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SHORT COMMUNICATION

Why do muscles lose torque potential when activated within their agonistic group?

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ABSTRACT

Agonistic muscles lose approximately 20% of their individual torque-generating capacity when activated with their agonistic muscles compared with when stimulated in isolation. In this study, we (1) tested if this loss in torque was accompanied by a corresponding loss in force, thereby testing the potential role of changes in moment arms between conditions; (2) removed all inter-muscular connections between the quadriceps muscles, thus determining the potential role of inter-muscular force transmission; and (3) systematically changed the inter-muscular pressure by performing experiments at different activation/force levels, thereby exploring the possible role of inter-muscular pressure in the loss of torque capacity with simultaneous muscle activation. Experiments were performed in a New Zealand white rabbit quadriceps model (N=5). Torque and force were measured during activation of femoral nerve branches that supply the individual quadriceps muscles while activating these branches simultaneously and in isolation. Regardless of joint angle and inter-muscular connections between muscles, the differences in torque values between the simultaneous and the isolated activation of the quadriceps muscles were also observed for the directly measured force values. Mean differences in simultaneous and isolated muscle activation remained similar between the intact and separated conditions: torque difference 21±5% of maximum isometric torque of intact condition (MIC_{torque}), versus 19±6% MIC_{torque}, respectively, and force difference 18±3% MIC_{force} versus 19±7% MIC_{force}, respectively. The absolute torque loss was independent of the force, and thus presumably the inter-muscular pressures. Based on these results, we conclude that the torque deficit observed during simultaneous compared with isolated muscle activation is not primarily caused by moment arm, inter-muscular pressure or inter-muscular force transmission. The mechanisms underlying loss of force capacity during agonistic muscle contraction remain unknown.

KEY WORDS: Muscle properties, Connective tissue, Moment arm, Inter-muscular, Pressure

INTRODUCTION

A basic assumption typically made in muscle mechanics is that muscle properties determined for an individual muscle remain the same when the muscle contracts in concert with its agonistic muscles. Recently, however, it was shown that the maximal torque generating potential of individual muscles of the rabbit quadriceps group decreases, on average, by 20% when the muscles contract simultaneously (de Brito Fontana et al., 2018).

The mechanisms causing this reduction in torque are not understood. Differences in moment arm between conditions cannot be ruled out (Maganaris et al., 1998; Tsaopoulos et al., 2007), since only quadriceps torque and not force was measured in this previous study. If, during simultaneous activation, the moment arms of the quadriceps muscles were reduced in a systematic manner, then the differences in knee joint torques for individual and simultaneous muscle activation could be explained without an associated change in the force potential of the muscles between the two conditions.

In addition, inter-muscular force transmission has been shown to affect muscle forces in the presence of large relative displacements of one of the agonistic muscles relative to the rest of the muscles in that group (Bernabei et al., 2015; Maas, 2019; Maas et al., 2004, 2003; Maas and Sandercock, 2010; Tijs et al., 2015). However, whether the loss in force-generating potential during agonistic activation originates from inter-muscular connections is not known.

Another aspect to consider is the difference in inter-muscular pressure and associated transversal forces between simultaneous and individual agonistic muscles activation. Transversal forces are thought to decrease the ability of muscles to generate force (Siebert et al., 2016, 2014a,b), and greater inter-muscular pressure in the simultaneous compared with the individual activation of agonistic muscles could be the cause for the loss in force-generating potential observed by us previously (de Brito Fontana et al., 2018). If so, then one may argue that the amount of force loss with simultaneous agonistic activation should be smaller at lower levels of activation, and associated lower muscle forces and lower inter-muscular pressures (Reinhardt et al., 2016).

