The influence of knee angle on human quadriceps femoris performance

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2007

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Summarizing discussion

In this thesis we set out to investigate the extent to which the central nervous system is able to adapt activation of the knee extensors to length - and fatigue induced changes of the muscles' contractile properties. Neural activation of the knee extensors was investigated using superimposed electrical stimulation and surface EMG; in addition the energy consumption of the superficial knee extensors was measured using near - infrared spectroscopy. Using this combination of methods insight was obtained in the underlying mechanisms that relate motor control during sub - maximal isometric contractions at different muscle lengths, which have been discussed in the corresponding chapters. Nevertheless, some other issues are worthwhile to address and are discussed below after a brief summary of the main findings of this thesis.

Summary

Knee extensor endurance during sustained isometric contractions had previously been shown to be greater at short vs. longer muscle lengths (8, 14). In **chapter 2** we investigated the role of central activation, using superimposed stimulation, and blood flow in muscle - length dependent endurance (11). Time to torque failure for intermittent isometric knee extensions was ~ 60% greater at the 30° (short muscle length) vs. the 90° (long muscle length) knee angle (0° = full extension). The use of a cuff, occluding blood flow to the knee extensors throughout the fatiguing contractions, eliminated any potential effects of knee angle - dependent differences in muscle perfusion. At torque failure central activation ratios obtained using superimposed stimulation were very high and similar at both knee angles. The greater endurance at 30° compared to 90° was therefore concluded not to originate from knee angle - dependent differences in central activation at torque failure. It was postulated that (some of) the differences in endurance between knee angles could be related to differences in metabolic cost at different knee angles.

This was confirmed as at extended knee angles fatigability (8, 14) and muscle oxygen consumption (mVO_2, (4, 10)) during sustained submaximal isometric contractions were found to be less compared to flexed knee angles. Furthermore, at low torques mVO_2 was reported to be less in the rectus femoris muscle than in the vastus lateralis and medialis muscle (4). In **chapter 3** we hypothesized that these findings could be accounted for by a respective knee angle - and a muscle - dependent activation. By the simultaneous measurement of rectified surface EMG (rsEMG), as a measure of muscle activation, and mVO_2 during isometric contractions of the m. quadriceps, the contribution of knee angle - and a muscle - dependent activation could be determined. The results show that a tendency for less muscle activation (15 - 20%) contributes, but certainly cannot account for the substantially lower mVO_2 (~ 60%) at 30° vs. 60 and 90° knee angles. Moreover, at low contraction intensities a (s)lower (increase in) m. rectus femoris mVO_2 suggested a less intense activation of this muscle compared to the vasti.

Besides the reports of a muscle length - dependence of fatigue (6, 11, 13, 18), fatigue is also dependent on the relative force level during muscle contraction (7). Equal relative contraction intensities, derived by normalizing to the maximal voluntary contraction (MVC) at each knee angle, are often used to investigate and compare muscle fatigue at different knee angles (8, 14). If the MVC is used as a gold standard, any differences in maximal voluntary activation during the MVC between knee angles will erroneously create differences in the relative contraction intensities between knee angles. This could make it relatively easier to perform isometric contractions at one knee angle compared to another. Generally, the maximal voluntary activation during an MVC, measured using superimposed stimulation, is used as an indication of a subjects' ability to reach the maximal force capacity of the muscle. However, due to uncertainties in the determination of this maximal force capacity (5, 15), the relationship between relative voluntary force and voluntary activation was investigated in **chapter 4.** This type of relationship can only be properly evaluated using subjects with exceptional ability for maximal voluntary activation of the knee extensors. Already at a relative torque level of ~ 79%MVC a voluntary activation level of ~ 92% was calculated in these subjects. A subsequent ~ 34% increase in EMG was measured for a further ~ 18% torque increase for which a mere ~ 6% increase in voluntary activation was calculated. It was therefore concluded that using the conventional interpolated twitch torque method, voluntary activation does not represent relative voluntary torque. In addition, small increases in relative torque lead to disproportionate (relative to torque) increases in EMG as MVC is approached.

