Integration of intrinsic muscle properties, feed-forward and feedback signals for generating and stabilizing hopping

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It was hypothesized that a tight integration of feed-forward and feedback-driven muscle activation with the characteristic intrinsic muscle properties is a key feature of locomotion in challenging environments. In this simulation study it was investigated whether a combination of feed-forward and feedback signals improves hopping stability compared with those simulations with one individual type of activation. In a reduced one-dimensional hopping model with a Hill-type muscle (one contractile element, neither serial nor parallel elastic elements), the level of detail of the muscle’s force–length–velocity relation and the type of activation generation (feed-forward, feedback and combination of both) were varied to test their influence on periodic hopping. The stability of the hopping patterns was evaluated by return map analysis. It was found that the combination of feed-forward and proprioceptive feedback improved hopping stability. Furthermore, the nonlinear Hill-type representation of intrinsic muscle properties led to a faster reduction of perturbations than a linear approximation, independent of the type of activation. The results emphasize the ability of organisms to exploit the stabilizing properties of intrinsic muscle characteristics.

Keywords: locomotion; muscle; exploitive actuation; force–length–velocity; return map; stability

1. INTRODUCTION

In biomechanical simulations, a muscle is often represented by a Hill-type muscle model. In this model, the muscle force exerted to a limb depends on the current state of the muscle, i.e. muscle length, muscle contraction velocity and muscle activation, whereas force–length and force–velocity relations are intrinsic properties of a muscle, activation is an extrinsic variable that is considered to adjust the muscle for different tasks.

Physiologically, an appropriate muscle activation is generated via motor commands from the central nervous system consisting of the brain and spinal cord. When coming from the brain via descending pathways, the motor commands could depend on a movement error signal, i.e. the current deviation from a planned movement trajectory, as the quantity to be minimized [1]. In engineering, this method is termed negative feedback control. As an alternative to negative feedback control, generation of discrete and rhythmic movements could be provided in a feed-forward manner. Rhythmic feed-forward activation patterns [4–6] could be generated by central pattern generators (CPGs) [7], which were proved to exist in biology and are conceptionally used in biomechanical models. CPGs are hierarchically on a lower level than the brain [8] and presumably located in the spinal cord [9].

The central nervous system incorporates peripheral sensory information from proprioceptive muscle sensor organs [6,10,11], e.g. muscle spindles (length and velocity of stretch and contraction) and Golgi tendon organs (muscle force). While negative feedback control necessarily depends on the feedback of sensory information

*Rhythmic patterns could also be seen as repeated discrete movements [2]. Hogan & Sternad [3] proposed a concept to define and distinguish the characteristics of rhythmic patterns. They stated that the complex biological movements may be a superimposition of both, discrete and rhythmic tasks.
(error signal), CPG feed-forward control may also require sensory information to reset or to adapt the phase of the rhythmic signal [12–16]. Apart from this centralized incorporation of sensor signals, there is evidence of decentralized circuits, which directly couple sensor signals to muscle stimulation in direct feedback loops [7,17].

Such decentralized proprioceptive feedback could also be responsible for generating a certain movement. For example, Geyer et al. [18] showed that proprioceptive signals can produce a muscle activation pattern resulting in periodic human hopping. Here, the hopping movement is neither a result of a planned trajectory nor a predetermined pattern, but a result of the direct coupling of proprioceptive sensory signals to muscle activation. The hopping model of Geyer and colleagues consisted of a two-segment leg with one Hill-type knee extensor muscle (contractile and series elastic element). Three different proprioceptive signals (muscle force, length and contraction velocity) were delayed, gained and added or subtracted to a stimulation bias. The resulting stimulation was fed back to the muscle via excitation–contraction coupling. Positive force feedback (FFB) and positive length feedback (LFB) were found to generate appropriate activation patterns for periodically stable hopping. Furthermore, such decentralized feedback could rapidly adapt to disturbances and thus, stabilize bouncing gaits. In contrast, in the literature, several authors used feed-forward activation patterns to actuate hopping models for human jumping [19–21] and hopping [22].