In this study, we aimed to investigate these three potential causes for the observed losses in torque-generating potential during simultaneous muscle activation compared with activation of the individual muscles alone: (i) differences in moment arms; (ii) differences in inter-muscular force transmission; and/or (iii) differences in inter-muscular pressures between the two conditions. We hypothesized that the observed torque loss with simultaneous rabbit quadriceps activation is not associated with changes in muscle moment arms or caused by inter-muscular force transmission, but is associated with differences in inter-muscular pressure. Therefore, we expected to observe (i) a similar amount of loss of muscle force as there was a loss in muscle torque; (ii) that removing inter-muscular connections, thereby removing inter-muscular force transmission, would not affect force or torque loss; and (iii) that decreasing inter-muscular pressures, achieved by decreasing activation/force levels, would result in a smaller loss in

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torque-generating potential of quadriceps muscles during simultaneous compared with isolated activation.

MATERIALS AND METHODS

Five female New Zealand white rabbits were used in this study (age, 10–12 months; strain=HRA[NVW]SPF; and average body mass, 4.0 kg). All procedures were approved by the University of Calgary Animal Ethics Committee.

Animal preparation

Before the experiment, rabbits were tranquillized with 1 ml kg^{-1} Atravet (25 mg ml^{-1}; Vetoquinol NA. Inc., Lavaltrie, QC, Canada) and held under anesthesia with a 2% isoflurane/oxygen mixture. After completion of the experiments, animals were euthanized with an overdose injection of Euthanyl (MTC Pharmaceuticals; Cambridge, ON, Canada). The branches of the femoral nerve responsible for the innervation of vastus lateralis (VL), vastus medialis (VM) and rectus femoris (RF) muscles were carefully dissected, and one custom-designed, nerve cuff type electrode was placed on each of the three nerve branches (Han et al., 2019). To avoid cross-talk between the stimulating electrodes, Kwik-Cast (World Precision Instruments, Saraota, FL, USA) was placed around the nerve cuffs (Han et al., 2019). During the experiments, rabbits were fixed in a stereotaxic frame (Sawatsky et al., 2012) in a supine position. The pelvis and femoral epicondyles were pinned to keep the hip at a flexion angle of 130–140 deg.

Experimental protocol

VL, VM and RF muscles were stimulated through electrical stimulation of the corresponding nerves using a dual output stimulator (Grass S8800, Astro/Med Inc., Longueil, QC, Canada) in four experimental conditions: VL nerve branch activation alone, VM nerve branch activation alone, RF nerve branch activation alone and activation of all three nerve branches together. Knee extensor torques were measured using a torsional load cell and a servomotor (Parker Hannifin Corporation, Irwin, PA, USA) using Windaq data collection software (Dataq Instruments, Akron; collection card, DI-400, 12 bit) and a customized MATLAB program (The MathWorks, Natick, MA, USA).

Cross-talk in this study was avoided by visual and tactile inspection of the muscles during all isolated contractions of VL, VM and RF and by carefully examining the torque–voltage recruitment curves for each individual muscle. The examination of torque–voltage curves confirmed that the voltage applied during the experiments was well within the safety margin and considerably below the intensity required to activate neighboring muscles through cross-talk (Han et al., 2019). Knee extensor torques using this preparation are highly repeatable with a correlation coefficient of 0.99 for three consecutive contractions at 90 deg of knee angle (Han et al., 2019).

Three of the five rabbits also underwent a submaximal activation testing protocol. For these animals, the knee was maintained at a 90 deg angle for all activation levels. Varying activation and force levels were achieved by stimulating the muscles at frequencies ranging from 20 to 100 Hz, except for VM where the minimum frequency of stimulation varied from 40 Hz (N=2) to 55 Hz (N=1) because of the low VM forces and the difficulties in measuring torque reliably below these frequencies. A pause of 2 min was allowed between contractions to minimize fatigue and avoid potentiation effects caused by irregular inter-stimulation intervals.

For two rabbits, maximal activation testing was also performed at different muscle lengths corresponding to knee flexion angles ranging from 40 deg to 120 deg, with the muscles intact initially, and then with the muscles separated by removing all inter-muscular connections through blunt dissection. To ensure that there were no adhesions formed between muscles following blunt separation, the separated muscles were covered in mineral oil to allow for 'frictionless' movement between muscle surfaces. To measure the resultant knee joint extensor torques and the associated knee extensor forces, an implantable force transducer (IFT) (Herzog et al., 1996a,b; Korvick et al., 1996; Xu et al., 1992) was used to measure muscle force. A small incision was made in the patellar tendon to insert the IFT.

