Motor Patterns in Human Walking and Running

G. Cappellini,1 Y. P. Ivanenko,1 R. E. Poppele,2 and F. Lacquaniti1,3,4

1Department of Neuromotor Physiology, Scientific Institute Foundation Santa Lucia, Rome, Italy; 2Department of Neuroscience, University of Minnesota, Minneapolis, Minnesota; and 3Department of Neuroscience and 4Centre of Space Bio-medicine, University of Rome Tor Vergata, Rome, Italy

Submitted 24 January 2006; accepted in final form 1 March 2006

Cappellini, G., Y. P. Ivanenko, R. E. Poppele, and F. Lacquaniti. Motor patterns in human walking and running. J Neurophysiol 95: 3426–3437, 2006; doi:10.1152/jn.00081.2006. Despite distinct differences between walking and running, the two types of human locomotion are likely to be controlled by shared pattern-generating networks. However, the differences between their kinematics and kinetics imply that corresponding muscle activations may also be quite different. We examined the differences between walking and running by recording kinematics and electromyographic (EMG) activity in 32 ipsilateral limb and trunk muscles during human locomotion, and compared the effects of speed (3–12 km/h) and gait. We found that the timing of muscle activation was accounted for by five basic temporal activation components during running as we previously found for walking. Each component was loaded on similar sets of leg muscles in both gaits but generally on different sets of upper trunk and shoulder muscles. The major difference between walking and running was that one temporal component, occurring during stance, was shifted to an earlier phase in the step cycle during running. These muscle activation differences between gaits did not simply depend on locomotion speed as shown by recordings during each gait over the same range of speeds (5–9 km/h). The results are consistent with an organization of locomotion by recordings during each gait over the same range of speeds (5–9 km/h). The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

INTRODUCTION

Walking and running are generally considered as distinct gait modes with strikingly different mechanics and energetics. Humans change gait to increase locomotion speed while saving energy. Thus oxygen consumption is lower for walking than for running below the transition speed, whereas it is higher above this speed (Margaria 1976). In walking, the body vaults up and over each stiff leg in an arc, analogous to an inverted pendulum (Cavagna et al. 1976) (Fig. 1A). Kinetic energy in the first half of the stance phase is transformed into gravitational potential energy, which is partially recovered as the body falls forward and downward in the second half of the stance phase. Running, instead, is analogous to bouncing on a pogo stick (Full and Koditschek 1999; Raibert 1986) (Fig. 1A). As a leg strikes the ground, kinetic and gravitational potential energy is temporarily stored as elastic strain energy in muscles, tendons, and ligaments and then is nearly all recovered during the propulsive second half of the stance phase. The walking gait may also be defined by the existence of a double support phase during stance, whereas running has a “flight” phase during which neither limb is in ground contact.

Walking and running are the two most common forms of human gait. Although they share some basic kinetics and kinematics, the two gaits are also distinctly different so the transition from walking to running is obvious. In fact, both kinematics and kinetics change abruptly in going from a walking gait to a running gait (Hreljac 1993; Minetti et al. 1994; Nilsson et al. 1985). For example, the gait transition is accompanied by an abrupt decrease in ground contact time by ~35% and an ~50% increase in peak ground reaction force. There are also a number of gait parameters that change monotonically with increasing speed during both walking and running, including increased step length and cycle duration and decreased stance duration (Nilsson et al. 1985). Many of these changes are associated with increasing intensity of muscle activation (Ivanenko et al. 2006; Prilutsky and Gregor 2001; Winter and Yack 1987).

The mechanisms that underlie the changes associated with speed and gait changes are still not well understood. In general, the mechanics of locomotion and the associated muscle activity have been more thoroughly studied in the human than has the neural control. For the latter, we must rely largely on extrapolations from animal models. A number of experimental findings from animals and humans suggest that different locomotion patterns may result primarily from peripheral factors, like muscle performance or sensory feedback (Pearson 2004; Smith et al. 1993) and/or by a reconfiguration of the neural network (Gillis and Biewener 2001; Grillner 1981) or by modulating the parameters of a basic network (Collins 2003; de Leon et al. 1994; Golubitsky et al. 1999; Grillner and Zangger 1979; Orlovsky et al. 1999; Pribe et al. 1997).

An important result from the animal studies was the demonstration that the entire range of speeds and locomotion gaits can be generated in the cat by varying only the intensity of stimulation of the mesencephalic locomotor region (MLR) (Mori et al. 1989; Shik 1983; Shik et al. 1966). The gait determined by this “central command” was automatically adapted to the external conditions (such as slope of the road or body loading) by “peripheral” mechanisms. Increasing only the strength of the MLR stimulation could increase the speed of forward progression, and at stronger stimulation levels, the animal changed the locomotion gait from out-of-phase coordination (walk or trot) to in-phase coordination (run or gallop). Areas anatomically similar to the MLR in the cat have also
been found to serve a similar function in fish, reptiles, birds, and primates (Jordan 1991; Mori et al. 1996).

