

## VARIATIONS IN FORCE–TIME HISTORIES OF CAT GASTROCNEMIUS, SOLEUS AND PLANTARIS MUSCLES FOR CONSECUTIVE WALKING STEPS

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### Summary

Force-sharing among muscles during locomotion has been studied experimentally using ‘representative’ or ‘average’ step cycles. Mathematical approaches aimed at predicting individual muscle forces during locomotion are based on the assumption that force-sharing among muscles occurs in a consistent and unique way. In this study, we quantify normal variations in muscular force–time histories for step cycles executed at a given nominal speed, so that we can appreciate what it means to analyze ‘representative’ or ‘average’ step cycles and can evaluate whether these normal variations in muscular force–time histories are random or may be associated with variations in the kinematics of consecutive step cycles. Forces in gastrocnemius, soleus and plantaris muscles were measured for step cycles performed at a constant nominal speed in freely moving cats. Gastrocnemius forces were always larger than peak plantaris or soleus forces. Also, peak gastrocnemius forces typically occurred first after paw contact, followed by peak soleus and then peak plantaris forces. Furthermore, it was found that variations in muscular force–time histories were substantial and were systematically related to step-cycle durations. The results of this study suggest that findings based on ‘representative’ or ‘average’ step cycles for a given nominal speed of locomotion should be viewed cautiously and that variations in force-sharing among muscles are systematically related to variations in locomotor kinematics.

### Introduction

The distribution problem in biomechanics can be described by a set of equations aimed at calculating the forces of structures in and around a joint from the known resultant joint moment and force. The constraints associated with the distribution problem are that a given resultant joint moment and force are satisfied at any instant in time by the moments produced by the internal structures crossing the joint (e.g. Manter, 1938; Crowninshield and Brand, 1981). The major structures that can satisfy resultant joint moments and forces

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are muscles, ligaments and bones. However, ligamentous and bony forces are typically eliminated or neglected when solving the distribution problem theoretically, leaving just the muscular forces for the equilibration of the resultant joint moments (e.g. Seireg and Arvikar, 1973; Crowninshield, 1978; Pedotti *et al.* 1978; Patriarco *et al.* 1981; Dul *et al.* 1984a,b; Herzog, 1987a,b). Even when considering only muscular forces, the mathematical description of a typical joint and the corresponding muscles yields an indeterminate set of equations: there are more unknown muscular forces than rotational degrees of freedom at the joint. For such systems, there exists, generally, an infinite number of possible muscular force–time combinations that satisfy a given resultant joint moment. However, theoretical approaches aimed at solving the distribution problem give one solution, thus implicitly assuming that a given resultant moment (and consequently a given movement) is executed with identical force–time histories of the muscles involved.

Experimental measurements of muscular activity (EMG) or muscular forces show distinct differences between cycles of repeated movements (Manter, 1938). For example, muscular forces in cat ankle extensors vary for consecutive step cycles executed at constant nominal speeds (Walmsley *et al.* 1978; Hodgson, 1983; Herzog *et al.* 1993). These variations are typically small and were implicitly associated with corresponding changes in the kinematics of walking. However, Hoffer *et al.* (1989) showed force records from the cat medial gastrocnemius muscle that doubled from one step to the next, and O'Donovan *et al.* (1983) reported one-to fourfold changes in forces of the cat flexor digitorum muscle for consecutive step cycles. These latter authors state that such 'unpredictable bursts of FDL activity' were observed in most experimental sessions 'often without overt disturbance in the animal's gait.' Therefore, the question arises whether variations in muscular forces for a given movement are random within the kinematic constraints, or whether variations are systematic and reflect subtle changes in the kinematics of different step cycles. Furthermore, the use of a 'representative' or 'typical' step cycle (e.g. Hoffer *et al.* 1989) for deriving general results must be questioned when faced with results reported in the literature that show changes in muscular forces exceeding 100% for consecutive step cycles (O'Donovan *et al.* 1983; Hoffer *et al.* 1989). The purpose of this study was to quantify normal variations in muscular force–time histories for step cycles executed at a given speed, and to evaluate whether these variations are associated with corresponding variations in the kinematics of consecutive step cycles.

