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The mechanics of agonistic muscles

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ABSTRACT

Introduction: In this study, we tested two assumptions that have been made in experimental studies on muscle mechanics: (i) that the torque-angle properties are similar among agonistic muscles crossing a joint, and (ii) that the sum of the torque capacity of individual muscles adds up to the torque capacity of the agonist group.
Methods: Maximum isometric torque measurements were made using a specifically designed animal knee extension dynamometer for the intact rabbit quadriceps muscles (n = 10) for knee angles between 60 and 120°. The nerve branches of the vastus lateralis (VL), vastus medialis (VM) and rectus femoris (RF) muscles were carefully dissected, and a custom made nerve cuff electrode was implanted on each branch. Knee extensor torques were measured for four maximal activation conditions at each knee angle: VL activation, VM activation, RF activation, and activation of all three muscles together.
Results: With the exception of VL, the torque-angle relationships of the individual muscles did not have the shape of the torque-angle relationship obtained when all muscles were activated simultaneously. Furthermore, the maximum torque capacity obtained by adding the individual torque capacities of VL, VM and RF was approximately 20% higher than the torques produced when the three muscles were activated simultaneously.
Discussion: These results bring into question our understanding of in-vivo muscle contraction and challenge assumptions that are sometimes made in human and animal muscle force analyses.

1. Introduction

When analyzing the mechanics of agonistic muscles crossing a joint, some basic and simplifying assumptions are often made implicitly, especially in experimental studies. These include that: (i) the torque-angle properties of agonistic muscles crossing a joint are similar in shape, and (ii) that the sum of the torque capacity of individual muscles adds up to the torque capacity of the agonist group. Despite the appeal of these assumptions, and their use in the literature, their validity remains unknown (Epstein and Herzog, 1998; Herzog, 2017; Sandercock and Maas, 2009; Tijs et al., 2014).

Regarding the first assumption, the relative contribution of each agonist muscle to the total muscle group torque is often thought to be independent of joint angle in experimental studies. Force contributions are primarily calculated based on a muscle's physiological cross-sectional area (e.g., de Brito Fontana et al., 2014; Finni et al., 2003; Ichinose et al., 2000, 1997; Ishikawa et al., 2003; Kawakami et al., 1998). However, there are multiple factors that may influence the contribution of a muscle to the maximum isometric torque at a given joint angle, for example: the force-length relationship, the length-dependent activation, and the relationship between changes in joint angle, muscle tendon unit length and fascicle length (Gordon et al., 1966; Lieber and Fridén, 2000; Lutz and Rome, 1994; Rassier et al., 1999; Vaz et al., 2012). These factors may change differently for the individual muscles comprised in an agonistic group, thereby affecting the torque potential of a muscle relative to the torque potential of the agonistic group.

On the other hand, in theoretical models of the human musculoskeletal system, physical and biological parameters, such as muscles' anatomy, fascicle lengths, tendon slack lengths, and electromyographic activity, are often used to account for differences in the force-length properties of individual muscles during forward simulations and inverse dynamics approaches (Delp et al., 1990; Erdemir et al., 2007; Fidelus, 1969; Hatze, 1977; Hoy et al., 1990). Although neuromusculoskeletal modeling and simulation has proliferated in the biomechanics research community over the past 25 years, there is still a lack of verification and validation standards, and experimental data regarding individual agonistic

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muscle properties are necessary for proper calibration and validation of models (Hicks et al., 2015).

Regarding the second assumption, it is important to consider that muscles are, in their natural anatomical situation, intimately interconnected and packed within connective tissues, such as the epimysium and fascia (Maas and Sandercock, 2010; Purslow, 2008). Upon contraction, muscles deform and exert pressure on each other. These deformations for a given muscle may depend on the activation and force produced by the other muscles within the anatomic confines of an agonistic group and may, in turn, affect the force potential of muscles (Maas and Sandercock, 2010; Purslow, 2010; Raiteri et al., 2016; Reinhardt et al., 2016). Since muscle properties are typically evaluated in maximally activated muscles, it seems relevant that these interactions are also evaluated in the fully active state. During submaximal contractions, inter-muscular pressures are likely low and may not be sufficient to affect force generating potential of individual muscles (Tijs et al., 2014).

If indeed the torque generating potential of a muscle stimulated in isolation is different from that of the same muscle when activated simultaneously with the muscles of its agonistic group, then the resulting discrepancy may need to be accounted for in experimental and theoretical studies of human movement. While great advances have been made in our comprehension of muscle properties in isolated muscles, fibres, myofibrils, and sarcomeres (Abbott and Aubert, 1952; Edman et al., 1982; Gordon et al., 1966; Hill, 1938; Joumaa and Herzog, 2010; Leonard et al., 2010; Rack and Westbury, 1969; Rassier and Herzog, 2004), our understanding of muscle properties and functions of individual muscles within their agonistic group remains limited (Jarc et al., 2013; Maas and Sandercock, 2010; Tijs et al., 2014).

