Antagonistic Co-contraction Can Minimise Muscular Effort in Systems with Uncertainty

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Abstract

Muscular co-contraction is often seen in human movement, but can currently not be predicted in simulations where muscle activation or metabolic energy is minimised. Here, we intend to show that minimal-effort optimisations can predict co-contraction in systems with random uncertainty. Secondly, we aim to show that this is because of mechanical muscle properties and time delay. We used a model of a one-degree-of-freedom arm, actuated by two identical antagonistic muscles, and solved optimal control problems to find the controller that minimised muscular effort while remaining upright in the presence of noise with different levels. Tasks were defined by bounding the maximum deviation from the upright position, representing different levels of difficulty. We found that a controller with co-contraction required less effort than

purely reactive control. Furthermore, co-contraction was optimal even without activation dynamics, since nonzero activation still allowed for faster force generation. Co-contraction is especially optimal for difficult tasks, represented by a small maximum deviation, or in systems with high uncertainty. The ability of models to predict co-contraction from effort or energy minimization has important clinical and sports applications. If co-contraction is undesirable, one should aim to remove the cause of co-contraction rather than the co-contraction itself.

Keywords: Optimal Control, Co-contraction, Effort Minimisation

1 Introduction

Recently, predictive simulations have been used to predict gait in different scenarios, such as walking with a prosthesis [1], an exoskeleton [2], or in a way that reduces the axial knee contact force [3], and running with different shoe midsole materials [4]. Predictive simulations are usually formulated as an optimal control problem in which the objective includes a term related to muscular activation effort or metabolic energy. The optimisation represents the inherent optimisation performed in the central nervous system, and the solutions represent an optimal movement trajectory, and the open-loop muscle activation patterns that produce this trajectory.

Currently, predictive simulations do not take into account uncertainty in the system, even though uncertainty has been shown to be important for movement decisions [5, 6, 7]. Uncertainty can be caused by sensory noise [8] or because of the environment, e.g. when walking on slippery terrain. In linear systems, the certainty equivalence principle states that the optimal trajectory with uncertainty is the same as without [9]. However, this is not true for nonlinear human dynamics [10]. Similarly, the optimal muscle stimulation pattern is likely different in systems with uncertainty.

A typical feature of predictive simulations is that antagonistic co-contraction is min-

imised. Co-contraction is the simultaneous activation of the agonist and antagonist muscle around a joint. It increases the instantaneous muscle stiffness due to the nonlinear mechanical properties of the muscle, and consequently prevents movement. Co-contraction is often seen in human movement (e.g. [11]), especially in individuals with impairments. For instance, co-contraction is observed in gait of persons with a transtibial amputation (TTA gait), between the muscles of the upper leg on the intact sides [12, 13]. However, simulations found by solving optimal control problems failed to predict this co-contraction [1]. Similarly, co-contraction is not predicted in static optimisation [14, 15].

Co-contraction does not produce external forces or work while it requires effort and metabolic energy [16], and therefore co-contraction is often described as inefficient [17, 18]. The benefit of co-contraction in human movement has been described as an increase in joint stiffness and stability [16, 19, 20, 21], a reduction of stress in the joint ligaments [22], and lower tibial shear force [22]. However, these objectives are typically not included in the optimal control problem that generates the predictive simulation. Effort and energy expenditure increase with co-contraction, and co-contraction will thus not be predicted from such an optimal control problem. One approach to increase accuracy of predictive simulations is to include additional optimisation objectives to the optimal control problem, and tune the solution by weighting them appropriately (e.g. [23]). However, from an evolutionary perspective, it would be attractive to explain co-contraction by the single objective of effort or energy minimization [24]. This would mean that humans robustly choose movements based on a simple objective, instead of a combination of different objectives related to energy or effort and stability.

In fact, a system with uncertainty benefits from the stiffness that is provided by co-contraction to prevent undesired movement. This control approach might require less effort than a reactive control approach that corrects afterwards. Hogan [16] proposed that co-contraction is required because the time delay in the nervous system does not allow a human to rely solely on reactive control, and therefore a combination of energy-efficient

reactive and inefficient co-contraction is required [16]. This was confirmed using stochastic open-loop optimal control by Berret and Jean [25]. However, Berret and Jean did not allow feedback control. Therefore, it is still unknown if a control strategy combining co-contraction with reactive control requires less energy than a control strategy with only reactive control.

