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Motor units are recruited in a task-dependent fashion during locomotion

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Summary

Muscle fibres have a range of contractile properties from fast to slow. Traditional understanding of muscle fibre recruitment suggests that the slower fibres within a mixed muscle are used for all contractions including those at rapid speeds. However, mechanical arguments predict that some locomotor tasks are best performed by solely the faster fibres. Motor recruitment patterns can be indicated by the spectral properties of the myoelectric signals. High- and low-frequency myoelectric spectra that have similar spectral power indicate the activity of faster and slower motor units, respectively. In this study, the myoelectric signals in humans were measured from nine muscles of the leg during walking and running at 1.5, 3 and 4.5 m s^{-1}. The myoelectric spectra for 20 points in each stride were calculated using wavelet techniques, and the spectral properties quantified using principal component analysis. Bursts of muscle activity were characterized by hysteresis in the myoelectric frequencies, with different frequencies occurring at different times, indicating time-varying shifts in the motor recruitment patterns. This hysteresis occurred at all locomotor speeds tested. It is likely that the different types of motor unit are recruited in a task-dependent fashion during locomotion.

Key words: muscle fibre recruitment, myoelectric signal, principal component analysis, PC loading, hysteresis, task dependence.

Introduction

Animals typically use their muscles in a sub-maximal fashion during routine movements. The motor units, which are the functional contractile unit of the muscles, are thus not all used for each movement task. It remains an interesting and unresolved question as to how and why animals select the use of particular motor units to drive different movement tasks. Different motor units within a mixed mammalian muscle may be used for different phases within a gait cycle; for instance, some motor units in the sartorius of a walking cat are activated during concentric contractions and some are activated during eccentric contractions (Hoffer et al., 1981). Such populations of motor units may form task groups that are selectively recruited for different kinematic conditions during each stride (Loeb, 1985). Mammalian motor units have a range of contractile properties (Burke et al., 1971) that affect their function. However, it has not been established whether the mechanical requirements for movement govern the recruitment of different types of motor unit.

In synergistic muscles with different contractile properties, the faster muscle may be selectively used for faster tasks, and this has been demonstrated for the paw-shake in the cat (Smith et al., 1980; Fowler et al., 1988) and swimming in the blue gilled sunfish (Jayne and Lauder, 1994). However, little is known about how mammals recruit their motor units for different movement tasks within a mixed muscle. There are mechanical (Rome et al., 1988) and energetic reasons (Woledge et al., 1985) to suppose that the faster motor units within a mixed muscle should be selectively used for faster tasks. Indeed, jumping in the bushbaby involves the selective use of the faster muscle fibres in the mixed muscles of the vastus lateralis and gastrocnemius (Gillespie et al., 1974). The mechanical benefits of using faster motor units for faster activities should hold true across a range of locomotor speeds and for different dynamic tasks within each stride, but such task-dependent recruitment has not yet been observed. Thus, the purpose of the present study was to investigate whether patterns of motor unit recruitment varied within a stride at a range of locomotor speeds.

The myoelectric signals that are emitted from an active muscle contain information about the muscle fibre types that generated the signal. Faster muscles generate higher frequencies within the myoelectric spectra than do slow muscles (Elert et al., 1992; Gerdle et al., 1988; Kupa et al., 1995; Moritani et al., 1985; Solomonow et al., 1990), and distinct high and low frequency bands have recently been identified that characterize activity from faster and slower muscle fibres, respectively, in rainbow trout, cats, rats and humans (Wakeling et al., 2002; Wakeling and Syme, 2002; Wakeling and Rozitis, 2004). Myoelectric signals with different frequencies but the same power indicate the activity of different motor units. Therefore, in the present study, we tested the hypothesis that myoelectric bursts with

distinct frequencies but the same power would occur at different times within each stride during walking and running.

Materials and methods

Six recreational runners (age 33.0±3.0 years; height 180.1±3.0 cm; mass 76.7±3.2 kg; mean ± S.E.M.) ran on a motorized treadmill on a horizontal grade. Initially, subjects ran for a 5-min warm-up period at a velocity of 3 m s^{-1}. Subjects were then tested during walking at 1.5 m s^{-1} and during running at 3 and 4.5 m s^{-1}. Each speed was tested for 45 s followed by a 45 s rest. The order of the three speeds was randomized to make a block, and the block was repeated six times.