It was expected that muscular force–time histories would vary slightly from one step to the next. If these variations were systematic, it should be possible to relate them to corresponding changes in the kinematics of walking. However, if the variations were random and occurred within the kinematic constraints, they may reflect the mathematically indeterminate nature of the neuromusculoskeletal system (e.g. Crowninshield and Brand, 1981; Dul *et al.* 1984b; Herzog and Binding, 1992). In this case, it would not be possible to relate force variations to changes in walking mechanics.

### Materials and methods

Direct force measurements from gastrocnemius, soleus and plantaris muscles were

obtained from seven outbred, male cats (mass 3.5–4.5 kg) walking and trotting at a variety of systematically changing speeds. Complete force–time histories from all muscles of interest and for a minimum of 19 consecutive step cycles were obtained from four of the seven animals at a nominal walking speed of  $1.2 \text{ m s}^{-1}$ . These data were analyzed to evaluate step-by-step variations in the force–time histories of gastrocnemius, soleus and plantaris muscles. The partial results obtained from the remaining three animals were consistent with the information presented here.

Walking trials were executed on a motor-driven treadmill. The treadmill was 1 m long, thus leaving some space for the animals to move backwards and forwards; therefore, the treadmill speed (in this case,  $1.2 \text{ m s}^{-1}$ ) represents a nominal or average walking speed of the animal. For animals 1, 2, 3 and 4, the number of steps used in the analysis was 43, 25, 20 and 19, respectively. All experiments were filmed using a video camera (Motion Analysis, Santa Rosa, CA) with its optical axis perpendicular to the plane of movement. Video data were collected at rates of 60 Hz for animal 1, and 200 Hz for animals 2, 3 and 4. Step-cycle times were measured from the video records and were defined as the time period from footfall of the left (instrumented) hindlimb of step  $n$  to the corresponding footfall of step  $n+1$ .

Treadmill locomotion has been reported to differ in some aspects compared with overground locomotion in the cat (Wetzel *et al.* 1975), and this may have influenced some of the results reported here. However, these differences appeared to be mostly associated with the interlimb coordination (Wetzel and Stuart, 1976) and appeared to be strongly affected by changes in the treadmill speed, by the head position of the animal and by the avoidance of punishment [i.e. an air-shock to encourage the animal to walk (Wetzel *et al.* 1975; Wetzel and Stuart, 1976)]. The step cycles analyzed in this study were carefully selected in order to avoid introducing large differences between the treadmill locomotion and what is observed during overground locomotion. The selection of the steps used for analysis was performed with the help of the high-speed video records; only steps where the head and tail were held high, and where footfall occurred at the same location relative to the treadmill ( $\pm$  about 1.0 cm), were accepted for analysis. Furthermore, any punishing procedures, such as air-shock, were strictly avoided.

Simultaneous force measurements were obtained from gastrocnemius, soleus and plantaris muscles of the left hindlimb using ‘buckle’-type tendon force transducers (Walmsley *et al.* 1978; Herzog and Leonard, 1991; Herzog *et al.* 1992). Homemade, E-shaped, stainless-steel tendon force transducers (Fig. 1) were surgically implanted onto the tendons of gastrocnemius, soleus and plantaris muscles under strictly sterile conditions with the animals deeply anesthetized. These tendons may be accessed and separated by cutting the tendinous sheath surrounding the entire Achilles tendon. Soleus and plantaris transducers were fixed on the most distal, and the gastrocnemius transducer on the most proximal, aspect of the respective tendons to avoid interference between transducers. The open ends of the E-shaped transducers were closed using a suture to prevent slippage of the transducers relative to the tendons. Leads from the transducers were pulled subcutaneously to a connector on the back of the animal. From this connector, force signals were transferred to and stored in a computer (PC386) using a cable. Each tendon force transducer was connected *via* this cable to a force gauge



Fig. 1. Tendon transducer used for the recording of forces from cat soleus (small units on the scale shown are 1 mm). The holes at the end of the top and bottom bar of the E-shaped transducer are for suturing the transducer in place.

amplifier (model 2100, Micromeritics Group) to complete a Wheatstone bridge. Force data were collected at a frequency of 250 Hz for animal 1 and 625 Hz for animals 2, 3 and 4.

