The role of intrinsic muscle properties for stable hopping – stability is achieved by the force-velocity relation

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A reductionist approach was presented to investigate which level of detail of the physiological muscle is required for stable locomotion. Periodic movements of a simplified one dimensional hopping model with a Hill-type muscle (one contractile element, neither serial nor parallel elastic elements) were analyzed. Force-length and force-velocity relation of the muscle were varied in three levels of approximation (constant, linear and Hill-shaped nonlinear) resulting in nine different hopping models of different complexity. Stability of these models was evaluated by return map analysis and the performance by maximum hopping height. The simplest model (constant force-length and constant force-velocity relation) outperformed all others in maximum hopping height but was unstable. Stable hopping was achieved with linear and Hill-shaped nonlinear characteristic of the force-velocity relation. The characteristics of force-length relation marginally influenced hopping stability. The results of this approach indicate that the intrinsic properties of the contractile element are responsible for stabilization of periodic movements. This connotes that a) complex movements like legged locomotion could benefit from stabilizing effects of muscle properties, and b), technical systems could benefit from the emerging stability when implementing biological characteristics into artificial muscles.

Key words: stabilization; preflex; elasticity; actuator; Hill model
1. Introduction

Human and animal locomotion is governed by periodic movements. Thereby, the center of mass oscillates in vertical direction (Cavagna et al., 1977; Enoka, 2008). This oscillatory movement is a result of the interplay between gravitational force and leg force (Blickhan, 1989). Active forces in the leg are generated by muscles. To understand how the complex musculo-skeletal system can generate adequate leg forces, knowledge of the intrinsic muscle properties is necessary. Hill (1938) described and separated the intrinsic properties for a single muscle represented by a serial elastic and a contractile element with force-length and force-velocity relationship. This work has inspired many researchers to create biomechanical models that range from the detailed description of force production in muscle fibers to large scale musculo-skeletal modeling of human and animal movements.

With musculo-skeletal models it is possible to ask for the functional role of specific muscle properties observed in real muscle. For a single maximum height jump, van Soest et al. (1994) observed that variations of starting positions have little effect on jumping height when the muscles are activated by the same predefined muscle activation pattern. For squat jumping, it was shown that perturbations have much less influence on take-off posture when the model is actuated by muscle dynamics instead of joint moment control (van Soest & Bobbert, 1993). Therefore, it appears that muscle properties are able to compensate for perturbations and facilitate the convergence of dynamic explosive movements. The authors concluded that the intrinsic muscle properties represented by the force-length-velocity function in Hill-type muscle models act like a zero time delay peripheral feedback system. Thus, the mechanical properties of the muscle itself represent a functional feedback system. Because of the zero time delay, Brown and colleagues (1995) coined the term “preflex” for all mechanical actions, whether stabilizing or not, emerging from these intrinsic properties.

In hopping simulations, the interplay of predefined activation pattern and preflex properties of the mechanical system was found to compensate for unexpected changes in surface stiffness and further, predict adjustments of leg stiffness (van der Krogt et al., 2009) as known from experiments (hopping: Moritz & Farley 2004, running: Ferris et al. 1999). While van der Krogt et al. (2009) showed that passive preflex dynamics can negotiate perturbations, Geyer et al. (2003) demonstrated that a combination of muscle properties and predefined activation pattern can also generate stable periodic movements like vertical hopping. In addition, Geyer and colleagues discussed the necessity of specific muscle properties for the stabilization of hopping movements. They found that for hopping the force-length relationship can be neglected without losing periodic stability. In similar way, McMahon (1984), Hogan et al. (1987) and Blickhan et al. (2007) mentioned a stabilizing effect of the force-velocity characteristic. Gerritsen et al. (1998) explicitly showed, that a walking model with disabled force-velocity relation could not compensate for dynamic perturbations.

All studies mentioned above discussed the effects of intrinsic muscle properties for sup-
porting the stabilization of movements. However, since these studies analyzed complex multi segmental movement dynamics (e.g. two or more segment model for hopping and walking), interaction effects come into play. The geometric properties of the linkage system (Wagner & Blickhan, 1999) and the co-activation of antagonistic muscles (Wagner & Blickhan, 2003) are known to influence stability. Additionally, in a Hill-type muscle-tendon complex (represented by contractile element, serial and parallel elastic elements) it is unclear whether stability emerges from the properties of the contractile element itself, or the passive elastic elements, or the interaction of all three components.

Concerning the properties of the contractile element, it is unknown which level of biologically observed complexity of the force-length and force-velocity curves is required for a given movement task. While many researchers focused on finding models that fit experimental data (e.g., Winters & Woo, 1990; Günther et al., 2007; Guschlbauer et al., 2007; Siebert et al., 2008) as accurately as possible, there are indications that only specific features of these complex relations are responsible for particular capabilities of muscle. For example, Blickhan et al. (2003) stated that the slope of the force-velocity relation supports (self-) stabilization. Hence, a linear approximation of this Hill curve could be sufficient. Although linear muscle properties are not present in nature, they would be of wide interest in engineering as this could help to simplify actuator design and control.