Therefore, we would like to investigate if we can predict co-contraction with a traditional effort cost function for an uncertain system. We aim to show that a control strategy with co-contraction requires less effort than a control strategy without co-contraction for certain tasks in systems with uncertainty. Our secondary aim is to examine if co-contraction is optimal due to time delay. We recently proposed a solution method for optimal control problems of human movement to include uncertainty [10], which can be used to study these aims. We solve optimal control problems that include system uncertainty to investigate if the optimal control strategy includes co-contraction, and does not rely solely on reactive control. We also remove the activation dynamics from the muscle, and solve optimal control problems to investigate if co-contraction is still optimal without the time delay of the activation dynamics due to nonlinear muscle mechanics. We expect a lower level of co-contraction to be optimal, because the reactive control is faster.

2 Methods

Muscle tendon units (MTUs) are commonly modelled using the Hill-type model. The basic Hill-type model consists of two elements: the contractile element (CE), which models the active component of the muscle, and the series elastic element (SEE), which models passive elements connected to the muscle in series, such as the tendon and aponeurosis [26]. Stiffness is nonlinear in the CE, in its force-length relationship, and in the SEE, which is modelled as a spring with a quadratic stiffness [27]. Furthermore, the maximum force is also limited by the shortening velocity [28], meaning that a force cannot be generated

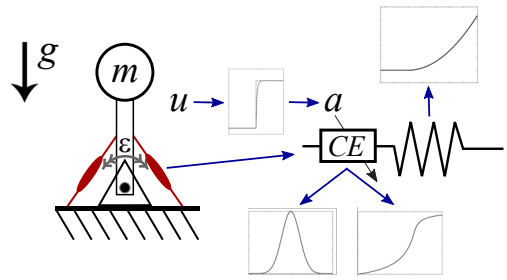

Figure 1: Overview of the arm used in this study. It has one rotational degree of freedom at the base, and is operated by two identical muscle-tendon units (MTUs). The MTUs consist of a series elastic element, modelled as quadratic spring, and a contractile element (CE) with activation dynamics, a force-length relationship, and a force-velocity relationship. Uncertainty, ε, is added to the base of the arm. The MTU is also modelled without activation dynamics to separate the effect of time delay.

instantly from a non-contracted muscle. Finally, a time delay is present in the activation dynamics of the CE.

We used a simple one degree-of-freedom arm controlled by two muscles, as shown in figure 1, to show that a control strategy with co-contraction minimises effort in an uncertain environment. The arm was connected to the ground via a revolute joint, operated by two identical MTUs with an equal but opposite moment arm. Muscular activation caused the MTUs to apply a force to the arm, and an imbalance between the force in both MTUs caused a moment around the joint. We solved optimal control problems to find the optimal controller for the arm such that effort is minimised. Tasks were simulated by bounding the maximum deviation from the upright position. A decreasing maximum deviation angle represents increasing difficulty. We solved these problem for a common Hill-type model, and a Hill-type model without activation dynamics.

2.1 Dynamics Model

The arm was modelled as a one degree of freedom pendulum with length $l = 0.6$ m and weight $m = 2$ kg. The state was described using angle, θ, and angular velocity, ω, yielding

the following dynamics:

$$\dot{\theta}(t) = \omega(t) \tag{1}$$

$$\dot{\omega}(t) = -\frac{g}{l}\sin(\theta(t)) + \frac{\tau(t)}{ml^2} + \varepsilon(t) \tag{2}$$

where $g = 9.81$ m/s^2 denotes gravity, $\varepsilon \sim \mathcal{U}(-b, b)$ the uncertainty of the system, drawn from a uniform distribution with limits b, and $\tau(t)$ the torque that was applied at the base of the arm, which is determined from the MTU force as follows:

$$\tau(t) = F_{SEE,1}(t)d - F_{SEE,2}(t)d \tag{3}$$

where $d = 2$ cm is the equal and opposite moment arm.

The arm was controlled by two identical MTUs, which were modelled as two element Hill-type muscles with a CE with activation dynamics, a force-length relationship, and a force-velocity relationship, and a quadratic spring to model the SEE (see figure **??**. The force in the SEE was determined as follows:

$$F_{SEE} = k_{SEE}F_{max}(l_{SEE}(t) - l_{SEE(slack)})^2 \quad \text{if} \quad l_{SEE}(t) > l_{SEE(slack)} \tag{4}$$

with stiffness $k_{SEE} = \frac{1}{(0.05 l_{SEE(slack)})^2}\ F_{max}$/m, slack length $l_{SEE(slack)} = 5$ cm, and length $l_{SEE}(t)$.