EMG measurement

Myoelectric activity was measured from the muscle bellies of the vastus medialis, rectus femoris, vastus lateralis, lateral gastrocnemius, medial gastrocnemius, soleus, biceps femoris, semitendinosus and tibialis anterior muscles of the right leg using round bipolar surface electrodes (Ag/AgCl; 10 mm diameter, 22 mm spacing). A ground electrode was placed on the fibular head. The EMGs were preamplified at source (bandwidth 10–500 Hz, 3 dB; Biovision, Wehrheim, Germany) and recorded at 3600 Hz (DAQCard-6062E; National Instruments, Austin, TX, USA). Myoelectric activity was recorded for 20 consecutive steps in the last 30 s of each running trial. An accelerometer mounted on the right shoe measured the time of heel-strike.

EMG analysis

The myoelectric signals (Fig. 1A) were resolved into their myoelectric intensities in time–frequency space using wavelet techniques (von Tscharner, 2000). The intensity is a close approximation of the power of the signal contained within a given frequency band, and the intensity spectrum is equivalent to the power spectrum from the myoelectric signal.

Strides were demarked by the time of heel-strike, and further subdivided into 20 equal time-windows. Stride times were thus normalized to a time of 100% and began at heel-strike. The mean intensity spectrum was calculated for each time-window (Fig. 1B,C). The first wavelet covered a frequency band of 2–12 Hz, which is typically associated with movement artefacts. If the myoelectric intensity resolved by the first wavelet was greater than the maximum intensity resolved by the higher wavelets then the data from that trial were considered noisy and not analyzed further. Intensities resolved by the first wavelet were then ignored, so the final analysis considered the total frequency band of 10–524 Hz).

The mean myoelectric intensity for each muscle and subject for the 4.5 m s^{-1} trials was calculated and used to normalize the spectra for the respective muscles and subjects. One matrix of spectra was compiled from the normalized spectra for all muscles and all subjects. The principal components (PCs) were calculated from the covariance matrix of the matrix of

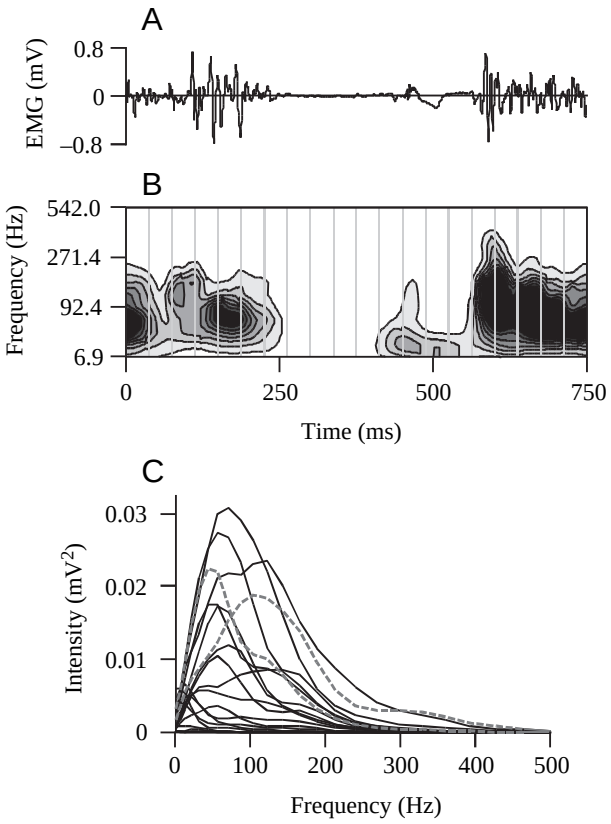

Fig. 1. (A) Myoelectric signal from the biceps femoris for one stride of running at 4.5 m s^{-1}. Heel-strikes occurred at times of 0 and 750 ms. (B) The mean myoelectric intensity for 20 consecutive strides is shown as a function of time and frequency, with high intensities denoted by dark shading. The 20 time-windows that divide the stride are indicated by the vertical grey lines. (C) The myoelectric intensity spectra for each of the 20 time-windows shown in B.

spectra (Wakeling and Rozitis, 2004). The PCs were calculated with no prior subtraction of the mean data and so describe the components of the entire signal (Wakeling and Rozitis, 2004).