The question remains, however, as to whether this descending control modulates a basic “motor program” for walking and running (for instance, a set of nonlinear oscillators with bifurcations at critical transitional points) or a separate set of oscillators for each distinct gait. In either case, a gait transition might be subject to feedback concerning critical peripheral factors. A recent line of investigation relevant to the neural generation of locomotor patterns is based on the identification of elementary units of muscle activation (Bizzi et al. 1991, 2002; Davis and Vaughan 1993; d’Avella and Bizzi 2005; Giszter et al. 2001; Hart and Giszter 2004; Hultborn 2001; Ivanenko et al. 2003; Kargo and Giszter 2000; Patla et al. 1985; Ting and Macpherson 2005; Tresch and Bizzi 1999). According to this approach, locomotor programs may be considered as a set of characteristic timings of muscle activation (Ivanenko et al. 2005). In fact, the same five basic activation components can account for the electromyographic (EMG) waveforms of 32 ipsilateral leg, trunk, and shoulder muscles during walking at speeds between 1 and 5 km/h (Ivanenko et al., 2004b). The same five components were also present when walking was combined with various voluntary motor tasks that required significantly different muscle usage (Ivanenko et al., 2005). If there is a common set of oscillators for walking and running, we might anticipate that muscle activation during running might also be accounted for, at least in part, by the same basic muscle activation components. If, however, separate sets of oscillators underlie the different gaits, we might expect that this would be associated with distinctly different timings of muscle activation. Although the analysis of individual EMG patterns of human running has been performed in numerous studies (see Prilutsky and Gregor 2001), the underlying common structure of the motor output has not been previously investigated.

Therefore the aim of this study was to examine how muscle activation depends on locomotion speed and on locomotion gait. The experimental design was to record kinematics and EMG activity from human subjects as they either walked or ran on a treadmill at each of several different speeds. We used statistical methods incorporating a linear decomposition of the EMG data to determine the general design of the motor output in walking and running.

**METHODS**

**Subjects**

Eight healthy subjects [6 males and 2 females, between 26 and 44 yr of age, 69 ± 10 kg (mean ± SD), 1.75 ± 0.07 m] volunteered for the experiments. All subjects were right-leg dominant. The studies conformed to the Declaration of Helsinki, and informed consent was obtained from all participants according to the procedures of the Ethics Committee of the Santa Lucia Institute.

**Experimental setup**

Subjects walked or ran on a treadmill (EN-MILL 3446.527, Bonte Zwolle BV, Netherlands) at different controlled speeds (3–12 km/h). They were asked to swing their arms normally and to look straight ahead. Subjects walked with their shoes on. Before the recording session, subjects practiced for a few minutes in walking and running on the treadmill at different speeds. In a standard protocol, subjects were asked to walk at 3, 5, 7, and 9 km/h and to run at 5, 7, 9, and 12 km/h so that we could compare walking and running at the same speeds (5, 7, and 9 km/h).

We also used a computer-controlled speed program that linearly increased and then decreased treadmill speed between 1 and 12 km/h to observe the recorded parameters during continuous speed changes (ramp speed condition, acceleration, and deceleration was set to 0.4 km · h⁻¹ · s⁻¹). Three subjects participated in this experiment. They were instructed to follow the changes in speed by remaining in place with respect to the treadmill when the belt velocity was changing. We also recorded during overground walking [at 5.6 ± 1.1 (SD) km/h] and running (9.6 ± 0.9 km/h). This allowed us to calculate the moments of forces (see following text) by asking subjects to step on a force plate located in the middle of a 7-m walkway.

**Data recording**

We recorded kinematic data bilaterally at 100 Hz by means of the Vicon-612 system (Oxford, UK) with nine TV cameras spaced around the walkway. Infrared reflective markers (diameter: 1.4 cm) were attached on each side of the subject to the skin overlying the following landmarks: gleno-humeral joint (GH), the midpoint between the anterior and the posterior superior iliac spine (ilium, IL), greater trochanter (GT), lateral femur epicondyle (LE), lateral malleolus.
(LM), heel (HE), and fifth metatarso-phalangeal joint (VM). The spatial accuracy of the system is better than 1 mm (root mean square). We recorded electromyographic activity by means of surface electrodes from 32 muscles simultaneously on the right side of the body. We used active Delsys electrodes (model DE2.1, Delsys, Boston, MA) applied to lightly abraded skin over the respective muscle belly. The signals were amplified (×10,000), filtered (20–450 Hz; Bagnoli 16, Delsys), and sampled at 1,000 Hz. Sampling of kinematic, force platform, and EMG data were synchronized.

