Muscle morphology of the vastus lateralis is strongly related to ergometer performance, sprint capacity and endurance capacity in Olympic rowers.

Adapted from:
Abstract

Rowers need to combine high sprint and endurance capacities. Muscle morphology largely explains muscle power generating capacity, however, little is known on how muscle morphology relates to rowing performance measures. The aim was to determine how muscle morphology of the vastus lateralis (VL) relates to rowing ergometer performance, sprint and endurance capacity of Olympic rowers. Eighteen rowers (12♂, 6♀, 17 competed at the 2016 Olympics) performed an incremental rowing test to obtain $\dot{V}O_{2\text{max}}$, reflecting endurance capacity. Sprint capacity was assessed by Wingate cycling peak power ($PO_{\text{peak}}$). VL morphology (volume, physiological cross-sectional area (PCSA), fascicle length ($L_f$) and pennation angle) was derived from 3D ultrasound imaging. Thirteen rowers (7♂, 6♀) completed a 2000-m rowing ergometer time trial. Wingate $PO_{\text{peak}}$ and $\dot{V}O_{2\text{max}}$ were also normalized to lean body mass$^{2/3}$ to eliminate body size differences. Muscle volume largely explained variance in 2000-m rowing performance ($r^2=0.85$, $p<0.001$), $\dot{V}O_{2\text{max}}$ ($r^2=0.65$, $p<0.0001$), and Wingate $PO_{\text{peak}}$ ($r^2=0.82$, $p<0.001$). Normalized $\dot{V}O_{2\text{max}}$ and Wingate $PO_{\text{peak}}$ were negatively related in males ($r=-0.94$, $p<0.001$). $L_f$, not PCSA, attributed to normalized Wingate $PO_{\text{peak}}$. In conclusion, VL volume largely explains variance in rowing ergometer performance, sprint and endurance capacity. Normalized sprint capacity associates with $L_f$ rather than PCSA, therefore athletes may benefit from long fascicles.
Muscle volume largely explains performance, sprint and endurance capacity in Olympic rowers


1. **Rowing ergometer performance requires sprint and endurance (explained variance)**

   81% Sprint
   90% Endurance
   98%

2. **Muscle volume VL strongly relates to performance, sprint and endurance capacity**

   \[ r = 0.92 \]
   \[ r = 0.91 \]
   \[ r = 0.81 \]
   \[ r = 0.83 \]
   \[ r = 0.70 \]
   \[ r = 0.71 \]
   \[ r = 0.66 \]
   \[ r = 0.60 \]
   \[ r = 0.70 \]

   male
   female

3. **Sprint and endurance capacity are inversely related (♂)**

   \[ r = -0.94 \]  
   \[ p < 0.001 \]

   * scaled for body size and composition

Muscle volume VL explains ergometer performance, sprint and endurance capacity

Athletes may benefit from long fascicles
Introduction

Rowing challenges athletes to optimize both endurance and sprint capacity. The 2000-m rowing races require substantial aerobic energy contribution (~70-87%), but rowers are also physically strong compared to other endurance athletes. Rowing performance is predicted by both maximal oxygen uptake (VO_{2max}) and all-out anaerobic sprint capacity. Consequently, endurance and sprint (i.e. force and power generating) capacities are complementary determinants of 2000-m rowing performance in competitive female rowers, in male and female world championship rowers, and (inter)national male rowers. Although endurance and sprint capacities are known predictors of rowing performance, it remains unknown how elite rowers establish both a high endurance and sprint capacity.

Combining high sprint and endurance capacity is challenging. Increasing both muscle fiber size and muscle fiber oxidative capacity is strongly endeavoured, but also difficult, as these are inversely related across species (including untrained humans), within animal species, and within trained cyclists. In addition, training-induced muscle adaptations are conflicting. When athletes perform concurrent endurance and resistance training, muscle hypertrophy and strength gains induced by resistance training are compromised. Assessment of muscle properties, such as morphology of knee extensors in rowers, may provide insights in how sprint and endurance capacities are concurrently established. For instance, maximal force exertion by the muscle attributes to sprint capacity and is determined by the summation of cross-sectional areas of all muscle fibers, whereas a smaller muscle fiber diameter implies a shorter oxygen diffusion distance to the core of the muscle fiber, which is beneficial for high steady state oxidative metabolism. However, data on muscle morphology of rowers is limited and very little is known on how muscle morphology of elite rowers relates to their sprint capacity, endurance capacity and 2000-m rowing performance.

