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

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ABSTRACT

Muscular co-contraction of antagonistic muscle pairs is often observed in human movement, but it is considered inefficient and it can currently not be predicted in simulations where muscle activation or metabolic energy is minimized. Here, we investigated the relationship between minimizing effort and muscular co-contraction in systems with random uncertainty to see if muscular co-contraction can minimize effort in such system. We also investigated the effect of time delay in the muscle, by varying the time delay in the neural control as well as the activation time constant. We solved optimal control problems for a one-degree-of-freedom pendulum actuated by two identical antagonistic muscles, using forward shooting, to find controller parameters that minimized muscular effort while remaining upright in the presence of noise added to the moment at the base of the pendulum. We compared a controller with and without an feedforward control. Tasks were defined by bounding the root mean square deviation from the upright position, while different perturbation levels. We found that effort was minimized when the feedforward control was nonzero, even when the feedforward control was not necessary to perform the task, which indicates that co-contraction can minimize effort in systems with uncertainty. We also found that the optimal level of co-contraction increased with time delay, both when the activation time constant was increased and when neural time delay was added. Furthermore, we found that for controllers with a neural time delay, a different trajectory was optimal for a controller with feedforward control than for one without, which indicates that simulation trajectories are dependent on the controller architecture. Future movement predictions should therefore account for uncertainty in dynamics and control, and carefully choose the controller architecture. 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.

Understanding human movement is one of the key goals in biomechanics research. During the last 60+ years, the energy optimality of movement has been shown in different experimental and simulation work. Using experiments, Ralston showed that people choose their walking speed to minimize the metabolic energy expenditure per distance travelled in 1958 (Ralston, 1958). Since then, the minimization of energy expenditure in movement has been confirmed for different other parameters, such as step frequency (Zarrugh et al., 1974), step width (Donelan et al., 2004) and vertical movement of the center of mass (Ortega and Farley, 2005; Gordon et al., 2009). Furthermore, walking and running emerge as energy-optimal gaits at their respective speeds when optimal simulations are created with simple passive-dynamic walking models (Srinivasan and Ruina, 2006). Static optimization has revealed that muscle forces can be explained by minimizing an objective related to effort (Crowninshield and Brand, 1981). Simulations with complex musculoskeletal models, where an objective related to energy minimization is minimized, have also revealed a motion that looks very similar to walking (Ackermann and Van den Bogert, 2010; Koelewijn et al., 2018). Energy minimization also makes sense from an evolutionary

perspective (Wall-Scheffler, 2012).

However, certain human behaviours seem to contradict the notion that movements are energy optimal, a prime example being antagonistic co-contraction of muscles. Antagonistic co-contraction is the activation of both agonist muscles, which support a movement, and antagonist muscles, which oppose a movement, around a joint. It increases the instantaneous muscle stiffness due to the nonlinear mechanical properties of the muscle, and consequently prevents movement. Co-contraction does not produce external forces or work while it requires effort and metabolic energy (Hogan, 1984), and therefore co-contraction is often described as inefficient (Falconer and Winter, 1985; Winter, 2005). The benefit of co-contraction in human movement has been described as an increase in joint stiffness and stability (Hogan, 1984; Hirokawa et al., 1991; Jiang and Mirka, 2007; Selen et al., 2005), a reduction of stress in the joint ligaments (Baratta et al., 1988), and lower tibial shear force (Baratta et al., 1988).

From what is known about human movement, it would be unlikely that a human behaviour exists that is not energy-optimal. Therefore, we hypothesize that co-contraction is optimal in practice, due to noise in the movement. Noise can be caused by external uncertainty, such as due to wind, but noise is also present internally in sensory and motor neurons (Bays and Wolpert, 2007). As a result, human control should constantly correct any deviations caused by noise. Furthermore, a neural time delay is present in the control due to the travel time required through sensory and motor neurons. Therefore, the stiffness added by co-contraction prevents any unwanted deviations due to noise, could be more energy efficient than a reactive control approach, where deviations are corrected after their occurrence.

To investigate our hypothesis, we can use tools from stochastic optimal control. The notion of energy optimality has allowed researchers to study human movement using tools from optimal control (He et al., 1989; Park et al., 2004; Ackermann and Van den Bogert, 2010). Then, the goal is to find the optimal input, which could be described by a control law (He et al., 1989; Park et al., 2004), or parameterized over time (Ackermann and Van den Bogert, 2010), that minimizes an objective, while performing the desired task. However, commonly, the dynamics are described using a deterministic model, which does not account for the internal or external noise (Anderson and Pandy, 2001; Miller et al., 2013; Ackermann and Van den Bogert, 2010; Koelewijn et al., 2018). Another option is to linearize the system (He et al., 1989; Park et al., 2004), and use e.g. linear quadratic Gaussian control Todorov (2005). However, human walking is nonlinear, while the internal noise is signal dependent and thus nonlinear as well, meaning that the assumptions of linear quadratic Gaussian control do not hold. Instead, to account for the noise, we should use stochastic optimal control while allowing for the system to be nonlinear.

However, the solution to stochastic optimal control problems can only be estimated using time-consuming approaches. When solving a stochastic optimal control approach for nonlinear systems, the

stochastic Hamilton-Jacobi-Bellmann equation should be solved. However, these equations become intractable for high dimensions (Kappen, 2005). Therefore, several methods have been developed that estimate the solution of optimal control problems for nonlinear systems. The most commonly used approach is the Monte Carlo method (Tiesler et al., 2012; Sandu et al., 2006a). In this method, a large number of forward simulations are performed, where the uncertain variables are sampled from their distribution. Using the solution of each of the forward simulations, a distribution of the outcome variables is provided. This method requires a large number of simulations to obtain an accurate solution (Sandu et al., 2006a). Another approach is based on the theory of generalized polynomial chaos, which states that a second order stochastic process can be approximated by a combination of stochastic basis functions. When combined with a collocation method, this approach can solve optimal control problems faster than a Monte Carlo method (Tiesler et al., 2012; Sandu et al., 2006a,b). We have recently developed such an approach to solve stochastic optimal control problems for human gait based on sampling and direct collocation (Koelewijn and van den Bogert, 2020). However, this method still does not scale well to models with a large number of degrees of freedom.

Instead of using collocation, forward shooting could be an appropriate alternative to investigate our hypothesis. Historically, optimal control problems of gait were solved with forward shooting, but these problems required many computer hours to solve, and often gait cycles were not periodic (Anderson and Pandy, 2001; Miller et al., 2013). Direct collocation reduced the optimization time to less than one hour for three-dimensional gait simulations (Falisse et al., 2019; Nitschke et al., 2020) and thereby greatly enhanced the possibilities for gait simulations. Recently though, advances have also been achieved using forward shooting, especially in combination with reflex models (Ong et al., 2019; Koelewijn and Ijspeert, 2020), and nowadays this method, e.g. using the software SCONE (Geijtenbeek, 2019), can also efficiently solve optimal control problems with a predefined controller structure and a relatively smaller number of optimization variables.