In this study, we aim to prove whether and to what extend the previously suggested origin of stability relies on the shape of the force-velocity dependency of the contractile element itself. We hypothesize that already an isolated contractile element with force-velocity relation (linear or non-linear) is capable of creating and stabilizing a one-dimensional periodic hopping movement. We use this simplified model approach to exclude the interaction effects mentioned above (geometry, antagonistic muscle pairs, passive elastic components of Hill-type models). In fact, it is not our goal to reflect real human hopping as closely as possible, but rather to find the minimal requirements for creating and stabilizing periodic bouncing movements.

2. Methods

2.1. Simplified hopping model

The hopping model idealized the body as a point mass $m$ which is accelerated by gravitation in negative $y$ direction and by the idealized leg force generated by a single 'leg muscle' in positive $y$ direction (figure 1). The leg force was assumed to be identical to the muscle force $F_m$ as no leg segmentation was considered. As a consequence of this simplification this conceptual 'leg muscle' had to push rather than to pull. In contrast to biological muscles this resulted in reversed signs in the force-length and force-velocity relations (see section 2.2), but had no effect on the underlying muscle mechanics. The muscle force acted only during ground contact when the vertical distance $y$ of the mass to the ground was smaller than the rest-length of the leg ($y \leq L_0$). The equation of motion for this model
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Figure 1: Hopping model consisting of a point mass $m$ representing the body and a conceptual 'leg muscle' which generates the force in positive $y$-direction. The 'leg muscle' is reduced to an inverse contractile element (inverse CE) which produces a pushing rather than pulling force during stance (indicated by the black arrows). The sketch on the right visualizes that this is equivalent to a pulling contractile element clamped in a stiff mechanical construct to redirect the force. For the optimization (section 2.4), hopping cycles, as defined by two subsequent apices and cycle time $T$, are used. $y_0$ is the release height and $h = y_1 - L_0$ the hopping height. Stance phase occurs when the distance $y$ of the mass to the ground is $y \leq L_0$ (indicated by the shaded area).

was:

$$m \ddot{y} = -mg + \begin{cases} 0 & y > L_0 \text{ flight phase} \\ F_{in} & y \leq L_0 \text{ ground contact} \end{cases}$$

(1)

To generate a periodic hopping movement alternating stance- and flight phases had to be generated by the muscle force.

2.2. Muscle model

Muscle force was generated by a Hill-type contractile element:

$$F_{in} = A(t) Fl Fv F_{max},$$

(2)

where $A(t)$ is activation state, $Fl(y)$ the force-length relation, $Fv(\dot{y})$ the force-velocity relation and $F_{max}$ the maximum isometric contraction force of the muscle. As neither serial nor parallel elastic elements were considered, muscle length $L = \min(y, L_0)$ and contraction velocity $v = \dot{L}$ solely depended on the position and velocity of the mass.
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\[ F_m = A(t) F_l F_v F_{\text{max}} \]

Figure 2: Muscle force \( F_m \) is defined by a Hill-type approach with combinations of constant, linear, and non-linear approximations of the force-length (\( F_l \)) and the force-velocity (\( F_v \)) relation resulting in nine different muscle models. These models are labeled according to the scheme \( M[Fl \text{ approximation}, Fv \text{ approximation}] \). Top left is the simplest model which disregards all physiological muscle dynamics. Bottom right is the most complex model which is most physiological approximation to the dynamical behavior of real muscle. From top to bottom force-length complexity increases. From left to right force-velocity complexity increases. Activation patterns \( A(t) \) are obtained by optimization. Maximum isometric force is \( F_{\text{max}} = 2.5 \text{ kN} \), approximately three times body weight (see table 1). The maximum operating ranges during optimal periodic hopping are indicated by the gray areas.
2. Methods

Fl and Fv were represented in three levels of detail (constant, linear and Hill-shaped nonlinear) of the physiologically observed intrinsic muscle properties (figure 2). For Fl these relations were:

$$Fl = \begin{cases} 1 \\ k(L_0 - L) \\ \exp \left[ c \frac{L - L_{opt}}{L_{opt}w} \right] \end{cases} \begin{array}{l} \text{constant} \\ \text{linear} \\ \text{Hill} \end{array}$$

(3)

where $k$ describes the spring constant for the linear approximation, $L_{opt}$ the optimal length of the muscle for maximum force, $w$ the width, and $c$ the curvature of the bell-shaped force-length relation as described in Hill-type muscle models (e.g. Geyer et al., 2003). The force-velocity relations were

$$Fv = \begin{cases} 1 \\ 1 - \mu v \\ \frac{\nu_{max} - v}{\nu_{max} - K v} \\ \frac{\nu_{max} - v}{N + (N - 1)\frac{\nu_{max} - v}{\nu_{max} - \nu_{max}}} \end{cases} \begin{array}{l} \text{constant} \\ \text{linear} \\ v > 0 \\ v \leq 0 \end{array}$$