If it is assumed that biologically both actuation concepts are present and involved in locomotion [11,23,24], the question arises what functional benefit is achieved by the combination of these mechanisms [6]? In a model for insects, Proctor & Holmes [16] found that an isolated antagonistic musculoskeletal system can partially compensate the effects of an additional load if feed-forward CPG activation is combined with tonic proportional FFB. Also from an engineering perspective, Kuo [25] demonstrated a performance advantage by the combination of feed-forward and feedback controllers. The advantage is that the sensitivity of feed-forward control against perturbations and the sensitivity of feedback strategies to sensor noise can be reduced. While this approach considers the combination of different control schemes, it does not consider the dynamics emerging from the interaction of the control system with intrinsic properties of the underlying musculo-skeletal system [6,26].

Interestingly, the stability of human hopping models fundamentally relies on the representation of intrinsic muscle properties (e.g. constant, linear or nonlinear force–length–velocity relation) and is less influenced by the activation pattern itself [22]. Furthermore, the force–velocity relation was found to be necessary for hopping stabilization while the force–length relation could be removed. This result holds for optimized predetermined activation [22] as well as proprioceptive feedback [18] generated activation. It becomes obvious that a tight integration of intrinsic properties with feed-forward and feedback actuation is a key feature of locomotion [24,27], especially in challenging environments, e.g. uneven terrain [26].

Therefore, we hypothesize an improvement of stability in hopping movements through the integration of adequate representation of intrinsic muscle properties and the combination of feed-forward and feedback actuation.

To test this hypothesis, we analysed two template models for human hopping. The intrinsic muscle properties were represented in different levels of detail, as proposed in Haefelf et al. [22]: a reduced model with only linear force–length relation and a complex model with Hill-type force–length and force–velocity relations. Both models were driven by different feedback modes as well as a combination of feedback and feed-forward activation, and investigated for stability.

2. METHODS

2.1. Hopping model

The one-dimensional human hopping model used for this study was described in detail by Haeflef et al. [22]. In summary, it idealized the body as a point mass \( m \) at height \( y \) which was accelerated by a leg force \( F_m \) and gravity.

\[
\ddot{y} = -mg + \begin{cases} 
0 & y > L_0 \text{ flight phase} \\
F_m & y \leq L_0 \text{ ground contact}.
\end{cases}
\] (2.1)

The leg force was generated by a single muscle represented by a Hill-type contractile element producing the muscle force

\[
F_m = A(t) F_l F_v F_{max},
\] (2.2)

where \( A(t) \) was the activation state, \( F_l(y) \) the force–length relation, \( F_v(\dot{y}) \) the force–velocity relation and \( F_{max} \) the maximal isometric contraction force of the muscle. No gearing between leg force and muscle force was represented (figure 1).

The concept of template models [28] is discussed in §4.4.


\[ F_{m} = A F_l F_v F_{\text{max}} \]

**Figure 2. Muscle force \( F_m \) is defined by a Hill-type approach where \( A \) represents the muscle activation, \( F_l \) the force–length relation, \( F_v \) the force–velocity relation and \( F_{\text{max}} \) the maximum isometric force [22]. The activation either is generated by proprioceptive feedback (adapted from Geyer et al. [18]) or is an optimized feed-forward pattern \( A(t) \) or a combination of both. In the case of feedback, the stimulation is generated from force/velocity/length signals, which are delayed (by \( \delta \)), amplified by the gain \( G \) and added to the pre-stimulation \( STIM_0 \) before being coupled to the activation (ECC, equation (2.3)). Force–length and force–velocity relation are represented in different levels of detail. In the simple model \( M[\text{const, lin}] \), there is no force–length dependency considered, and the force–velocity relation is a linear approximation. In the more complex model \( M[\text{Hill, Hill}] \), \( F_v \) and \( F_l \) have nonlinear Hill-type dependencies. The maximum operating ranges during optimal periodic hopping are indicated by the grey areas. The force–length relation is plotted in reference to the leg compression \( \Delta L = y - L_0 \). (Online version in colour.)**

\( F_l \) and \( F_v \) were represented in different approximations (linear, nonlinear) to the physiologically observed characteristics [22, fig. 2]. Here, we show the results for the simplest model allowing stable periodic hopping \( M[\text{const, lin}] \) and the most realistic model \( M[\text{Hill, Hill}] \) (figure 2).

