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CONTROL OF POSITION AND MOVEMENT IS SIMPLIFIED BY COMBINED MUSCLE SPINDLE AND GOLGI TENDON ORGAN FEEDBACK

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SUMMARY

Human muscle has two primary sensors: *Muscle Spindles* (*MSs*), typically assumed to signal length and changes in length of the muscle fibres, and *Golgi tendon organs* (*GTOs*), assumed to sense the force delivered by muscle. Unlike *MSs*, *GTOs* do not play a prominent role in current theories of human motor control. Here we show that due to the mechanical interaction of muscle fibres with tendon, a simple feedback loop based only on spindle afferents is not effective. We propose that *GTO* signals can be used to compensate for tendon stretch, and we show using simulations with detailed musculoskeletal models that together with *MS* afferents they can be used for simple yet very effective feedback control. The analyses in our study shed light on the role of *GTOs* and on the potential reasons why strong connections between muscle spindles and *GTOs* exist in the human nervous system.

INTRODUCTION

GTOs do not play a prominent role in current theories of movement control. This might be because their function is not well understood and that –in motor control studies– tendons, in which *GTOs* are situated, are often ignored altogether. Yet, there is ample evidence in the literature that both tendons and *GTOs* play an important role in the dynamics of the musculoskeletal system.

MSs are suggested to help the control of joint position and velocity by low-level spinal feedback. However, *MSs* cannot detect changes in muscle-tendon complex (*MTC*) length that occur due to tendon stretch. Hence, in the real system feedback using *MSs* alone may result in poor control.

GTOs are typically seen as force sensors[1]. However, since tendon behavior is largely elastic, we propose that the signals from *GTOs* can alternatively be seen as a proxy for tendon length. As a result, *GTOs* combined with *MSs* can be effectively used to code *MTC* length (l_{MTC}) and, because l_{MTC} is one-to-one related to joint position, can thus be used for feedback control of joint position.

In this study, we first carried out a simple mathematical analysis to assess static errors when controlling the elbow joint position with a biceps muscle (tendon length ≈ 20 cm) using *MSs* feedback only. Then we used detailed musculoskeletal models of the arm to assess the response quality when feeding back either *MS* afferents alone or a combination of spindle and *GTO* afferents. Finally, we incorporate the proposed feedback scheme in an optimally

controlled fast whole arm movement and assessed its robustness against perturbations.

METHODS

The 1DOF and 2DOF musculoskeletal models of the arm used here have been fully described elsewhere [2,3]. In short, the models consisted of 3 segments, interconnected by 2 hinges (representing glenohumeral and elbow joint) and driven by either 4 (1DOF) or 6 (2DOF) lumped Hill-type muscles. The models were restricted to move in a horizontal plane at shoulder height. The upper arm of the 1DOF model was fixed at 45° . Tendons were modelled as quadratic springs stretching 5% at maximal isometric force.

MSs were assumed to provide accurate information about the *CE* length (l_{CE}) and contraction velocity (v_{CE}). Muscle activation (*STIM*) depended on an open-loop part ($stim_{open}$) and a feedback part. With only spindle feedback, *STIM* was:

$$STIM(t) = stim_{open}(t) + k_p[l_{CEref}(t) - l_{CE}(\Delta t)] + k_d[-v_{CE}(\Delta t)]$$

where Δt is the time minus a 25ms time delay and k_p , k_d are feedback constants. With combined feedback, *STIM* equaled:

$$STIM(t) = stim_{open}(t) + k_p[l_{MTCref}(t) - l_{CE}(\Delta t) - l_{SE}(\Delta t)] + k_d[-v_{CE}(\Delta t)]$$

where l_{MTCref} is the reference l_{MTC} equalling the l_{MTC} at a desired joint angle. In case of fast 2DOF reaching movements, $stim_{open}$ was the optimal *stim* minimizing the sum of squared *stim* for a 30cm movement in 400 ms. $stim_{open}$ was identified using a sparse non-linear optimal control solver (SNOPT; Tomlab Optimization Inc., Pullman, WA).

We assessed the responses of the 1DOF model to 1) a position perturbation, 2) a sudden change in co-contraction and 3) an external constant torque perturbation. The 2DOF movements were perturbed using a 30ms torque of ± 10 Nm. Feedback parameters for optimization were: 1) k_p , k_d were identical for all muscles, 2) homonymous feedback only, 3) constant gains during the simulations and 4) only optimized for one response.

RESULTS AND DISCUSSION

Fig.1 left panel shows the static error (se) due to tendon stretch as a function of force of the biceps (e.g. as consequence of increasing weights held in the hand). Two important observations can be made: 1) at maximal isometric force there is a very large se and 2) due to non-linear characteristics of the tendon, se is substantial at even

low forces. The right panel of Fig.1 shows the response to a transient position perturbation. With only *MS* feedback the model responds much faster, yet introduces large *se* depending on the feedback gain: the higher the gain the higher the error. When spindle afferents were combined with signals from the GTOs, no end-point error occurred, yet with the known advantage of negative PD feedback leading to faster responses. Responses to other perturbation types show similar results and are not shown in this abstract.