Data analysis

The torque and force obtained in each condition was normalized, respectively, to the torque and force obtained at the angle of maximum force during simultaneous activation with the muscles intact (non-separated muscles) [% maximum isometric contraction (%MIC)]. The total knee extensor torque was compared at the different activation levels between two conditions referred to as SUM and SIM. The SUM torque was obtained by adding the torques produced by VL, VM and RF when these muscles were stimulated in isolation, and the SIM torque was obtained when all three muscles (VL, VM, RF) were activated simultaneously using identical stimulation as for the SUM conditions. The difference between SUM and SIM was compared across all experimental conditions.

In order to investigate possible changes in moment arm between the SUM and SIM conditions, torque was divided by force and compared before and after blunt separation of the inter-muscular connections (intact×separated). The effect of submaximal activation (changing inter-muscular pressures) on the difference between SUM and SIM was analyzed based on a linear regression equation between torque differences and torque level (i.e. torque during simultaneous contraction) for each individual animal data (R^2 and slope) and for pooled data. This analysis was conducted for absolute differences, SUM−SIM (Nm), and for relative differences, which were normalized to the torque produced at each activation level, (SUM−SIM)/SUM. In addition, the association between torque level (across submaximal contractions) and torque differences was assessed using Spearman correlations (P<0.05) of rabbit pooled data (N=3).

RESULTS AND DICUSSION

The sum of the maximum torque capacity for the isolated stimulation of VL, VM and RF (SUM) exceeded the maximum torque capacity for simultaneous stimulation (SIM) of all muscles of the agonist group by 10–50% across all levels of activation (Fig. 1A) and angles (Fig. 1B). Removing the inter-muscular connections between VL, RF and VM did not eliminate the differences in torque production between SIM and SUM. For the intact condition, differences in torque averaged across angles were 17±6% of the maximum isometric torque for the intact condition (MIC$_{torque}$) for rabbit 1 and 25±5% MIC$_{torque}$ for rabbit 2, and, for the separate condition, 18±6% MIC$_{torque}$ and 19±5% MIC$_{torque}$, respectively. Regardless of joint angle and inter-muscular connections, differences in force were similar to those observed for torque: in the intact condition, 14±4% MIC$_{force}$ for rabbit 1 and 21±2% MIC$_{force}$ for rabbit 2, and, in the separated condition, 17±4% MIC$_{force}$ for rabbit 1 and 20±8% MIC$_{force}$ for rabbit 2. In Fig. 2, we show an estimation of changes in moment arms across conditions.