\( M[\text{const, lin}] \) had a constant \( F_l \) and a linear \( F_v \) dependency:

\[ F_{lM[\text{const, lin}]} = 1 \]

and

\[ F_{vM[\text{const, lin}]} = 1 - \mu v, \]

where \( \mu \) describes the slope of the linear force–velocity curve. \( M[\text{Hill, Hill}] \) had nonlinear Hill-type \( F_v \) and \( F_l \) dependencies:

\[ F_{vM[\text{Hill, Hill}]} = \exp \left[ -c \left( \frac{L - L_{\text{opt}}}{L_{\text{opt}} w} \right)^3 \right] \]

and

\[ F_{lM[\text{Hill, Hill}]} = \begin{cases} \frac{v_{\text{max}} + v}{v_{\text{max}} - K v} & v > 0 \\ N + (N - 1) \frac{v_{\text{max}} - v}{v_{\text{max}} - v_{\text{opt}}} & v \leq 0 \end{cases} \]

where \( L_{\text{opt}} \) is 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 [18]. For the concentric phase (\( v > 0 \)), \( K \) is the curvature parameter and \( v_{\text{max}} \) the maximum contraction velocity. The eccentric phase (\( v \leq 0 \)) is characterized by an equation based on Geyer et al. [18], where \( N \) represents the dimensionless force \( F_m/F_{\text{max}} \) at \( v = -v_{\text{max}} \). Parameter values were chosen to represent human hopping (table 1).

The model was implemented in MATLAB v. 7.4 (R2007a) using the SIMULINK v. 6.6 toolbox (Mathworks Inc., Natick, MA, USA). The embedded ODE45 integrator with a maximum step size of \( 10^{-12} \) s and absolute and relative error tolerance of \( 10^{-6} \) was used for the simulation.

### 2.2. Activation by proprioceptive feedback

The excitation–contraction coupling (ECC), which relates muscle activation state \( A(t) \) to the stimulation input \( STIM(t) \), is described by a first-order differential equation

\[ A(t) = STIM(t) - \tau \frac{dA(t)}{dt}, \quad (2.3) \]

where \( \tau \) is a time constant [18]. Muscle stimulation \( 0 \leq STIM(t) \leq 1 \) is generated from the proprioceptive feedback signals \( F \) (muscle force), \( v \) (contraction velocity) and \( L \) (muscle length). Here, these proprioceptive signals are multiplied by the gain factors \( G_F \), \( G_v \), \( G_L \), respectively, and delayed by \( \delta \).

\[
\begin{align*}
STIM(t) = & \begin{cases} STIM_0 + G_F (L(t - \delta) - L_{\text{eff}}) & LFB \\
STIM_0 + G_v (v(t - \delta) - v_{\text{eff}}) & VFB \\
STIM_0 + G_L (L(t - \delta) - L_{\text{eff}}) & \text{ALLFB}.
\end{cases}
\end{align*}
\]

(2.4)
Stability against perturbations of release height was activation. If a perturbation remains constant from step to step (|S| = 1), the model has indifferent behaviour (neutrally stable). The return maps were calculated for release heights of 1.01...1.20 m.

2.5. Simulation protocol

To generate biologically relevant hopping patterns, the feedback parameters (gains and offsets) were optimized with respect to two criteria (for details, see appendix A): periodic hopping height was chosen as the primary optimization goal in order to generate hopping patterns with enough ground clearance to allow for significant perturbations. The secondary criterion was a hopping frequency of f ≈ 2 Hz, which corresponds to preferred human hopping frequencies [31,32]. The optimization was repeated nine times (table 2). The resulting feedback-driven hopping patterns were tested for stability against perturbations in landing height (compare §2.4). In addition, hopping patterns generated by the combination of feedback and feed-forward signals (according to equation (2.5)) were tested for stability. The optimization process for the feed-forward patterns Aopt is described elsewhere [22].