Therefore, we will investigate our hypothesis that co-contraction is energy optimal on a nonlinear system with uncertainty. We will solve optimal control problems using forward shooting in SCONE on the simplest possible problem where co-contraction can occur: to find the optimal muscle controls for a one degree of freedom pendulum, controlled by two muscles at the base, to remain upright while noise is applied to the pendulum base. We use this problem to investigate if a control strategy with more co-contraction requires less effort than a control strategy with less co-contraction for certain tasks in systems with uncertainty, even when a strategy with less co-contraction is possible. We will also use this problem to examine the relationship between co-contraction and time delay, both in the muscle and neural time delay between a sensory stimulus and an action. To do so, we will repeat the optimal

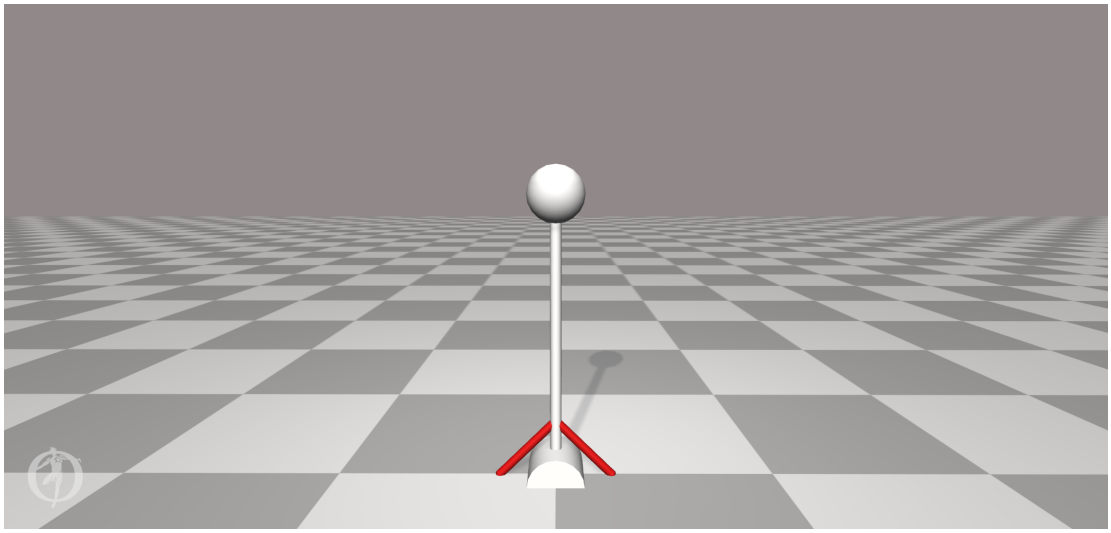

Figure 1. Pendulum used in this study. The pendulum has one rotational degree of freedom at the base, and is operated by two identical muscle-tendon units (MTUs). The MTUs are modeled as ”Thelen2003Muscle” (Thelen, 2003).

control problems with different neural time delays, by introducing a time delay in the controller, and with increased activation time constant in the muscle to investigate the relationship between co-contraction and time delay.

METHODS

We developed a one degree-of-freedom pendulum model, operated via two muscle-tendon units (MTUs) in OpenSim (Seth et al., 2018) (Figure 1). The pendulum was modelled as a point mass of 1 kg, located 50 cm from a revolute joint, which connected the pendulum to the ground. We set the default value of its degree of freedom to π, or the upright position, which we defined as the angle $\theta = 0$. We attached identical MTUs on both sides of the revolute joint to operate the pendulum. These MTUs were attached to the ground with a $\pm$ 10 cm offset, and attached to the pendulum at 10 cm above the joint. The MTUs were modelled as ”Thelen2003Muscle” (Thelen, 2003) with identical parameters (Table 1). The optimal fiber length and tendon slack length were chosen such that the muscle was approximately slack in the upright position.

Controller model

We designed two controllers to determine the MTU input from the pendulum angle and angular velocity. To compare the effect of co-contraction, one controller had feedforward control and feedback control, while the other only had feedback control. In the first controller, we created a constant feedforward stimulation, which represents co-contraction for a static task. We created feedback control using proportional-derivative control, which penalized any deviation from the upright position and any angular velocity. Since the

Table 1. Default muscle model parameters.

Parameter	Value and unit
Maximum isometric force	$F_{max} = 2000$ N
Maximum shortening velocity	$v_{CE(max)} = 10\ l_{CE(opt)}$/s
Maximum force during lengthening	$g_{max} = 1.8\ F_{max}$
Optimal fiber length	$l_{CE(opt)} = 7$ cm
Activation time constant	$T_{act} = 10$ ms
Deactivation time constant	$T_{deact} = 40$ ms
Tendon slack length	$l_{SEE,slack} = 8$ cm
Pennation angle at optimal	$\phi_{opt} = 0.2$ rad
Tendon strain at isometric force	$e_{SEE,iso} = 0.033$
Passive muscle strain at isometric force	$e_{PEE,iso} = 0.6$
Active force-length shape factor	$K_{act} = 0.5$
Passive force-length shape factor	$K_{pas} = 4$
Force-velocity shape factor	$A_f = 0.3$

problem is symmetric, the feedforward control was the same for both MTUs, while the feedback control had an opposite sign between the MTUs. Therefore, the full input for muscle i, u_i, was calculated as follows:

$$u_i(t) = u_0 \pm (K_P\theta(t-\Delta t) + K_D\omega(t-\Delta t)), \tag{1}$$

where u_0 denotes the feedforward control, K_P the position feedback gain, K_D the derivative feedback gain, ω the angular velocity of the pendulum, and Δt the neural time delay.

The second controller was exactly the same, but we set the feedforward control to 0.01, the minimum muscle activation, such that only feedback control was used:

$$u_i(t) = 0.01 \pm (K_P\theta(t-\Delta t) + K_D\omega(t-\Delta t)). \tag{2}$$

Optimal Control Problem and Simulations

We solved optimal control problems to optimize controller parameters for different tasks. The goal was to find the control parameters that minimized muscular effort during a 20 s simulation while remaining close to the upright position position, under the influence of perturbations added to the base of the pendulum. We defined the precision of the tasks using a maximum root mean square (RMS) deviation from the upright position over the full simulation. We chose this task description instead of bounding the maximum deviation to ensure that co-contraction was not required due to one large perturbation that could not be overcome by the muscles otherwise. We also defined a fall, which ended the simulation, when the joint angle deviated more than 1 rad from the upright position. All simulations started from the upright position

and zero angular velocity. This yields the following optimization description:

$$\text{For dynamic system} \quad \dot{x} = f(x(t), u(t)) \tag{3}$$

$$\text{with initial conditions} \quad \theta(0) = 0,\ \omega(0) = 0, \tag{4}$$

$$\underset{u_0, K_P, K_D}{\text{minimize}} \quad J(u(t)) = \frac{1}{2T}\int_{t=0}^{T} u_1(t)^2 + u_2(t)^2 \mathrm{d}t \tag{5}$$

$$\text{subject to} \quad \theta_{RMS} = \sqrt{\frac{1}{T}\int_{t=0}^{T} \theta(t)^2 \mathrm{d}t} \quad \leq \theta_{RMS,max} \tag{6}$$

$$T \quad \geq 20, \tag{7}$$

where $f(x(t), u(t))$ describe the dynamics, derived with OpenSim (Seth et al., 2018), T the duration of the simulation, θ_{RMS} the RMS deviation of the angle, and $\theta_{RMS,max}$ the maximum RMS deviation, or the desired task precision.