We confirmed the previous result (de Brito Fontana et al., 2018) that simultaneous activation of the rabbit quadriceps muscles results
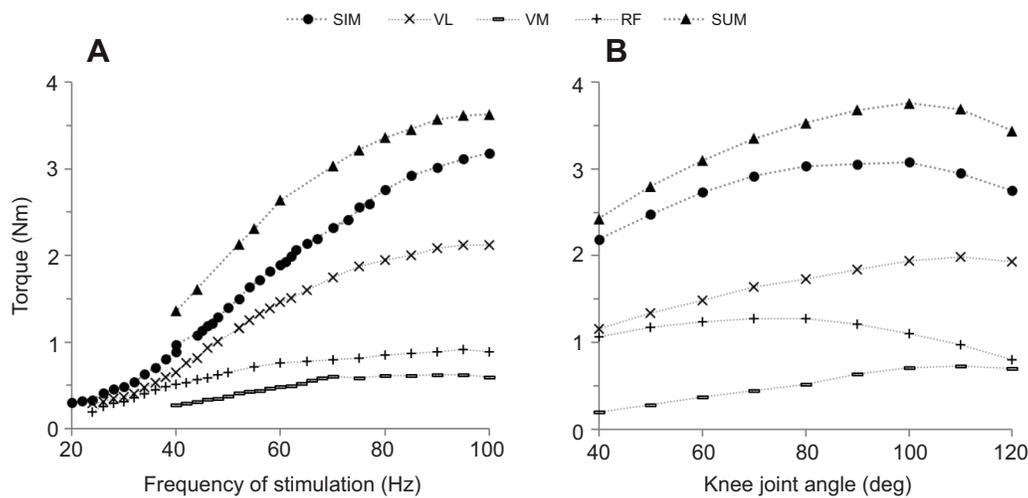
Fig. 1. Exemplar individual rabbit data for knee extensor torques measured when the entire quadriceps muscle is stimulated simultaneously and individually. Experiments were performed at different frequencies of activation at 90 deg of knee flexion (A, N=1 of 3 rabbits) and at different knee angles (0 deg equals full knee extension) for a stimulation frequency of 100 Hz (B, N=1 of 2 rabbits). Knee extensor torque was measured when the entire quadriceps muscle was stimulated simultaneously (SIM) and individually (VL, vastus lateralis; VM, vastus medialis; RF, rectus femoris). The torque produced as a result of the sum of the individual muscle torques (SUM) was greater than that resulting from simultaneous stimulation of the quadriceps muscles using identical muscle activation. All results are for intact muscles (inter-muscular connections intact).

in a loss in torque and additionally showed that there is a corresponding loss in muscle force. In previous studies, it was not clear whether the loss in torque was caused by a change in moment arm between SIM and SUM. Moment arms of some muscles have been shown to change with force (Maganaris et al., 1998; Tsaopoulos et al., 2007). Often, however, the changes observed are in the opposite direction of that which could explain the loss in torque. Our findings, of similar losses in knee extensor torques and directly measured knee extensor forces, suggest that moment arms did not change in a significant manner between the SIM and SUM conditions in our experiments. This result can also be observed by the superposition of moment arm data across conditions (Fig. 2).

It has been argued that inter-muscular force transmission may be an important component of force transmission of an entire muscle
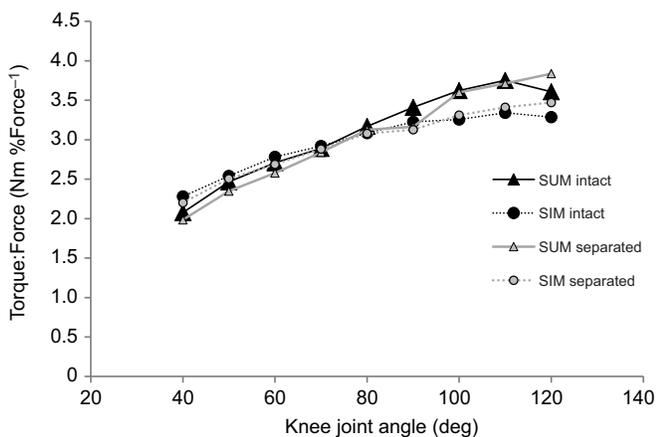

Fig. 2. Ratio between torque and force at different knee joint angles for quadriceps muscles stimulated simultaneously (SIM) and individually (SUM). Data are shown for one rabbit (same as Fig. 1, right) for the intact condition (inter-muscular connections were intact) and the separated condition (where the inter-muscular connections were removed by blunt dissection). Although an increase in the ratio is observed as the knee is flexed, there is close overlap among curves, indicating that moment arms remained approximately the same across conditions.

group (Bernabei et al., 2015; Huijing and Baan, 2001; Maas and Sandercock, 2010). In the case of a rupture of one muscle for example (Maas and Sandercock, 2008), force can be substantially transferred to the neighboring muscles through inter-muscular connections. However, the role of inter-muscular force transmission in a normal animal system when agonistic muscles contract and deform/displace in synchrony much less studied, thus functionally, the role of inter-muscular force transmission remains unclear.