3D ultrasound imaging enables quantification of muscle morphology, retrieving muscle volume and muscle architecture from the same 3D ultrasound voxel array. Muscle volume represents the total amount of contractile tissue, which influences total energy consumption and power generating capacity of the muscle. Mechanical muscle power is by definition the product of muscle force and shortening velocity, as experimentally shown in human and animal muscle. Muscle force is proportional to the number of sarcomeres arranged in parallel, i.e. muscle physiological cross-sectional area (PCSA). Force exerted on the tendon is, however, reduced by the pennation angle of the fascicles, which increases with muscle hypertrophy. Prime determinants of maximal shortening velocity are the number of sarcomeres arranged in series, i.e. fascicle length (L_s), and myosin heavy chain type distribution within the muscle. Performance potential of a muscle group will therefore be enhanced by enlarged muscle volume through increases in L_s and/or PCSA. Indeed, trained male rowers have larger quadriceps muscle volume, thus a higher performance potential, in comparison to male controls. Muscle architecture may be critical for how high endurance and sprint capacity are combined. PCSA increases with muscle fiber hypertrophy in response to resistance training. Muscle fiber cross-sectional area (FCSA) is, however, inversely related to muscle fiber VO_{2max}. This suggests that enlarging FCSA not only increases pennation angle, but also constrains oxygen diffusion (as it increases the diffusion distance). In turn, muscle fiber VO_{2max} of the m. vastus lateralis strongly relates to whole-body VO_{2max} during cycling, which is an important determinant.
of endurance capacity. Therefore, a knee extensor muscle volume with a large PCSA is likely associated with a lower endurance capacity (assuming muscle fiber number is constant), while a long $L_f$ may circumvent the negative effect of muscle fiber hypertrophy on oxygen diffusion and muscle fiber $\dot{V}O_{2\text{max}}$. Assessment of muscle morphology will complement insights in physiological determinants of rowing performance and in how endurance and sprint capacity are established.

The aim of this study was to determine how muscle morphology of the m. vastus lateralis relates to 2000-m rowing ergometer performance, sprint capacity and endurance capacity of Olympic rowers. Rowing is a complex movement that requires recruitment of many muscles crossing multiple joints. In the present study, we assessed morphology of the m. vastus lateralis (VL), because activation of the quadriceps muscles, such as the VL, is essential to the power production in rowing\textsuperscript{25,26}. Moreover, within the rowing stroke, activation of the VL contributes to a smooth transition into recovery\textsuperscript{25} and from recovery into the propulsion phase\textsuperscript{26}. We hypothesized that 2000-m rowing performance, endurance capacity and sprint capacity are highly related to muscle volume, representing the total amount of contractile tissue. When normalized for body size differences, we expect that a long fascicle rather than large PCSA facilitates athletes to combine relatively high sprint and endurance capacities.

**Methods**

**Participants**

Eighteen rowers (8 heavyweight male, 4 lightweight male, 4 heavyweight female and 2 lightweight female rowers) volunteered to participate in this study (Table 4.1). Participants competed in different disciplines at the 2016 Olympics (17 rowers) or at the international level (1 rower), and included Olympic medallists. Rowers had on average 7.0 ± 2.8 years of international competitive experience and trained for ≥12 sessions per week. All oarsmen were sweep rowers, of whom six rowed on bow side and six on stroke side and female rowers consisted of five scull rowers and one sweep rower on stroke side. Irrespective of this distribution, it should be noted that stroke side of sweep rowers and leg dominancy do not lead to asymmetries in muscle morphology, muscle activation, force and peak power production\textsuperscript{27-29}. Prior to participation, experimental procedures of the study were explained and all participants provided written informed consent. Participants were instructed to perform no strenuous exercise and consume no alcohol within the last 24 hours before each test, and were instructed not to consume food, caffeinated beverages or dietary supplements during the last three hours before each test. The study was conducted according to the principles of the Declaration of Helsinki and was approved by the medical ethics committee of the VU medical centre, Amsterdam, the Netherlands (NL54282.029.15).

**Rowing ergometer performance**

Rowing performance was obtained from a 2000-m time trial on a rowing ergometer (Concept II, Model D, Morrisville, VT, USA). Rowers were instructed to finish the time trial as fast as possible and were free to select their preferred damper setting. After the time trial, finish time and average power output were obtained from the ergometer display. Since measurements were performed during the pre-Olympic season and given the physiological and psychological strain of the time trial, it was not possible to incorporate the 2000-m rowing performance within the
training schedules of all athletes. The 2000-m rowing ergometer performance was obtained in 13 rowers (7♂, 6♀).