The CE added two states to the dynamics: the activation, a, and the contractile element length, l_{CE}. The CE dynamics were modelled implicitly using the imbalance of forces

between the series elastic element and the contractile element:

$$F_{SEE}(t) - a(t)f(l_{CE}(t))g(v_{CE}(t))F_{max} = 0 \tag{5}$$

with:

$$f(l_{CE}(t)) = \exp\left(-\left(\frac{l_{CE}(t)-l_{CE(OPT)}}{wl_{CE(OPT)}}\right)^2\right) \tag{6}$$

$$g(v_{CE}(t)) = \begin{cases} \frac{v_{CE(max)}+v_{CE}(t)}{v_{CE(max)}-v_{CE}(t)/A} + \beta v_{CE}(t) & \text{if } v_{CE} \leq 0 \\ \frac{g_{max}v_{CE}(t)+c_3}{v_{CE}(t)+c_3} + \beta v_{CE}(t) & \text{if } v_{CE} > 0 \end{cases} \tag{7}$$

$$\tag{8}$$

where $f(l_{CE})$ is the force-length relationship, and $g(v_{CE})$ the force-velocity relationship, with a small damping term, with coefficient β, for numerical stability. All parameters are described in table 1.

The activation dynamics introduced a time delay and smoothing between the stimulation and activation. The dynamics were defined as follows, given the parameters in table 1:

$$\dot{a}(t) - (u(t) - a(t))\left(\frac{u(t)}{T_{act}} + \frac{1-u(t)}{T_{deact}}\right) = 0 \tag{9}$$

where $u(t)$ denotes the muscle stimulation,

Table 1: Muscle model parameters.

Parameters	Value (unit)
Maximum isometric force	$F_{max} = 1100$ N
Maximum shortening velocity	$v_{CE(max)} = 10\ l_{CE(opt)}$/s
Maximum force during lengthening	$g_{max} = 1.5\ F_{max}$
Optimal fiber length	$l_{CE(opt)} = 7$ cm
Activation time constant	$T_{act} = 12$ ms
Deactivation time constant	$T_{deact} = 47.6$ ms
Hill parameter	$A = 0.25$
Width of the force-length curve	$w = 0.56$
Damping coefficient	$\beta = 0.001\ F_{max}s/l_{CE(opt)}$

We also developed a muscle model without activation dynamics for our secondary aim. In this model, the stimulation was fed into the contractile element dynamics directly instead of the activation. Then, only the contractile element length was added to the dynamics state.

2.2 Controller model

The MTU input was determined using a combination of open-loop and closed-loop control. The open-loop control modelled the co-contraction, because a static task was performed in our work. The closed-loop control models reactive control, which was active once the arm deviates from its desired, upright position. The full input for muscle i was calculated as follows:

$$u_i(t) = u_{0,i} + K_{P,i}\theta(t) + K_{D,i}\omega(t) \tag{10}$$

where $u_{0,i}$ denotes the open-loop control input of muscle i, $K_{P,i}$ a position feedback gain for muscle i, and $K_{D,i}$ a derivative feedback gain for muscle i. The stimulation was truncated at zero when the full input, $u_i(t)$ was negative. The co-contraction input and feedback gains of the two muscles were independent.

2.3 Optimal Control Problem

The control parameters were optimised by solving an optimal control problem. The goal was to find the control parameters that minimised the muscular effort, while different tasks were simulated by limiting the deviation allowed from the upright position, creating the following objective problem:

$$\underset{[u_{0,1}\ u_{0,2}\ K_{P,1}\ K_{P,2}\ K_{D,1}\ K_{D,2}]^T}{\text{Minimise:}} \quad \int_{t=0}^{T} u(t)^2 \mathrm{d}t \tag{11}$$

$$\text{Subject to:} \quad \dot{x}(t) = f(x(t), u(t), \varepsilon(t)) \quad 0 \leq t \leq T \tag{12}$$

$$x(0) = x(T) \tag{13}$$

$$|\theta(t)| < \theta_{bound} \qquad 0 \leq t \leq T \tag{14}$$

where equation 12 denotes the dynamics (equations 2, and 5- 9), equation 13 denotes a periodicity constraint to ensure that the state at the beginning and the final time, T, is equal, and equation 14 represents the task, which limits the maximum deviation from the

upright position to θ_{bound}. The periodicity constraint was used to ensure that the motion could theoretically continue infinitely long.

2.4 Simulations

The optimal control problems were solved with different noise limits: $b = [0\ 1\ 2.5\ 5\ 7.5\ 10]^T$. The solution is trivial for $b = 0$, because in that case no co-contraction or feedback control is required, but the muscle states that yielded static equilibrium were found in the optimisation. The solution for $b = 0$ is then used as initial guess for $b = 1$, which is then used as initial guess for $b = 2.5$, and so on. The noise limit, b, was divided by the square root of the time step to create a dimensionless value. These problems were repeated 10 times with different noise samples to account for variability due to the uncertainty. We investigated the effect of task difficulty by varying θ_{bound}, using $\theta_{bound} = [5\ 10\ 15\ 20]^T$ (see equation 14).

