Coordinating Muscles and Limbs for Postural Control in the Cat

J. Lucas McKay, Lena H. Ting

1Electrical and Computer Engineering, Georgia Institute of Technology
2Biomedical Engineering, Emory University and Georgia Institute of Technology

Introduction
A recent study from our laboratory demonstrated that muscle activity and force produced during the automatic postural response in cats can be decomposed into a small set of five underlying “functional muscle synergies” (Torres-Oviedo et al. 2006). Each functional muscle synergy specifies both a pattern of hindlimb muscle activation and a correlated “synergy force vector” at the ground. In particular, synergies from the control condition were sufficient to reproduce responses from other biomechanical configurations (anterior-posterior “stance distances”).

Forces produced at these different biomechanical configurations change systematically. At the self-selected “preferred” stance distance, forces are directed diagonally towards and away from the center of mass. At shorter stance distances, a wider range of force directions are observed. Here, we demonstrate that forces produced during the postural response cannot be predicted from biomechanical or energetic considerations alone. We hypothesized that the forces produced during postural response arise due to interlimb coordination of functional muscle synergies across the hindlimbs. Our results suggest neural mechanisms that coordinate redundant muscles and limbs determine postural forces.

Methods
1. Propose two neural controllers to perform an idealized postural task
   - Biomechanically redundant “task”: generate a 1N net force with the hindlimbs.
     - Intertlimb redundancy and muscular redundancy
     - Multiple possible coordination strategies
     - 12 horizontal plane directions
     - Several stance distances

   A priori information: “Internal model” of the force produced by each synergy or muscle
     - One leg shown
     - Shadmehr and Mussa-Ivaldi 1994; Kawato 1999
     - Hypothesized neural controllers: positive least-squares combination of 1) muscle synergy activation vs. 2) individuated muscle activation.
       - e.g., minimize “signal-dependent noise”; Harris and Wolpert 1998

2. Apply the neural controllers to a 3D, static musculoskeletal model of the hindlimbs
   - Relates muscle activation to endpoint force
     - 62 muscles, 14 degrees of freedom at 6 anatomical joints
     - Burkholder and Nichols 2004; McKay et al. 2007
   - Postures based on kinematic data of each cat in each stance distance.

3. Synergy controller: muscle patterns are optimal combinations of synergies
   - Minimize total synergy activation while achieving the postural task, \( \text{F}_{\text{net}} \)
   - Calculate muscle synergies numerically based on experimentally-measured synergy force vectors
   - Cross-validate results with two different criteria
     - “Minimum-noise” Harris and Wolpert 1998
     - “Maximum-force” Valero-Cuevas et al. 1998
   - Resulting synergy force vectors rotate with limb axis, as predicted by Torres-Oviedo et al. (2006).
     - McKay and Ting in review

4. Muscle controller: muscle patterns based on minimizing energetic expenditure

5. Compare predicted force patterns to experimentally-measured postural forces.

Results

<table>
<thead>
<tr>
<th>Frame</th>
<th>MEASURED RIGHT HINDLIMB FORCES</th>
<th>SYNERGY CONTROLLER</th>
<th>MUSCLE CONTROLLER</th>
</tr>
</thead>
<tbody>
<tr>
<td>SHORT</td>
<td>( R^2 = 0.80 )</td>
<td>( R^2 = 0.80 )</td>
<td>( R^2 = 0.11 )</td>
</tr>
<tr>
<td>SHORT</td>
<td>( 0.5 )</td>
<td>( 0.72 )</td>
<td>( 0.72 )</td>
</tr>
<tr>
<td>LONG</td>
<td>( 2.5 ) N</td>
<td>( 0.23 )</td>
<td>( 0.30 )</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Frame</th>
<th>Source Data</th>
<th>Synergy Controller</th>
<th>Muscle Controller</th>
</tr>
</thead>
<tbody>
<tr>
<td>SHORT</td>
<td></td>
<td>Predicts average postural forces well in all postural configurations and perturbation directions, particularly Long stance.</td>
<td></td>
</tr>
<tr>
<td>SHORT</td>
<td></td>
<td>Predicts changes with stance distance associated with “force constraint” behavior.</td>
<td></td>
</tr>
<tr>
<td>SHORT</td>
<td></td>
<td>Regions where the limb is not used are also predicted (i.e., directly lateral in Shortest stance)</td>
<td></td>
</tr>
<tr>
<td>Preference</td>
<td></td>
<td>Predicts average postural forces poorly throughout the workspace.</td>
<td></td>
</tr>
<tr>
<td>Preference</td>
<td></td>
<td>Predicts little or no change with stance distance.</td>
<td></td>
</tr>
<tr>
<td>Preference</td>
<td></td>
<td>Predicts “opposite” diagonal axis in Shortest stance - a fundamentally different postural strategy.</td>
<td></td>
</tr>
</tbody>
</table>

Interpretation
Muscle activation patterns, force coordination patterns are not completely determined by task mechanics – different neural coordination strategies result in markedly different coordination patterns. Is the synergy coordination strategy non-“optimal?” Optimal coordinating synergies results in more energetic expenditure than optimally coordinating muscles. Is there a cost for control? What is the role of homeostatic mechanisms? Should the synergy coordination solution converge to the muscle coordination optimum, e.g., Hoyt and Taylor 1981? 

Proprioceptive reference frames for sensory information may underlie synergy organization. Length and orientation of the limb are important variables (Bosco et al. 2000); synergy force vectors are fixed in this frame and may aid in computation.

References
Burkholder Tj and Nichols Tr. Three-dimensional model of the hind limb. Journal of Biomechanics. 36:219-228, 2004

Acknowledgements
The authors gratefully acknowledge Gelsy Torres-Oviedo for insightful discussions and providing synergy force vector data. Experimental data was courtesy of Jane Macpherson. Funding provided by NIH grant HD46922.