(4)

where the linear approximation equals one at zero velocity and creates higher forces during landing (equivalent to the eccentric contraction phase for muscles during hopping) than during take off (equivalent to concentric contraction). $\mu$ describes the slope of the linear force-velocity curve. The nonlinear approximation was derived from Hill’s equation (Hill, 1938) in the concentric phase ($v > 0$) where $K$ is the curvature parameter and $v_{max}$ the maximum contraction velocity. The eccentric phase ($v \leq 0$) was characterized by an equation based on Seyfarth et al. (2000), where $N$ represents the dimensionless force $F_m/F_{max}$ at $v = -v_{max}$ (eccentric force enhancement). The signs in $Fv$ and $Fl$ were a result of the arrangement as an inverse contractile element (pushing ‘leg muscle’).

The parameters for the model (table 1) were derived from Geyer et al. (2003). The adapted parameters reflect the fact that in this model the inverse contractile element had to substitute the principle function of the whole leg during hopping. In human hopping maximum ground reaction forces of $F_{GRF,max} \approx 3 \times mg$ (Farley et al., 1991; Grabowski & Herr, 2009) and leg compressions of $\Delta L \approx 10\%L_0$ (Granata et al., 2002; Grabowski & Herr, 2009) can be observed. Therefore, the maximum isometric force for the Hill-type force-length relation of the substitute muscle was chosen to be $F_{max} \approx 3 \times mg$. Optimal muscle length was set to $L_{opt} = 0.9 \times L_0$. Therefore, the model exerted typical human maximum ground reaction forces at typical human maximum leg compressions. Parabola width $w$ and curvature $c$ caused the $Fl$ to drop to $0.8 \times F_{max}$ at touch down/take off muscle length. Therefore, the muscle operated on the ascending limb and the plateau region of the force-length relation (figure 2).
2. Methods

Table 1: Model parameters. Derived from Geyer et al. (2003).

<table>
<thead>
<tr>
<th>parameter</th>
<th>value</th>
</tr>
</thead>
<tbody>
<tr>
<td>leg rest length $L_0$</td>
<td>1 m</td>
</tr>
<tr>
<td>body mass $m$</td>
<td>80 kg</td>
</tr>
<tr>
<td>gravitational constant $g$</td>
<td>10 ms$^{-2}$</td>
</tr>
<tr>
<td>maximum isometric muscle force $F_{\text{max}}$</td>
<td>2.5 kN</td>
</tr>
<tr>
<td>optimal muscle length $L_{\text{opt}}$</td>
<td>0.9 m</td>
</tr>
<tr>
<td>width $w$</td>
<td>0.45 m</td>
</tr>
<tr>
<td>curvature $c$</td>
<td>-29.96</td>
</tr>
<tr>
<td>maximum velocity $v_{\text{max}}$</td>
<td>-3.5 ms$^{-1}$</td>
</tr>
<tr>
<td>curvature constant $K$</td>
<td>1.5</td>
</tr>
<tr>
<td>eccentric force enhancement $N$</td>
<td>1.5</td>
</tr>
<tr>
<td>linear $Fl$ normalized spring constant $k$</td>
<td>10 m$^{-1}$</td>
</tr>
<tr>
<td>linear $Fv$ slope $\mu$</td>
<td>0.25 ms$^{-1}$</td>
</tr>
</tbody>
</table>

Parameters of the Hill-type force-velocity relation $v_{\text{max}}$ and $K$ were chosen such that $Fv = 0.5$ at a velocity of $v = 1$ m/s (take off velocities are usually > 1 m/s). The eccentric force enhancement was set to $N = 1.5$ (van Soest & Bobbert, 1993). Leg length $L_0 = 1$ m and body mass $m = 80$ kg were estimated for an adult man. The gravitational constant was rounded to $g = 10$ ms$^{-2}$.

The common feature of Hill-type force-length relation and its linear approximation was $F = F_{\text{max}}$ at leg length $L = L_{\text{opt}} = 0.9 \times L_0$ (figure 2). The linear approximation of the force-velocity relation resulted from the requirements of no effect at isometric conditions ($Fv = 1$ for $v = 0$) and similar maximum force enhancement during impact ($Fv = N = 1.5$ for $v = -2$ m/s).

The model was implemented in Matlab 7.4 (R2007a) using the Simulink 6.6 toolbox (Mathworks Inc., Natick, MA, USA). The embedded ODE45 integrator with a maximum step size of $10^{-3}$ s and absolute and relative error tolerance of $10^{-12}$ was used for the simulation. Results were verified with a tenfold higher accuracy.