Maximal incremental test

\( \dot{V}O_{2\text{max}} \) is one of the main determinants of endurance capacity\(^{10,30}\), and was obtained from a maximal incremental test to voluntary exhaustion. The test consisted of a 7×4 min exercise protocol with 1-min rest between blocks on the Concept II ergometer (Model D). During the first four minutes, targeted power output was set at 40% of previously determined 2000-m mean power for men and at 45% for women, which was increased by 8% every 4-min block\(^{31}\). The last 4-min exercise block was an all-out block. Respiratory data were recorded breath-by-breath using open circuit spirometry (Cosmed Quark CPET, Cosmed S.R.L., Rome, Italy) and prior to every test, the volume transducer and gas analyzer were calibrated according to manufacturer’s instructions. Data was converted to second-by-second data and \( \dot{V}O_{2\text{max}} \) was calculated as highest 30-s moving average value achieved during the test to voluntary exhaustion.

Wingate test

To obtain peak power generating capacity, a primary determinant of sprint capacity, participants performed a 30-s Wingate test on a bicycle ergometer (Monark 894 E Peak Bike, Monark Exercise AB, Vansbro, Sweden)\(^{32}\). The bicycle ergometer is designed to accurately measure accelerations with high temporal resolution, more so than a rowing ergometer. The test was preceded by a 10-min warm-up (brake weight 1-1.5 kg) with three 10-s accelerations and a 2-min rest interval. Workload was set at 8% body mass for females or 10% for males and was automatically applied

<table>
<thead>
<tr>
<th>Table 4.1. Participant characteristics</th>
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<tr>
<td>n</td>
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<tr>
<td>Age(^a) (year)</td>
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<tr>
<td>Body mass (kg)</td>
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<tr>
<td>Lean body mass(^d) (kg)</td>
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<tr>
<td>Height(^c) (cm)</td>
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<tr>
<td>Rowing performance 2000 m(^d) (s)</td>
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<td>Rowing performance 2000 m(^d) (W)</td>
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<tr>
<td>( \dot{V}O_2\text{max} ) (L∙min(^{-1}))</td>
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<tr>
<td>Wingate PO(_{\text{peak}}) (W)</td>
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<tr>
<td>Wingate PO(_{\text{mean}}) (W)</td>
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<tr>
<td>Wingate fatigue index (%)</td>
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<tr>
<td>KE isometric torque (N∙m)</td>
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<tr>
<td>VL volume (cm(^3))</td>
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<tr>
<td>VL PCSA (cm(^3))</td>
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<tr>
<td>VL L(_{f}) (cm)</td>
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<tr>
<td>VL ( \theta ) (°)</td>
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</tbody>
</table>

Notes: * significantly different from females, p<0.05, ** significantly different from females, p<0.01, \(^a\) non-parametric data were tested by a Mann-Whitney U test. \(^b\) lean body mass was obtained in 10♂ and 5♀ rowers. \(^c\) 2000-m rowing performance was obtained in 7♂ and 6♀ rowers. Abbreviations: F, female; M, male; ES, effect size male-female differences; LW, lightweight; HW, heavyweight; KE, knee extension; VL, vastus lateralis muscle; PCSA, physiological cross-sectional area; L\(_{f}\), fascicle length; \( \theta \), pennation angle, i.e. the angle between fascicle and its distal aponeurosis; n, number of participants;
to the flywheel when cadence exceeded 70 revolutions per minute. Participants were instructed to remain seated and received strong verbal encouragement throughout the test. Peak (highest 1-s) power output ($P_{peak}$), average power, and fatigue index (drop from $P_{peak}$ to minimal power expressed as percentage of $P_{peak}$) were obtained from the Wingate test.

**Isometric knee extension**

For assessment of force generating capacity, an important determinant of sprint capacity, isometric knee extension (KE) torque of the right leg was measured using a custom-made dynamometer. Participants were firmly secured with straps over hips and shoulders, and the lower leg was protected by a shin guard and strapped to a force transducer (KAP E/200Hz, Bienfait B.V. Haarlem, The Netherlands), which was placed ~26.6 cm distally from the knee joint to measure force exertion at the shin. Hip flexion angle was set at 85° and knee flexion angle at 60°, which approximates optimal knee joint angle for maximal knee extension torque\(^3\), with 0° corresponding to full hip or knee extension. Active knee angle was set after alignment of the anatomical knee axis with the dynamometer rotation axis, while participants exerted a submaximal isometric contraction during knee extension. Knee extension torque was obtained by multiplication of measured forces (sampled at 1 kHz) with the lever arm. After a warm-up of three submaximal isometric contractions, participants performed a maximum of five attempts to attain peak isometric KE torque, while receiving online visual feedback of their force tracings. Peak isometric KE torque was the highest 100-ms moving average obtained from the 5-s isometric contractions.

