Muscle synergies reflect optimal control of task-level variables during balance

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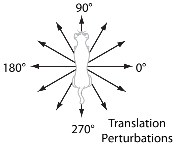
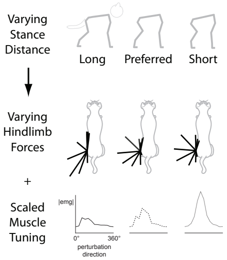
Introduction

Our goal is to understand the biomechanical and neural mechanisms underlying the force constraint strategy during balance tasks in cats [1-3]. When postural perturbations are issued as translations of the support surface, limb forces are elongated away from the center of mass (CoM), independent of the perturbation direction. When the distance between the fore- and hind-feet is shortened, a wider range of force directions is observed. Increased muscle activity is also observed at shorter postural configurations.



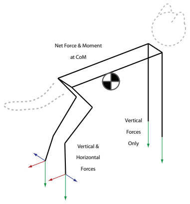
We previously rejected the hypothesis that limb forces during balance reflect limitations in the biomechanical force production capability of the hindlimb, suggesting that limb forces reflect active neural control mechanisms. We showed that a detailed hindlimb model was able to produce forces in any direction, unlike those observed in balance [4]. However, constraining the muscles in the hindlimb model to activate in muscle synergies based on experimental data [5] improved the match to balance forces, suggesting that limb force directions during balance are shaped by active neural control.

Here, we sought to model the active neural control mechanisms of balance, which requires contributions of all four limbs, rather than simply the constraints of an isolated limb. We hypothesized that limb forces and muscle activity during balance reflect an optimal motor solution for task-level control of the CoM with all four limbs. During balance tasks, the nervous system must achieve the task-level goal of controlling the CoM [6, 7]; however, appropriate CoM forces and moments can be produced with many different patterns of muscle activation due to redundancy among the muscles and limbs. The nervous system may resolve this redundancy by optimally controlling muscles to minimize energetic cost [8, 9]. Muscle synergy patterns may also emerge from, or approximate, the optimal control of individual muscles [10, 11].



In a static quadrupedal model, we tested whether task-level of the CoM with either muscles or muscle synergies was able to predict limb forces and muscle tuning observed in different postural configurations.

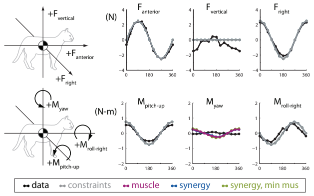
Methods



1. We tested whether task-level control of the CoM in a detailed quadrupedal model was able to predict forces and muscle activity across postural configurations.
    - The model has detailed hindlimbs (static, 31 muscles, 7 DoF, [4]) and abstract forelimbs. CoM height was estimated from morphological parameters.
    - Because forelimb horizontal-plane forces are not always observed in balance tasks [2], the forelimbs were constrained to produce vertical forces only.
2. We predicted forces and muscle activity while constraining CoM forces and moments to values observed in 3 intact cats.
    - 3 or 4 postural configurations for each cats = 11 total.
    - 12 translation perturbation directions; 5 cm amplitude, 15 cm/sec velocity.
3. To approximate "energy," we minimized the activation of either 31 muscles per limb or 5 muscle synergies per limb.
    - Muscle synergy model: e = W•c; e: muscle activation (31D); W: muscle synergy matrix (31D•5D); c: muscle synergy coefficients (5D). Muscle synergies were adapted from experimental force data [4,5].
    - We minimized two cost functions: sum-squared muscle activation (∑e2) or sum-squared muscle synergy activation (∑c2).
4. We compared predicted limb forces quantitatively to experimental data.
5. We tested whether predicted muscle activity exhibited tuning curve scaling with postural configuration.
6. We compared the total energetic cost and simulation time predicted by muscle control and muscle synergy control to each other.

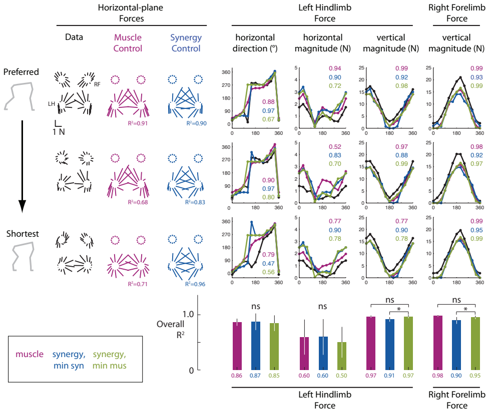
Model predictions vs. Data

Muscle control and muscle synergy control both produced physiological CoM forces+moments across postural configurations.