Each measured spectrum can be reconstructed from the vector product of the PC weightings and the PC loading scores (e.g. Fig. 2C). The majority of the signal for any given myoelectric spectrum is defined by the first two PCs, and the relative PC I and PC II loading scores give a measure of the frequency of the myoelectric signal. The angle θ was thus defined by ArcTan (PC I score/PC II score) and used as a measure of the myoelectric frequency for each spectra (Fig. 2; Wakeling and Rozitis, 2004).

A multivariate analysis of covariance (MANCOVA) was used to test the hypothesis that the myoelectric frequency differed at different times within each stride (Minitab Inc., State College, PA, USA). The response variable was θ, the measure of myoelectric frequency. The subject code, time-window and locomotor velocity were used as factors in the test, and the myoelectric intensity used as the covariate. The MANCOVA was repeated for each muscle tested.

Results

Myoelectric intensities occurred at different frequencies at different times in each stride, illustrated by the broken grey lines in Fig. 1C, which show distinct myoelectric frequencies occurring for similar myoelectric intensities.

The first two principal components of the myoelectric intensity spectra described 82.8% of the signal. The weighting for PC I had a shape similar to that for a myoelectric intensity spectrum (Fig. 2A). The myoelectric intensity for each of the time-windows correlated with the PC I score with a correlation coefficient of r=0.98. The weighting for PC II had a negative region at frequencies below 60 Hz and a positive region at frequencies above 60 Hz (Fig. 2B). Intensity spectra could be reconstructed from the vector product of the PC weightings and the PC loading scores. Reconstructed spectra with positive intensities across all frequencies (a physiological constraint) occur for a range of θ and result in two extreme spectra with mean frequencies of 54.7 Hz and 125.9 Hz (Fig. 2C).

The stride durations during walking and running at 1.5, 3.0 and 4.5 m s^{-1} were 1050±1, 746±1 and 694±1 ms, respectively. As the running velocity increased, the myoelectric intensity increased for all muscles tested, and this is illustrated by the greater PC I loading scores in Figs 3–5.

Each burst of muscle activity can be visualized by a loop of PC I–PC II loading scores in the PC I–PC II scoring plane (Figs 3–5). For instance, during walking, the biceps femoris showed a single burst of activity from approximately 85% of one stride to 5% of the next. When the velocity increased to a run at 3.0 m s^{-1}, the biceps femoris showed a pause in myoelectric activity at heel-strike, and the activity extended into two bursts: the first burst from 75% to heel-strike and then a second burst from heel-strike to 30% of the stride (Fig. 3A). In some cases, for instance the tibialis anterior activity during walking (Fig. 3C), the paths of PC I–PC II loading scores showed little hysteresis and lay on a vector projecting from the origin. These paths indicate that the myoelectric frequency remained steady throughout the burst of activity. In other cases, for instance the tibialis anterior activity during running at 4.5 m s^{-1} (Fig. 3C), the loops of PC I–PC II loading scores showed a marked hysteresis. These loops indicate that the myoelectric frequency changed during the burst of activity. In some cases, PC I–PC II loading scores followed anticlockwise loops, for instance the rectus femoris activity during running at 3.0 m s^{-1} (Fig. 4B), and these loops indicated a gradual decrease in the myoelectric frequency as the burst of activity progressed. In other cases, PC I–PC II loading scores followed clockwise loops, for instance the medial and lateral gastrocnemius activity during running at 3.0 m s^{-1} (Fig. 5A,B), and these loops indicated a gradual increase in the myoelectric frequency as the burst of activity progressed. The PC loading scores from between 20 880 and 34 560 spectra were included in each MANCOVA, and for all muscles there was a significant effect of the time-window on the angle θ (P<0.001).