We also solved the optimisation problem with the open-loop control input fixed at $u_0 = [0\ 0.05\ 0.1\ 0.15\ 0.2]^T$, to show that the optimal objective is lowest when there is co-contraction, and the open-loop control input is nonzero. The problems with fixed input were repeated five times. The solutions with $b = 20$ and the lowest objective were used for comparison.

Finally, we compared the MTU model to an MTU model without activation dynamics to investigate the effect of time delay. The optimal control problem with free open-loop control input was repeated with an MTU model without activation dynamics. Again, these problems were repeated 10 times. We compared the co-contraction input, as well the optimal state trajectories and inputs for the system with and without activation dynamics.

All optimal control problems were solved with direct collocation, with 3000 collocation points and a duration of 3 s, and a backward Euler formulation. The muscle models, the arm dynamics and the controller, as well as their derivatives, were coded in MATLAB (Mathworks, Natick, MA, USA). IPOPT 3.11.0 was used to solve the resulting optimisation

Table 2: Optimal controller parameters for each system noise limit.

System noise limit	Open-loop muscle input		Proportional gain		Derivative gain	
	Muscle 1	Muscle 2	Muscle 1	Muscle 2	Muscle 1	Muscle 2
$b = 0$	0.0	0.0	0.0	0.0	0.0	0.0
$b = 1$	$2.5 \cdot 10^{-6}$	$2.9 \cdot 10^{-4}$	0.0098	-0.024	$5.9 \cdot 10^{-4}$	-0.0014
$b = 2.5$	0.018	0.020	0.61	-0.73	0.011	-0.013
$b = 5$	0.075	0.062	2.4	-2.6	0.0095	-0.016
$b = 7.5$	0.14	0.11	4.8	-5.1	0.010	-0.024
$b = 10$	0.20	0.16	7.9	-8.2	0.0099	-0.025

problems [29].

3 Results

3.1 Optimal Controllers

Table 2 shows the optimal controller parameters for each system noise limit, for the smallest maximum angle θ_{bound}, averaged over 10 repetitions with different noise samples. With increasing system noise, the open-loop muscle input and position gains increased. The derivative gains increased only slightly, and mostly for muscle 2.

Figure 2 shows the average objective function over five repetitions for different tasks as a function of the open-loop control input for the problem with the largest noise, $b = 10$. For none of the tasks, zero open-loop control input yielded the lowest objective. Instead, an open-loop control input $u_0 = 0.05$ was optimal, expect for $\theta_{bound} = 5$ deg, where $u_0 = 0.15$ was optimal. This shows that co-contraction input minimises effort in a stochastic environment, especially when little deviation from the desired position is allowed.

Figure 3 shows the co-contraction input of the optimal solutions as a function of the maximum angle, θ_{bound}, and system noise limit, averaged over 10 repetitions. As expected, no co-contraction was optimal in a deterministic system, with $b = 0$. For all systems with noise, the optimal solution was a control strategy with co-contraction, since both open-loop control inputs were nonzero. The amount of co-contraction increased with an increasing

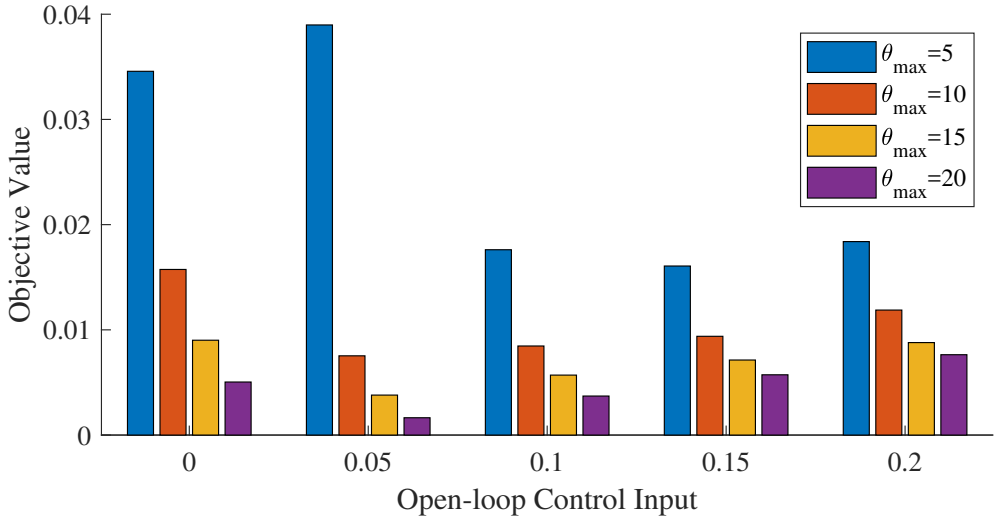

Figure 2: Objective value as a function of open-loop control input for different tasks for the system with the largest limit, $b = 10$.

system noise limit and with a decreasing maximum angle.