The following 32 muscles were recorded from all eight subjects: tibialis anterior (TA), flexor digitorum brevis (FDB), gastrocnemius lateralis (LG), gastrocnemius medialis (MG), soleus (SOL), peroneus longus (PERL), vastus lateralis (Vlat), vastus medialis (Vmed), rectus femoris (RF), sartorius (SART), biceps femoris (long head, BF), semitendinosus (ST), adductor longus (ADD), tensor fascia latae (TFL), gluteus maximus (GM), gluteus medius (Gmed), external oblique (OE), internal oblique (OI), latissimus dorsi (LD), iliopectineus (ILIO), rectus abdominis, superior portion (RAS), erector spinae recorded at T1, T9, and L2 (EST1, EST9, ESL2, respectively), biceps brachii (BIC), triceps brachii (TRIC), deltoideus, anterior and posterior portions (DELTA and DELTP, respectively), trapezius, inferior and superior portions (TRAPS and TRAPI, respectively), sternocleidomastoideus (STER), and splenius (SPLE). Electrode placement for the erector spinae muscle was 2 cm lateral to the spinous process, for SOL—about 2 cm distal to the medial head of the gastrocnemius, for RAS—about 3 cm lateral of the umbilicus (also see Winter 1991). Before the electrodes were placed, the subject was instructed about how to selectively activate each muscle (Kendall et al. 1993), while EMG signals were monitored, so as to optimize the EMG signal and minimize cross-talk from adjacent muscles during isometric contractions.

During overground locomotion, we also recorded the ground reaction forces \( F_x, F_y, \) and \( F_z \) under the right foot at 1,000 Hz by a force platform \((0.9 \times 0.6 \text{ m}, \text{Kistler 9287B, Zurich, Switzerland})\). At the end of the recording session, we made anthropometric measurements on each subject. These included the mass and stature of the subject, the length and circumference of the main segments of the body (Zatsiorsky et al. 1990).

Data analysis

BIOMECHANICAL ANALYSIS. The gait cycle was defined with respect to the right leg movement, beginning with right foot contact with the surface (touch-down). The body was modeled as an interconnected chain of rigid segments: IL-GT for the pelvis, GT-LE for the thigh, LE-LM for the shank, and LM-VM for the foot. For walking and running, the gait cycle was defined as the time between two successive foot contacts of the right leg corresponding to the local minima of the HE marker. The timing of the lift-off was determined analogously (when the VM marker elevated by 3 cm). The touch-down and lift-off times were used to verify the time plate recordings (when the vertical ground reaction force exceeded 7% of the body weight), and we found that the kinematic criteria we used predicted the onset and end of stance phase with an error <2% of the gait cycle duration (see also Borghese et al. 1996). The data were time-interpolated over individual gait cycles on a time base with 200 points.

EMG-ANALYSIS. Raw data were numerically rectified, low-pass filtered with a zero-lag Butterworth filter with cutoff at 10 Hz, time-interpolated over a time base with 200 points for individual gait cycles and averaged. Each trial for a given speed included ≥10 consecutive gait cycles (typically 15).

Joint moments of force

For the overground locomotion records, the moments of forces (with extensor moments being positive) at the ankle, knee, and hip joints of the right leg were calculated using measured kinematics, force plate data, anthropometric data taken on each subject, and the traditional Newton-Euler inverse dynamics model (Bresler and Frankel 1950). The moments were normalized to the body mass.

Factor analysis

We applied a principal component analysis (PCA) to each of several data sets consisting of normalized EMG patterns over a step cycle. Factor analysis (FA) used here has been thoroughly described in our previous papers (Ivanenko et al. 2003, 2004b, 2005). Briefly, the steps involve calculation of the correlation matrix, extraction of the initial principal components (PCs), application of the varimax rotation, calculation of factors scores (referred to as temporal activation components in the text), factor loadings (weighting coefficients across muscles), and percent of variance accounted for (PV) by each temporal component in the total data set. The aim of FA is to represent the original EMG data set \( E \) as \( t \) matrix, where \( m \) the number of muscles and \( t = 200 \) for all conditions because EMG data were time-interpolated over individual gait cycles to fit a normalized 200-point time base) as a linear combination of \( n \) basic temporal components \( E = W C + \text{residual} \), where \( W \) are weighting coefficients or loadings \( m \times n \) matrix) and \( C \) are basic temporal components \( n \times t \) matrix).