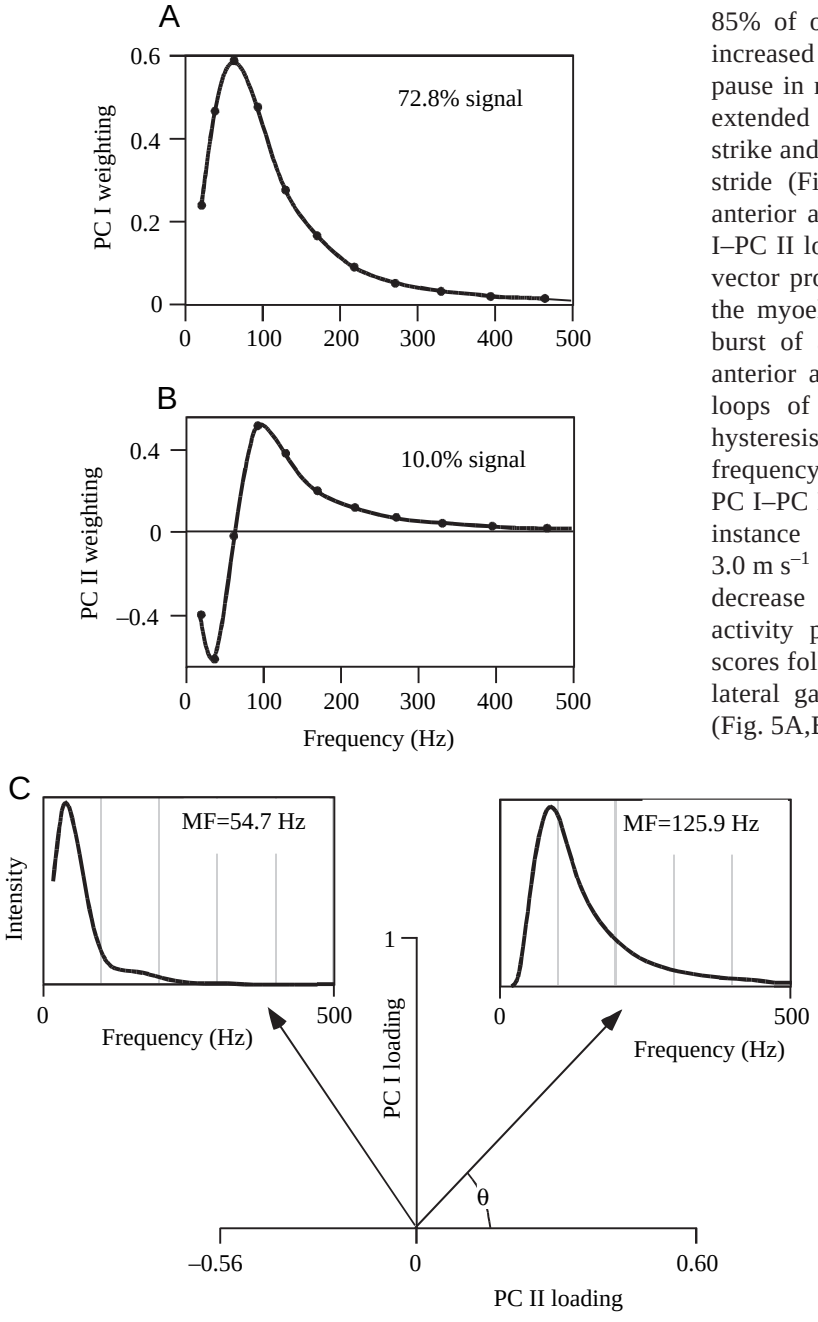

Fig. 2. Weightings for (A) the first principal component (PC I) and (B) the second principal component (PC II) shown with the proportion of the signal that this component describes. (C) Intensity spectra reconstructed from the vector product of the PC loading scores and the PC weightings. The mean frequencies (MF) for the reconstructed spectra are shown. The angle θ is a measure of the relative PC I and PC II loading scores and of the myoelectric frequency.