3. RESULTS

3.1. Hopping with proprioceptive feedback

The direct feedback was found to be capable of producing activation patterns similar to the optimal activation pattern (figure 3). For model M[const, lin] only minor deviations from the optimal activation pattern were found during stance phase (figure 3a). For model M[Hill, Hill], FFB and the hybrid feedback ALLFB reproduced the optimal activation Aopt from Haeufle et al. [22] fairly well (figure 3b). LFB activation pattern shows a similar shape but with shorter duration (resulting in reduced hopping height). VFB cannot capture the quick rise of the optimal activation pattern after touchdown. The resulting force patterns (figure 3c,d) reflect the earlier-described observations of the activation patterns. Peak forces of all activation schemes are similar in model M[const, lin] (Fmax ≈ 3 kN). In model M[Hill, Hill], peak forces rise up to Fmax ≈ 3.6 kN for all activation types except for VFB with Fmax ≈ 2.4 kN.

Regarding the hopping height, model M[const, lin] reached with all four feedback types nearly the optimal feed-forward periodic hopping height of h = 11.9 cm (yfix = 1.119 m) (table 2). In the nonlinear model M[Hill, Hill], FFB and the hybrid feedback ALLFB reached the highest hopping height (FFB: h = 6.6 cm; ALLFB: h = 6.7 cm). Hybrid feedback does not reach much higher hopping heights in any model than a single feedback. Hopping height was lowest for all models with VFB.

When comparing muscle model complexity, we found increasing model complexity to result in decreasing periodic hopping height (M[const, lin]: 11.5 cm ≤ h ≤ 11.6 m and M[Hill, Hill]: 5.5 cm ≤ h ≤ 6.7 cm; table 2).

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Table 1. Model parameters for human hopping. The biological relevance of these parameters is suggested in Haeufle et al. [22].

<table>
<thead>
<tr>
<th>parameter</th>
<th>value</th>
</tr>
</thead>
<tbody>
<tr>
<td>leg rest length L0</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 m s⁻²</td>
</tr>
<tr>
<td>optimal isometric muscle force Fmax</td>
<td>2.5 kN</td>
</tr>
<tr>
<td>width w</td>
<td>0.45 m</td>
</tr>
<tr>
<td>curvature c</td>
<td>30</td>
</tr>
<tr>
<td>maximum velocity vmax</td>
<td>-3.5 m s⁻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 Fv slope μ</td>
<td>0.25 m s⁻¹</td>
</tr>
<tr>
<td>stimulation activation coupling time constant τ</td>
<td>10 ms</td>
</tr>
<tr>
<td>feedback signal delay δ</td>
<td>15 ms</td>
</tr>
</tbody>
</table>

STIM0 represents the pre-activation; voff and Loff denote a muscle spindle signal offset [18]. Four feedback types are considered: force feedback (FFB), velocity feedback (VFB), length feedback (LFB) and the combination of all three signals in a hybrid feedback (ALLFB). In all feedback types, the signal propagation delay δ was set to 15 ms as an estimate of afferent pathway properties from spinal cord to leg muscles [18].

2.3. Combined feed-forward and feedback

We previously presented maximum height hopping generated by optimal activation patterns Aopt(t) [22]. These optimal activation patterns represent a feed-forward signal. Here, feed-forward and proprioceptive feedback signals are combined:

\[ A_{\text{comb}}(t) = A_{\text{FF}}(F(t), v(t), L(t)) + \left(1 - A_{\text{FF}}\right) \times A_{\text{opt}}(t), \]

where 0 ≤ AFF ≤ 1 is the weighting factor between feedback (AFF = 1) and optimal feed-forward (AFF = 0) activation.

2.4. Stability analysis: apex return map

Stability against perturbations of release height was investigated by mapping the dependency of apex height y1 on release height y0 using an apex return map y1(y0) [29,30]. A periodic solution is characterized by y1 = y0 and, thus, is represented in the apex return map as a fixed point, yfix with y1(y0) = y0 = yfix. The optimization process favoured 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 return map in the neighbourhood of a fixed point is a measure for stability against infinitesimal perturbations. The trajectory converges to its periodic solution after a small perturbation if |S| < 1. Therefore, we called models with |S| < 1 stable. A model is unstable for perturbations growing from step to step (|S| > 1).
Table 2. Results of the optimization: for the characteristics of the periodic hopping patterns (stability $S$, periodic hopping height $y_{\text{fix}}$ and hopping frequency $f$) mean ± s.d. of the optimization results (nine repetitions) are shown. The values for optimal feed-forward activation are taken from Haeufle et al. [22]. From all nine repetitions of the optimization, the feedback parameters resulting in the highest periodic hopping height were used for further analysis (§3.2). In this table, these optimal feedback parameters are reported and additionally, the standard deviation of the optimization indicated by $D$. STIM0 is the stimulation bias, $G_F$, $G_v$ and $G_L$ are the gains in the force, velocity and length feedback circuits. $v_{\text{offset}}$ and $L_{\text{offset}}$ represent a signal offset. Length gains $G_L$ are negative owing to the ‘inverse’ contractile element (figure 1).