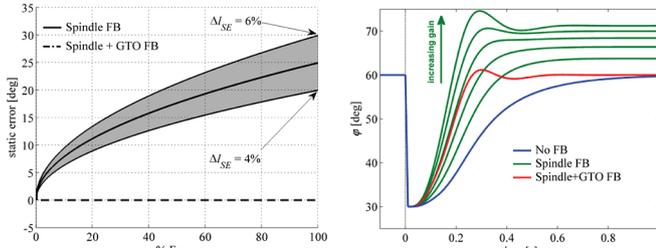


Figure 1 Left panel: Static error with spindle feedback. Right panel: Response to position perturbation. Adapted from [4].

Fig. 2 shows simulated *unperturbed* fast 2DOF movements as well as fast movements observed experimentally (in gray: mean ± 1 std; see [4]). The left panel depicts the hand path, the right upper panel the shoulder position and the lower the elbow position. Simulations of the musculoskeletal model with only the optimal *stim_{open}* (blue) shows good resemblance with the movement observed experimentally (note that because of overlap, the blue line is hardly visible). Adding feedback of only *MS*s caused the movement to deviate substantially and to not arrive on target. When *GTO* information also was added, movement was very similar to the model without feedback and experimental data. It should be noted that the suggested feedback loops were not an integral part of the optimal control problem, but were simply added to an optimal *stim_{open}* that was found for the system without feedback.

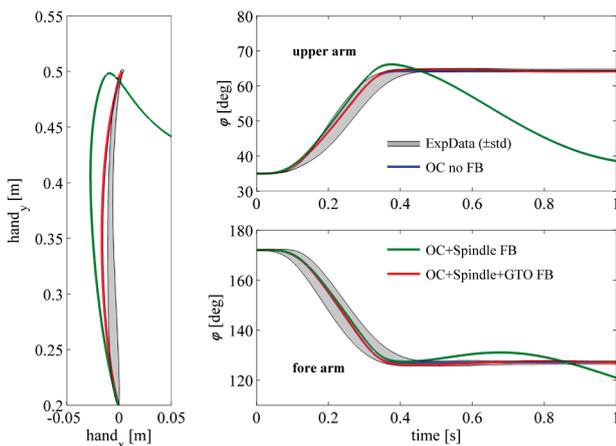


Figure 2 Experimental data and model simulations of fast point-to-point movements. Adapted from [4].

Fig. 3 shows simulations similar to that in Fig. 2, however 0.2s after onset the movements were perturbed with transient torques (± 10 Nm) in the shoulder. The difference between the model with and without the proposed feedback was apparent only after 0.4s; the end time of the unperturbed movement. This is because up to that moment, *STIM* was dominated by the open loop *stim*. Together with Fig.2, these

results show that once a suitable *stim_{open}* is found, the suggested feedback can be readily added without substantially increasing the computational demands for the CNS.

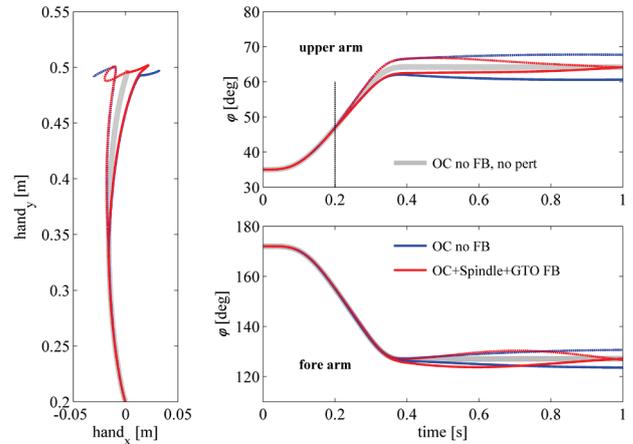


Figure 3 Simulated responses to torque perturbations during fast point-to-point movements. Adapted from [4].

In this study we suggest that the combination of *MS*s and *GTO*s can be used together to effectively feedback *MTC* length. Recent human physiological data indeed showed that l_{MTC} length is well predicted by a combination of spindle and *GTO* output[5]. Interestingly, spindle and *GTO*s are frequently found in line with and attached to each other to form 'tendon organ-spindle dyads'[6]. Furthermore, recent neurophysiological data suggests that all spindle (Ia and II) and *GTO* afferents excite monosynaptically interneurons that directly excite α -motoneurons[7].

These experimental data on both the sensors and interneurons in the spinal cord are consistent with (but do not prove) the idea that the suggested combined feedback from muscle spindles and *GTO*s is physiologically plausible. In turn, the theoretical analyses of this study might shed light over the reasons as to why such strong physiological couplings between spindles and *GTO*s are present, namely because of the result of the mechanical interaction between the contractile element and tendon in the musculoskeletal system.

CONCLUSIONS

The results of this study show that *Golgi-tendon organ* afferents may be seen as a proxy for muscle force dependent tendon length. In combination with muscle spindle afferents, *GTO* afferents may be used in low-level spinal feedback to help to control joint position and velocity.

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