**Muscle morphology**

Muscle morphology of m. vastus lateralis (VL) was determined using 3D ultrasound imaging, which demonstrates high reproducibility and validity ($r>0.98$) and is previously described in detail\(^4,5\). In short, B-mode ultrasound images of the right VL were obtained using a 5-cm linear probe (Technos MPX, ESAOTE S.p.A. Italy), while the participant was positioned with hip angle at 85° and knee flexion angle at 60°. The shank was secured with straps to prevent leg displacement or rotation. Multiple longitudinal scans were made of the VL from lateral to medial border, with the ultrasound probe in transverse orientation. The location and orientation of the probe were monitored by a motion capture system (Optotrak Certus, NDI, Waterloo, Canada) and synchronized with the ultrasound images (25 Hz) to construct a 3D voxel array, using customized software in Matlab (Mathworks Co, Natick, Massachusetts, USA).

From this 3D ultrasound reconstructed voxel array, the origin and distal muscle belly end of the VL were identified using 3D image processing software (MITK; www.mitk.org). Muscle volume was derived from manual segmentation of transversal cross-sections along the VL length in MITK. Interactive interpolation was used to confirm identification of muscle boundaries. Note that visible adipose tissue and connective tissue incursions were carefully excluded from segmentation. Fascicle length ($L_f$) and pennation angle between fascicle and distal aponeurosis ($\theta$) were obtained from the mid-longitudinal ‘fascicle’ plane at a position 2/3\(^{rd}\) along the muscle belly (distal to the trochanter major, Figure. 4.1). The mid-longitudinal plane was defined by the vector between origin and distal end of the VL and a line representing the shortest distance between the tangent of the distal aponeurosis and the projection of this vector onto the anatomical cross-section 2/3\(^{rd}\) along the muscle belly (distal to the trochanter
Physiological cross-sectional area (PCSA) was calculated by dividing muscle volume by $L_f$. Because muscle force exerted on the patellar tendon is reduced by its pennation angle, PCSA was also multiplied by cosine of the pennation angle to obtain the effective PCSA³⁴.

**Normalized sprint and endurance capacity**

Maximal power of an organism scales with its body size. To assess biological differences in peak power and aerobic power production, we removed effects of body size by normalizing $\dot{V}O_{2\text{max}}$ and Wingate PO$_{\text{peak}}$ to lean body mass$^{2/3}$³⁵. Isometric scaling predicts mass and volume to be proportional to body mass (BM), cross-sectional or surface areas to be proportional to BM$^{2/3}$ and linear dimensions such as height or $L_f$ to be proportional to BM$^{1/3}$³⁶. Time is also considered a linear dimension¹. Consequently, $\dot{V}O_{2\text{max}}$ (volume*time$^{-1}$) and PO$_{\text{peak}}$ (work*time$^{-1}$) are proportional to BM$^{2/3}$. As body fat mass substantially influences body mass but does not contribute to maximal power, peak power and aerobic power are expected to be a linear function of (body mass – body fat)$^{2/3}$³⁵. Lean body mass (LBM) was determined from the sum of 4 skinfolds³⁷ in 15 participants (10♂, 5♀), due to limited availability of athletes during the pre-Olympic season.

**Statistics**

All data are presented as individual values or as mean±SD. Differences between male and female rowers were assessed by independent T-test or Mann-Whitney U test. Effect sizes were calculated as Cohen’s d from group means and pooled standard deviations. Relationships between morphological variables (volume, PCSA, $\theta$, $L_f$), (normalized) endurance and sprint capacity ($\dot{V}O_{2\text{max}}$, Wingate PO$_{\text{peak}}$, and KE torque) and 2000-m rowing average power were assessed by (partial) Pearson’s correlations and linear regressions. Effect sizes of relationships were assessed by Pearson's correlations and coefficients of determination. Stepwise multiple regression analysis was used to predict 2000-m rowing performance (average power) from $\dot{V}O_{2\text{max}}$, Wingate PO$_{\text{peak}}$, and KE torque or from morphological variables. Predictors were included in the model if a significant $R^2$ change (p<0.05) was reported. Results are reported if assumptions for multiple regression analysis were met, demonstrating independent errors (indicated by a Durbin-Watson score between 1 and 3), no multicollinearity between predictors (reflected by a variance inflation factor

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**Figure 4.1.** Muscle morphology of the vastus lateralis muscle (VL) was characterized by 3D ultrasound imaging. A) A reconstructed voxel array of the VL of a heavyweight oarsman is shown in 3D, including longitudinal (blue), transversal (green) and coronal (red) planes. B) Fascicle length and pennation angle were obtained from the mid-longitudinal ‘fascicle’ plane. The mid-longitudinal plane is defined by the vector between origin and distal end of the VL and a line resembling the shortest distance between the tangent of the distal aponeurosis and the projection of this vector within the anatomical cross-section at 2/3rd of the muscle belly length (distal to the trochanter major).
<10 and tolerance >0.2), and homoscedasticity of residuals (normal distribution of standardized residuals). Sex differences in the relationship between significant predictors and 2000-m rowing performance were tested by ‘enter’ multiple regressions (predictor, sex and predictor-sex), and were acknowledged if the interaction effect was significant. Findings were considered to be significant if p<0.05.