<table>
<thead>
<tr>
<th>muscle model</th>
<th>feedback</th>
<th>FFB</th>
<th>VFB</th>
<th>LFB</th>
<th>ALLFB</th>
<th>$A_{\text{opt}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fl</td>
<td>Fv</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>const</td>
<td>lin</td>
<td>$S = 0.4479 ± 0.0005$</td>
<td>$y_{\text{fix}} = 1.1154 ± 0.0002$ m</td>
<td>$f = 2.001 ± 0.001$ Hz</td>
<td>STIM0 = 0.186±0.017</td>
<td>$G_F = (7.11 \Delta 0.27) \cdot 10^{-4}$</td>
</tr>
<tr>
<td>Hill</td>
<td>Hill</td>
<td>$S = 0.26 ± 0.04$</td>
<td>$y_{\text{fix}} = 1.066 ± 0.007$ m</td>
<td>$f = 2.1 ± 0.2$ Hz</td>
<td>STIM0 = 0.027±0.02</td>
<td>$G_F = (9.71 \Delta 0.14) \cdot 10^{-4}$</td>
</tr>
</tbody>
</table>
3.2. Hopping stability with combined feedback and feed-forward

The return maps (figures 4 and 5) show that optimal feed-forward activation as well as all feedback types result in stable hopping ($|S| < 1$). All pure feedback types ($w_{FB} = 1$) showed a return map with positive slope ($0 < S < 1$) (thick coloured lines) at the fixed point, while pure feed-forward activation ($w_{FB} = 0$) resulted in return maps (thick black lines) with a negative slope ($-1 < S < 0$) (see also figure 6). These two observations hold for both muscle models M[const, lin] and M[Hill, Hill].

The return maps further show that the whole range of investigated disturbances in release height ($y_0 = 1.0 \ldots 1.2$ m) were compensated as the hopping was attracted to the fixed point (undisturbed hopping pattern). Only VFB in the M[Hill, Hill] model has a limited range of release heights ($y_0 < 1.09$ m).

Combinations of optimal feed-forward activation and different feedback modes (figures 4 and 5, thin lines) resulted in return maps with slopes $S$ between the two extreme cases, namely pure optimal activation with $w_{FB} = 0$ and pure feedback with $w_{FB} = 1$.

Comparing the simple linear and the more complex nonlinear model, we found smaller differences in the complex model between the return maps of optimal feed-forward and pure feedback activation. This becomes prominent by the closer alignment of the return maps (figure 4 versus figure 5). Further, the perturbation is diminished faster in the complex model (flatter return maps). A higher hopping stability is indicated in the more complex model (except for VFB) by smaller values of $|S|$ (table 2).

4. DISCUSSION

Dickinson [6] stated that ‘future studies of motor control should address the dynamic coupling among CPGs, sensory feedback, mechanical preflexes and the environment.’ In this paper, we integrated mechanical muscle properties, feed-forward and feedback signals, and tested their capabilities in generating and stabilizing hopping.

We were able to show that the combination of feed-forward and direct feedback improves hopping stability and that the more complex Hill-type representation of intrinsic muscle properties generally leads to a faster reduction of perturbations independent of the type of activation.