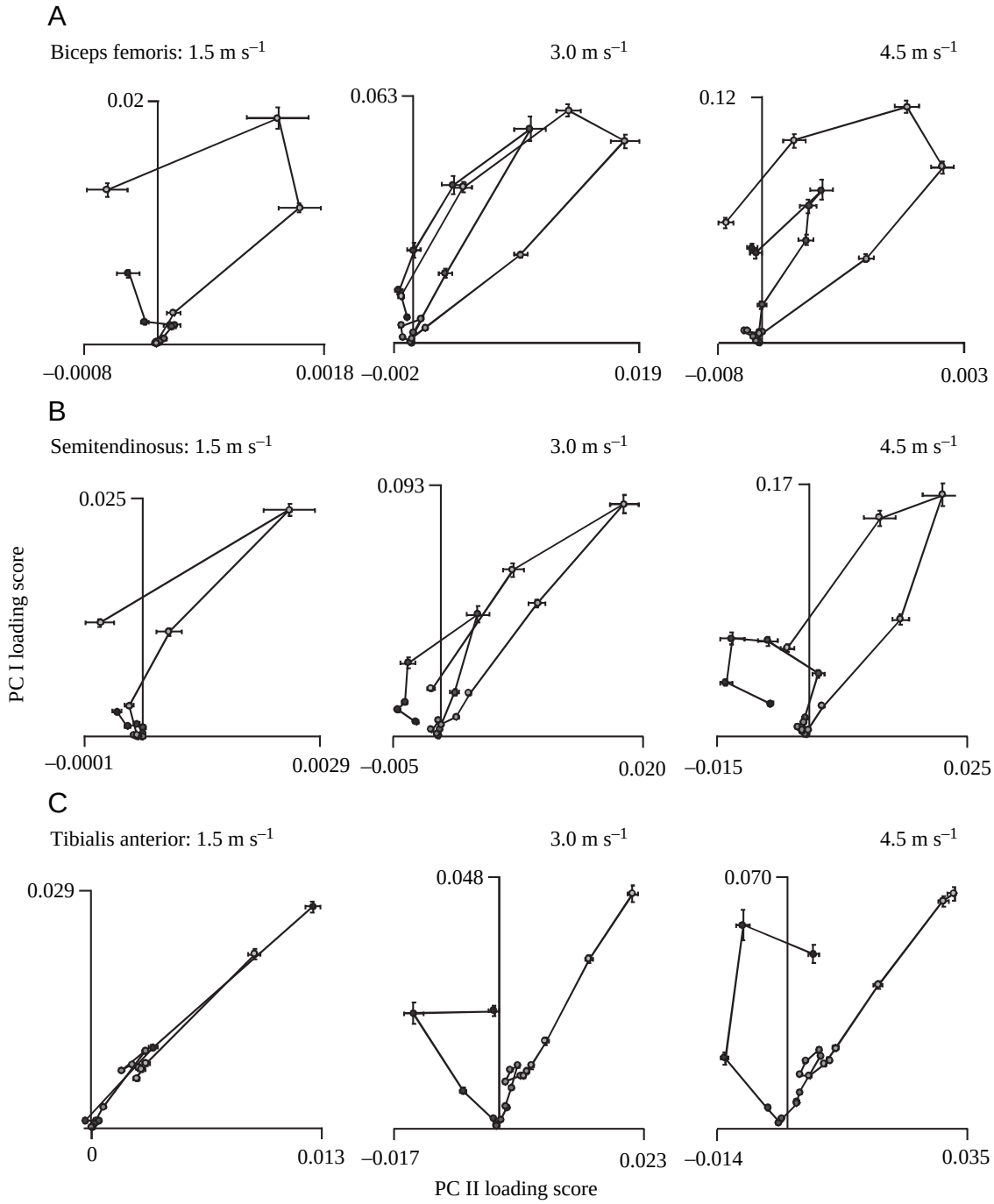

Fig. 3. Principal component loading scores for PC I and PC II during walking and running for the leg flexors. Each point shows the mean ± S.E.M. loading scores pooled from the six subjects (N>348). The 20 points on each graph show the PC loading scores at the 20 successive time-windows during each stride, graded from black immediately after heel-strike to light grey immediately before the next heel-strike. Data are shown for the biceps femoris (A), the semitendinosus (B) and the tibialis anterior (C).

Discussion

The lower-extremity muscles are activated for distinct periods within each stride. Activated muscle generates force and performs or absorbs mechanical work during concentric and eccentric phases of a contraction, and all of these functions are utilized during locomotion. The myoelectric intensity is a measure of the activation level and is predicted well by the PC I loading score. During each stride, the bursts of muscle activity correspond to increases in PC I loading score, and these occur at different times for antagonistic muscles with opposing function. For instance, the hamstring muscles showed greatest activity before the foot touches down (Fig. 3), whereas the quadriceps group shows greatest activity soon after heel-strike (Fig. 4).