**Results**

Table 4.1 summarizes age, body mass, height, 2000-m rowing ergometer performance, sprint and endurance capacity and muscle morphology in female, male and all rowers. The 2000-m rowing ergometer performance was strongly related to (both) endurance and sprint capacity (r=0.95, p<0.01 and r=0.90, p<0.01 respectively, n=13). Multiple regression analysis revealed that $\dot{V}O_{2max}$ and Wingate $PO_{peak}$ together explained 98% of the variance in 2000-m ergometer power ($R^2=0.98$, p<0.001).

![Muscle volume largely explains 2000-m rowing ergometer performance (A), $\dot{V}O_{2max}$ (B) and Wingate $PO_{peak}$ (C)](image)

Individual values (upper panel 7♂ and 6♀, lower panels 12♂ and 6♀) are shown for male rowers (△) and female rowers (○). The thick solid line represents the best linear fit based on individual values and the dotted lines represent the 95% prediction interval.
PCSA explained 68% ($r^2=0.68$, $p<0.001$) and fascicle length 43% ($r^2=0.43$, $p<0.05$) of the variance in ergometer performance, while pennation angle was not related to 2000-m rowing ergometer performance ($r^2=0.004$, $p=0.774$). Multiple regression analysis revealed that VL volume was the primary morphological determinant explaining 85% of variance in 2000-m rowing ergometer power ($r^2=0.85$, $p<0.001$, $n=13$, see Figure 4.2 and Table 4.2).

\(\dot{V}O_2^{\text{max}}\), Wingate PO\(\text{peak}\), and maximal isometric KE torque were related to VL muscle volume (Figure 4.2 and Table 4.2, $n=18$). Also PCSA and \(L_f\) were positively related to Wingate PO\(\text{peak}\), \(\dot{V}O_2^{\text{max}}\) and maximal isometric KE torque (Table 4.2). In females, PCSA was strongly related to Wingate PO\(\text{peak}\) and KE torque, while in males \(L_f\) was moderately related to Wingate PO\(\text{peak}\) and KE torque. Taken together, these results show that VL volume largely explained the variance in 2000-m rowing ergometer performance, endurance capacity and sprint capacity.

![Image of graphs](image)

Figure 4.3 indicates that \(\dot{V}O_2^{\text{max}}\) and Wingate PO\(\text{peak}\) are a function of volume or size. When divided by body mass, \(\dot{V}O_2^{\text{max}}\) and Wingate PO\(\text{peak}\) were not significantly related in males and were not significantly related in females ($r=-0.68$, $p<0.05$ and $r=-0.60$, $p=0.21$ respectively, Figure 4.3A). \(\dot{V}O_2^{\text{max}}\) and PO\(\text{peak}\) normalized to LBM\(^{2/3}\) were not related in females, but showed an inverse relationship in male rowers ($r=-0.94$, $p<0.001$, Figure 4.3B) consistent with the inverse relationship between muscle fiber \(\dot{V}O_2^{\text{max}}\) and FCSA\(^8,10\). \(\dot{V}O_2^{\text{max}}\) per LBM\(^{2/3}\) was not significantly related to PCSA ($r=0.28$, $p=0.31$, $n=15$), muscle volume ($r=0.22$, $p=0.43$) or \(L_f\) ($r=0.13$, $p=0.64$). Wingate PO\(\text{peak}\) per LBM\(^{2/3}\) was positively related to muscle volume ($r=0.67$, $p<0.01$, $n=15$) and \(L_f\) ($r=0.66$, $p<0.01$), but not to PCSA ($r=0.37$, $p=0.18$). Thus, normalized sprint capacity was inversely related to normalized endurance capacity in male rowers. Unexpectedly, normalized endurance capacity was not related to PCSA. \(L_f\), but not PCSA, attributed to normalized sprint capacity.
Table 4.2. Pearson correlations and 95% confidence intervals of relationships between muscle morphology and 2000-m rowing performance, endurance capacity and sprint capacity (i.e. power and force generating capacities).