3.2 Optimal Trajectory

Figure 4 shows the arm angle, input torque, muscle input, activation, contractile element length, and muscle force of an optimal trajectory. The solution with the lowest objective is given for $\theta_{bound} = 5$ deg and noise limit $b = 10$. The arm angle remained within 5 degrees from the upright position (top left). The input torque ranged between -20 and 20 N, and its

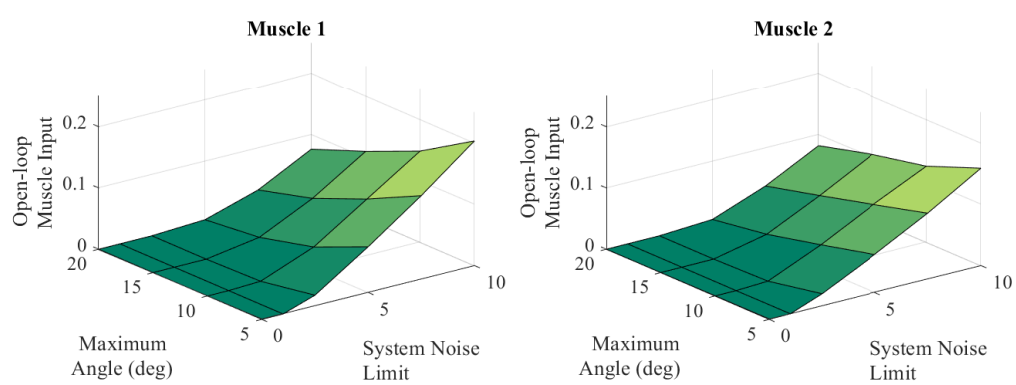

Figure 3: Average co-contraction input of optimal solution as a function of maximum angle, θ_{bound} and system noise limit, b. The co-contraction input increases with increasing system noise limit, and with decreasing maximum angle.

trajectory had a similar shape to the am angle (top right). The input signal varied between -1 and 1 (middle left), but was truncated at 0 before it was put in to the MTU model, such that the activation is always positive (middle right). The bottom graphs show that the muscle was co-contracting, since the contractile element length was generally smaller than optimal (bottom left), while both muscles regularly generated force at the same time for 84% of the simulation (bottom right).

3.3 Optimal Controller and Trajectory without Activation Dynamics

Figure 5 shows the optimal co-contraction input as a function of the system noise limit for the MTU model with and without activation dynamics. The average open-loop muscle input is shown for $\theta_{bound} = 5$ deg. The amount of co-contraction was very similar between the two MTU models, and slightly lower for the MTU model without activation dynamics.

Figure 6 shows the optimal arm angle trajectory, torque input, muscle input, contractile element length, and muscle force for the MTU model without activation dynamics, for the same solution as figure 4. The results look similar to the results with activation dynamics. However, the main difference is that without activation dynamics, there was force in both muscles for only 46% of the simulation, compared to 84% for the MTU model with activation dynamics.

4 Discussion

We aimed to show that a control strategy with muscular co-contraction requires less muscular effort in a system with noise than a purely reactive control strategy. We solved optimal control problems on a one degree-of-freedom arm operated with two identical, antagonistic muscles, where the aim was to minimise effort, and optimised open-loop and closed-loop controller parameters. We showed that the optimal solution had nonzero open-loop input, and thus co-contraction, in a system with noise. The level of co-contraction increased with