In our study, removal of all inter-muscular connections between VL, VM and RF, and ensuring a virtually frictionless movement between the target muscles by the addition of mineral oil, did not eliminate the loss of torque/force in the SIM compared with the SUM condition. This finding does not exclude the possibility that extra-muscular force transmission pathways, as defined by Maas and Sandercock (2010) play a different function in the SIM and SUM conditions, but given the present evidence, this seems rather unlikely.

We hypothesized that the main cause for the observed differences in torque/force between the SIM and SUM conditions could be differences in the inter-muscular pressure. When stimulating all muscles simultaneously, there is likely a pressure buildup between the individual muscles of the agonistic group. Reinhardt et al. (2016) showed that inter-muscular pressure increases almost linearly with increasing muscle force for the rabbit triceps surae muscles, and the same is likely true for other muscle groups. In contrast, one would expect inter-muscular pressures to be small (negligible) if only a single muscle is activated at any given time.

Siebert et al. (2014b) demonstrated that increasing the transverse pressure exerted on the rat gastrocnemius muscle by a plunger (from 1.3 N cm^{-2} to 5.3 N cm^{-2}) resulted in an almost linear decrease in muscle force (from 4.8% to 12.8%) and later showed that the loss in force is independent of the contact area but is associated with the magnitude of the transverse force exerted (Siebert et al., 2016). The resulting pressure values tested in their experiments are within the range of observed inter-muscular pressures in agonistic muscles (Reinhardt et al., 2016) and produced losses in force in a similar range to what we and others observed with SIM contractions (de Brito Fontana et al., 2018; Han

et al., 2019; Perreault et al., 2002; Tijs et al., 2014). Therefore, we expected an increasing difference in torque and force between SIM and SUM for increasing knee extensor forces. In contrast to our hypothesis, however, the relative torque deficit between the SIM and SUM conditions increased with decreasing levels of muscle force and associated decreases in inter-muscular pressures.

For submaximal contractions, there was a significant negative correlation ($R=-0.72$, $P<0.001$) between pooled data of knee extensor torque and the percent difference in torque generating potential between SIM and SUM (Fig. 3A), while there was no significant relationship between knee extensor torque and the absolute torque differences between SIM and SUM ($R=-0.13$, $P=0.523$) (Fig. 3B). The slope of this latter relationship for individual rabbits was always below 0.001, and R^2 values were 0.07 for Rabbit 1 and below 0.01 for Rabbit 2 and 3.

Our results seem to contradict the findings by Siebert et al. (2014b) who found an increasing loss of muscle force when transversal/lateral pressures exerted on the muscle were increased. However, our findings do not rule out intermuscular pressure categorically as a mechanism for the force loss, as there might be other factors that could offset a transverse loading effect. All experiments on lateral pressure application on muscles and associated force loss were done for maximal tetanic contractions (Siebert et al., 2016, 2014a,b). If muscles contracting sub-maximally are more sensitive to the effect of external pressure, it is possible that, even with the surrounding muscles less active, and exerting lower inter-muscular pressures during sub-maximal compared with maximal activation, the absolute torque loss may remain similar across muscular activation levels. Future studies should be designed to investigate the effect of transversal loading on muscles for submaximal contractions. Our results suggest that submaximal agonistic force production is affected by the loss in force during simultaneous agonistic muscle stimulation and that the

(absolute) magnitude of this force loss is similar to that observed for maximal contractions.

Another feature that is distinctly different between inter-muscular pressure built up for simultaneous contractions of agonistic muscles and the experiments with externally applied lateral pressures is that, in the latter case, the pressure is applied by placing a weight on the lateral aspect of the muscle with the muscle aligned horizontally. Upon contraction and muscle deformation, the weight is free to move and is typically lifted against gravity. For the *in vivo* quadriceps contractions in our case, the muscles are surrounded by layers of connective tissue, and muscle deformation during contraction is constrained. Furthermore, instead of having a constant transversal load and pressure, inter-muscular pressure likely builds up gradually during force development in agonistic muscles.