Some of the deeper muscles around the hip have a rather complex architecture depending on the hip joint angle (Delp et al. 1999), and indeed we cannot rule out a possibility that there might be some cross-talk in our recordings of muscles like ILIO. Nevertheless, our averaged records (the major peak of activity around lift-off) are consistent with those reported in the literature (Andersson et al. 1997; Rab 1994) and obtained using a simulated biomechanical model of bipedal stepping (Zajac et al. 2003). A FA could theoretically be compromised by electrical cross-talk among adjacent muscle recordings (De Luca and Merletti 1988; Nene et al. 2004). However, if cross-talk did exist, it would most likely have affected only the weighting coefficients assigned to each component in accounting for the activity of a muscle that was contaminated by cross-talk (Ivanenko et al. 2004b).

In the present study, unless a component explained at least as much as 3% of the total variance, we dropped it. The higher-order components were generally variable and not significant (see RESULTS). To assess similarities of activation components across subjects and speeds, we used the following parameters: timing of the main peak and the width of the main peak (Ivanenko et al. 2005). The five basic components were ordered according to the timing of the main peak. The width of the main peak was estimated by measuring the full-width at half-maximum (FWHM). The half of maximum was calculated as a point corresponding to the mid-height between the peak value and the mean value between 2 minima (1 to the left, another 1 to the right with respect to the main peak). In the case of "boundary" peaks (close to the foot contact), we used only descending or ascending part of the component profile to calculate the half-width at half-maximum and then multiplied it by 2, under the assumption of the symmetrical profile.

Independent component analysis and nonnegative matrix factorization

Different statistical methods have been developed to assess a linear decomposition of the original set of data based on different assumptions (Tresch et al. 2006). Thus factor analysis with varimax rotation constrains the analysis to orthogonal (uncorrelated) factors. Although factor analysis of EMG activity was thoroughly documented for human locomotion and we could thus compare our results with those reported in the literature (Davis and Vaughan 1993; Ivanenko et al. 2003, 2004b, 2005; Merkle et al. 1998; Olree and Vaughan 1995), we also performed two other decomposition-related statistical analyses:
independent component analysis (ICA) and nonnegative matrix factorization (NMF).

We performed an informax ICA (Bell and Sejnowski 1995) using the function “runica” in the EEGLAB package (v4.5; www.sccn.ucsd.edu/ee abolab/) (Delorme and Makeig 2004) running on Matlab v7. The rationale for this analysis is that unlike PCA (FA), ICA aims at extracting unknown hidden components from multivariate data using only the assumption that the unknown components are mutually independent (Hart and Giszter 2004).

We also applied a NMF using the multiplication algorithm described by Lee and Seung (1999) that constrains the temporal components and weighting coefficients to be nonnegative. The rationale for application of the NMF was that our data consisted of nonnegative values (rectified EMG activity), and the NMF constraint allows only additive not subtractive combinations (d’Avella and Bizzi 2005).

All methods were applied to the same data set in each task and the results across methods and tasks (walking vs. running) were compared. We reduced the dimensionality of the data to the same final number of temporal components as in the FA for both the ICA and NMF analyses. Using the correlation matrix for factor analysis (see preceding text) automatically implies normalization of each EMG waveform to its SD value. To compare the results of FA with those of ICA and NMF, the amplitude of EMG waveforms was normalized by their mean SD values prior to the application of ICA and NMF. This is reasonable because we were mainly interested in rhythmic patterning elements in the control of locomotion (temporal components) rather than in muscle synergies (weighting coefficients) and because the amplitude of EMG activity was roughly similar when walking and running at the same speed (see RESULTS).

Statistics

A factor analysis was performed using Statistica v6.0 (StatSoft). Statistical analyses (Student’s t-tests) were used to compare the half-widths of the component peaks (FWHM) in walking and running. Statistics on correlation coefficients was performed on the normally distributed, Z-transformed values.

RESULTS

General characteristics of walking and running

Running and walking gaits are usually adopted for different speeds of locomotion, with a preferred transition occurring at \(~7\) km/h for most human subjects (Nilsson et al. 1985). Some major differences between the two gaits are illustrated in Fig. 1A. During walking, the leg tends to behave like a rigid strut, and the joints remain relatively extended throughout the stance phase (Lee and Farley 1998). In contrast, during running, the major leg joints undergo substantial flexion and extension during stance as the leg behaves in a more spring-like manner.

Both running and walking can occur, however, over a wide range of speeds (Minetti et al. 1994). We examined both gaits at 5, 7, and 9 km/h and walking alone at 3 km/h and running alone at 12 km/h. Although increases in locomotion speed in both gaits were accomplished by increasing both the cadence and stride length, the duration of the stance phase was always >50% of the gait cycle for walking and <50% for running (Fig. 1C). This difference corresponds to a change from a double support phase during walking to a single support during running, which is then accompanied by a greater ground reaction force occurring shortly after foot contact at the beginning of the cycle (Fig. 1B).