<table>
<thead>
<tr>
<th>Group</th>
<th>Rowing performance 2000m (W)</th>
<th>$\dot{V}O_\text{2max}$ (L·min$^{-1}$)</th>
<th>Wingate $PO_{\text{peak}}$ (W)</th>
<th>KE torque (N·m)</th>
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<tr>
<td></td>
<td>All M F</td>
<td>All M F</td>
<td>All M F</td>
<td>All M F</td>
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<tr>
<td>$n$</td>
<td>13 7 6</td>
<td>18 12 6</td>
<td>18 12 6</td>
<td>18 12 6</td>
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<tr>
<td>VL volume (cm$^3$)</td>
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<td></td>
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<tr>
<td></td>
<td>0.92** 0.57 0.74</td>
<td>0.81** 0.50 0.61</td>
<td>0.91** 0.83** 0.77</td>
<td>0.78** 0.56 0.91*</td>
</tr>
<tr>
<td></td>
<td>[0.75-0.98] [-0.33-0.92] [-0.17-0.97]</td>
<td>[0.55-0.93] [-0.11-0.83] [-0.40-0.95]</td>
<td>[0.76-0.97] [0.48-0.95] [-0.11-0.97]</td>
<td>[0.48-0.91] [-0.02-0.86] [0.38-0.99]</td>
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<tr>
<td>VL PCSA (cm$^3$)</td>
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<td></td>
<td>0.83** 0.23 0.88*</td>
<td>0.70** 0.36 0.78</td>
<td>0.72** 0.45 0.85*</td>
<td>0.56* 0.18 0.95**</td>
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<td></td>
<td>[0.51-0.95] [-0.64-0.84] [0.22-0.99]</td>
<td>[0.35-0.88] [-0.27-0.77] [-0.09-0.97]</td>
<td>[0.38-0.89] [-0.16-0.81] [0.11-0.98]</td>
<td>[0.13-0.81] [-0.44-0.68] [0.58-0.99]</td>
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<td>VL $L_f$ (cm)</td>
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<td>0.66* 0.33 -0.10</td>
<td>0.60** 0.30 -0.15</td>
<td>0.70** 0.60* -0.03</td>
<td>0.69** 0.61* 0.05</td>
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<td>[0.17-0.89] [-0.56-0.87] [-0.84-0.78]</td>
<td>[0.18-0.83] [-0.34-0.74] [-0.86-0.75]</td>
<td>[0.35-0.88] [0.04-0.87] [-0.82-0.80]</td>
<td>[0.33-0.88] [0.06-0.88] [-0.79-0.83]</td>
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<tr>
<td>VL $\theta$ (°)</td>
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<tr>
<td></td>
<td>-0.06 -0.06 0.36</td>
<td>-0.12 -0.06 0.01</td>
<td>-0.04 -0.02 0.48</td>
<td>-0.26 -0.29 0.05</td>
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<td>[-0.50-0.44] [-0.59-0.56] [-0.54-0.93]</td>
<td>[-0.65-0.23] [-0.74-0.34] [-0.79-0.83]</td>
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Notes: Rowing performance is the average power output over a 2000-m ergometer rowing performance, F, female; M, male; KE, knee extension; VL, vastus lateralis muscle; PCSA, physiological cross-sectional area; $L_f$, fascicle length; $\theta$, pennation angle, i.e. the angle between fascicle and its distal aponeurosis; $n$, number of participants. For Pearson correlations * illustrates significant, $p<0.05$; ** significant, $p<0.01$. 

Muscle morphology of the vastus lateralis
Discussion

This study shows that volume of m. vastus lateralis could explain a large proportion of the variance in 2000-m rowing ergometer performance, sprint capacity and endurance capacity. Following normalization to lean body mass\(^{2/3}\), sprint and endurance capacity were negatively related in males, but not related in females. Unexpectedly, a large PCSA did not seem detrimental for normalized \(\dot{V}O_{2\text{max}}\), while \(L_f\) and not PCSA, attributed to normalized \(P_{\text{Opeak}}\).

Sprint and endurance capacity of our rowers were complementary determinants of their 2000-m rowing ergometer performance, illustrating the high aerobic and anaerobic demands of a 2000-m rowing race\(^1\). Our findings of Olympic rowers (\(R^2=0.98\)) are in line with previous observations in competitive female rowers (\(R^2=0.96\))\(^4\), world rowing finalists (\(R^2=0.96-0.98\))\(^5,6\) and (inter) national male rowers (\(R^2=0.85\))\(^7\). Ergometer testing is not confounded by environmental effects (e.g. wind or water current) and therefore facilitates standardized assessment of rowing performance. In addition, 2000-m rowing ergometer performance together with body mass predict 2000-m rowing performance on water (i.e. body mass affects water drag forces, but not drag forces of the rotating ergometer flywheel)\(^38\). Thus, morphological determinants of ergometer performance are also relevant for on-water rowing performance.