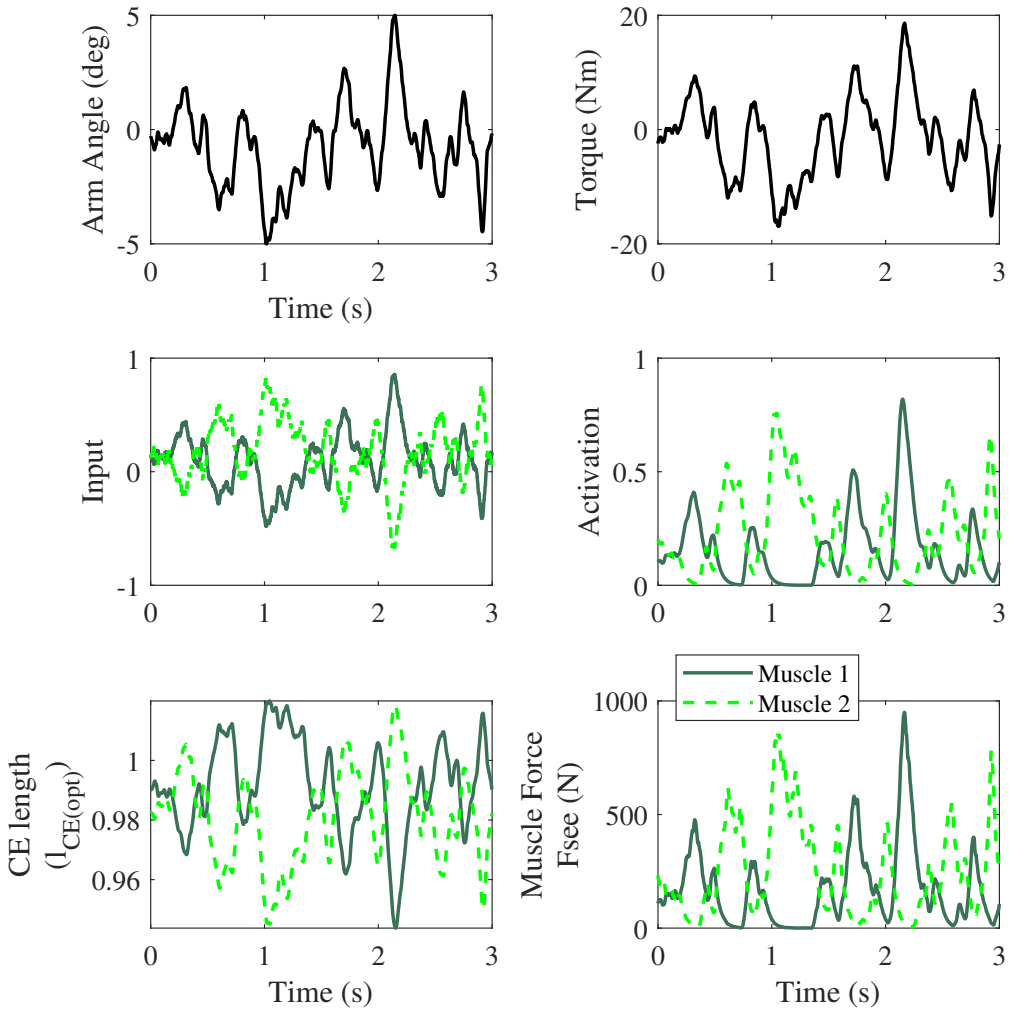

Figure 4: Optimal arm angle (top left), input torque (top right), muscular input (middle left), muscular activation (middle right), contractile element (CE) length (bottom left), and muscle force (bottom right). The solution shown had the lowest objective, for $\theta_{bound} = 5$ deg and noise limit $b = 10$.

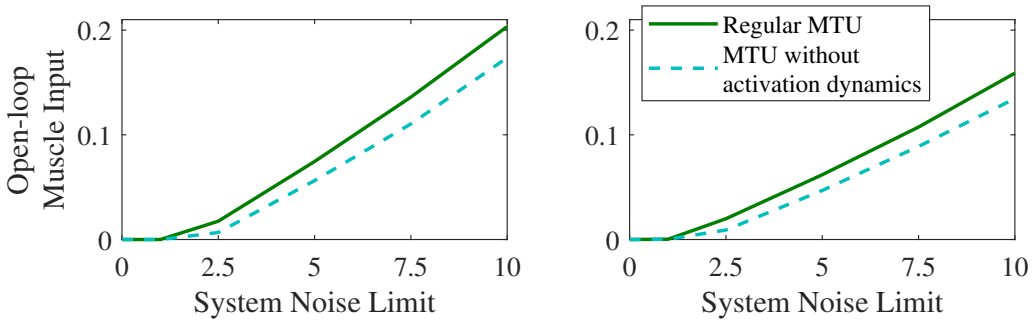

Figure 5: Co-contraction input of optimal solution with and without activation dynamics in the MTU. The co-contraction input increases with the system noise limit, b, similarly for both systems.

the system noise level (table 2). We also showed that if the open-loop control was fixed, the objective was larger with zero open-loop control than nonzero open-loop control (figure 2). Furthermore, the level of co-contraction increased when the maximum deviation angle decreased (see figure 2 and figure 3), which shows that a higher level of co-contraction is optimal for more difficult tasks. In practice, every system has uncertainties, due to internal noise in the neural control or due to randomness in the environment. Therefore, these results show that in practice a control strategy with co-contraction minimises effort. This means that the common claim that co-contraction is inefficient [17, 18] is incorrect.