2.3. Protocol of the simulation experiment

Nine muscle models of different complexity resulted from the combination of different approximations of $Fl$ and $Fv$. These models were labeled according to the scheme $M[Fl$ approximation, $Fv$ approximation] (figure 2). For example $M[\text{linear}, \text{Hill}]$ stands for the muscle model with linear $Fl$ and Hill-shaped nonlinear $Fv$. With the constant option it was possible to suppress the influence of either relation.

For each of the nine muscle models, muscle activation patterns $A(t)$ were optimized to generate periodic hopping movements (paragraph 2.4). These optimal hopping patterns
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were tested for stability against perturbations in release height (paragraph 2.5). Additionally, spring-like behavior of the model during ground contact was evaluated (paragraph 2.6).

2.4. Optimal activation

To generate a periodic hopping movement the muscle activation pattern \( A(t) \) was optimized for maximum periodic hopping height with a genetic algorithm (population of 200 individuals, 100 generations, 3 repetitions for verification, details see appendix A). Each individual represented an activation pattern \( A_i(t_i) \) on a grid with 5 possible activation states \( A_i \epsilon \{0, 0.25, 0.5, 0.75, 1\} \) at time intervals of \( t_{i+1} - t_i = 25 \text{ ms} \) after apex. Activation \( A(t) \) was linearly interpolated between grid points. These activation patterns were applied to single-cycle simulations (Geyer et al., 2003). A hopping cycle started at an apex (upper point of flight phase, \( \dot{y} = 0 \)) with release height \( y_0 \) and ended at the subsequent apex with apex height \( y_1 \) (figure 1). The fitness function \( P \) of each individual was calculated from the hopping height \( h = y_1 - L_0 \) and hopping cycle duration \( T \) normalized to 1 s:

\[
P = h \times \begin{cases} 1 & T \leq 0.5 \text{ s} \\ 2(1 - T) & T > 0.5 \text{ s} \end{cases}
\]

where performance \( P \) equals the hopping height for cycle durations of \( T < 0.5 \text{ s} \) and was reduced for cycle durations of \( T > 0.5 \text{ s} \). This restriction of hopping cycle time was necessary due to the simplicity of the linear models. As the linear force-length relation included no physical limit for muscle contraction, hopping height could increase infinitely with longer hopping cycle duration. \( T = 0.5 \text{ s} \) corresponded to preferred human hopping frequencies of \( \approx 2 \text{ Hz} \) (Melvill-Jones & Watt, 1971; Farley et al., 1991).

2.5. Stability analysis - apex return map

Stability against perturbations of release height was investigated by mapping the dependency of apex height \( y_1 \) on release height \( y_0 \) using an apex return map \( y_1(y_0) \) (Full et al., 2002; Rummel & Seyfarth, 2008). A periodic solution is characterized by \( y_1 = y_0 \) and, thus, is represented in the apex return map as a fixed point \( y_{\text{fix}} \) with \( y_1(y_0) = y_0 = y_{\text{fix}} \). The optimization process described above favored such solutions. A perturbation of release height \( (y_{\text{fix}} + \Delta y_0) \) generally caused a deviation of the hopping height \( (y_{\text{fix}} + \Delta y_1) \). For a stable fixed point the perturbation diminishes during the cycle \( (|\Delta y_0| > |\Delta y_1|) \). Thus, the slope \( S = dy_1/dy_0 \) of the returnmap in the neighborhood of a fixpoint is a measure for stability against infinitesimal perturbations. The trajectory converges to its periodic solution after a small perturbations if \( |S| < 1 \). Therefore, we called models with \( |S| < 1 \) stable. A model is unstable for perturbations growing from step to step (\( |S| > 1 \)). If a perturbation remains constant from step to step (\( |S| = 1 \)) the model has indifferent behavior. The return maps were calculated for release heights of 1.01 \( \cdots \) 1.20 m.
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2.6. Spring like behavior

Spring like behavior of the model during periodic hopping was evaluated with the elasticity coefficient $C_{\text{EL}}$ (Geyer et al., 2003)

$$C_{\text{EL}} = \left(1 - \frac{D}{D_{\text{max}}}\right)^2$$

where $D$ is the net area (sum of all areas) enclosed by the force-length trace and $D_{\text{max}} = \max(F_m) \times \max(y - L_0)$ during stance. The coefficient $C_{\text{El}}$ provides a measure of how closely the leg approximates perfectly elastic behavior ($C_{\text{El}} = 1$).

3. Results

3.1. Optimal activation, hopping height and elastic behavior

For each muscle model (figure 2) the optimal activation pattern $A(t)$ is shown in figure 3. Without force-velocity dependency ($F_v = \text{const.}$, left column) full activation was predicted ($A(t) = 1$). With linear or Hill-type force-velocity relation the optimal activation patterns showed the following characteristic: in the beginning of ground contact the activation is low ($A(t) \leq 0.25$), then it rises to maximum activation after approximately 20-40% of ground contact and remains at this maximum level until the end of the contact.