We used SCONE (Geijtenbeek, 2019) to solve these optimal control problems via forward shooting. Since SCONE does not allow for constraints, we constructed an objective, J_{SCONE}, to ensure that effort was minimized, while our constraints were met. To do so, we added two objective terms to the objective of minimizing effort, such that the RMS deviation was penalized once it was larger than maximum RMS deviation, and another penalty was added when a simulation finished in less than 20 s. Therefore, we created the following objective to achieve the desired behaviour:

$$J_{SCONE}(x(t), u(t)) = \quad J(u(t)) \tag{8}$$

$$+ \quad 100 + 10\theta_{RMS} \quad \text{if } \theta_{RMS} > \theta_{RMS,max} \tag{9}$$

$$+ \quad 1000(20 - T) \quad \text{if } T < 20\ s. \tag{10}$$

During forward shooting, perturbations were added to the moment at the base of the pendulum. We ensured that the same perturbations were added each iteration by fixing the random seed. The perturbations were added as external moment to the pendulum each 0.1 s, starting at t = 0 s. The random moment was drawn from a uniform distribution with a given amplitude, representing the task difficulty. We repeated each problem with 3 random seeds to account for variation due to the variability of the problem. All files used in SCONE, including the OpenSim model file, can be found in Koelewijn (2021).

Analysis

To investigate the effect of co-contraction on effort, we first visualized the landscape of feedforward control and required effort by solving optimizations with fixed levels of feedforward control. We use a maximum RMS deviation of 5 deg, a perturbation amplitude of 100 Nm, and a time delay of 10 ms. Then, we solved optimizations with the feedforward control, u_0, fixed between 0.02 and 0.22 with increments of

0.02 to investigate how the effort objective, $J(u(t))$ changes with the feedforward control. We also solved an optimization where the feedforward control is optimized, and compared this result to the solutions with fixed feedforward control.

To investigate the relationship between task precision and task difficulty, we solved optimizations for the controller with feedforward control for a range of tasks by varying the maximum RMS deviation (task precision) between 2 and 5 deg, with increments of 1, and by varying the perturbation amplitude (task difficulty) between 75 and 150 Nm, with increments of 25 Nm. Here, the neural time delay was equal to 0 ms. First, we discarded the tasks for which the combination of precision and difficulty could not be solved, meaning that the simulations did not last the full 20 s or the RMS deviation was larger than the maximum. Then, we selected the tasks for which the optimal feedforward control was larger than 0.01, the minimum activation, and investigated if the largest activation was close to 1. If this was the case, feedforward control is optimal not because of effort minimization, but it is required to perform the task, because the MTU strength would be insufficient. Finally, for the tasks where the optimal feedforward control was larger than 0.01 and the maximum activation was not close to 1, we also solved optimizations for the controller without feedforward control. We compared these solutions to those with feedforward control for the tasks where both simulations lasted the full 20 s and where the RMS deviation was equal to or below the maximum. For those simulations, we compared the objective value, so the required effort, the feedback gains, and the co-contraction index (CCI) between the two simulations. We calculated the CCI as follows (Falconer and Winter, 1985):

$$CCI = \frac{2\left(\int_{t_1}^{t_2} u_1(t)\mathrm{d}t + \int_{t_2}^{t_3} u_2(t)\mathrm{d}t\right)}{\int_{t_1}^{t_3} u_1(t) + u_2(t)\mathrm{d}t}, \tag{11}$$

where $[t_1, t_2]$ is the time period where the activation in MTU 1 is lower than in MTU 2, and $[t_2, t_3]$ denotes the time period where the stimulation in MTU 2 is lower than in MTU 1.

Next we investigated the effect of adding neural time delay. We used the task with maximum RMS deviation of 5 degrees, and perturbation amplitude of 100 Nm. We solved optimizations for both controllers with neural time delays between 5 ms and 25 ms, with increments of 5 ms. We investigated how the feedforward control developed with increasing neural time delay. Then we compared the solutions for the controller with and without feedforward control input using the objective, the CCI, and the controller gains as described before. Again, we only compared solutions for which the simulations lasted the full 20 s and the desired task precision was met. We also compared the optimal trajectories of the pendulum angle, muscle activation, muscle length, and muscle force for the controller with feedforward control to these optimal trajectories without feedforward control to investigate how these variables changed between

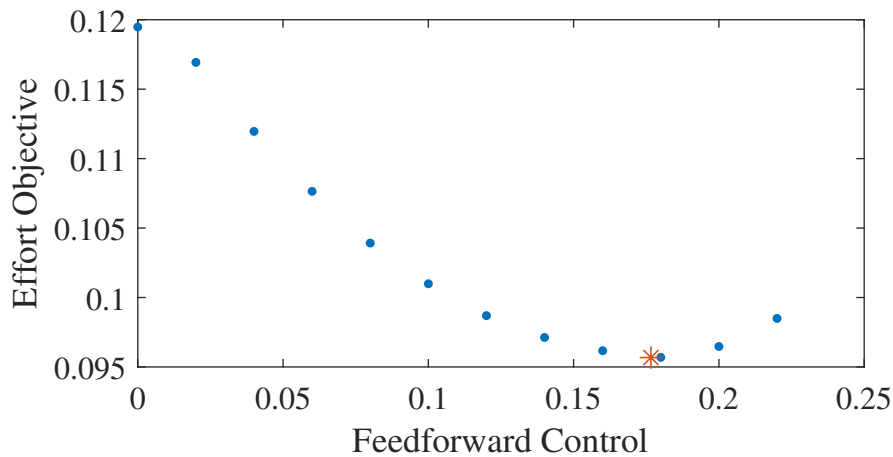

Figure 2. Effort objective as a function of the feedforward input. The blue dots show the optimal solutions found with prescribed feedforward input. The red star shows the optimal solution when feedforward input was optimized.

both solutions.

Then we investigated the effect of the muscle activation time using the same task as for the neural time delay. We solved optimizations for both controllers with activation time constants ranging between 0.01 and 0.09 with increments of 0.02, while setting the neural time delay to 0 ms. Our analysis was very similar to the neural time delay; we investigated how the feedforward control developed with increasing activation time constant. Then we again compared the solutions for the controller with and without feedforward control using the objective, CCI, and controller gains as described before, selecting only those solutions for which the simulations lasted the full 20 s and the desired task precision was achieved. We also compared the simulation outcomes between the two controllers, as well as to the simulation outcomes of the controller with neural time delay.