Our secondary aim was to investigate if co-contraction is optimal due to the time delay. Therefore, the same problem was solved for an MTU model without activation dynamics. We showed again that a nonzero open-loop control input, and thus co-contraction, is optimal without the time delay of the activation dynamics (see figure 5). To further investigate the effect of the different mechanical properties of the muscle, we also investigated several simplified models where nonlinear components of the muscle model were replaced by linear components. These simplified models showed that co-contraction is not optimal in an MTU without time delay or force-length and force-velocity properties, while co-contraction is optimal in an MTU model with a linear SEE and a CE with and without activation dynamics. This shows that especially active muscle properties cause co-contraction to be optimal. These results are presented in the supplementary material.

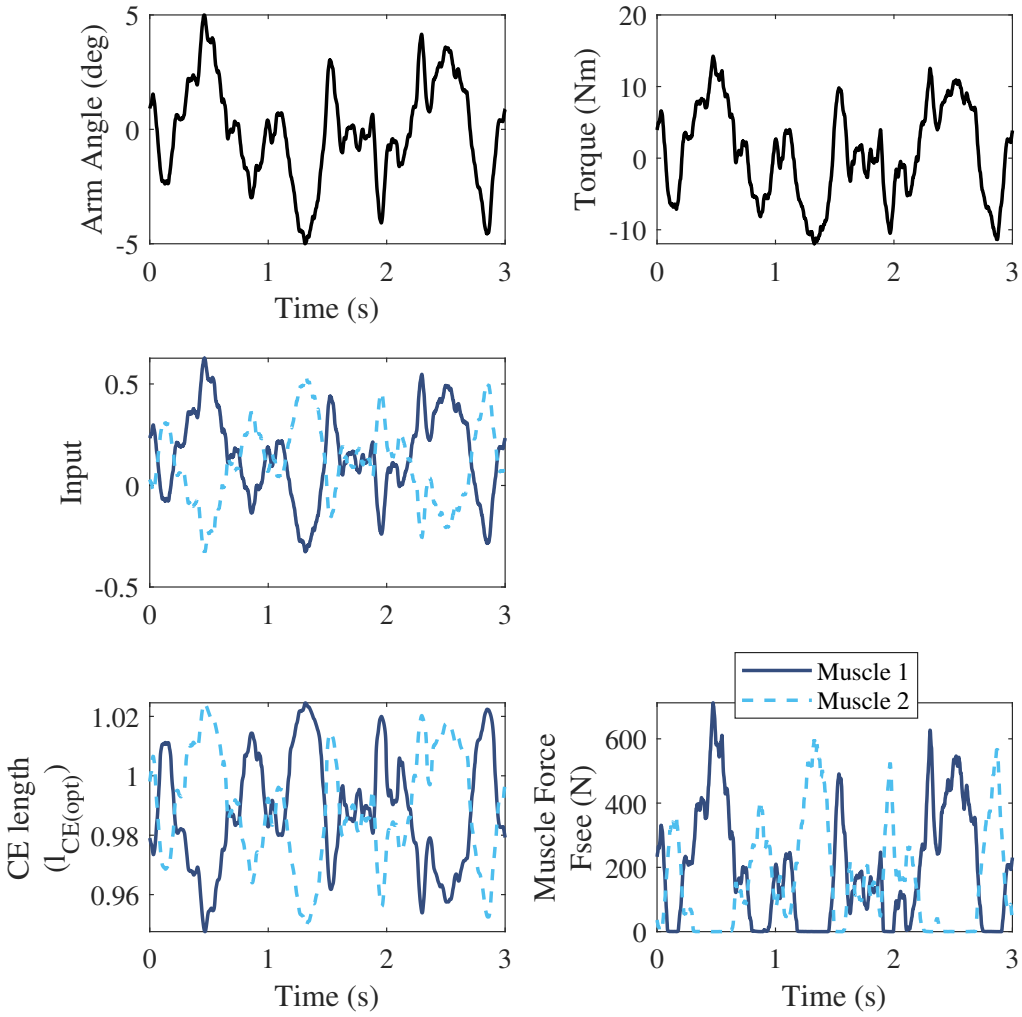

Figure 6: Optimal arm angle (top left), input torque (top right), muscular input (middle left), contractile element (CE) length (bottom left), and muscle force (bottom right) for the system without activation dynamics in the MTU. The solution shown had the lowest objective, for $\theta_{bound} = 5$ deg and noise limit $b = 10$.

As expected, the optimal level of co-contraction was slightly lower in the MTU model without activation dynamics than in the regular MTU model. Furthermore, the amount of time that force was produced in both muscles also decreased from 84% to 46% of the simulation without activation dynamics (see figure 4 and 6). We suspect that a nonzero level of co-contraction input was still optimal due to the force-velocity properties. When a muscle is activated and shortens, the force-velocity properties limit the maximum force that can be generated at a high shortening velocity, thereby acting as a time delay between activation and force generation. Therefore, co-contraction input is still optimal, since then the contractile element remains shortened, allowing for faster force generation.