One possible cause for the differences in torque and force between the SIM and SUM conditions might be associated with differences in muscle deformations when muscles are activated individually compared with when they are activated simultaneously with all muscles of the agonistic group. In an isolated preparation of the frog plantaris muscle, however, constraining radial expansion during contraction by using a rigid tube did not result in a significant loss of maximum isometric force but in a reduction in shortening and in the mechanical work that could be produced during low-level submaximal contractions (Azizi et al., 2017). Future studies should focus on the possible difference in deformations in muscles during simultaneous and isolated activation as different changes in fascicle length, pennation angle and muscle gearing could potentially explain the loss in torque generating potential during simultaneous activation (de Brito Fontana and Herzog, 2016; Eng et al., 2018; Vaz et al., 2012).

Inter-muscular pressure was not measured in this study; therefore, we cannot be certain how pressures increased with muscle force. However, previous studies (Reinhardt et al., 2016), and pilot data from our lab on the rabbit quadriceps muscles, show a linear increase between torque/force and inter-muscular pressure. A limitation of the rabbit quadriceps preparation is that the force contributions of VL, VM and RF during the SIM conditions cannot be measured independently, as they share a common distal tendon and have no discernible tendons proximally for individual muscle force measurements for the SIM conditions. In addition, the fourth head of the quadriceps muscle group, the vastus intermedius, was not activated in our experiments because of the difficulty in accessing its nerve branch without damaging crucial nerve and muscle structures. It would be of great interest and might provide additional insights into the mechanics of the force loss for the SIM compared with the SUM condition, if the individual muscle forces of the quadriceps were known at any instant in time for the SIM conditions. With an average loss in torque/force production of 20% for the SIM condition, we do not know whether this loss is similarly distributed among the quadriceps muscles, or if one muscle is more affected than the others.

Conclusion

Based on the results of this study, we conclude that inter-muscular pressure, changes in moment arm and inter-muscular force transmission are likely not contributing to the force deficit observed in the SIM compared with the SUM conditions in the rabbit quadriceps muscles. The mechanisms underlying the loss of force in simultaneous compared with isolated muscle activation remain unknown, but possible explanations remain, such as differences in muscle deformations and fascicle length differences
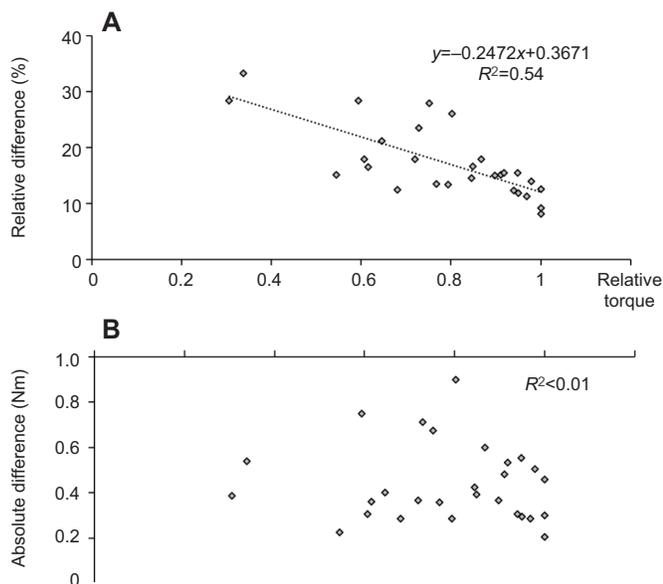

Fig. 3. Differences between the torques produced by vastus lateralis, vastus medialis and rectus femoris during simultaneous (SIM) stimulation, and the torques obtained from the sum of stimulating VM, VL and RF independently (SUM) as a function of relative torque (SIM normalized to maximum) during maximal and submaximal stimulation. (A) Differences in relative terms [(SUM–SIM)/SUM×100]. (B) Differences in absolute terms (pooled data, $n=3$). Note that the percentage change in torque between SIM and SUM increases for decreasing levels of torque.

between these conditions. It is also important to highlight that our findings suggest that everyday movements performed at low levels of activation and force can be affected by this force loss in simultaneous muscle stimulation.

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