The purpose of this study was to analyze systematically the torque-angle relationship of muscles within an agonistic group. Specifically, we tested two hypotheses related to the assumptions introduced above: (i) that the torque-angle curves of all muscles (normalized to their peak torque) are similar, and (ii) that the sum of the isometric torque capacity of the individual agonist muscles activated in isolation adds up to the torque capacity of the entire group activated simultaneously. These hypotheses were tested for the specific case of the rabbit knee extensor muscles where we used individual nerve stimulation of the vastus lateralis (VL), vastus medialis (VM) and rectus femoris (RF) muscles in isolation or in combination of all three.

2. Methods

Experiments were performed on the right quadriceps muscles of 10 skeletally mature New-Zealand white female rabbits (average mass 4.0 kg; range 3.0–5.4 kg, Covance Inc., headquartered in Princeton, NJ, US). Approval for all procedures was obtained from the University's Animal Ethics Committee.

Rabbits were tranquilized with 1 ml/kg Atravet (25 mg/ml; Vetoquionol NA. Inc., Lavaltrie, QC, Canada) and held under anesthesia with a 2% isoflurane/oxygen mixture. After the experiment, animals were euthanized with an overdose injection of Euthanyl (MTC Pharmaceuticals; Cambridge, ON, Canada) into the lateral ear vein.

The branches of the femoral nerve responsible for the innervation of VL, VM, and RF were carefully dissected. One custom nerve cuff electrode was placed on each of the three branches, allowing for electrical stimulation of the three muscles individually or together. Then, Kwik-Cast (World Precision Instruments, Saraota Fl, USA) was injected around the nerve cuffs. Rabbits were fixed supine in a stereotaxic frame (Sawatsky et al., 2012) with the pelvis and femoral epicondyles pinned to keep the hip angle at 130–140° (180°, full extension of the hip) and to stabilize the proximal segment of the knee. The knee center of rotation (lateral epicondyle) was carefully aligned with the rotational axis of a servomotor (Parker Hannifin Corporation, Irwin, PA, USA) which controlled (Motion Planner, Rohnert Park, CA, USA) the angle of the tibia in relation to the femur. Passive knee flexion and extension was performed to verify that the servomotor and knee joint axes remained aligned throughout the entire range of motion tested. Knee joint moments were acquired using Windaq data collection software (Dataq Instruments, Akron) and a customized MATLAB program (The MathWorks, Natick, MA, USA) (Leumann et al., 2015). Stimulation of the nerves was given through a dual output stimulator (Grass S8800, Astro/Med Inc., Longueil, QC, Canada), which was synchronized with the servomotor. Torque-angle curves of the quadriceps group and the individual quadriceps muscles were obtained for knee angles ranging between 60 and 120° (0°, full extension of the knee). Kinematic analysis of rabbits hopping in unrelated experiments indicated that this range reflects the primary functional range of the knee.

There were four experimental conditions for each knee angle: VL activation alone, VM activation alone, RF activation alone, and activation of all three muscles together. Nerve stimulation was performed at a frequency of 100 Hz, using rectangular 0.1 ms pulses for 500 ms. The stimulation current was set at twice the level that was found to produce maximal forces to ensure recruitment of all motor units of the quadriceps muscle group. A pause of 2 min was given between tests. Fatigue throughout the protocol was assessed by repeating the first torque measurement at the end of all testing. For three of the ten animals, contractions were performed for every 10° knee angle, while for the remaining animals, measurements were made every 20° and polynomial interpolation was used to estimate the data points at the intermediate knee angles.

The total knee extensor torque for the entire muscle group was calculated by adding the torques produced by VL, VM and RF when stimulated in isolation (SUM), and this torque was compared to that obtained when all muscles were activated simultaneously (ALL).

Normal distribution of the data was confirmed through Shapiro-Wilk testing. Two two-factor (*condition* × joint angle) repeated measures ANOVA were used for analysis. The first was used to test differences between muscles (VL, VM, RF, and entire group) for the normalized joint torques across knee angles and the second was used to test for differences between the sum of the individual muscle torques (SUM) and the torques produced when all muscles were stimulated simultaneously (ALL).

3. Results

There was a significant interaction ($p < 0.001$) between joint angle and muscle (VL, RF, VM, and ALL) for the normalized torques, indicating that the shape of the torque-angle relationship differed among muscles/group (Fig. 1). VL and the agonist group (simultaneous stimulation of all muscles - ALL) worked primarily on an ascending slope and a plateau of their respective torque-angle relationships, reaching peak torque values at a knee angle of 100°. VM worked almost exclusively on an ascending torque-angle region (peak torque at 110–120°), and RF had a substantial portion of its torque-angle relationship on a descending slope, reaching its peak torque at 90°.

The sum of the maximum torque capacity for the isolated stimulation of VL, VM and RF was approximately 20% higher than the maximum torque capacity for simultaneous stimulation of all muscles of the agonist group ($p < 0.001$) and for all joint angles ($p = 0.997$ for interaction between effects) (Fig. 2). Confidence