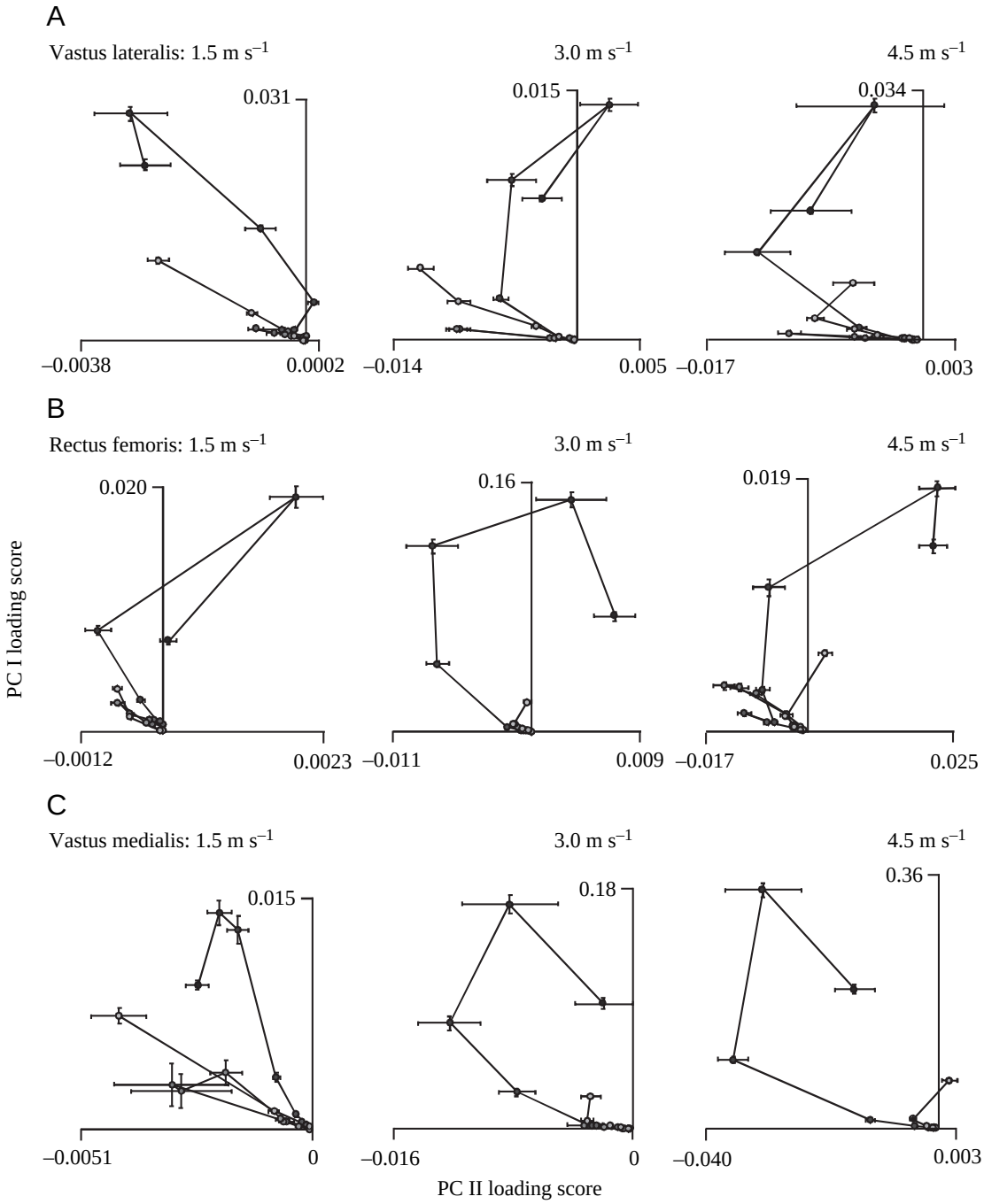

Fig. 4. Principal component loading scores for PC I and PC II during walking and running for muscles in the quadriceps group. Each point shows the mean ± S.E.M. loading scores pooled from the six subjects (N>342). The 20 points on each graph show the PC loading scores at the 20 successive time-windows during each stride, graded from black immediately after heel-strike to light grey immediately before the next heel-strike. Data are shown for the vastus lateralis (A), the rectus femoris (B) and the vastus medialis (C).