Muscle volume explains a large proportion of the variance in 2000-m rowing ergometer performance, sprint and endurance capacity

Volume of m. vastus lateralis showed the strongest relationship with 2000-m rowing ergometer performance, sprint capacity and endurance capacity (\(r^2=0.60-0.85\)). The VL volume of our male rowers was 900 cm\(^3\) (body mass ~90 kg). Previous studies have demonstrated VL volumes of 750 cm\(^3\) in trained male rowers (body mass ~75 kg)\(^23\) and 550-675 cm\(^3\) in male controls (body mass ~65 and ~75 kg, respectively)\(^23,34\). VL volume was strongly related to Wingate \(P_{\text{Opeak}}\) and \(\dot{V}O_{2\text{max}}\), illustrating that the muscle power generating capacity and oxygen consumption are strongly related to the total amount of contractile tissue. As VL volume may be influenced by differences in sex and/or body size, we performed additional partial correlations controlling for sex and body size, which revealed that VL volume and rowing ergometer performance were still strongly related after controlling for sex-differences (\(r=0.72, p=0.018\)), but were unrelated after controlling for body size-differences (LBM\(^{2/3}\)) (\(r=0.23, p=0.516\)). In support of this finding, VL volume was found to be strongly correlated to LBM\(^{2/3}\) (\(r=0.95, p<0.001\)). These results imply that VL volume explained variance in 2000-m rowing ergometer performance independent of sex-differences, but not independent of body-size differences in this homogeneous group of Olympic rowers. Based on these results, athletes may seek to obtain maximal ergometer performance by maximizing their (VL) muscle volume within the limits of their weight class.

For improving rowing performance by increasing muscle volume, two considerations are of relevance. First, training-induced changes in muscle size strongly impact muscle architecture. During muscle hypertrophy, muscle fibers require a larger attachment area onto the aponeurosis. This is facilitated by lengthening of the aponeurosis, as observed during adolescence\(^14\), or by increasing the pennation angle, which effectively decreases the attachment area on the aponeurosis\(^20\). Moreover, muscle hypertrophy and changes in \(L_f\) both affect muscle optimum length\(^20\). During muscle activation, alterations in pennation angle contribute to muscle length...
changes (i.e. shortening velocity), while higher pennation angles reduce effective force exertion on the tendon\(^{20}\). In longitudinal studies, one should consider these architectural changes in response to training.

Second, muscle force and power are not solely determined by muscle volume, but also depend on specific force, the muscle force per effective PCSA, which can be estimated for the quadriceps femoris muscle (QF) of our rowers. First, force exerted by the QF was calculated by dividing KE isometric torque by patellar moment arm. Patellar moment arm estimated at optimal knee joint angle is very similar between participants (average 4.7–4.8 cm)\(^{34,39}\), and was assumed to be 4.75 cm in all rowers. M. vastus lateralis volume yields -34% of the total QF volume in rowers\(^{23}\), and this percentage is similar for PCSA\(^{39}\), which we took into account. Specific force was then calculated to be 29 N\(\cdot\)cm\(^{-2}\) in female and 32 N\(\cdot\)cm\(^{-2}\) in male rowers, which was slightly higher than that of male controls\(^{40}\) and similar to the 30 N\(\cdot\)cm\(^{-2}\) reported for male controls after 9 weeks of strength training\(^{39}\). Note that hypertrophied muscle fibers of body-builders have demonstrated a lower fiber specific force than muscle fibers of power athletes and controls\(^{41}\). Our Olympic rowers also demonstrated a large PCSA and muscle volume, though not at the cost of their specific force. It remains to be established whether elite rowers may further enhance 2000-m rowing performance by obtaining a higher specific force.

**Inverse relationship between normalized endurance and sprint capacity**

To investigate intrinsic properties of the neuromuscular system, \(\dot{V}O_{2\text{max}}\) and Wingate PO\(_{\text{peak}}\) were normalized to LBM\(^{2/3}\). High normalized, rather than absolute, sprint and endurance capacities are essential to 2000-m rowing performance on water, as water resistance increases with body mass. \(\dot{V}O_{2\text{max}}\) and Wingate PO\(_{\text{peak}}\) per body mass were inversely related in males (\(r=-0.68, p<0.05, 12\sigma\)), and not significantly related in a small group of females (\(r=-0.60, p=0.21, 6\sigma\)). Since PO\(_{\text{peak}}\) and \(\dot{V}O_{2\text{max}}\) scale with body size\(^{36}\), a scale-invariant relationship was obtained after normalization to LBM\(^{2/3}\). This relationship was non-significant in females, but evidently inverse in male rowers (\(r=-0.94, p<0.001, 10\sigma\)). Sex differences were still present after normalization to LBM\(^{2/3}\), as these are largely (but not fully) reduced by normalization to LBM\(^{42}\), likely because of reduced oxygen supply in females due to lower hemoglobin concentrations\(^{43}\). Our cross-sectional results indicate an inverse relationship between normalized endurance and sprint capacity in oarsmen that is consistent with the inverse relationship between muscle fiber \(\dot{V}O_{2\text{max}}\) and FCSA\(^{8,10}\).