The resulting maximum periodic hopping height $y_{\text{fix}}$ (table 2) strongly depended on the complexity of the model. The highest hopping height was predicted by the simplest model M[constant, constant] with $y_{\text{fix}} = 1.145 \text{ m}$. With constant $F_v$, increasing the complexity of the force-length relation resulted in a reduction of $y_{\text{fix}}$ by up to 0.048 m to 1.097 m. When introducing a force-velocity dependency (linear, or Hill-type $F_v$) the maximum hopping height depended less on $Fl$ (variation $\Delta y_{\text{fix}} < 0.015 \text{ m}$), but was further reduced with increasing complexity of $F_v$ (linear $F_v y \approx 1.11 \text{ m}$, Hill $F_v y \approx 1.07 \text{ m}$).

The elasticity coefficient predicted fully spring like behavior ($C_{\text{EL}} = 1$) in all models without force-velocity dependency ($F_v = \text{const.}$). In all other models $C_{\text{EL}}$ was reduced ($0.54 < C_{\text{EL}} < 0.76$).

3.2. Stability of optimal hopping patterns

Models with no force-velocity dependency ($F_v = \text{const.}$) showed a returnmap where the hopping height after ground contact always equalled the release height ($y_1 = y_0 \forall y \in [1, 1.2]$, figure 4, left column). These models were indifferent ($S = 1$), i.e., perturbations neither diminished nor grew.

Stable hopping patterns were found for all models with force-velocity relation (figure 4, central and right column). We found that with increasing complexity of the force-velocity relation, stability was also increasing: the slope of the returnmap was between $-0.87 <
Figure 3: Optimized hopping characteristics for different muscle models. Results for individually optimized activation $A(t)$ (dashed lines), trajectories of the mass (upper solid line) and muscle forces $F_m$ (lower solid line) for maximum hopping performance. The shaded areas indicate stance phase. The models are labeled according to the scheme $M[Fl\text{ approximation}, Fv\text{ approximation}]$: From top to bottom force-length complexity increases. From left to right force-velocity complexity increases. The activation during flight phase has no effect on the model during periodic hopping, but may affect muscle force during perturbed cycles (e.g. extended ground contacts).
3. Results

Table 2: Results for optimal activation patterns. The results for the different models are labeled according to the scheme M\[Fl approximation, Fv approximation\] as indicated by the icons. $y_{fix}$ is the optimal periodic hopping height. $S$ is the slope of the returnmap at the periodic hopping height which indicates stable hopping for $|S| < 1$ (all models with linear and Hill-type force-velocity relation). For definitions of elasticity coefficient $C_{EL}$ and hopping performance $P$ see equations (6) and (5).

<table>
<thead>
<tr>
<th>M[constant, constant]</th>
<th>M[constant, linear]</th>
<th>M[constant, Hill]</th>
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<tbody>
<tr>
<td>$S = 1$</td>
<td>$S = -0.87$</td>
<td>$S = -0.02$</td>
</tr>
<tr>
<td>$y_{fix} = 1.145$ m</td>
<td>$y_{fix} = 1.119$ m</td>
<td>$y_{fix} = 1.076$ m</td>
</tr>
<tr>
<td>$C_{EL} = 1$</td>
<td>$C_{EL} = 0.597$</td>
<td>$C_{EL} = 0.579$</td>
</tr>
<tr>
<td>$f = 2$ Hz</td>
<td>$f = 1.97$ Hz</td>
<td>$f = 1.99$ Hz</td>
</tr>
<tr>
<td>$P = 1.145$</td>
<td>$P = 1.102$</td>
<td>$P = 1.071$</td>
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<tbody>
<tr>
<td>$S = 1$</td>
<td>$S = -0.86$</td>
<td>$S = -0.52$</td>
</tr>
<tr>
<td>$y_{fix} = 1.097$ m</td>
<td>$y_{fix} = 1.113$ m</td>
<td>$y_{fix} = 1.061$ m</td>
</tr>
<tr>
<td>$C_{EL} = 1$</td>
<td>$C_{EL} = 0.662$</td>
<td>$C_{EL} = 0.767$</td>
</tr>
<tr>
<td>$f = 2$ Hz</td>
<td>$f = 1.86$ Hz</td>
<td>$f = 1.93$ Hz</td>
</tr>
<tr>
<td>$P = 1.097$</td>
<td>$P = 1.029$</td>
<td>$P = 1.023$</td>
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<tr>
<td>$S = 1$</td>
<td>$S = -0.41$</td>
<td>$S = -0.10$</td>
</tr>
<tr>
<td>$y_{fix} = 1.137$ m</td>
<td>$y_{fix} = 1.114$ m</td>
<td>$y_{fix} = 1.070$ m</td>
</tr>
<tr>
<td>$C_{EL} = 1$</td>
<td>$C_{EL} = 0.627$</td>
<td>$C_{EL} = 0.543$</td>
</tr>
<tr>
<td>$f = 2$ Hz</td>
<td>$f = 1.96$ Hz</td>
<td>$f = 1.98$ Hz</td>
</tr>
<tr>
<td>$P = 1.137$</td>
<td>$P = 1.091$</td>
<td>$P = 1.059$</td>
</tr>
</tbody>
</table>
3. Results

