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**Should the neural–mechanical behaviour of a muscle be coupled or co-vary?**

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To produce a torque about a joint in the human body there must be sufficient drive to excite motor neurones in the spinal cord to discharge action potentials. The number of motor neurones that are recruited, and the rate at which those motor neurones discharge action potentials, is directly linked to the summation of twitch forces in the muscle. However, the potential to generate a torque also depends on the mechanics of all of the muscles crossing the joint. Mechanical properties such as the muscle pennation angles, physiological cross-sectional areas, and moment arms will ultimately determine the mechanical advantage of the system. Based upon the inextricable link between neural and mechanical factors in generating joint torques, whether isometric or causing body segment motion, a fundamental question emerges regarding whether these factors are coupled or co-vary. For instance, would the goal of the system be to produce large and small torques only (i.e. ↑ neural drive and ↑ mechanical advantage, or ↓ neural drive and ↓ mechanical advantage), as would be the case if the two were coupled? This behaviour would result in large joint torques for the performance of high-intensity strength tasks, as well as very small torques for the performance of low-intensity postural tasks. Alternatively, if neural and mechanical factors co-vary (i.e. ↑ neural drive and ↓ mechanical advantage, or vice versa) then it would result in the ability to more appropriately grade joint torque, as well as probably conserve metabolic energy through less overall work demand.

A recent study in *The Journal of Physiology* by Hudson et al. (2009) examined the relationship between neural and mechanical factors in the first dorsal interosseous muscle (FDI) of the hand. By using this particular muscle, the authors were able to circumvent many of the limitations traditionally associated with making the neural–mechanical comparisons at joints controlled by many muscles. The results from that study led the authors to conclude that the neural drive to the FDI muscle and the mechanical advantage of the muscle are coupled when the thumb changes position. The remainder of this note will focus on the impact of the study and the interpretation of the results, specifically with regard to whether the neural drive to the muscle and the muscle mechanics should co-vary or be coupled when performing motor tasks.

The study by Hudson et al. (2009) recorded end-point forces produced (i) by ulnar nerve stimulation and (ii) during static index finger flexion efforts, with the thumb positioned in a number of ‘thumb up’ and ‘thumb down’ postures. Although a seemingly minor postural adjustment, ulnar nerve stimulation resulted in a 60% larger end-point twitch force in the thumb down position compared to thumb up. Furthermore, ultrasound results indicated that, relative to thumb up, the thumb down posture caused a 65% increase in the distance between the FDI tendon and the lateral tubercle of the second metacarpal, which was used to estimate FDI moment arm magnitude. Thus, the mechanical advantage for FDI force transmission across the metacarpophalangeal (MCP) joint was significantly increased with the thumb down, regardless of muscle force. Based on the mechanics, end-point force is directly proportional to the MCP joint torque, via the geometric configuration of the system. In other words, since the index finger was splinted and MCP joint angle remained constant, moment arm magnitude was the main geometric factor determining how effectively FDI muscle force was transformed into end-point force. The end-point forces generated by supramaximal ulnar nerve stimulation (i.e. constant neural input) illustrate the proportionality between MCP joint torque and end-point force (a 65% increase in moment arm → 60% increase in end-point force). However, the mechanics are only one aspect of generating joint torques. Can, or does, the central nervous system exploit such a mechanical advantage under voluntary conditions?

In the second experiment, Hudson et al. (2009) used electromyography (EMG) to examine how the neural drive adjusts to changes in thumb posture during voluntary isometric force contractions. The improved mechanical effectiveness of the thumb down position would imply that the nervous system could decrease its neural input to the FDI muscle to generate the same voluntary force as in the thumb up posture. Stated differently, it might be expected that the neural input would co-vary with moment arm magnitude. However, the results of the second study demonstrated a 28% increase in FDI muscle activity when transitioning from thumb up to thumb down, despite the constant end-point force. Although the identified coupling supported the authors’ hypothesis, the results appear to represent a mechanical paradox. Have the authors identified a situation where the nervous system fails to capitalize on an enhanced mechanical advantage for more efficient finger force production, or does a downplayed factor exist which would indicate a co-variance of neural and mechanical factors? Since it is not imperative that the nervous system implement a single strategy, it is pertinent to explore how both coupling and co-variance are reasonable control strategy options for a given system. In addition, the possibility that some factors could be coupled while others co-vary must be considered.

The treatment of EMG data as an indication of neural input (control signal) to the FDI supports the coupling of neural and mechanical factors. Why would the nervous system couple neural input with moment arm magnitude? Within the context of the presented studies, neural input is the key factor in muscle force modulation, while posture-related changes in FDI muscle mechanics are deemed minor. However, the intrinsic design, or architecture, of muscle has been posited as a way to alter the effectiveness of the neural input (Lieber & Friden, 2000). A posture-related decrease in muscle force-generating capacity would necessitate an increase in neural activation to generate a set level of muscle force thereby reducing neural effectiveness. At the level of the muscle, thumb flexion (i.e. moving to thumb down) is likely to shift the
superficial belly of the FDI toward shorter muscle fibre lengths. Assuming the FDI operates on the ascending limb of the force–length relationship, this shift would cause a decrease in the force-generating capacity of the muscle. Although speculative, this assertion is supported by previous biomechanical modelling of the third dorsal interosseous muscle (Meunier et al. 2004), which is architecturally similar to FDI (Jacobson et al. 1992). Thus, while neural input is coupled with moment arm magnitude, it could also co-vary with muscle force–length concurrently such that the increased EMG signal accommodates to yield the same end-point force in both postures.

Alternatively, it is important to remember that finger flexion force produced by activation of the FDI represents the involvement from its two muscle bellies. The muscle fibres of the two heads of the FDI merge as they approach the MCP joint; however, it is the length and line of action of the superficial head which is most likely altered by changes in thumb posture. The line of pull of the superficial head supports index finger abduction (thumb adduction) as its primary function, thus its presumed contribution to MCP flexion may be generous, regardless of thumb posture. Certainly, EMG recorded using surface electrodes is likely to be dominated by motor units from the superficial head. In general, thumb down postures (abduction–adduction) are more functionally relevant for activities involving object manipulation, by stabilizing objects between the thumb and index finger (Santello et al. 1998). Therefore, the increased FDI signal in thumb down postures may reflect greater action of the superficial head to facilitate coordination of the thumb and index finger in preparation for functional grasping tasks. In this case it would seem most reasonable that the neural drive and muscle mechanics would co-vary to enable finer control of the digits.

The control of joint torques generated by the human body is complex, even when examining a ‘simple’ system like the muscles surrounding the MCP joint. Ultimately, there is an interaction between neural and mechanical factors for each muscle. It is possible that both coupling and co-variance of these factors occurs for every muscle, and likely that the adopted strategy is task dependent. For instance, tasks that demand strong forces probably demonstrate coupling of the neural–mechanical system, while fine object manipulation would require co-variance. This may even extend to all muscles surrounding a joint such that some would function in a coupled manner while others would co-vary, once again, dependent on the task. Whichever occurs, the study by Hudson et al. (2009) has presented an interesting case that spans the fields of neurophysiology and biomechanics and displays the importance of the two fields working together to understand the operation of the human motor system.

References


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