RESULTS

We found that for the example task, the effort objective is not minimized without any feedforward input, but when the feedforward input is equal to just below 0.18 (Figure 2). The relationship between the feedforward control and effort objective seems quadratic, since the required effort increased both when more or less feedforward control was used. These results show that even when it is possible to have no co-contraction, it requires less effort to have feedforward control and thus co-contract both muscles.

A comparison of different tasks with varying precision and difficulty

We found that co-contraction was optimal for a subset of the tested tasks with a sufficiently high precision, defined by the maximum RMS deviation, and difficulty, defined by the perturbation amplitude (Table 2). Though all tasks could be simulated for the full simulation time of 20 s, it was not possible to meet the

desired precision for all tasks. If this was the case, no optimal feedforward control was reported as the optimization was not considered successful. Furthermore, for the perturbation amplitude of 150 Nm, we found that co-contraction was required because the maximum activation was reached ($a > 0.995$). However, for the four cells with bold font in Table 2), we found co-contraction was an optimal control strategy, with the maximum activation below 0.93.

Table 2. Optimal feedforward controls for experiment 1. Bold font indicate the tasks for which co-contraction was optimal without requiring maximum activation. A dash indicates that the desired task precision was not achieved, meaning that the constraint on the root mean square (RMS) deviation was not met.

RMS angle	Perturbation amplitude (Nm)			
(deg)	75	100	125	150
2	0.010	**0.056**	-	-
3	0.010	0.010	**0.084**	-
4	0.010	0.010	**0.046**	0.210
5	0.010	0.010	**0.017**	0.133

We found that for two of the four highlighted tasks, it was possible to also use the controller with only feedback control, which required more effort, while for the other two tasks, the required precision was not achieved without feedforward control (Table 3). For the tasks with perturbation amplitude of 125 Nm, and maximum RMS angle of 4 or 5 degrees, we found that the objective is smaller for the optimal solution with co-contraction than for the optimal solution without co-contraction, while for the other two solutions, the actual RMS deviation was larger than the maximum, so the desired task precision was not achieved. When comparing the controllers with and without feedforward control, we find that the position and derivative gains of the optimal controller are smaller with feedforward control than without, and that this difference increases when the level of the optimal feedforward control increases. Furthermore, also the CCI is four times higher with feedforward control than without, and it increases with the level of the optimal feedforward control.

The effect of increased neural time delay

We found that the optimal feedforward control increased with an increasing neural time delay in the control (Fig. 3), and that the controller with feedforward control yielded lower objectives, and thus lower effort, than the controller without feedforward control (Table 4). The minimum feedforward control of 0.01 was optimal without neural time delay. The optimal feedforward control then increased in a somewhat linear fashion with the neural time delay, and co-contraction was optimal for all nonzero time delays. With a time delay of 10 ms or less, it was also possible to meet the required task precision without feedforward control (Table 4), and the objective was higher without feedforward control than with feedforward control. The difference in the objective with and without feedforward control increased

Table 3. Comparison of the RMS, objective, feedback gains, and co-contraction index (CCI) of the optimal solutions with and without co-contraction for the highlighted tasks. The objective (required effort) is given for all tasks that achieved the required precision. The position and derivative gain, as well as the CCI, are only reported for the tasks which achieved the required precision with and without feedforward control.

	Perturbation amplitude	100	125	125	125
	RMS angle	2.0	3.0	4.0	5.0
Actual RMS deviation	No feedforward control	2.7	3.6	4.0	5.0
	With feedforward control	2.0	3.0	4.0	5.0
Objective	No feedforward control	-	-	0.1005	0.0893
	With feedforward control	0.0839	0.1244	0.1001	0.0892
Position gain	No feedforward control	-	-	4.113	2.975
	With feedforward control	-	-	3.864	2.920
Derivative gain	No feedforward control	-	-	0.251	0.220
	With feedforward control	-	-	0.232	0.219
CCI	No feedforward control	-	-	0.77%	0.98%
	With feedforward control	-	-	2.84%	2.87%

for larger time delays, when optimal feedforward control was larger as well. Similar to the comparison of tasks without neural time delay (Table 3), we found that the optimal position and derivative gain were lower with feedforward control than without feedforward control. Furthermore, the CCI was consistently higher for the simulation with feedforward control, and increased to 29.9% for a time delay of 10 ms, while without feedforward control, the CCI remained close to 1%.

Table 4. Comparison of the RMS, objective, feedback gains, and CCI of the optimal solutions with and without co-contraction with different neural time delays. The objective (required effort) is given for all tasks that achieved the required precision. The position and derivative gain, as well as the CCI, are only reported for the tasks which achieved the required precision with and without feedforward control.

	Time delay (ms)	0	5	10	15	20	25
RMS deviation	No feedforward control	5.0	5.0	5.0	6.3	8.0	10.4
	With feedforward control	5.0	5.0	5.0	5.0	5.0	5.0
Objective	No feedforward control	0.0499	0.0670	0.120	-	-	-
	With feedforward control	0.0499	0.0641	0.0957	0.134	0.171	0.207
Position gain	No feedforward control	2.134	2.432	2.784	-	-	-
	With feedforward control	2.134	2.098	1.730	-	-	-
Derivative gain	No feedforward control	0.187	0.178	0.225	-	-	-
	With feedforward control	0.187	0.160	0.145	-	-	-
CCI	No feedforward control	1.36%	1.50%	1.19%	-	-	-
	With feedforward control	1.36%	9.88%	29.9%	-	-	-

A comparison of the joint angles, muscle activation, contractile element length, and muscle force during a simulation with and without co-contraction reveals small differences that indicate a different strategy is used by the controllers with and without feedforward control (Fig. 4). The pendulum angle in the simulation with feedforward control is slightly closer to zero (upright) than for the simulation without feedforward control (Fig. 4A, e.g. around 8 s). This strategy allows for larger deviations for large

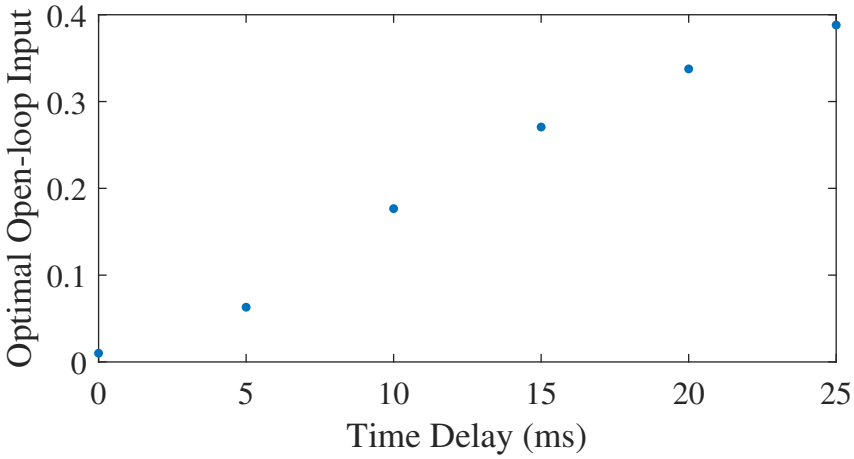

Figure 3. Optimal feedforward control as a function of neural time delay.

perturbations, e.g. at 9.8 s. Furthermore, in the simulation with feedforward control, the activation peaks are lower, while during periods with low activation, the activation is higher than in the simulation without feedforward control (Fig. 4B). The contractile element length is generally smaller for the simulation with feedforward control than for the simulation without feedforward control (Fig. 4C). Consequently, peak muscle forces are also lower in the simulation with feedforward control than in the simulation without feedforward control, but the difference between the peaks is smaller for the muscle force than for the activation. Furthermore, activation peaks, and therefore muscle force peaks are slightly delayed in the simulation with feedforward control compared to the simulation without feedforward control (Fig. 4B and 4D).

