SENSORY REGULATION OF MUSCLE ACTIVITY DURING WALKING IN CONSCIOUS CATS

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INTRODUCTION

Our previous work on decerebrate cats suggested that force feedback, originating from Golgi tendon organs (GTOs), makes a substantial contribution to ankle extensor activity accounting for approximately 50% of suprathreshold activity at longer muscle lengths [1]. To test the functional significance, we determined the contribution of force feedback to muscle activity during walking in conscious cats with intact central nervous systems.

METHODS

We trained 2 cats to walk on a pegway that could be adjusted to different slopes (Figure 1; +25, +10, 0, -10, -25 degrees). One peg measured ground reaction force. Video analysis yielded joint kinematics. To isolate the MG muscle, other major ankle extensors (LG, Sol, and Pl) were denervated 4 days prior to data collection. Implanted EMG electrodes measured muscle activity. Using inverse dynamics and moment-arm measurements, we estimated MG force, length, and velocity. The estimates allowed the use of mathematical models [2] to predict muscle spindle (Ia and II afferents) and GTO activity (Ib afferents).

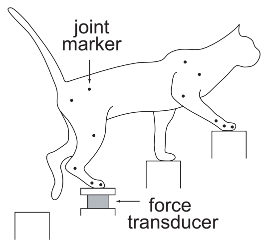

Figure 1:

RESULTS AND DISCUSSION

As expected, greater slopes resulted in increased muscle activity and force at longer muscle lengths during stance (Figure 2). Due to this increase in force, predicted Ib activity increased strongly with length. Predicted Ia and II activity, however, was nearly independent of length because muscle velocity decreased at longer muscle lengths. This suggested that changes in muscle activity were due primarily to force feedback allowing the use of a simple model of the neuromuscular system to estimate the pathway loop gain ($K{\cdot}M$; Figure 3). This gain ranged from ~0.2 at short muscle lengths to ~0.6 at longer muscle lengths demonstrating that force feedback was of modest importance downhill, accounting for 20% of total activity and force, and of substantial importance uphill, accounting for 60%. This length dependence was due to the intrinsic force-length property of muscle, *M*. The gain of the pathway that converts muscle force to motoneuron depolarization, *K*, was independent of length. These findings emphasize the general importance of feedback in generating ankle extensor activity during walking in the cat and suggest the intriguing possibility that feedback automatically compensates for changes in slope without requiring different descending commands.

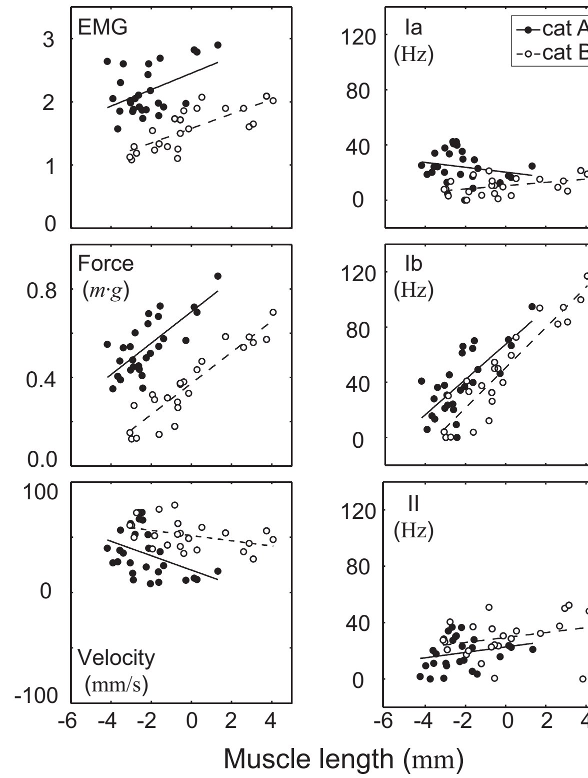

Figure 2: Relationship between muscle length and muscle activity, force, velocity, and predicted proprioceptor activity during stance. A positive velocity denotes a lengthening muscle. Symbols represent the average value over 50 ms beginning 50 ms after ground contract. Lines are best-fit linear regression lines.

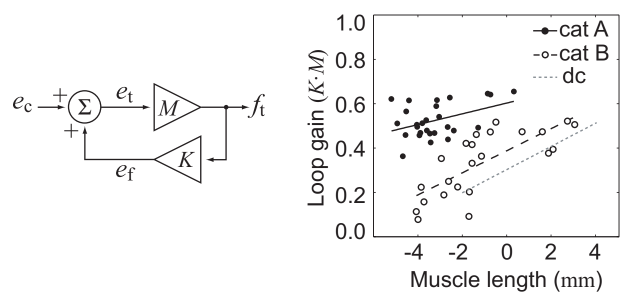

Figure 3: Left: Force feedback model. Total muscle activity, e_t, and force, f_t, are measured variables. e_c, the central contribution to e_t, was estimated as the y-intercept of the regression line for the relationship between e_t and f_t. We solved for the remaining variables. Right: Relationship between loop gain and muscle length. Symbols represent the average values and lines represent linear regressions. The dotted line shows that previous decerebrate experiments yielded similar results to current findings.

REFERENCES

1. Donelan JM, et al.. *J Neuro Physiol* **92**, 2093-2104, 2004.
2. Prochazka A. *Prog Brain Res* **123**, 133-142, 1999.