THE EFFECT OF TEMPERATURE ON RESIDUAL FORCE ENHANCEMENT IN SINGLE SKELETAL MUSCLE FIBERS

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INTRODUCTION

Residual force enhancement (or force enhancement) has been defined as an increased steady-state isometric force following stretching of an active fiber or muscle compared to the steady-state force obtained for purely isometric contractions at the corresponding length (Edman et al, 1982). Although this phenomenon has been observed consistently in skeletal muscles for more than half century, the underlying mechanism is not yet clear.

The aim of this study was to determine whether residual force enhancement is caused by specific, stretch-induced changes in cross-bridge kinetics. In a previous study, we observed a vastly increased amount of force enhancement in fibers treated with the phosphate release blocker BDM (Rassier and Herzog, 2004). This result was explained with a stretch-induced change of the ratio of weakly-to-strongly-bound cross-bridges towards the strongly bound state. Aside from using BDM, the ratio of weakly-to-strongly-bound cross-bridges can also be biased towards the weakly bound state by lowering temperature (Wang & Kawai, 2001). Therefore, we hypothesized that if force enhancement is associated with a facilitation of transition of weakly to strongly bound cross-bridges, low temperature should produce greater force enhancement than high temperature experiments.

METHODS

Single fibers (n = 11) were dissected from lumbrical muscles of the frog (R. Pipiens) for all experiments. Isolated fibers were suspended between a motor arm and a force transducer inside an experimental chamber filled with Ringer’s solution (pH=7.2). Sarcomere lengths were measured using a laser diffraction technique. After determining the plateau of force-length relationship, an isometric reference contraction was performed at the final length. This was followed by an active stretch of 10% or 15% of optimal fiber length at a speed of 40% optimal fibre length/s. For all tests, contraction duration was 3.5s and stiffness was measured with a step stretch (20µm over 1ms) 0.2ms before deactivation. Experiments were performed at two different temperatures (7 and 20°C). Force enhancement was measured 10ms before the length step for stiffness measurement. Force was normalized to fiber cross-sectional area and stiffness was calculated by dividing normalized force by elongation.

RESULTS AND DISCUSSION

Fiber stiffness in the force-enhanced state was similar to that observed during the isometric reference contractions. Values of force/stiffness, which are assumed to represent the average force per cross-bridge, were significantly greater in the force-enhanced state than in the isometric reference contraction (table1). This result suggests that the increased isometric force following active stretch is caused by an increase in the average force per cross-bridge rather than an increase in the number of attached cross-bridges. The average isometric reference force at 20°C was slightly greater than that measured at 7°C, but the difference was not statistically
significant. Stiffness was significantly increased at 7ºC compared to 20ºC (table1). Force enhancement was significantly greater at 7ºC compared to 20ºC, and correspondingly, the enhancement of ratio of force/stiffness was greater (figure1, table2).

Figure 1: Raw force-time histories of active stretch (solid, S) and isometric reference contraction at the corresponding final length (dashed, I) at 7ºC (A, 18.3% FE) and 20ºC (B, 13.0% FE) temperature.

This result suggests that force enhancement at low temperatures is higher than at high temperatures, because of a bigger proportion of weakly bound cross-bridges at the low temperature and a stretch-induced facilitation of the transition of weakly to strongly bound cross-bridges. This result is consistent with previous results in which BDM was used to bias the ratio of weakly to strongly bound cross-bridges towards the weakly bound state.

SUMMARY/CONCLUSIONS
Force enhancement was greater at low compared to high temperatures, as expected, thereby supporting the hypothesis that force enhancement is associated with a stretch-induced conversion of weakly-to-strongly-bound cross-bridges.

REFERENCES

ACKNOWLEDGEMENTS
Canada Research Chairs Program, CIHR and NSERC of Canada

Table 1: 10% stretch. Force, Stiffness and Force/Stiffness (mean ± SE). *Stretch significantly different from isometric reference contraction, p<.05. † 7 ºC significantly different from 20ºC, p<.05.

<table>
<thead>
<tr>
<th></th>
<th>Force [N/mm²]</th>
<th>Stiffness [N/mm³]</th>
<th>Force/stiffness [mm]</th>
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<tbody>
<tr>
<td></td>
<td>7 ºC</td>
<td>20 ºC</td>
<td>7 ºC</td>
</tr>
<tr>
<td>Iso</td>
<td>0.172±0.017*</td>
<td>0.176±0.015*</td>
<td>7.69±0.60†</td>
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<tr>
<td>Stretch</td>
<td>0.189±0.017*</td>
<td>0.188±0.016*</td>
<td>7.77±0.63†</td>
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Table 2: Force enhancement (FE), Stiffness enhancement (SE) and Force/Stiffness enhancement (F/stiff E) (mean ± SE). # 7 ºC significantly different from 20ºC, p<.05.

<table>
<thead>
<tr>
<th></th>
<th>10% stretch [%]</th>
<th>15% stretch [%]</th>
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<tbody>
<tr>
<td></td>
<td>FE #</td>
<td>SE</td>
</tr>
<tr>
<td>7 ºC</td>
<td>10.43 ± 1.06</td>
<td>1.70 ± 1.09</td>
</tr>
<tr>
<td>20 ºC</td>
<td>6.83 ± 0.61</td>
<td>0.65 ± 1.15</td>
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