The effect of a longer activation time

We found that the optimal feedforward control increased with an increasing activation time constant (Fig. 5), and that the controller with feedforward control led to lower objectives, and thus lower effort, than the controller without feedforward control. Similar to the neural time delay (Fig. 3), the optimal feedforward control increased somewhat linearly with the activation time constant. For the activation time constant of 0.03, it was possible to meet the desired task precision also without co-contraction. This solution had a higher objective (0.0934 vs. 0.0879) without feedforward control. The CCI was nonzero for both solution, and lower without feedforward control than with (0.94% vs. 14.1%).

Contrary to what was found for the neural time delay, we did not find a different strategy between both controllers when increasing the activation time constant, and we saw smaller differences in the pendulum angle, muscle activation, contractile element length, and muscle force when comparing both controllers than for the neural time delay (Fig. 6). The pendulum angle was very similar and the peak deviation at 9.8 s comparable between both controllers (Fig. 6A). Both controllers also yielded very similar

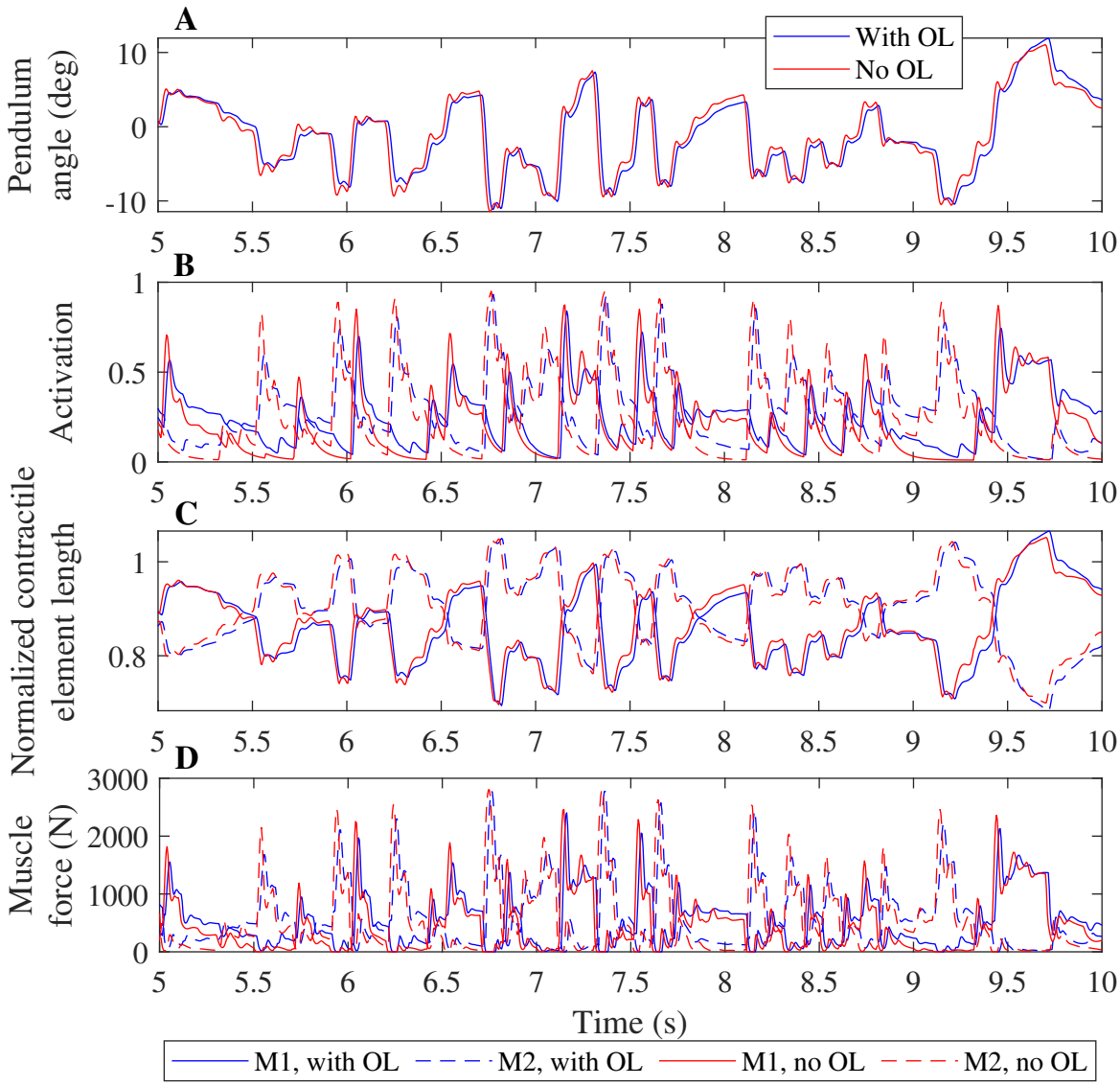

Figure 4. Comparison of simulations with and without feedforward control, for a neural time delay of 10 ms. Pendulum angle (A), activation (B), contractile element length (C), and muscle force (D) for the solution with feedforward control (blue) and without (red) are plotted for 5 seconds of the 20 second simulations. A solid line is used for muscle 1 (M1) and a dashed line for muscle 2 (M2) in figures B-D.

contractile element lengths, though the controller with feedforward control generally had slightly smaller extremes than the controller without feedforward control (Fig. 6C). Similar to Fig. 4B, we observed smaller activation peaks and larger activation during periods where activation is low for the controller with feedforward control than for the controller without feedforward control (Fig. 6B), which led to similar small differences in muscle force (Fig. 6D), which again were smaller than observed in Fig. 4D.