Figure 4: Hopping stability with optimal activation. The models are labeled according to the scheme $M[F_l$ approximation, $F_v$ approximation]. The returnmaps $y_i(y_0)$ show the relation between release height $y_0$ and subsequent apex height $y_{i+1}$ for all nine muscle models. Release height varied between $1.0 \text{ m} < y_0 < 1.2 \text{ m}$. Intersections of returnmaps (thick lines) with diagonals (dashed lines) indicate fixpoints $y_{\text{fix}}$ (periodic solutions with $y_{i+1} = y_0$). The slope $S = \frac{dy_{i+1}}{dy_0}$ of the returnmap in the neighborhood of a fixpoint indicates stable hopping if $|S| < 1$ as for models with linear (central column) and Hill-type (right column) force-velocity relation. Here, starting from a disturbed apex height ($y_0 = y_{\text{fix}} + \Delta y$) the system converges to the steady-state height in a few cycles. For models with constant force-velocity relation (left column) apex height always equals release height ($y_1 = y_0$). Thus, perturbations neither diminish nor grow ($S = 1$).
3. Results

Table 3: Results for mean activation. The results for the different models are labeled according to the scheme $M[F_{\text{f}} \text{ approximation, } F_{\text{v}} \text{ approximation}]$ as indicated by the icons. $y_{\text{fix}}$ periodic hopping height, $S$ slope of the returnmap at the periodic hopping height, $C_{\text{EL}}$ elasticity coefficient and $P$ hopping performance.

<table>
<thead>
<tr>
<th>Fl $\square$</th>
<th>M[constant, constant] unstable</th>
<th>M[constant, linear]</th>
<th>M[constant, Hill]</th>
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<tr>
<td>$S = -0.43$</td>
<td>$y_{\text{fix}} = 1.142 \text{ m}$</td>
<td>$C_{\text{EL}} = 0.627$</td>
<td>$S = -0.14$</td>
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<tr>
<td></td>
<td></td>
<td>$f = 1.70 \text{ Hz}$</td>
<td>$y_{\text{fix}} = 1.070 \text{ m}$</td>
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<tr>
<td></td>
<td></td>
<td>$P = 0.940$</td>
<td>$C_{\text{EL}} = 0.579$</td>
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<table>
<thead>
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<th>M[linear, constant] unstable</th>
<th>M[linear, linear]</th>
<th>M[linear, Hill]</th>
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<tbody>
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<tr>
<td></td>
<td></td>
<td>$f = 1.90 \text{ Hz}$</td>
<td>$y_{\text{fix}} = 1.020 \text{ m}$</td>
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<tr>
<td></td>
<td></td>
<td>$P = 1.042$</td>
<td>$C_{\text{EL}} = 0.790$</td>
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<th>M[Hill, constant] unstable</th>
<th>M[Hill, linear]</th>
<th>M[Hill, Hill]</th>
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<tbody>
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<td>$y_{\text{fix}} = 1.134 \text{ m}$</td>
<td>$C_{\text{EL}} = 0.641$</td>
<td>$S = -0.17$</td>
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<td></td>
<td></td>
<td>$f = 1.71 \text{ Hz}$</td>
<td>$y_{\text{fix}} = 1.082 \text{ m}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P = 0.942$</td>
<td>$C_{\text{EL}} = 0.658$</td>
</tr>
</tbody>
</table>

$S < -0.41$ for linear and $-0.52 < S < -0.02$ for Hill-type force-velocity relation. All tested perturbations (release heights of $1.01 \cdots 1.20 \text{ m}$) could be compensated.

3.3. Stability with mean activation pattern

As part of the differences between models could be caused by differences in activation pattern, we derived a mean activation pattern $A_{\text{mean}}$. The optimal activation patterns for models with force-velocity dependency had similar characteristics (paragraph 3.1, figure 3 central and right column). Therefore, we derived the mean activation pattern $A_{\text{mean}}$ across these six models. This more general activation pattern was then applied to all models (figure 5 and table 3) to extract the effect from intrinsic muscle properties only.

With $A_{\text{mean}}$, models without force-velocity dependency were unstable. Stable hopping patterns were found for all models with force-velocity relation. Again, increasing com-
plexity of the force-velocity relation resulted in increasing model stability: the slope of the returnmap was between $-0.64 < S < -0.40$ for linear and $-0.20 < S < -0.14$ for Hill-type force-velocity relation.