4.1. Performance of feedback modes

The results clearly prove that an optimal feed-forward activation pattern and a purely feedback-driven activation lead to similar periodic hopping behaviour. This becomes prominent because activation patterns and force patterns nearly remain the same for the feed-forward and feedback approaches (figure 3). This result is surprising because it reveals that decentralized feedback modes are as effective as centralized feed-forward activation. This stands in contrast to Geyer et al. [18], where the optimal activation pattern clearly...
outperformed the best feedback type (FFB) in hopping height with 19.6 cm versus 16.3 cm. Regarding the different feedback types, we found only minor differences in hopping height in the M[const, lin] model (less than 1 mm). The M[Hill, Hill] basically confirms the results of Geyer et al.\[18\] that FFB leads to highest periodic hopping. However, we found smaller differences in hopping height between FFB and LFB (approx. 1 cm in contrast to approx. 7 cm for the model in Geyer et al.\[18\]). The differences observed here between the feedback types might be amplified by the more complex structures in the model of Geyer et al.\[18\], i.e. segments, muscle acting over lever arm at joint and tendons acting in series to the muscle.

The resulting hopping heights vary between 5.5 cm ≤ h ≤ 11.6 cm (table 2). This is in accordance with a hopping height of up to h = 8.6 cm found for human periodic hopping at preferred hopping frequency [33]. In addition, the chosen hopping frequency of 2 Hz corresponds to the preferred frequency in human hopping [31,32]. Therefore, the criteria used for the optimization in this study (periodic hopping, f ≥ 2 Hz, maximum hopping height) led to biologically relevant hopping performance.

Regarding hopping stability, we found stable solutions for all feedback types. However, the capability to quickly reduce a perturbation is clearly better with force and LFB than with VFB, i.e. the slope of the return map |S| at the fixed point is flatter for FFB and LFB (figures 4 and 5). Furthermore, in the complex model M[Hill, Hill], VFB is not able to reject perturbations larger than 2 cm. This means that FFB and LFB outperform VFB with respect to hopping performance. This behaviour can be inherited by more complex models [18].

4.2. Benefits of combining feedback and feed-forward

Both optimal feed-forward and feedback activation can produce the same periodic hopping patterns. However, when introducing perturbations, the stabilizing response can be clearly distinct. The return maps of feed-forward activation have a negative slope (−1 < S < 0) at the fixed point, while the return maps of all feedback modes have a positive slope (0 < S < 1) (figures 4 and 5). Disturbances in case of a positive slope S are rejected in a monotonic manner (figure 6).
That means, that with every hop, the perturbation is reduced by a certain fraction $\Delta y_{i+1}/\Delta y_i \approx S$. In the case of feed-forward with a negative slope $S$, the consecutive apices are alternatingly too high or too low and only the norm $|\Delta y_{i+1}/\Delta y_i|$ of the perturbation is reduced in every cycle (figure 6). Despite this qualitatively different reaction to perturbations they diminish with both types of activation within a few cycles. Therefore, the type of stabilization (negative or positive slope) reflects system properties whose biological relevance is still unclear. Interestingly, only this difference facilitates a combination of feed-forward and feedback signals which results in optimal stability ($S = 0$).

In our study, the increased stability of the hopping simulations driven by feed-forward or feedback actuation in parallel compared with those simulations using exclusively one actuation type could be quantified. All return maps from combined activation lay within the range given by the pure signals (figures 4 and 5). At the fixed point, the slope of the return maps is closer to zero, implying faster reduction of perturbations than the pure activation schemes. Interestingly, this is only possible because feed-forward and feedback-actuated hopping results in alternating versus monotonic rejection of the perturbation (figure 6). In fact, only this difference allows the selection of a weighting factor $v$, resulting in patterns with slope $S = 0$, and thus facilitates a combination of feed-forward and feedback signals, which results in optimal stability. From these results, it can be predicted that a combination of feed-forward and feedback is beneficial to all systems, reacting to perturbations in this opposing way.

There is also experimental evidence of simultaneous contributions of feedback and feed-forward signals. For example, in human hopping both contribute to the early EMG burst after landing [37] or to adapt walking patterns against movement resistances [38]. Our study shows that one resulting benefit of the combination is an improved disturbance rejection. We can speculate about other benefits of the combination of feed-forward and feedback signals. One advantage could be that the organism can rely on a well-known and trained pattern but adds some flexibility by using sensory feedback. Also, the shape of the trained pattern could be much less critical if reflex pathways are

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Figure 5. Return maps for model $M[Hill, Hill]$ show the model reaction to perturbations in the apex height $y_0$ leading to a subsequent apex height $y_1$. For further description, see figure 4. The discontinuous return map with velocity feedback (VFB) (c) results from the following situation: if the release height is too high, the contractile element driven by the VFB does not produce enough force to generate the next push off, and the model collapses. (Online version in colour.)
provided at the same time. Or the redundancy of control possibilities could be a safety measure to compensate the (temporary) loss of one of the systems.

