Variability of neural activation during walking in humans: short heels and big calves


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People come in different shapes and sizes. In particular, calf muscle size in humans varies considerably. One possible cause for the different shapes of calf muscles is the inherent difference in neural signals sent to these muscles during walking. In sedentary adults, the variability in neural control of the calf muscles was examined with muscle size, walking kinematics and limb morphometrics. Half the subjects walked while activating their medial gastrocnemius (MG) muscles more strongly than their lateral gastrocnemius (LG) muscles during most walking speeds (‘MG-biased’). The other subjects walked while activating their MG and LG muscles nearly equally (‘unbiased’). Those who walked with an MG-biased recruitment pattern also had thicker MG muscles and shorter heel lengths, or MG muscle moment arms, than unbiased walkers, but were similar in height, weight, lower limb length, foot length, and exhibited similar walking kinematics. The relatively less plastic skeletal system may drive calf muscle size and motor recruitment patterns of walking in humans.

Key words: neural control; walking; heel length; medial gastrocnemius; humans

1. INTRODUCTION

Calf muscle size can vary greatly between individuals [1]. Some people have short, stout lower leg muscles, while others have long, slender leg muscles. A possible cause for these differences in calf muscle size is the difference in neural signals received by the muscles, because muscles respond to increased neural activation with hypertrophy [2]. These individuals would also generate relatively higher muscle forces when walking, since muscle force increases with amplitude of muscle activity [2,3]. Despite consistent kinematic patterns during walking, some variability exists in neural control patterns among individuals [4–8]. Generally, the differences in neural control patterns occur primarily in signal amplitude rather than in signal timing. For this study, we examine the relationship between the variability in the neural activation or motor recruitment pattern of walking, leg muscle size and skeletal morphology in healthy adults. We examine sedentary subjects to ensure that athletic training did not affect the inherent motor recruitment pattern of walking.

Furthermore, walking is a behaviour that nearly everybody can do well. In the current study, we hypothesize that individuals who recruit their muscles more strongly will have shorter heels without differences in kinematic patterns. Subjects with shorter heels will also have larger calf muscles, because those who recruit their muscles more strongly presumably generate higher forces in those muscles [2,3]. These higher forces correspond to shorter heels owing to the trade-off between force (F) and moment arm (r) to generate the given muscle moment or torque (M) needed about the ankle during walking (M = F · r). Similar to pulling a door closer to its hinge, the ankle must be extended by a greater force when muscles pull closer to the joint with a shorter heel.

2. MATERIAL AND METHODS

Five male and five female adults (ages 18–33, mean = 20.5 yrs; weight, 60.7 ± 9.0 kg; height, 1.69 ± 0.08 m) of normal body mass index (21.7 ± 1.6), who did not exercise regularly, volunteered for the study. The subjects walked barefoot on a motorized treadmill at five speeds (0.3, 0.6, 0.9, 1.2 and 1.5 m s⁻¹). Subjects walked for 2 min at a randomly selected speed before a 25 s recording period. All experiments were conducted in accordance with the IRB of Harvey Mudd College.

Motor recruitment patterns of the lower leg muscles were recorded using surface electromyography (sEMG; A-M Systems model 1800). Ultrasound determinations of muscle length and width were used to place the bipolar electrodes at the same location for each subject ([4] SENIAM). The sEMG signals were amplified 100× and filtered from 10 to 500 Hz with an amplifier (A-M Systems model 1800). Signals from the amplifier were acquired at 2500 Hz on a PC computer. The recordings were filtered in MATLAB with a second-order Butterworth band-pass filter from 20 to 400 Hz. Amplitudes of the sEMG signals were normalized relative to each subject’s maximum voluntary contraction (MVC) during standing calf raises. Amplitude values were obtained by finding the maximum average of a 10 ms period during the major burst for each stride at each speed. Burst durations were determined from an ensemble average generated from 4 to 12 complete strides from each speed [5,8]. Muscle bias equalled medial gastrocnemius (MG) amplitude (%MVC) divided by the sum of the MG and lateral gastrocnemius (LG) amplitudes (%MVC). Individuals were denoted ‘MG-biased’ if their bias values exceeded 0.67 during three or more of the five speeds. ‘Unbiased’ subjects walked with nearly equal amplitudes of their MG and LG muscles (bias = 0.34–0.66) at most speeds.

Morphological measurements of the three calf muscles were made using a B-mode, real-time ultrasound machine (Medasonics, 210DX; 7.5 MHz linear transducer, figure 1a,b; [9–11]). The effective mechanical advantage (EMA) of each subject’s right foot was determined by dividing the heel length, or in-lever of the calf muscles, (r) by the out-lever arm of the foot (R, figure 1c). Lengths between the lateral malleolus (LM), medial malleolus (MM) and posterior surface of the calcaneal (or Achilles) tendon were used to geometrically calculate r. R equalled the average lengths between LM and the fifth metatarsophalangeal (MTP) and MM to the first MTP (figure 1c).

The kinematics, or joint angle patterns, during walking were determined using three high-speed cameras (Oqus, 125 Hz) and a Qualysis Motion Capture System. Seven 2 cm reflective markers were attached to the right side of each subject centered at the first MTP, fifth MTP, LM (ankle), lateral condyle of the femur (knee), lateral center of rotation of the hip, iliac crest and the axis of rotation of the shoulder. Morphometrics of the limb were obtained using these same anatomical landmarks.

Statistics included unpaired t-tests to compare between MG-biased and unbiased groups and general linear models (GLM) corrected for height, weight and foot length to grade-predict (SAS Institute, Inc.). Differences were significant when p < 0.05. All data were calculated as mean ± s.d.