We have shown that co-contraction minimises effort in noisy systems. Previous work showed that uncertainty is taken into account when making control decisions [5, 6, 7]. Our work suggests that humans choose robust movement trajectories based on a single objective of effort minimization, while accounting for uncertainty, and not based on a complex objective with different components accounting for effort and stability, among others. De Luca and Mambrito [30] previously showed that co-contraction was observed in environments with uncertainty, and our work explains this observation by showing that this co-contraction minimises muscular effort. Therefore, predictions of human movements would be more accurate if uncertainty is taken into account. For example, by taking into account uncertainty, a predictive gait simulation with a lower-leg prosthesis model could predict the co-contraction that is observed in experiments in the upper leg on the prosthesis side. Then, predictive simulations could be used to improve prosthesis design, to find a design that is stable enough to not require co-contraction to minimise effort, because this co-contraction increases metabolic cost in gait of persons with a transtibial amputation [31].

Co-contraction of muscles is used as an indicator of impaired control [32]. However, our work shows that co-contraction does not necessarily indicate impaired function. Instead, co-contraction might be the most optimal control strategy for e.g. the elderly population, who have decreased strength and for whom falls could have dire consequences,

such as fractures [33] or even death [34]. The difficulty of the task was represented by the maximum deviation angle, θ_{bound}. Difficult tasks require one to remain close to the desired position, and are represented by a smaller maximum angle. Simpler tasks have a larger maximum deviation angle, since variation of the intended trajectory is allowed to a greater extent. By varying the maximum deviation angle, we showed that the optimal and expected level of co-contraction increases with the difficulty of the task. Elderly people, who have less room for error when walking, might aim to stay closer to the intended trajectory than younger people and therefore display more co-contraction.

We used a two-element Hill-type MTU model without a parallel elastic element (PEE). This model was chosen because the PEE will not be active when there is co-contraction, because its slack length is equal to at least the optimal fiber length. Recently, a winding filament model was introduced as alternative to a Hill-type muscle model [35]. It is expected that with a winding filament model there would be more advantages of co-contraction, since a contraction of the contractile element would then also lengthen the titan spring, further stiffening the muscle.

Noise can be present internally or externally. Internal noise is present in neural control, both in sensing [8] and stimulation, while external noise could be due to wind, or uneven ground. In this work, noise was added to the pendulum acceleration, which represents external noise. The problem was also repeated with internal noise, added to the joint angle to model sensor noise, or to the input, to model noise in stimulation. The solution was trivial with sensor noise, because the noise was removed from the system without feedback control, such that no control at all is required. When input noise was added, again it was optimal to not have feedback control, however with co-contraction.

The co-contraction input was not constrained to be the same for both muscles, despite the system being symmetric otherwise. However, such an equality constraint could have pushed to solution in a certain direction, which was undesired. Therefore, the co-contraction input of both muscles was left free. This caused the optimal co-contraction

input to be different between the two muscles, but the average over the different noise samples were similar, which shows that the difference was a side-effect of the uncertainty.

System uncertainty was modelled with uniform noise. This was chosen because the maximum deviation was bounded. If normally distributed noise was used, it is possible that the noise at one time instance is very large, which would cause the pendulum to deviate too far and not meet the task constraint. Then, co-contraction might have come out as a means to avoid that one large deviation, instead of as a reason to minimise effort. Uniform noise is bounded and therefore does not suffer from this issue.

The feedback to the muscles was based on the joint angle instead of the muscle force and length, which would be a better representation of the human sensory system. However, feedback on the muscle force and length is generally one-directional. Therefore, a more realistic feedback law would have introduced discontinuities in the Jacobian during the optimisation, which causes problems in gradient-based optimisation algorithm. Instead, it was chosen to use a simple feedback law with proportional and derivative feedback on the joint angle.

In conclusion, we showed that co-contraction minimises effort in an environment with uncertainty. Furthermore, the amount of co-contraction increases with the amount of uncertainty in the environment, and the difficulty of the task. We also showed that co-contraction is optimal due to time delay and mechanical properties of active muscle, and that the force-velocity properties cause co-contraction to be optimal even without time delay between sensors and muscle activation. Co-contraction is often thought of as inefficient and therefore avoided as much as possible. However, this work shows that co-contraction is not inefficient, but the combination of proactive and reactive control requires less effort than only reactive control. Therefore, training and rehabilitation should focus on removing the cause of co-contraction to increase movement efficiency, instead of removing co-contraction itself.

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Author Contributions

AK and AvdB conceived and designed the study; AK ran all simulations, analysed the results and drafted the manuscript, AvdB critically revised the manuscript; All authors gave final approval for publication and agree to be held accountable for the work performed therein.

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