Given this inverse relationship\(^{6,10}\), a large PCSA was also expected to be negatively related to \(\dot{V}O_{2\text{max}}\) normalized to LBM\(^{2/3}\). PCSA of the VL of our males was large (~87.5 cm\(^2\)) compared to the 75 cm\(^2\) in male controls\(^{34}\). However, unexpectedly, PCSA of the VL was not inversely related to normalized \(\dot{V}O_{2\text{max}}\). An explanation could be that the PCSA of elite rowers is made up of a large number of muscle fibers allowing fiber CSA to remain relatively small. Yet, biopsy studies on VL of elite oarsmen have shown large FCSAs in combination with a large fraction of slow-twitch fibers (~70%) that are characteristic for endurance athletes\(^{1,44}\). Another explanation for the absent relationship between PCSA and normalized \(\dot{V}O_{2\text{max}}\) could be that oxygen diffusion was enhanced in our rowers, providing sufficient oxygen supply from atmosphere to mitochondria, such that a large FCSA may be combined with high muscle fiber \(\dot{V}O_{2\text{max}}\). In line with this, oarsmen show a relatively dense capillary network\(^{1,44}\), which may explain these present findings.
Wingate PO\textsubscript{peak} normalized to LBM$^{2/3}$ was positively related to $L_f$ and not related to PCSA. More sarcomeres in series (longer $L_f$) appears beneficial for sprinters, as elite 100-m sprinters showed longer $L_f$ compared to long-distance runners and non-sprinters$^{45,46}$. An increase in fascicle length may be achieved by (eccentric) resistance training$^{22,47,48}$, but this also shifts optimal muscle torque/power generation towards higher contraction velocities$^{19,22}$. Taken together, a combination of high normalized sprint capacity and normalized endurance capacity may be achieved by long fascicles rather than a large PCSA.

**Study limitations**

Investigating a population of Olympic rowers provides the unique opportunity to obtain physiological determinants of rowing performance, as they have optimized their rowing technique and are uniquely trained to deliver the best 2000-m rowing performance. However, Olympic athletes form a small and rare population, and therefore, the sample size was small in the present study. These factors should be considered before translating the present findings to other populations.

Muscle morphology was assessed of the VL, which is part of the quadriceps femoris muscle and is essential to the power production in rowing$^{25,26}$. We did not measure variability in quadriceps musculature or region-specific variation in muscle architecture along the muscle length. Yet, recent findings indicate that m. vastus lateralis is the largest quadriceps muscle in both male and female rowers and that only slight differences ($\leq 2\%$) exist in volume distribution of quadriceps muscles between male and female rowers$^{28}$. Though muscle architecture varies along its length, inter-subject differences in one region are considerably similar to those in other regions of the m. vastus lateralis$^{49}$. As the region of our muscle architecture measurements was standardized, this would only have marginal effects on the correlations observed in the present study.

Maximal oxygen consumption is not the only determinant of endurance capacity. Nevertheless, maximal oxygen consumption is one of the main determinants of endurance capacity$^{10,30}$ and strongly relates to muscle fiber maximal oxygen consumption of the m. vastus lateralis$^{24}$.

The maximal power-producing capacity was assessed by the Wingate test and maximal KE force generating capacity by maximal isometric force. Though measurement of maximal dynamic force on a dynamometer may also enhance our understanding of the rowing performance, we assessed maximal isometric force. Dynamic force measurements involve activation of many muscles crossing multiple joints, whereas maximal isometric knee extension torque can be ascribed to only the knee extensor muscles, allowing determination of specific force.

**Practical applications**

Rowing ergometer performance requires both a high sprint and endurance capacity. Present findings show that a simple Wingate test and an incremental exercise test can be used to characterize athletes within the sprint-endurance continuum. For future (rowing) practice, these measures may also prove to be useful for identification of young talent and optimization of individual training strategies. Here we show that measurements of muscle morphology facilitate our understanding of how athletes achieve their performance. Future studies are warranted to validate how training strategies alter muscle morphology and whether these adaptations contribute to maximization of (rowing) performance.
**Conclusions**

Vastus lateralis muscle volume could explain a large proportion of the variance in 2000-m rowing ergometer performance, endurance capacity and sprint capacity. Therefore, athlete rowers may seek to maximize ergometer performance by maximizing their (vastus lateralis) muscle volume within the limits of the athlete's weight class. When scaled for differences in body size, normalized sprint and endurance capacity were inversely related in oarsmen, indicating that maximizing both capacities appears to be challenging. Normalized endurance capacity was unexpectedly not negatively related to PCSA, whereas normalized sprint capacity was positively associated with fascicle length, but not with PCSA. To maximize normalized sprint capacity, athletes may therefore benefit from long fascicles, but it remains to be established to which extent functional elongation of muscle fascicles can be achieved by training.
References