3. RESULTS

The sedentary subjects used one of two types of motor recruitment patterns in their triceps surae complex during walking (figure 2). Half of the subjects used an MG-biased recruitment pattern during which they...
activated their MG more strongly relative to their LG muscles during walking (figure 2a; n = 5). The other five subjects used an unbiased recruitment pattern activating their MG and LG muscles equally during walking (figure 2b). As subjects walked faster, motor recruitment patterns of the calf muscles for all subjects became less biased (figure 2c). MG amplitude did not differ between the MG-biased group (e.g. 53 ± 25%MVC at 0.9 m s\(^{-1}\)) and the unbiased group (37 ± 11%MVC). LG amplitudes were also similar between the MG-biased group (e.g. 21 ± 15%MVC at 0.9 m s\(^{-1}\)) and the unbiased group (29 ± 13%MVC). Muscle bias, or the relative amplitude of MG to LG muscles, however, was 30 per cent greater for the MG-biased walkers (average = 0.74 ± 0.06) than for unbiased walkers (0.57 ± 0.06; figure 2c; p = 0.001). Moreover, soleus (SOL) amplitudes did not differ among individuals. Finally, the MG-biased group generated shorter LG motor patterns relative to the unbiased group, even though the MG timing parameters did not differ. In summary, MG:LG duration in the MG-biased group (average = 1.80 ± 0.54) exceeded that of the unbiased group (average = 0.95 ± 0.08) by 90 per cent. Longer activation of the MG muscle correlated positively with MG-bias (GLM p = 0.008) during walking.

Normalized MG muscle size (MG thickness/lower leg length) in MG-biased walkers (0.060 ± 0.006) was 14 per cent larger than in unbiased walkers (0.051 ± 0.003; t-test p = 0.01). Relative LG and SOL sizes in MG-biased walkers did not differ from unbiased walkers. Pennation angle in all three muscles did not differ between the MG-biased and unbiased groups of walkers (figure 1b). By contrast, total muscle size, or the sum of the relative MG, LG, and SOL thicknesses, of the MG-biased walkers (0.150 ± 0.021) exceeded that of the unbiased walkers (0.129 ± 0.011) by 14 per cent. Stronger MG activation correlated with larger calf muscles (GLM p = 0.009; figure 2d).

Relative heel length (r/R), or EMA [12], of the MG-biased walkers (0.26 ± 0.02) was 24 per cent shorter than that of the unbiased walkers (0.32 ± 0.07; p < 0.05; figure 1c). In absolute terms, the in-lever arm of the calf muscles (r) in MG-biased walkers (3.31 ± 0.26 cm) was 25 per cent shorter than in unbiased walkers (4.14 ± 0.92 cm). By contrast, the out-lever arm of the foot (R) between the MG-biased group (13.04 ± 1.19 cm) and the unbiased group (13.10 ± 0.26 cm) did not differ. A shorter heel correlated with stronger relative neural activation signals (GLM p = 0.01; figure 2d).

Despite the differences in motor recruitment patterns, relative MG muscle size, and relative heel length, all kinematic measures, including adduction/abduction of the foot, and all other morphometric measures were similar between the two groups of walkers. Specifically, height, weight, leg length, lower leg length and foot length did not differ between the two types of walkers.

4. DISCUSSION

Few researchers have investigated the relationship between heel length, or EMA, and neural control, muscle size and the kinematics in humans during walking. Within an individual, ankle EMA does not vary with speed during walking [13], but shorter heels among elite runners correlate with better running economy [14,15]. During walking, if we assumed that the same torque is required about the ankle joint, shorter heels would require the generation of larger ankle extensor, or plantarflexor, forces. Additionally, to generate the same work at the ankle, a shorter heel would result in less muscle shortening and require even higher forces. In order to generate these higher forces at the ankle, these individuals activate their relatively thicker muscles for a longer
duration. Analogous to pulling a door, simple mechanics can explain the differences in calf muscle size among individuals. MG-biased walkers with shorter heels pull the door closer to the hinge, requiring higher forces from a larger MG muscle. Whereas, unbiased walkers pull the door farther from the hinge requiring lower forces from a smaller MG muscle.

Different people may have different activity pattern generators for walking because the biomechanics of their ankles differ. These findings may provide insight into the degree of plasticity in motor patterns to accommodate changes in demand and to resolve the determinants of the variability in muscle size and neural activation in humans. Understanding the variability in the motor recruitment patterns, muscle size, and biomechanics of walking in humans may help to guide the understanding of human gait disorders and their treatment.

All experiments were conducted in accordance with the IRB of Harvey Mudd College (HMC).

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**Figure 2.** (a,b) Representative motor recruitment patterns, or sEMG recordings, of the MG (black, upper), LG (blue, middle), and SOL (red, lower) muscles of an (a) MG-biased subject and (b) an unbiased subject walking at 0.9 m s⁻¹. (c) Muscle bias at all walking speeds. Individuals were denoted ‘MG-biased’ (open symbols) if their bias values exceeded 0.67 at most speeds. ‘Unbiased’ (closed symbols) subjects walked with nearly equal amplitudes of their MG and LG muscles (bias = 0.33–0.66) at most speeds. Each symbol type represents an individual (n = 10). (d) Relative heel length (squares) and relative MG thickness (pluses) vary with average bias. Heel length (r/R) decreases with average bias. The solid line represents the linear regression, heel length = 0.545 - 0.393 × bias (r² = 0.51; p = 0.01), while the dashed line represents the linear regression, relative MG thickness = 0.031 + 0.038 × bias (r² = 0.39; p = 0.009).