The myoelectric signals change in frequency during each stride, as shown by the relative PC I–PC II loading scores and the angle θ. Decreases in myoelectric frequency can occur during fatiguing contractions (Brody et al., 1991) and with decreases in muscle temperature (Petrofsky and Lind, 1980). However, in the present study, the randomized block design minimized such bias. Furthermore, the intra-stride cycling of myoelectric frequency occurs at a time scale too short to be significantly affected by levels of fatigue or temperature. The different myoelectric frequencies in this study thus represent the signals from different units within each muscle. Motor units form the functional contractile unit within the muscles (Sherrington, 1929) and can generate different myoelectric frequencies (Wakeling et al., 2002; Wakeling and Syme, 2002; Wakeling and Rozitis, 2004). The patterns of PC loading scores and the shape of the PC weightings were similar to those

distinguished from faster and slower motor unit activity in humans (Fig. 2; Wakeling and Rozitis, 2004). In the present study, the PC I and PC II explain 83% of the measured spectra, with the remaining 17% explained by PC III to PC XI. Variations in myoelectric frequency between muscles are accounted for by some of the loading scores of PC III to PC XI. The changes in θ in this study should thus be considered as a relative measure of the motor unit recruitment patterns rather than an absolute measure of frequency from the individual muscles. Nonetheless, the changes in myoelectric frequency observed within each stride in this study are most likely due to changes of the motor unit recruitment patterns.

The results from this study thus indicate that the motor unit recruitment patterns change through each stride, between locomotor speeds and gaits, and are also different between muscles (Figs 3–5). The recruitment of the motor units can be