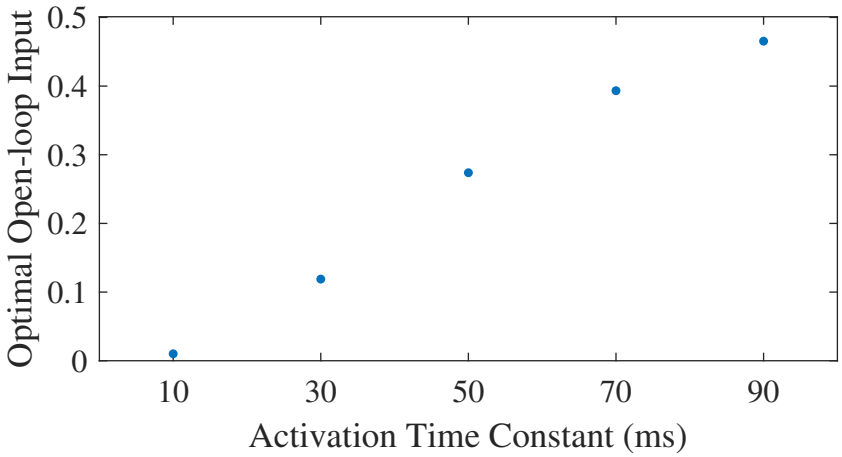

Figure 5. Optimal feedforward control as a function of activation time constant.

DISCUSSION

We investigated the relationship between co-contraction and effort minimization, and found that for certain tasks in systems with uncertainty, co-contraction minimizes effort. This co-contraction is created by applying a non-zero feedforward control to an antagonistic MTU pair. To show this, we solved optimal control problems for different tasks using controllers with and without feedforward control on a one degree-of-freedom pendulum while minimizing effort. We found different reasons that yielded an optimal feedforward control larger than the minimum muscle activation of 0.01. In some cases, co-contraction was necessary because otherwise the MTUs where not strong enough to successfully perform the task. However, in other cases, it was possible to also perform the task without feedforward control, but this required more effort. We also found that without feedforward control, the CCI was equal to around 1% for all tasks, meaning that the level of co-contraction is negligible. With feedforward control, it increased to 2.8% without time delay, to 14% with a larger activation constant, and to 30% with neural time delay for the tasks that could also be controlled without feedforward control. These results indicate that effort is minimized when an antagonistic muscle pair co-contracts, and that this co-contraction is especially optimal in muscles with time delay, either in the activation constant or through neural time delay. Therefore, we conclude that having feedforward control, and thus co-contraction, can minimize effort in environments with uncertainty, even when this co-contraction is not necessary.

We also investigated the relationship between time delay and co-contraction. To do so, we varied the activation time constant, and introduced a neural time delay in the control. For both, the amount of optimal feedforward control increased with an increase in time delay or time constant. In many cases, nonzero feedforward control was necessary to be able to solve the task. However, again, we found that certain tasks were solvable with and without feedforward control and that the combination of feedforward

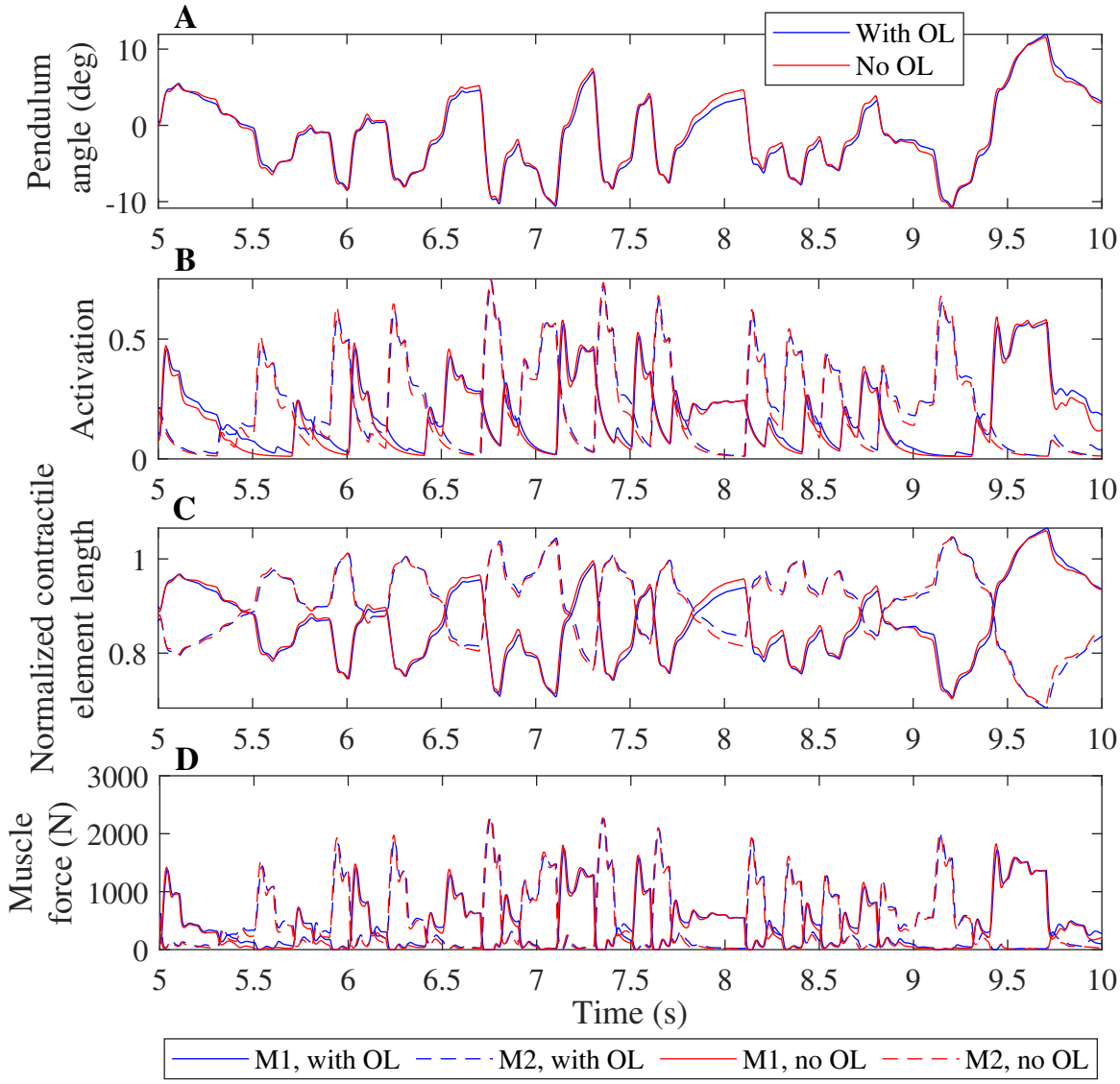

Figure 6. Comparison of simulations with and without feedforward control, for an activation time constant of 30 ms. Pendulum angle (A), activation (B), contractile element length (C), and muscle force (D) for the solution with feedforward control (blue) and without (red) are plotted for 5 seconds of the 20 second simulations. A solid line is used for muscle 1 (M1) and a dashed line for muscle 2 (M2) in figures B-D.

and feedback control, and thus antagonistic co-contraction, required less effort than only feedback control. We also found that with neural time delay, a different strategy was used with feedforward control than without, which changed the the optimal trajectory, while this change in strategy was not observed when the activation time constant was increased.