Figure 1D shows the normalized values (over all trials and subjects) of horizontal (VM_x) and vertical (VM_y) excursion of the foot plotted as function of speed. These global gait parameters exhibited the well-known monotonic relationship with increasing speed and different behaviors between walking and running (Nilsson et al. 1985).

Muscle activity patterns

The overall effect of speed on the average EMG activity was consistent with that reported in the literature (den Otter et al. 2004; Hogue 1969; Ivanenko et al. 2002; Murray et al. 1984; Nilsson et al. 1985), and it may be seen in Fig. 2. The intensity of distal leg activity is more similar across speeds, whereas the intensity of proximal leg and trunk activity increases much more with speed. Except for a few muscles like Bic, there is no obvious distinction in the intensity of muscle activation at the transition from walking to running (dotted vertical lines in Fig. 2A). However, there are differences in the patterns of activation at the transition, particularly in the distal leg muscles. The peak of LG activation shifts to an earlier phase in the cycle. Instead the changes in Vlat and ST activation are less obvious (Fig. 2B). The single cycle records at the gait transition points show that the difference in the activation timing of the calf muscles between walking and running occurs abruptly within a single step cycle (Fig. 2B). Some high-intensity muscle activation prior to the walk-to-run transition (see LG activity) is consistent with the idea that the activation of major leg muscles might act as a trigger for gait transition and explain why locomotion at nonpreferred speeds requires excessive muscle activation (Prilutsky and Gregor 2001).

The average EMGs for each muscle we recorded are illustrated in Fig. 3. They show the same basic result illustrated by Fig. 2 but with more detail. During walking, distal leg activity had about the same modulation intensity and overall pattern at all speeds although mean activity increased with speed. Proximal leg activity became more robust at the higher speeds in walking, and individual patterns of activity were often different at different speeds (see also Ivanenko et al. 2002; Winter and Yack 1987). The patterns of activity in trunk and abdominal muscles also tended to change dramatically as a function of speed. Cervical muscle activity, which was quite low at the lowest speeds, became significant at the higher speeds. There is an increase in the EMG activity of all muscles during running. In general muscles are most active around the time of foot contact.

The posterior calf muscles tend to function as one unit. During walking, the anterior muscles (TA) become active prior to lift-off and remain active throughout the swing phase and into the first 10% of the next cycle. The posterior calf muscles (MG, LG, SOL, PERL) are all active at ~40% of the cycle when the anterior muscles are relatively silent. With running, this pattern reverses so that the anterior muscles increase their activity during the mid part of the cycle, and the posterior muscles are active instead around the time of foot contact. This, in fact, is the most marked change in muscle coordination we observed in the transition between walking and running. These changes are associated with changes in leg and foot movements. In walking, the foot strikes the ground with the rear part of the heel and with a marked plantarflexion in the ankle. In running, on the other hand, initial contact is generally...
made with a more anterior part of the foot. Individual differences exist in the way the foot is placed on the ground (Chan and Rudins 1994; Rodgers 1988), which must also lead to differences in the activity pattern of muscles controlling the ankle.

EMG components: comparison of analytical methods

In our previous study (Ivanenko et al. 2005), we compared three different forms of factor analysis to find common components in the EMG patterns across muscles. Because each of these statistical approaches (FA, ICA, and NMF, see METHODS) places different restrictions on the outcomes, they might also extract different sets of activation components. We found, however, that the different algorithms converged to a similar solution about the temporal structure of the EMG activation patterns, both during normal walking and during walking combined with a voluntary movement.

We repeated this comparison here to determine whether the same components were also identified for EMG activity recorded during running. As before, we ordered the ICA and NMF components so that their waveforms matched the corresponding FA components (Fig. 4). The results were similar to those we reported previously (Ivanenko et al. 2005; see also Tresch et al. 2006) in that the three methods gave essentially the same result for both walking at 5 km/h (average waveform correlation with FA component \( r = 0.92 \pm 0.05 \) for ICA and \( 0.89 \pm 0.09 \) for NMF) and for running at 12 km/h (\( r = 0.94 \pm 0.03 \) for ICA and 0.87 \( \pm 0.11 \) for NMF). In addition, the loadings or weighting coefficients on particular muscles were also similar in the three methods. Finally, the total variance explained by basic temporal components was also similar. For instance, in Fig. 4, the percent of variance explained by all components was 87, 90, and 86% during walking and 90, 91, and 89% during running using FA, ICA and NMF, respectively.