4.3. Stability arises from exploitive actuation

In the literature, the paradigm exists that a feed-forward strategy cannot generate adaptive movement patterns ensuring stability for uneven terrain [25,35,39]. Our feed-forward-driven model can reject perturbations of more than 13 cm (for a 1 m leg length). Therefore, we can dispel such doubts about the feed-forward strategy not being able to properly adapt to altering terrain in hopping. Another paradigm is that instabilities arise from the signal delays in a pure feedback strategy [39]. Although our feedback-driven model incorporates signal delays of 15 ms, it results in very stable hopping patterns. In both cases, the key is the integration of the control strategy with intrinsic muscle properties. Several other studies confirm the role of intrinsic muscle properties for compensating perturbations, e.g. variations in starting position for explosive jumping [20], unexpected changes in surface stiffness during hopping [21], sudden external forces during walking [40] and perturbations while holding a load [41]. These intrinsic muscle properties may provide rapid responses to perturbations, for instance, mechanical preflexes as described by Brown & Loeb [42]. The control mechanism can rely on these mechanical properties and exploit them [43]. In this concept of exploitive actuation, furthermore, the movement trajectory has not to be planned and compared with the current movement, but rather emerges from the intrinsic properties of the actuated mechanical system itself [44,45].

The benefits of exploitive actuation for locomotion stability has also been demonstrated in several studies on insect locomotion [16,36,46,47]. Furthermore, a recent model addresses the integration of feed-forward and feedback activation in the context of intrinsic muscle properties [48]. They found that feedback can modulate muscle force to counteract strong impulsive perturbations. However, for the high stride frequency in rapid insect locomotion, it seems impossible that direct proprioceptive feedback alone could generate adequate muscle activations because of the neural time delays. Therefore, exploitive actuation might be even more important in insects, whereas feedback might play a more important role in mammalian locomotion [27].

In hopping, this exploitive actuation relies especially on the force–velocity relation. We observed that the nonlinear Hill-type force–velocity relation (figure 5) always resulted in a faster reduction of perturbations (smaller values of $|\dot{S}|$) than the linear approximation (figure 4). Because this holds for all types of activation pattern generation—pure feed-forward [22], or feedback, and their combination—our results reveal an independence of the activation type. Thus, the stabilizing capabilities seem to be mainly governed by the intrinsic muscle properties. Therefore, this hopping study is a strong case for the concept of exploitive actuation.

4.4. General implications for locomotion

The approach to understanding legged locomotion presented in this paper is inspired by the concept of templates and anchors [28]. In this concept, the complexity of a biological system is reduced to a model that describes and predicts a target behaviour with the least possible number of variables and parameters. Given the reductive nature, the analysis of such so-called template models facilitates the identification of underlying basic principles of locomotion. Template models can be anchored to be more representative of an organism by adding, for example, more morphological (segmentation of a leg, joints, muscles) and physiological details (muscle fibre orientation, behaviour of motor neurons and proprioceptive sensor properties). While templates are oriented on the global behaviour, anchors ‘provide causal explanations of detailed neural and musculo-skeletal mechanisms’ [28].

Following this concept, the model analysed in this article reduces the neuromechanical function of a leg (figure 7d) to a ‘muscle segment’ with Hill-type muscle properties (figure 7a). With this, it describes the basic function of legged systems in bouncing gaits, i.e. the vertical motion of the centre of mass, with alternating stance and flight phases. The muscle model itself represents the fundamental muscle characteristics.
and generates an active push off during stance phase. As the muscle operation requires a neural stimulation signal, we investigated two possibilities of neural movement generation for hopping. The major finding was that the simultaneous contribution of feed-forward and feedback could improve stability and reduce the response time to perturbations to one cycle.