Our results show that co-contraction, contrary to what is often thought (Falconer and Winter, 1985; Winter, 2005), is not inefficient, and that it is not chosen out of necessity (Hogan, 1984; Berret and

Jean, 2020), but also because it minimizes effort of movement in systems with uncertainty. Previous experimental work also showed already that uncertainty is taken into account when making movement decisions (Kim and Collins, 2015; Hiley and Yeadon, 2013; Donelan et al., 2004), and our results confirm this in simulation as well. De Luca and Mambrito (1987) previously showed that co-contraction was observed in environments with uncertainty, and our work explains this observation by showing that this co-contraction likely minimized muscular effort.

Our results have implications for predictive simulations of gait and other human movements, which are currently not sufficiently accurate for many applications. Instead of modeling dynamics deterministically, stochastic optimal control should be used to predict movements taking into account uncertainty. Currently, predictive simulations require a hand-crafted objective (Falisse et al., 2019) or a tracking term (Koelewijn and Van den Bogert, 2016) to be sufficiently accurate, while it makes sense from an evolutionary perspective that only an energy-related objective is used (Wall-Scheffler, 2012). By including uncertainty, it might be possible to improve simulation accuracy without the aforementioned additional objectives or tracking term. 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, which is currently not possible (Koelewijn and Van den Bogert, 2016). Then, predictive simulations could be used to improve prosthesis design, to find a design that is stable enough to not require co-contraction to minimize effort, because this co-contraction increases metabolic cost in gait of persons with a transtibial amputation (Waters and Mulroy, 1999).

Our results also highlight the care that should be taken when selecting parameters of the musculoskeletal system and the neural control algorithm. When we included neural time delay, a different trajectory was optimal for the controller with feedforward control than for the controller without feedforward control. This suggests that the choice of controller architecture could affect the results. Furthermore, we observed large differences in optimal feedforward control, and thus co-contraction level, when changing the activation time constant in a realistic range, since 10 ms is the default in OpenSim, while others use 35 ms (e.g. Lai et al. (2018)). This suggests that optimization results are also highly dependent on the choice of musculoskeletal parameters.

Co-contraction of muscles is used as an indicator of impaired control (Hortobágyi and DeVita, 2000). 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 (Winter, 1995) or even death (Kannus et al., 1999). The task difficulty was represented by the perturbation amplitude and by the task precision, because difficult tasks require one to remain close to the desired position, so to be

more precise. By varying the task precision and difficulty, we showed that the optimal and expected level of co-contraction increases with the task difficulty and precision. 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 chose to use a simple model of uncertainty, by adding a perturbing moment to the base of the pendulum. However, in reality, uncertainty is more complex, and can be present internally or externally. Internal noise means uncertainty in the neural control, both in sensing (Bays and Wolpert, 2007) and stimulation, while external noise could be due to many sources, such as wind or uneven ground. We repeated the problem with internal noise added to the joint angle, to model sensory noise, or to the input, to model noise in stimulation. The solution was trivial with sensory noise, because the noise was removed from the system when the feedback gains were zero, such that no control at all is required. When input noise was added, it was again optimal to have non-zero feedforward control.

We also ensured that different muscle model parameters did not affect the results. We identified the maximum isometric force and the tendon slack length as main parameters that could influence the result. The maximum isometric force was set somewhat arbitrarily in combination with the task difficulty and precision. For the same difficulty and precision, a higher maximum isometric force would yield that overall muscle activation could be reduced, until eventually no co-contraction was required, while a lower maximum isometric force would increase the amount of co-contraction required, until eventually the task could not be solved anymore. Furthermore, we tested the effect of the tendon slack length. Currently, the tendon is slack at a smaller than optimal fiber length. Therefore, we tested the scenario where the tendon was exactly slack at optimal fiber length and the scenario where the tendon was already active at optimal fiber length by repeating one task for both scenarios. We found that the result was very similar for all three scenarios, meaning that the optimality of co-contraction was not due to the choice of tendon slack length.

We assumed symmetry in control, and therefore only optimized for one feedforward control, which was applied to both muscles. Alternatively, we could have optimized parameters for both muscles separately. However, the problem is entirely symmetric otherwise, which means that the control should also be symmetric, and any asymmetry in the control would be caused by the specific noise sample used in the simulation. Furthermore, during preliminary simulations we found that the feedforward control, as well as the position and derivative feedback gain converged to the same value for both muscles when optimized separately, while this approach required a longer simulation time. Therefore, we chose to simplify and speed up our pipeline and implement a single controller for both muscles.

System uncertainty was modelled with uniform noise to bound the maximum possible perturbation. If

the perturbation moment was drawn from a normal distribution, it would be possible that the noise at a certain time instance is very large. Then, the optimal solution could have included co-contraction just to overcome this perturbation while still meeting the task constraint, while the muscles would not be strong enough otherwise, which would have affected our conclusion. Uniform noise is bounded and therefore its maximum is known.

In conclusion, we showed that co-contraction minimizes effort for certain tasks in uncertain environment, even when co-contraction is not necessary. Furthermore, the optimal amount of co-contraction increases with the task difficulty and precision, as well as with the activation time constant and the neural time delay. We also found that for controllers with neural time delay, the optimal trajectory was dependent on the controller used, which means that care should be taken when designing controller architecture. 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. Furthermore, optimal control problems of human gait should account for the nonlinearity of the human body and the system uncertainty to be able to create accurate movement simulations.

ACKNOWLEDGEMENTS

This research was supported by the National Science Foundation [grant number 1344954], by a Graduate Scholarship from the Parker-Hannifin Corporation, and by a faculty endowment from Adidas.