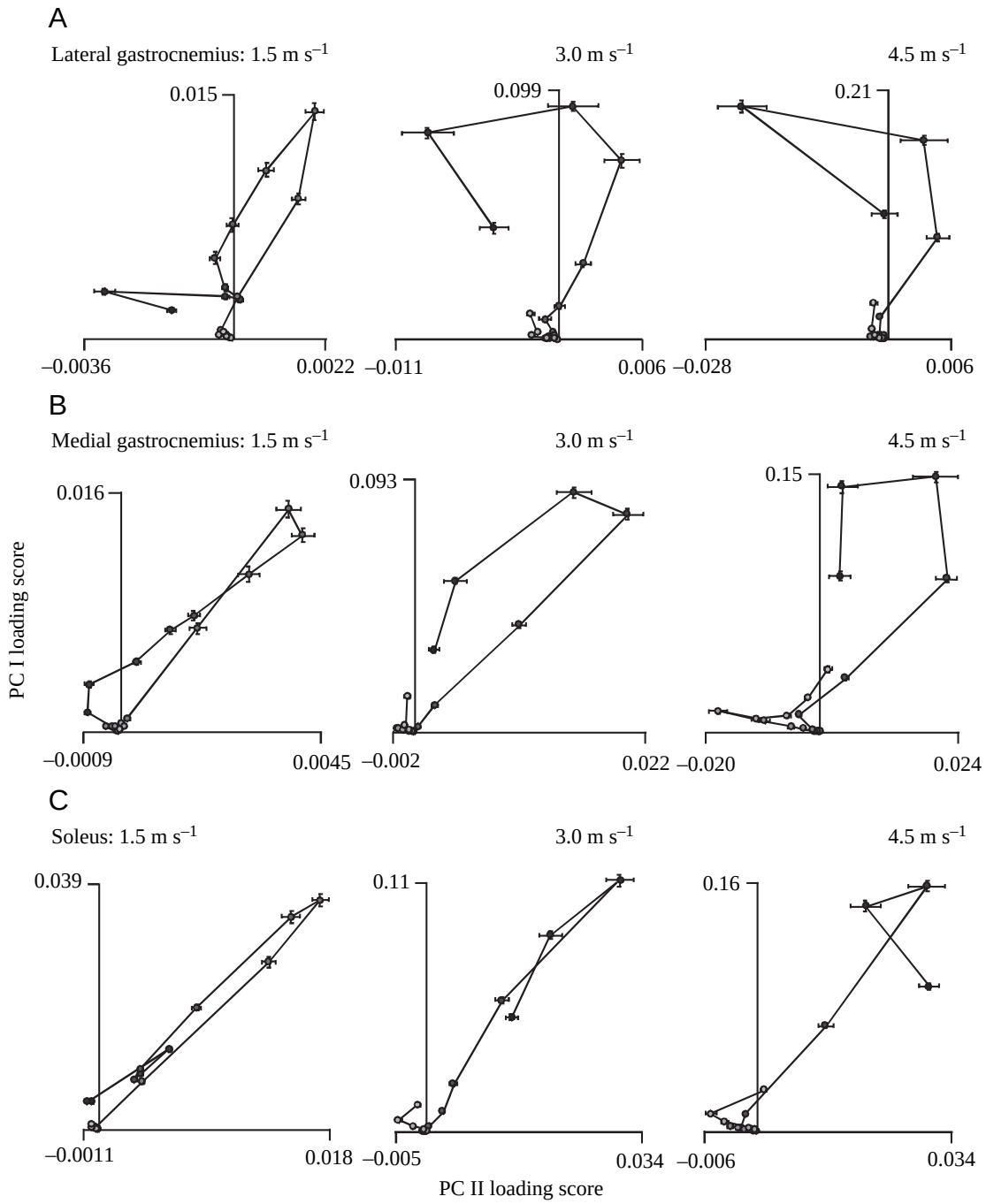

Fig. 5. Principal component loading scores for PC I and PC II during walking and running for muscles in the triceps surae group. Each point shows the mean ± S.E.M. loading scores pooled from the six subjects (N>348). The 20 points on each graph show the PC loading scores at the 20 successive time-windows during each stride, graded from black immediately after heel-strike to light grey immediately before the next heel-strike. Data are shown for the lateral gastrocnemius (A), the medial gastrocnemius (B) and the soleus (C).

considered to start with a basic plan of orderly recruitment determined by the excitabilities of the α-motoneurons (Henneman et al., 1974). The excitability of the motoneurons can be modulated by input from higher centres, for instance *via* the corticospinal tract. Superimposed on this plan, inhibitory interneurons within the spinal cord can modify the recruitment pattern, and, in particular, the Renshaw calls can cause reversals of the recruitment order (e.g. Ryall et al., 1972; Friedman et al., 1981; Broman et al., 1985). Furthermore, the sensitivity of the muscle spindles, which provide monosynaptic input to the α-motoneurons, is modulated by the fusimotor drive of the gamma efferents, which in turn cycles during each stride (Loeb, 1985). Motor unit recruitment is thus the result of complex neural integration that is able to shape the recruitment to different movement tasks.

Locomotion can place large energetic demands on an animal, and, indeed, during vigorous activity the metabolic rate of mammals can range from six times the resting rate in small mammals (Pasquis et al., 1970) to ~20 times the resting rate in larger athletic animals (Young et al., 1959). A large portion of this additional metabolic energy expenditure during movement results from muscular contractions, and thus recruiting the most appropriate motor unit to maximize power output or contractile efficiency may result in considerable energetic savings to the animal. Faster muscle fibres have higher rates of force development and relaxation than do slower fibres (Burke et al., 1971), and the maximum mechanical power output and efficiency during steady contractions occurs at 20–30% of their maximum shortening velocity, V_{max} (Hill, 1964; Kushermick and Davies, 1969). The faster motor units contain faster muscle fibres with higher V_{max} and so generate maximum power output and efficiency at higher shortening velocities than do slow fibres. Therefore, there is scope for a muscle to optimize its power production and efficiency by recruiting the most appropriate motor units for each contractile task. Matching the recruitment patterns to contractile requirements has the potential for reducing the metabolic energy expenditure for locomotion, and these patterns have been observed across anatomically distinct synergistic muscles during cat paw-shakes (Smith et al., 1980; Fowler et al., 1988) and swimming fish (Jayne and Lauder, 1994). Observations within mixed mammalian muscle have been limited to a study on the bushbaby in which selective recruitment of the faster motor units for jumping as opposed to running has been demonstrated within the mixed muscles of the vastus lateralis and gastrocnemius (Gillespie et al., 1974). The mechanical arguments discussed above, however, suggest that there should be a general pattern of matching contractile tasks to the recruited motor units that holds true across all locomotor speeds and gaits and also for the different movement tasks that occur within each stride.

Cycling of recruitment patterns within each stride may be a general feature of mammalian locomotion. It is likely that the motor units are recruited to match their contractile properties to the mechanical requirements for the motion, and these requirements change between gaits, speeds and within each stride. The demands on the muscle depend on its requirement to generate force during lengthening, shortening or isometric phases of each stride, and furthermore the demands of cross-bridge cycling may be utilized to dissipate mechanical energy during soft-tissue vibrations (Wilson et al., 2001). It is not known which movement tasks place selective demands on specific populations of motor unit, but this will be a necessary step in understanding the complexity of motor recruitment within mixed muscle during locomotion.

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