Factor analysis

Given the nearly equivalent results of the previous section, we again used the same FA approach as we did previously (Ivanenko et al. 2003, 2004b, 2005) to describe common
components in the EMG patterns across muscles. We analyzed EMG patterns separately for each subject and for each speed (Fig. 5). The basic result was that five temporal components accounted for between 83 and 99% of the total EMG waveform variance for all subjects across all conditions. The most significant component of order higher than five explained only 3.1 ± 1.1% of the total variance and was highly variable across subjects and conditions (component 6, Fig. 5).

The five components determined from the data recorded during walking were essentially the same as those we described previously (Ivanenko et al. 2004b), but they extend the range of those results to now include walking at 7 and 9 km/h. Five temporal components were also consistently found for all speeds during running (Fig. 5B). They each corresponded to a component derived from the walking data with the single clear exception of component 2. This component was substantially phase-shifted from a peak at ~45% of the cycle during walking to between 20 and 30% of the cycle during running.

As before, we found small but systematic shifts in the timing of the main peaks of the components to an earlier phase with
increasing speed (Fig. 6A). We showed earlier that these shifts tended to scale with the duration of the stance phase as that changed with speed (Ivanenko et al. 2004b). At the higher speeds used here (>3 km/h), the duration of stance did not decrease as much with speed as it did at lower walking speeds (1–3 km/h), so the component phase shifts were correspondingly less. There were also comparable phase shifts with speed during running. In fact, the phases of component 1, 3, 4, and 5 were essentially the same as we found at comparable speeds for walking (Fig. 6A). This might be slightly less clear in the case of component 5 because there may be a difference in the running and walking phases at 9 km/h.

The phase of component 2 seems to behave differently during walking and running. During walking the shift with speed is comparable to what we observed with the other four components. During running, however, not only is there a discrete phase shift with respect to the corresponding walking component, but the shift with speed seems to be greater. However, when we consider the phases relative to lift-off (end of stance) instead of relative to heel strike or touch-down, the phase of component 2 is consistently ~80% of the cycle (20% prior to lift-off) during both walking and running (Fig. 6B). In contrast, with lift-off as the reference, the phases of the other four components are no longer comparable during walking and running. In fact the phase of component 4 during walking aligns with component 3 during running and component 1 during walking aligns with the phase of component 5 during running. Moreover components 5 and 3 during walking and components 1 and 4 during running were not aligned with comparable components. Thus all but component 2 may be better represented by the reference to touch-down as we have also used in our previous studies.

The half-widths of the component peaks (FWHM) were essentially the same (~13% of the cycle duration) for each component across speeds (Fig. 6C). There was some tendency though for the running components 1 and 2 to be slightly wider (15–17%) at the lower speeds relative to the walking components ($P = 0.06$ for 5 km/h and $P = 0.05$ for 7 km/h, paired t-tests).

The total amount of waveform variance accounted for (PV) by each component was quite similar for walking and running, with components 4 and 5 typically accounting for less variance than the other three during both walking and running (Fig. 6D). Moreover, some differences that depended on walking speed, such as an increase in PV by component 3 and decrease by component 4 with increasing speed (Ivanenko et al. 2004b) seemed to hold also during running.

The relative strength of the effect of each activation component on a given EMG pattern is given by the component “loading” or “weighting coefficient” (Fig. 7B). We estimated any changes in weighting coefficients of the five temporal components between walking and running at the same speed (7 km/h) by correlating the set of weighting coefficients for various groups of muscles. We made separate comparisons for the leg and lower trunk muscles and the upper trunk and shoulder muscles for each corresponding component in running and walking (Fig. 7B). There was a fairly high consistency of relatively high correlation coefficients ($r_{\text{LEG}} = 0.68 \pm 0.17$) indicating that similar muscle groups in the limb and lower trunk were activated with common timing during walking and running. Interestingly the best correspondence was for component 2, indicating that the loading of component 2 on leg muscles was basically the same in walking and running in spite of the shift in the timing of component 2.

The consistency was much less, however, for the upper trunk and shoulder muscles ($r_{\text{TRUNK}} = 0.28 \pm 0.39$), where the biggest differences were seen with components 1 and 4. These components therefore participate in the activation of different groups of muscles in walking and running. It is obvious in fact the upper body and arm motion in particular tend to be much different in walking and running.

**DISCUSSION**

We examined muscle activation in human subjects over a range of speeds during both walking and running. Consistent with our previous result on the effects of walking speed (Ivanenko et al. 2004b), we found that speed changes during...
both walking and running are associated with increases in the intensity of muscle activation and only minor changes in their relative timings. The same five activation components accounted for muscle activity during either walking or running over the entire speed range tested. Moreover, in spite of significant differences in the overall characteristics of the two gaits, we found that major differences in muscle activation timing occurred only during stance, while walking and running timing was basically the same during the swing phase.