We speculated that this result is a general feature of legged locomotion and can be inherited to more realistic anchor models for the following reasons:

— the vertical oscillation of the centre of mass represents a movement primitive present in all legged gaits, whether it is hopping, running or walking [50]. Our reduced model predicts the global dynamics (centre of mass motion, ground reaction forces) for this vertical component and it further indicates how a muscle actuated legged system can cope with perturbations in ground height. In this respect it fulfils the Full & Koditschek requirements of a template because it defines 'the behaviour of the body that serves as a target for control' [28];

— although our analysis was done with parameters related to human hopping (table 1), in principle, a dimensionless analysis would lead to the same results and thus, could be applicable to animals of different size; and

— the literature already indicates that the mechanisms detected in our reduced model could be inherited by more complex musculo-skeletal models. For example, the hopping dynamics with FFB remain very similar in a two-segmented leg model driven by one muscle-tendon complex [18] (figure 7b). There, the reaction to perturbations showed the same monotonic behaviour found in our study. Furthermore, Geyer & Herr [49] showed that this FFB mechanisms could also generate and stabilize walking patterns in a more elaborate musculo-skeletal model with four segments and 14 muscles. This model could accurately predict human-like movement dynamics and even muscle activation patterns that remarkably resemble measured human electromyography (EMG) signals [cf. fig. 4 in 49]. Such an anchor evolution path towards human locomotion (figure 7) indicates that the feedback properties investigated on a fundamental level might not only remain valid in a more realistic model, but also synthesize behaviour observable in biology.

Therefore, we are confident that the advantages of combining feed-forward and feedback activation shown in this study are also advantageous for more complex musculo-skeletal systems. However, the proof of this speculation is open and could be tackled by the analysis of more elaborate (anchored) models.

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APPENDIX A. DETAILS OF THE GENETIC ALGORITHM

To determine the optimal feedback parameters, a genetic optimization algorithm was implemented. Each individual represents a set of five parameters with the limits: 0.001 ≤ STIM0 ≤ 1, 0 ≤ GF ≤ 2.5, 0 ≤ Ge ≤ 1.2, −100 ≤ GL ≤ 0, 1 ≤ Goffset ≤ 3, and −2 ≤ Loffset − 0.9. In the case of ALLFB, all parameters were optimized simultaneously. For the other feedback-types, the limits of the unnecessary parameters were set to 0. The initial population (n = 0) of individuals (parameter sets) was generated randomly. These parameter sets were applied to single-cycle hopping simulations from apex y0 to apex y1. The fitness function P of each individual was
calculated from the hopping height $h = y_f - L_0$ and hopping cycle duration $T$ normalized to 1 s:

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

(A1)

where performance $P$ equals the hopping height for cycle durations of $T < 0.5$ s and was penalized for cycle durations of $T > 0.5$ s. This restriction of hopping cycle time was necessary as the force–length relation in the model $M[\text{const, lin}]$ included no physical limit for muscle contraction and hopping height could have increased infinitely with longer hopping cycle duration.

Subsequent generations $(n + 1)$ were derived from the 50 fittest individuals (with highest performance $P$). Fifty per cent of the next generation $(n + 1)$ were identical copies of the 25 fittest individuals of generation $n$. 25 per cent were created by randomly scattered pairwise recombination and 25 per cent by mutation with a mutation rate of one out of five genes. To favour periodic solutions reached apex height $y_f$ was passed on as starting height $y_0$ for descendant individuals. Starting height of the initial population was $y_0 = 1.05$ m. The optimization was performed with 100 individuals for 100 generations and was repeated nine times. The best parameter set out of the nine repetitions was used for further analysis.

The feedback parameters resulting from nine repetitions of the optimization typically varied less than 15 per cent (table 2). For the ALLFB, on the other hand, variations were usually larger. However, the resulting differences in hopping height and stability were much smaller (table 2). This suggests that a nearly optimal hopping performance can be achieved with different sets of parameters, especially in the ALLFB case, and thereby only slightly affecting other results ($S$, $C_{IG}$, and $f$). Therefore, using only the set of parameters generating the highest periodic hopping height for further analysis still gives representative results for all feedback parameter sets from the optimization.

REFERENCES