4. Discussion

We hypothesized that an isolated contractile element with force-velocity relation (linear or non-linear) is capable of creating and stabilizing a one-dimensional periodic hopping movement.

The results show that for a given movement goal like maximum hopping height the simplest model without force-length and force-velocity relation reaches maximum performance (see §4.2). Stable hopping was only achieved with force-velocity relation (see §4.1).

4.1. Stability arises from the force-velocity relation

With the stepwise increment of model complexity it was possible to show that the force-velocity relation is responsible for the stabilization of periodic hopping patterns (figures 4 & 5). We found with increasing complexity of the force-velocity relation a faster convergence after small perturbations (smaller values of $|S|$ for the Hill-type than for the linear force-velocity relation). This finding is valid for optimal (table 2) and mean (table 3) activation patterns. Thus, the stabilizing effect rather originates from the force-velocity relation then from the shape of the activation pattern.

The stability $S$ is a measure for the convergence after a infinitesimal small perturbation. The rejection of larger perturbations is also shown in the returnmaps (figures 4 & 5). All models with force-velocity dependency (linear or Hill-type) could compensate for all tested perturbations (release heights of 1.01 ·· 1.20 m). Therefore, the only difference in the hopping pattern between linear and Hill-type force-velocity relation was a faster convergence after infinitesimal small perturbations with Hill-type force-velocity relation.

Furthermore, we found that stability can be achieved fairly well by a linear approximation of the force-velocity relation (Figs. 4 & 5). All models with linear force-velocity relation show stable periodic hopping patterns ($S = -0.87 ... - 0.40$, see tables 2 and 3). Blickhan et al. (2003) showed analytically for holding a load (static task) that the force-velocity relation has to have a negative slope (i.e., locally linear approximation) in order to stabilize the system. By fulfilling this criterion for the linear approximation of the force-velocity relation (negative slope), our results extend this conclusion to dynamic movements. While our model is reduced to a single contractile element, complex (non-linear) characteristics could become more important in larger scale and more redundant systems (Winters, 1995).

Several simulation studies on jumping (van Soest & Bobbert, 1993; van Soest et al., 1994), hopping (Geyer et al., 2003; van der Krogt et al., 2009) and walking (Gerritsen et al., 1998) discuss the specific role of the force-length-velocity relation of the contractile element for stabilization although all these models include multiple muscle-tendon complexes, segments
4. Discussion

Figure 5: Hopping stability with mean activation. The models are labeled according to the scheme $M[F_l$ approximation, $F_v$ approximation]. The returnmaps (solid lines, analogue to figure 4) indicate that all models with linear (central column) and Hill-type (right column) force-velocity relation show stable behavior with the same mean activation $A_{\text{mean}}$. Models with constant force-velocity relation are unstable.
and a certain geometrical arrangement of the muscle-tendon complexes with the segmented leg. From our results we can conclude that the intrinsic properties of the contractile element itself are responsible for stabilization. Therefore, features like the interaction of multiple muscles, multiple segments and the passive elastic components are not prerequisites for stability.

Whereas the force-velocity relation dominates the stability of our model, we found only marginally influence of the force-length relation (table 3, small variation in $S$). This confirms that the force-length relation is neither an important factor for stable hopping (Geyer et al., 2003) nor for perturbed walking (Gerritsen et al., 1998). The force-length relation could be more important in static, load compensating tasks (Gerritsen et al., 1998; Blickhan et al., 2003).

4.2. Increasing complexity reduces maximum performance

For nine muscle models of different complexity activation patterns were optimized for maximum hopping height. It was found that the simplest muscle model considered, with neither force-length nor force-velocity dependency ($M_{constant, constant}$), reaches the highest hopping height (table 2). This was expected as in the more complex models the factors in the force equation of the muscle model (equation 2) mostly reduce the maximum dynamic muscle force. Introducing the force-length relation limits the maximum dynamic muscle force as $0 \leq F_l \leq 1$ (figure 2). Although the force-velocity relation allows for higher muscle forces on the eccentric part ($F_v > 1$ for $\dot{y} < 0$), hopping height largely depends on muscle force during acceleration where the muscle operates on the concentric part ($\dot{y} > 0$). Here the force-velocity relation limits the muscle force as $F_v < 1$.

4.3. Damping effects of the force-velocity relation

The stabilizing function of the force-velocity relation arises from its damping effect. During periodic hopping dissipated and supplied energy are equal. When landing with higher velocities as caused by an unexpected lower landing position the eccentric force enhancement increases muscle force and therefore energy dissipation. This counteracts the perturbation. Lower landing velocities due to higher ground levels result in less dissipation and allow to regain hopping height. However, it is important to note important differences to a technical damper: 1) the damping effect in muscle occurs only when the muscle is activated and scales with the level of activation (as expressed by equation (2)), and 2) depending on the activation and movement dynamics muscles can function as power generator or energy absorber (Wilson et al., 2001; Ahn & Full, 2002), or as a combination of both as shown in this study.