**Speed versus gait effects**

Changes in locomotion speed are accompanied by changes in cycle length and cycle duration as well as in the fraction of the cycle devoted to stance or swing. Although such changes are also accompanied by changes in muscle activation patterns, most of these scale with the cycle duration so that changes in activation intensity seem to dominate (Andersson et al. 1997; den Otter et al. 2004; Ivanenko et al. 2004b; Murray et al. 1984; Prilutsky and Gregor 2001; Winter and Jack 1987). Gait changes on the other hand, such as the transition from walking to running, are often considered to involve a different muscle usage and not just more intense muscle activation. However, this is not what we found. The major change in muscle activation during running compared with walking was a phase shift attributable to a single activation component during stance, whereas the muscles activated by the shifted component remained the same. Increasing running speeds, from 7 to 12 km/h, was mostly accompanied by a similar activation of
leg muscles and somewhat more intense activation of trunk and shoulder muscles.

Muscle activation patterns recorded at 3 km/h were basically the same as those recorded at higher walking speeds with only few exceptions (e.g., TFL, ADD, Fig. 3). Instead, most of the 32 muscles we recorded exhibited more intense activation at higher speeds, and the activation timing was fully accounted for by five activation components (Ivanenko et al. 2004b). We expected though that running, which places different biomechanical demands on the neuromuscular system, would exhibit different muscle activation patterns. However, many muscle activation patterns were quite similar to those observed during walking. In fact, the five components that represent those patterns were each associated with the activation timing of nearly the same set of leg and lower trunk muscles during running and walking. The average correlation across weighting coefficients was 0.68 (range: 0.38 – 0.82). Thus these components seem to play essentially the same role in both conditions independently of speed [however, see Ivanenko et al. (2004b) and Fig. 6B, which shows a decrease in PV for component 4 and an increase for component 3 with increases in speed].

Gait changes

The activation of ankle extensors at an earlier phase of the locomotion cycle was the major EMG change we found to be associated with running compared with walking, and it reflects a difference in the support function of the leg in the two gaits.

One hypothesis proposed to account for the preferred transition to running with increasing speed predicts this difference in activation timing. It notes that at higher walking speeds, the ankle extensors are loaded toward the end of stance in an unfavorable portion of their force-velocity curve, so their force production is limited even as levels of activation increase. Shifting the activation to an earlier phase of stance shifts the activation to a more favorable force production range (Neptune and Sasaki 2005). This can also be seen as a shift in the ground reaction force ($F_z$) near the beginning of the cycle (Fig. 1B).

This shift of muscle activation timing from walking to running and the greater peak activation intensity during walking are both clearly evident in the EMG recordings from the posterior calf muscles (Fig. 3, MG, LG, PERL, and SOL). The

---

**Fig. 6.** Characteristics of activation temporal components. A: the timing (±SD) of the peaks of 5 common FA components across speeds and tasks. The 5 basic components are each characterized by a relatively narrow peak of activation at a particular phase of the cycle. Zero timing refers to the heel strike. Note the abrupt change in the timing of component 2 between walking and running. B: the timing of the same peaks referenced to the lift-off event. Gait cycle and 0 timing refers to the lift-off in this plot. Note the invariance of the timing of component 2 in walking and running when referenced to the lift-off event. C: the width (+SD) of the main peaks of components estimated as the full-width at half-maximum (FWHM). D: percent of variance explained by each component in the data sets obtained from all individual muscles.

---

**Fig. 7.** Activation temporal components derived from averaged muscle activity patterns (see Fig. 3). A: superimposed activation components in walking and running. Note a prominent phase shift of the timing of the main peak of the second component in running. B: weighting coefficients (across 32 muscles) of the 5 basic temporal components during walking and running at the same speed (7 km/h). The correlation of weighting patterns between walking and running is shown at the right of each record both for the leg/lower trunk [tibialis anterior (TA) – rectus abdominis, superior portion (RAS)] and upper trunk/shoulder [latissimus dorsi (LD) – sternocleido mastoideus (STER)] muscles separately.
timing shift is reflected in the activation components as a shift in the timing of component 2, which is weighted primarily on those same muscles. That is, component 2 accounts for the activation timing of basically the same muscles in both gaits. The preceding explanation about an earlier phase of ankle extensor activation implied a control based on optimal muscle performance using feedback information about muscle force production, length, and velocity. However, muscle performance may not contribute directly to the control of timing. The subjects in our study were able to use either gait voluntarily at 5, 7, and 9 km/h, and their muscle activation exhibited a similar discrete shift in timing between walking and running at each speed. It is also evident however, that component 2 timing shifted to progressively earlier phases in the cycle as running speed increased, indicating a possible role for muscle performance, as suggested by this hypothesis.