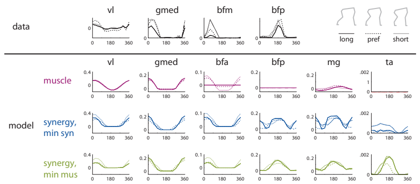
- Muscle synergy control satisfied CoM force + moment constraints in 10/11 postural configurations - shortest postural configuration of cat *Bi* was excluded.
- Because CoM yaw moments are typically of small magnitude (≤ 0.09 N-m) and do not contribute to stabilization of the CoM *per se*, CoM yaw moments were left unconstrained.
- Despite this, simulations produced small net CoM moments: Muscle control: ≤ 0.25 N-m; synergy control: ≤ 0.30 N-m; synergy control/min mus: ≤ 0.42 N-m.

Muscle control and muscle synergy control both predicted hindlimb and forelimb forces across perturbation directions and postural configurations.



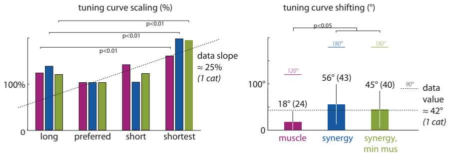
- Pronounced limb force changes with postural configuration were observed in 3/3 cats with muscle synergy control and 2/3 cats with muscle control.

Some flexors active during balance were not recruited by muscle control, but were recruited by muscle synergy control.



- VL,GMED,BFA,SOL (extensor tuning) recruitment: muscle control: (3/3 cats); muscle synergy control: (3/3).
- BFP+GRAC (flexor tuning) recruitment: muscle control: (0/3 cats); muscle synergy control: (3/3).
- TA (flexor tuning) recruitment: muscle control: (0/3); muscle synergy control: (2/3).
- MG (extensor tuning) was always recruited with "flexor" tuning.

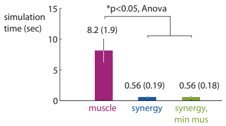
Muscle control and muscle synergy control both predicted increased muscle activity at shorter postural configurations.



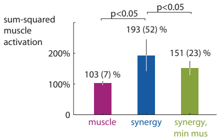
- Predicted muscle activity increased in shorter postural configurations, as in data.
- Some muscle activity increases were observed in long postural configuration, which was only observed in 1/14 recorded muscles.

Muscle control vs. Muscle Synergy control

Muscle synergy control decreased simulation time vs. muscle control.



Muscle synergy control increased energetic cost vs. muscle control.



Conclusions

1. Limb forces during balance in cats reflect a minimum-energy strategy for controlling the CoM with vertical forces at each limb and shear forces at the hindlimbs.
    - This work is the first demonstration of task-level balance control of CoM in a detailed model; previous pendulum models have not attempted to predict limb forces or multidirectional muscle tuning [6, 7].
    - A common neural controller - a single set of CoM force+moment constraints with energetic minimization - was able to predict variations in limb forces with postural configuration. However, unphysiological increases in muscle activity in long postural configuration suggest that some alterations to the neural controller over postural configurations (e.g., scaling of feedback gains) may be required.
    - The nervous system may not need to explicitly minimize yaw moment at the CoM, as optimal forces produced small yaw moments without explicit constraints.
2. A simplified neural control scheme based on muscle synergies can reproduce minimum-energy limb forces during balance.
    - Equivalence of muscle control and muscle synergy control has been demonstrated in various simulated motor tasks [12-14].
3. Flexor activation by muscle synergies suggests that the nervous system may minimize cost functions related to dynamic muscle recruitment during balance.
    - Although we treated the balance task as a static force production task in which extensor deactivation and flexor activation are equivalent, it actually occurs very quickly.
    - Penalizing deactivation time of muscles active in postural tone would encourage flexor activation; rewarding recruitment of muscles with fast fiber type would encourage ankle extensor function of MG.
4. Our results suggest that during balance tasks, the nervous system controls the CoM by optimally recruiting of a small number of muscle synergies, satisfying a tradeoff between energetic cost and computation time.
    - Muscle synergy control may provide faster computation during the time critical balance task. Reduced dimension control has been demonstrated to accelerate simulated motor learning [15].
    - The additional muscle activation required for muscle synergy control may not be physiologically demanding, particularly over of the short duration of the postural response (~1 second).

Acknowledgments

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