The shape of the optimized activation patterns can be related to the damping effects of the muscle (sect. 3.1, Fig. 3). Muscle models with linear or Hill-type force-velocity relation can produce less force during leg extension ($F_v < 1$ in concentric contraction) than during
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leg shortening (eccentric contraction, force enhancement up to $1.5 \times F_{\text{max}}$). This behavior of the muscle has to be compensated by the activation. Therefore, the activation is reduced during breaking phase to counteract the force enhancement and to allow the leg to compress sufficiently. Acceleration before take off happens under maximum activation to counteract the drop in the force-velocity function of the muscle.

As pointed out in sections 4.1 and 4.2 the force-velocity relation as an intrinsic property of the actuator stabilizes hopping height but affects the maximum hopping height. An alternative would be to implement a velocity-depending force in an actuator by introducing a physical damper. This implies inherent energy losses within the mechanical system. To overcome this disadvantage the damping needs to be adjusted, e.g. by applying feedback control. In the biological muscle this is achieved without sensory feedback by taking advantage of the intrinsic force-velocity relation.

4.4. Elastic behavior is lost without tendon and geometry

The results indicate a loss of spring like behavior ($C_{\text{EL}} \ll 1$) when including the force-velocity relation. On this abstract level (only contractile element) stable hopping is only possible without spring like behavior. However, the hopping model of Geyer et al. (2003) showed elastic leg behavior ($C_{\text{EL}} \approx 0.95$) and stability. Here, the contractile element is in series with an elastic tendon. They discussed that the model became unstable when they removed the force-velocity dependency of the contractile element. Apparently, the tendon properties support spring-like leg behavior, while stability comes from the intrinsic properties of the contractile element. Thus, a complete muscle-tendon complex integrated in a segmented leg can inherit the stability of the intrinsic muscle properties and also exhibit spring-like leg behavior.

4.5. The conceptual hopping model as a template for bouncing gaits

Hopping can be understood as a primitive movement which is essential for legged locomotion as it accounts for the periodic vertical oscillation of the center of mass (Blickhan & Full, 1993; Farley et al., 1993; Farley & González, 1996). Here, this fundamental pattern was modeled based on a single ‘leg muscle’ counteracting gravity. In contrast to the spring mass model, which can describe a vertical hopping motion as well, the muscle-based model can further stabilize the system energy. In this way, our hopping model exhibits the effects of intrinsic muscle properties to compensate for energetic perturbations in periodic tasks even, without the need of sensory feedback. With this it is a candidate as a template model (Full & Koditschek, 1999) for legged locomotion which complements the existing models based on stiff (McGeer, 1990) or spring-like leg function (Blickhan, 1989). The extension of these conservative template models by the here proposed muscle-based model opens the field for novel conceptual non-conservative gait models, which provide limit cycle stability (Full et al., 2002) during locomotion.
4.6. Technical systems can inherit effects of intrinsic muscle properties

In biology, authors emphasize the role of passive mechanisms for stabilizing and controlling movements. Recent results give evidence that much of the control in animal (e.g., Daley et al., 2009) and human (e.g., Grimmer et al., 2008) locomotion on uneven terrain relies on intrinsic muscle properties. Technical systems such as robots or prostheses could benefit from intrinsic properties of muscle like actuators by inheriting their stabilizing effects (Nishikawa et al., 2007). As pointed out in the previous sections, our main finding is the necessity of the force-velocity relation for dynamic stability. Thus, a technical implementation of force-velocity relation in actuators could help to compensate for disturbances and therefore to reduce control effort. In order to implement such properties, some researchers tried to create artificial muscles with properties similar to those of biological muscle. For example Klute et al. (2002) added a parallel hydraulic damper to a flexible pneumatic actuator to imitate the force-velocity relation in a technical muscle-tendon complex. The design of the artificial muscles was a trade off between maintaining simplicity while mimicking biological characteristics to the greatest degree possible. The result was a first-order approximation to both, the physiological force-length and force-velocity relation. Our results support the idea of such simple constructions as already linear (first-order) approximations of biological characteristics can stabilize periodic movements. Therefore, we suggest to implement technical actuators with such biologically inspired properties to exploit intrinsic properties.

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A. Details of the Genetic Algorithm

The initial population ($n = 0$) of activation patterns was generated randomly. Subsequent generations ($n + 1$) were derived from the fittest 100 individuals (with highest performance $P$, see equation 5). 50% of the next generation ($n+1$) were identical copies of the fittest 100 individuals of generation $n$, 25% were created by random scattered pairwise recombination and 25% by mutation with a mutation rate of one out of five genes. To favor periodic solutions reached apex height $y_1$ was passed on as starting height $y_0$ for descendant individuals. Starting height of initial population was $y_0 = 1.05$ m.

References


References


References