Other proposals to explain the transition to running also involve parameters that are expected to change continuously with speed such as the pendulum-related limitations for the frequency of leg oscillations, metabolic energy expenditure (Margaria 1976), or an increased “sense of effort” due to the exaggerated swing-related activation of ankle knee and hip flexors (Prilutsky and Gregor 2001) or have some critical value like a critical velocity of ankle flexion (Hreljac 1995), critical forces (Farley and Taylor 1991; Raynor et al. 2002), or a critical angle between the thighs (Minetti et al. 1994; see also Biewener et al. 2004; Brisswalter and Mottet 1996; Cavagna et al. 1976; Kram et al. 1997; Neptune and Sasaki 2005; Nilsson et al. 1985; Thorstensson and Robertsson 1987). Although such speed-related parameters may account for a bifurcation in behavior, they do not easily account for a discrete change, which can occur over a large range of speeds.

Our analysis suggests another possibility, namely that the motor program activates ankle extensors at a fixed interval preceding lift-off. We found that this timing, corresponding to component 2 activation at 20% of the cycle prior to lift-off, was basically the same over the entire speed range for both walking and running (Fig. 6B). Thus the propulsive force generated as a result of this activation timing occurred at the end of stance for both gaits. Although this timing may produce a more efficient force production during running due to the biomechanical factors discussed in the preceding text, it is also a simple strategy requiring only that the timing of one component be coordinated with lift-off, which may in turn simply depend on sensory information about the transition from stance to swing. The effect, however, is to coordinate the swing and stance phases in the two gaits.

According to this hypothesis, the timing of components 1, 3, 4, and 5 are referenced to the beginning of the cycle at heel strike or touch-down, whereas component 2 occurs at a phase that is appropriate for launching the swing phase. This implies that the invariant relative timing of the five muscle activation components we have noted for walking does not represent a basic unit for all locomotion. As we found for running, the relative timing of component 2 timing can be disassociated from the timing of the four components because their phases are referenced to different events in the locomotion cycle. The relative timing of other components might also be gait dependent in some way so that other forms of locomotion gait (e.g., hopping, skipping) could also have different relative component timings that are invariant only for a particular gait pattern.

This might be expected if component timing (or CPG phase) can be directly controlled by sensory input or descending commands (Pearson 2004).

This may also relate to experimental work in frogs suggesting that a small collection of unit burst generators of synergistic muscle activity can be triggered by sensory input to produce corrections and other adjustments of spinally organized trajectories (Hart and Giszter 2004; Kargo and Giszter 2000). In humans, several researchers have provided support for a segmental movement generation and superposition of short bursts or fixed timing elements to control upper limb point to point and cyclic motions (e.g., Krebs et al. 1999). This is not unlike our previous observation about the coordination of voluntary motor acts with walking (Ivanenko et al. 2005). In that case, the five activation components associated with walking were also present in the combined motor behavior, and a new component with task-related timing was superimposed. Thus to coordinate the stance and swing phases in both walking and running, four of the activation components remain invariantly timed with respect to the beginning of the stance phase. The other component (2) is inserted to correspond with the phase of the lift-off and therefore shifts its phase during running (Fig. 8).

This interpretation implies that the same basic motor program consisting of five distinct muscle activation phases characterizes both walking and running at various speeds. It also

![FIG. 8. Hypothetical motor programs for walking (A) and running (B) in terms of the characteristic timing of muscle activations. In both programs, 4 activation components (1, 3, 4, and 5) occur relative to the touch-down (TD) phase of the cycle and component 2 occurs relative to the lift-off (LO) phase, at about 20% of the cycle preceding LO. As 1 gait mode is switched to the other, the timing of LO relative to TD changes along with the relative timing of component 2 with respect to the other 4 components.](image-url)
implies that peripheral factors like the transition to the swing phase may have essential modulatory roles affecting the relative timing of activation. It is not clear, however, to what extent these influences might contribute to the basic program to provide an appropriate and invariant kinematic pattern (Lacquaniti et al. 1999).

Conclusions

In summary, gait changes and speed changes each have specific effects on muscle activation during locomotion. Nevertheless, the diverse biomechanical demands of running and walking and of locomoting at different speeds are met by surprisingly similar general template of muscle activation. The walking and running motor program in humans may be considered as a sequence of five temporal activation components relative to the stance and swing phase of the locomotion.

Grants

This work was supported by the Italian Ministry of Health, Italian Ministry of University and Research, and Italian Space Agency.

REFERENCES