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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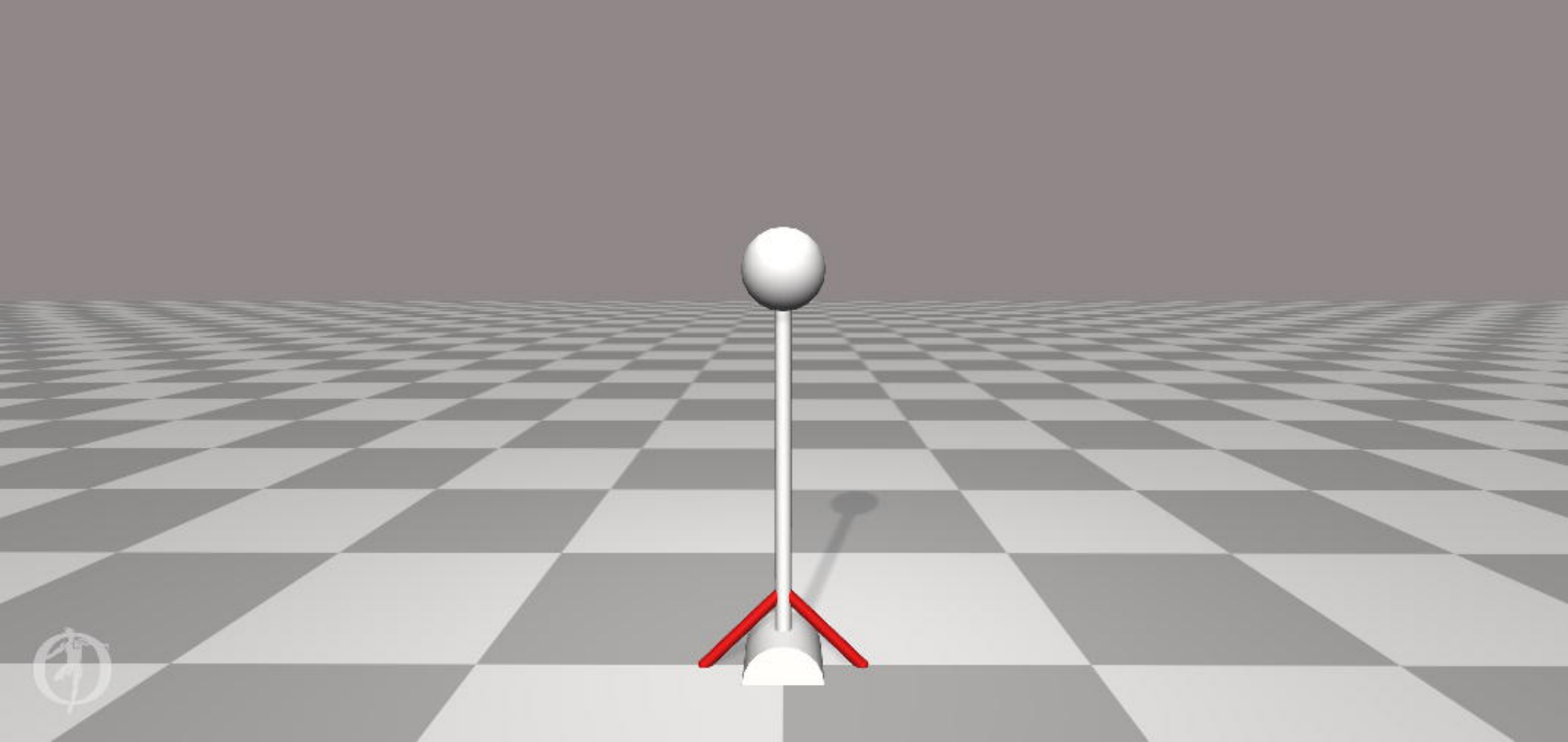

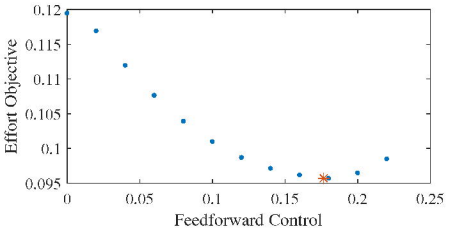
0.12
0.115
0.11
0.105
0.1
0.095
Effort Objective
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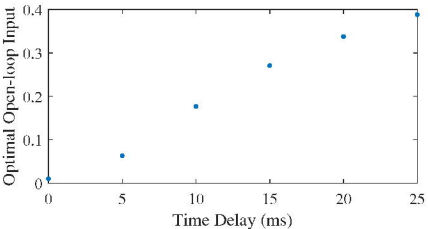
0.05
0.1
0.15
0.2
0.25
Feedforward Control


Optimal Open-loop Input
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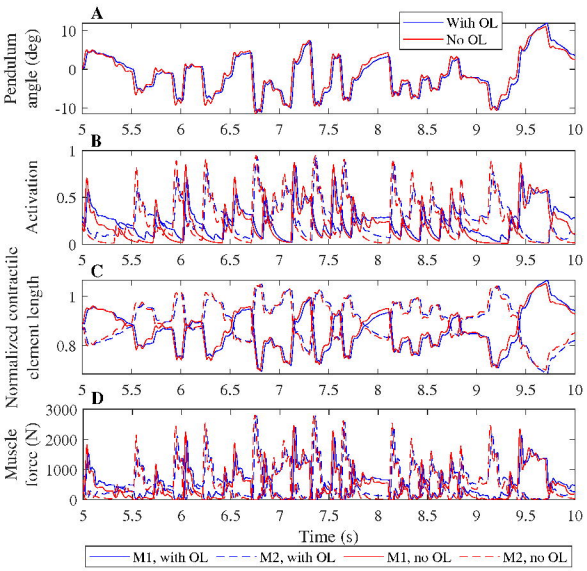
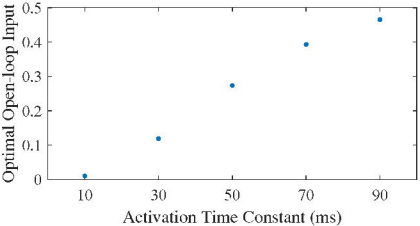
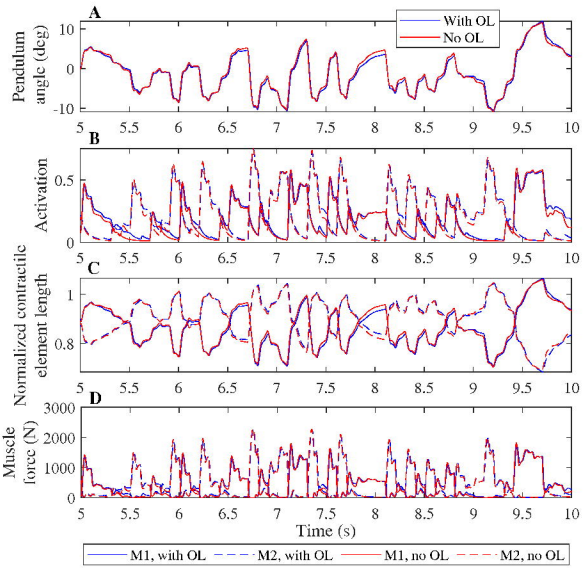
0.3
0.2
0.1
0
0
5
10
15
20
25
Time Delay (ms)


A
With OL
No OL
Pendulum angle (deg)
10
0
-10
B
Activation
1
0.5
0
C
Normalized contractile element length
1
0.8
D
Muscle force (N)
3000
2000
1000
0
5
5.5
6
6.5
7
7.5
8
8.5
9
9.5
10
Time (s)
M1, with OL
M2, with OL
M1, no OL
M2, no OL


Optimal Open-loop Input
0.5
0.4
0.3
0.2
0.1
0
10
30
50
70
90
Activation Time Constant (ms)


A
With OL
No OL
Pendulum angle (deg)
10
0
-10
B
Activation
0.5
0
C
Normalized contractile element length
1
0.8
D
Muscle force (N)
3000
2000
1000
0
5
5.5
6
6.5
7
7.5
8
8.5
9
9.5
10
Time (s)
M1, with OL
M2, with OL
M1, no OL
M2, no OL