Despite an as accurate as possible determination of the maximal torque capacity of the muscle in **chapter** 3 using superimposed stimulation, the findings in **chapter 4** illustrated that very small differences in voluntary activation could still coincide with substantial differences in relative torque. Since mVO_2 was measured at equal relative intensities at different knee angles in **chapter 3**, a knee angle - dependent effect of neural activation could not be excluded. To definitively exclude this potential knee angle - dependent effect of neural activation on the measurement of mVO_2, in **chapter 5** mVO_2 was measured during electrically evoked and maximal voluntary quadriceps contractions. By using this approach insight into the mechanisms limiting endurance at different knee angles was gained. Any differences in mVO_2 between knee angles during the electrically evoked contractions could be attributed to differences that originated at the level of the muscle. Additional differences in mVO_2 between knee angles found during the long lasting (15s) MVCs are then a consequence of processes (e.g. maximal voluntary activation) that may affect neural activation. It was hypothesized that during electrical stimulation where mVO_2 is maximal, the difference in mVO_2 between extended (30°) and flexed (90°) knee angles would be less compared to MVC contractions. During voluntary contractions mVO_2 was found to be ~ 50% less at extended vs. flexed knee angles. The ~ 20% lower mVO_2 found during electrically induced contractions must originate from differences that reside within the muscle. Therefore, 60% ([50 – 20] / 50 * 100%) of the total mVO_2 difference during voluntary contractions is the result of a lower neural activation at extended knee angles.

What causes the muscle length - dependent fatigue?

Fatigability had been shown to be less at short compared to longer muscle lengths for the m. tibialis anterior (6, 18), the elbow flexors (13), and knee extensors (8, 11, 14) and therefore appears to be a general phenomenon.

In **chapter 2** differences in blood flow and central activation at the point of torque failure were eliminated as possible causes for the lower fatigability at short muscle length. Potentiation was suggested to be responsible for some of the lower fatigability at short muscle length by Place et al. (17). In their study a greater twitch potentiation at short compared to long muscle length was reported after a voluntary sustained contraction of the knee extensors at 20%MVC. They suggested that a slower development of central fatigue during the sustained contraction at short compared to longer knee extensor muscle length could partly explain the lower fatigability at shorter muscle length.

Futhermore in a recent study by MacNaughton and MacIntosh (12) part of the muscle length - dependence of fatigue was attributed to a relatively greater underestimation of active force at long vs. short muscle lengths. As the underestimation was of minor importance at lengths below optimum muscle length, these findings were of little relevance to the experiments described in the present thesis and other studies investigating fatigue of the knee extensors (8, 14). The knee angles investigated in these experiments most likely correspond to a knee extensor muscle length at or below optimum (9, 21).

Another explanation for the lower fatigability at short vs. longer muscle length could be a reduced energy requirement at short muscle length as at short muscle lengths there would be a lower number of energy consuming cross - bridges (6). However, in studies on isolated mammalian muscle (16, 20) and frog muscle (1, 2) energy consumption was reported to be similar at short and optimum muscle length. Only at *very* short muscle length has energy consumption been reported to be lower compared to optimum muscle length (3, 19). Although the knee extensors studied in this thesis are probably operating on the ascending limb of the length - tension relationship at 30° (9, 21), it seems unlikely that this corresponds to the *very* short muscle length mentioned by de Haan et al. (3) and Sandberg and Carlson (19). Nevertheless mVO_2, established as a measure for energy consumption (4), was shown to be ~ 60% less at 30° (short muscle length) vs. 60 and 90° (long muscle length) angles in **chapter 3**. Furthermore, in the same chapter it was estimated that at most 10% of this difference in mVO_2 could be accounted for by a difference in muscle activation, measured using surface EMG.

It was shown in **chapter 4** that minor differences in voluntary activation could coincide with substantial differences in relative torque. As explained above, this may have contributed to the ~ 60% difference in mVO_2 reported between knee angles in **chapter 3**. In **chapter 5**, using only highly motivated subjects capable of high levels of voluntary activation at each knee angle, a smaller yet still substantial ~ 50% difference in mVO_2 was found between knee angles during long lasting MVCs. In the same chapter neural activation was eliminated as a confounding factor by using electrically evoked contractions of the knee extensors. A ~ 20% lower mVO_2 remained at the 30° compared to the 90° knee angle during electrical stimulation. The exact mechanism that causes this ~ 20% difference is unclear and remains to be elucidated, but must reside at the level of the muscle as the use of electrical stimulation excluded any knee angle - dependent differences in neural activation. However, 60% ([50 – 20] / 50 * 100%) of the total mVO_2 difference during voluntary contractions must be the result of a lower neural activation at extended knee angles. The consistent previous findings of a similar energy consumption at short and optimum muscle lengths (1, 2, 16, 20) seem difficult to reconcile with the ~ 20% difference in mVO_2 reported in this thesis and needs further investigation. The ~ 20% difference in mVO_2 found in the present thesis however, could account for the consistent finding (8, 11, 13, 14, 17) of a lower fatigability at short compared to long muscle lengths.