



Muscle contributions to propulsion and braking during walking and running: Insight from external force perturbations



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ABSTRACT

There remains substantial debate as to the specific contributions of individual muscles to center of mass accelerations during walking and running. To gain insight, we altered the demand for muscular propulsion and braking by applying external horizontal impeding and aiding forces near the center of mass as subjects walked and ran on a treadmill. We recorded electromyographic activity of the gluteus maximus (superior and inferior portions), the gluteus medius, biceps femoris, semitendinosus/membranosus, vastus medialis, lateral and medial gastrocnemius and soleus. We reasoned that activity in a propulsive muscle would increase with external impeding force and decrease with external aiding force whereas activity in a braking muscle would show the opposite. We found that during walking the gastrocnemius and gluteus maximus provide propulsion while the vasti are central in providing braking. During running, we found that the gluteus maximus, vastus medialis, gastrocnemius and soleus all contribute to propulsion.

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1. Introduction

Steady state walking and running involve first braking and then propulsion during each stance phase. Numerous researchers have studied how individual muscles contribute to whole body braking/propulsion, yet substantial disagreement regarding the specific roles of different muscles remains (Table 1).

Early seminal studies focused on correlating measured ground reaction force (GRF) with the timing and amplitude of electromyographic activity (EMG). These studies generally found that during walking the ankle plantarflexors [reviewed in [7]] and the gluteus maximus provided propulsion [1]. Running studies generally attribute propulsion first to the soleus and gastrocnemius but also to the gluteus maximus, hamstrings and vasti [1,16,17,20,21]. However, temporal correlation is not causation; an individual muscle may provide braking impulse even when net GRF is propulsive. Another complication is electromechanical delay, i.e. activation precedes muscle force development which persists

long after activation has diminished. The onset delay is ~30 ms and the relaxation time can be up to 300 ms [23].

More recently, computer simulation studies have quantified the individual muscular contributions to the GRF. Simulation has the advantage of cleanly parsing individual muscular contributions to GRF using measured kinematics and can be adapted to include complex muscle parameters. In walking, simulation studies agree the ankle extensors contribute to propulsion during the second half of stance [3,4,8,12], and some have also found minor contribution to braking in the first half of stance by one or both plantarflexors [4,6,8,12]. The vasti are thought to produce braking forces [e.g. 6,8,9,11]. In running, modeling studies suggest that the hamstrings and plantarflexors primarily produce forward acceleration [8,22]. With numerous muscles acting about any given joint, infinite possible muscle activation patterns can drive any given motion. Because of subtle implicit assumptions in the modeling process (tendon slack and fiber lengths) musculoskeletal models may not distinguish between solutions for the independent roles of muscles acting across the same joint. For example, substantial debate remains about the functions of the hamstrings and gluteals at the hip [6,8,9,11,12].

Changing speed and incline are common natural perturbations to propulsion and braking demand. Faster walking speeds are associated with overall larger horizontal GRF's, presumably

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Table 1

Review of literature on propulsion and braking during walking and running. Green represents propulsion while red represents braking. ↑ indicates a finding that the muscle contributes to propulsion. ↓ indicates a finding that the muscle contributes to braking. ○ indicates a finding that the muscle does not contribute to propulsion/braking (i.e. “we find that the hamstrings did not contribute to propulsion”). Data from the present study includes only our findings regarding muscles primary actions.

Walking	GMax	GMed	Vasti	Ham	Sol	Gas
[1] Stern et al. 1980	↑					
[2] Yang and Winter 1983			○	○	↑	↑
[3] Kepple et al. 1997			↑		↑	
[4] Pandy 2001				↓	↑	↓
[5] Gottschall and Kram 2002					○	↑
[6] Neptune et al. 2004	↑ ↓		↓	↑	↑	↓
[7] Rose and Gamble 2005					↑	↑
[8] Sasaki and Neptune 2006	↑ ↓	○	↓	↑	↑ ↓	↑
[9] Liu et al. 2006	↓	↑		○	↑	↑
[10] Lay et al. 2007	○		○	○	↑	↑
[11] Liu et al. 2008	↓	↑	↓	↑	↑	↑
[12] Neptune et al. 2008	○		○	○	↑ ↓	↑
[13] McGowan et al. 2009	↑	○	↑	○	↑	○
[14] Peterson et al. 2011	↓		↓	↑	↑ ↓	↓
[15] Franz et al. 2013	↑		↑	↑	↑	↑
Ellis et al. 2014	↑ ○	○ ○	↓ ○	○ ○	○ ○	↑ ○

Running	GMax	GMed	Vasti	Ham	Sol	Gas
[16] Winter 1983 (b)	↑				↑	↑
[17] Simonsen et al. 1985	↑		↑	↑	↑	↑
[18] Ounpuu et al. 1990			↑		↑	
[19] Montgomery et al. 1994	○		↑	○	○	○
[20] Novacheck et al. 1998	↑	↑	↑	↑	↑	↑
[21] Lieberman et al. 2006	↑			↑		
[8] Sasaki and Neptune 2006	↑ ↓	○	↓	↑ ○	↑ ↓	↑ ↓
[22] Hamner et al. 2010	○	↑	↓	↑ ○	↑	↑
Ellis et al. 2014	↑ ○	○ ○	↑ ○	○ ○	↑ ○	↑ ○

requiring additional muscular force. Studies that varied speed and cadence during walking have shown that the quadriceps and plantarflexors produce propulsion [2,14]. Peterson et al. [14] also suggested that the gluteus maximus and the plantarflexors contribute to braking in early stance. During inclined locomotion, a component of gravity acts parallel to the ground, which must be overcome through additional muscular action. Studies of uphill walking have found heightened activity of the ankle extensors indicating their role in propulsion [10,15]. However, these natural perturbations remain imperfect tests because changing speed and grade are tied to the kinematic need to step up the slope or to step more quickly.

Experimenters have also directly manipulated the need for propulsion and braking [5,13,24]. These artificial perturbation experiments allow researchers to attribute changes in muscle activity to altered propulsive demand. McGowan et al. [13] applied waist weights while lifting subjects vertically, effectively increasing the need for muscular acceleration/deceleration without changing the demand for weight support. They then used a computer simulation to calculate the net horizontal work produced by each leg muscle, finding that the soleus contributes more net horizontal trunk work than all of the other studied leg muscles combined. One challenge with this approach is that a change in body mass alters the need for both propulsion and

braking. Previously, Gottschall and Kram [5] applied near-constant horizontal aiding and impeding forces at subject's center of mass (CoM). They showed that the gastrocnemius produces propulsive accelerations during normal walking, with the soleus contributing when there is a heightened demand. This approach can be critiqued because it creates an artificial forward or backward pitching moment about the ankle. However, their results are similar to up and downhill walking studies, where no artificial pitching moment is present [10,15].

Here, we used the same artificial experimental perturbation as Gottschall and Kram [5], extending their work to comprehensively address nine candidate leg muscles during both walking and running. We reasoned that muscles creating propulsive forces would increase in activity when external horizontal impeding forces were applied to the body and decrease in activity when external horizontal aiding forces were applied. Similarly, muscles contributing to braking would decrease in activity with external impeding force and increase in activity with external aiding force.

Additionally, many previous studies have focused on muscular action in normal locomotion [e.g. 6,11,22]. We hope to go further and distinguish between primary and supplemental propulsive/braking action. We define a muscle as primarily propulsive/braking if it provides that action during normal, unperturbed locomotion. We expected to gain the most insight from slight aiding conditions where muscular effort is reduced below normal. We consider an increase in EMG under slightly aiding conditions as indicating that a muscle provides primary braking while a decrease indicates that a muscle provides primary propulsion. In contrast, a muscle that provides supplemental action will increase in activity selectively at higher aiding or impeding forces. Such recruitment might parallel natural activation during higher demand situations such as when accelerating or moving up or downhill.

We hypothesized that the gastrocnemius and soleus are the primary muscles that contribute to propulsion during walking while the vasti (e.g. vastus medialis) are primarily responsible for braking. We further hypothesized that the gluteus maximus, hamstrings, gastrocnemius and soleus all provide propulsion during running and that the vasti provide braking.

2. Methods

2.1. Subjects

Ten healthy, physically active individuals volunteered for this study (5 M/5 F, age 26 ± 5 years, height 1.73 ± 0.06 m, mass 66 ± 9 kg, mean ± 1 SD) as per the Institutional Review Board of the University of Colorado Boulder.

2.2. Protocol

Each subject first warmed up by walking on a treadmill for 5 min at 1.25 m/s. They then performed six experimental conditions first at a walk (1.25 m/s) and then a run (3 m/s). The experimental protocol began and ended with normal walk and normal run trials. Between the normal walk/run pairs, subjects completed four perturbation conditions in a random order, each of which involved external impeding or aiding forces. The perturbation conditions were 10% body weight (BW) impeding (10I), 5% BW impeding (5I), 5% BW aiding (5A), 10% BW aiding (10A). All trials were 1 min in duration.

2.3. Horizontal pulling apparatus

Our pulling apparatus was similar to that of Gottschall and Kram [5] (Fig. 1). It applied a nearly constant horizontal force to the

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