Five to seven days after transducer implantation, the cats had fully recovered from surgery as assessed by subjective observation of their walking and running movements, and as determined by the measured symmetry in stance times of their hindlimbs during these locomotor activities. After data had been collected, the tendon force transducers were calibrated in a terminal experiment with the animals deeply anesthetized. For calibration, each tendon was individually separated from its insertion site with a piece of bone. A series of at least 15 known weights was hung from each tendon, and a regression analysis between the transducer signals and the known forces was used to derive calibration curves. All transducers used in this experiment gave a linear output ( $r^2$  values for linear least-squares regressions were always larger than 0.990), showed almost perfect reliability and had no visible hysteresis. A static calibration could be used because it had been shown previously that static and dynamic calibrations are equivalent for this type of force transducer (e.g. Walmsley *et al.* 1978; W. Herzog, V. Zatiorsky, B. I. Prilutsky and T. R. Leonard, unpublished tests).

In order to assess means and standard deviations of the muscular forces over all step cycles, force-time histories were normalized with respect to stride-cycle duration. Means

and standard deviations of muscular forces were then calculated for the same relative instants in time. Time zero (in absolute and relative terms) always represented the start of the stance phase. In order to assess the relative contributions of each muscle to the total Achilles tendon force, individual muscle forces were normalized with respect to total Achilles tendon force for corresponding instants in time. Total Achilles tendon force was calculated as the sum of the forces of gastrocnemius, soleus and plantaris. A least-squares linear regression approach was used to relate force and timing variables to step-cycle times. The level of significance for all statistical tests was set at  $\alpha=0.01$ . The data collection was performed in a single day for each animal.

### Results

Fig. 2A–C shows the mean absolute force ( $\pm 1$  s.d.) of gastrocnemius, soleus and plantaris muscles over 43 steps as a function of relative time for animal 1. Approximately the first 60% of the time shown on the graphs corresponds to the stance phase, and the remaining 40% to the swing phase, of the step cycle. During the stance phase, gastrocnemius, soleus and plantaris muscles are active, high forces are produced and variations in force, indicated by the standard deviation curves, are considerable. During the swing phase, absolute values of the muscular forces and the corresponding standard deviations are small in all muscles.

Fig. 3A–D shows the mean absolute forces of gastrocnemius, soleus and plantaris of all four animals superimposed on one another and the sum of the forces of all three muscles, i.e. the total Achilles tendon force. Soleus forces typically contributed the least to the total Achilles tendon force at this speed of walking. Gastrocnemius forces were typically largest for about the first 25% of the step cycle and then became similar in magnitude to the plantaris forces for the remainder of the step cycle. On average (and also for most individual step cycles), the gastrocnemius muscle reached peak force first in all animals, followed by the soleus and then the plantaris muscle. Average peak force for the total Achilles tendon occurred at approximately the same time as the peak soleus forces.

Fig. 4A–C shows the mean force–time histories of gastrocnemius, soleus and plantaris muscles of animal 1, plus the corresponding mean force–time histories of the three steps yielding the highest (High) and the lowest (Low) peak forces. Note that the mean curves for the highest and lowest peak forces were obtained from different step cycles for the three muscles and that all step cycles were normalized with respect to time. In the gastrocnemius and soleus muscles, peak forces in the ‘high’-force steps are achieved through a steeper relative slope of the force–time curve for the initial part of the stance phase than in the ‘low’-force steps. For the plantaris muscle, the initial relative slope for all three force–time histories shown is similar, and the slopes start to differ only at force levels close to the peak force of the ‘low’-force step cycles. The average relative slopes of the descending part of the force–time histories during the stance phase (approximately from time 15% to time 60%) are similar for all conditions (i.e.  $-0.50$  N/%, Low;  $-0.51$  N/%, Mean; and  $-0.54$  N/%, High; Fig. 3B) in the soleus muscle. For gastrocnemius ( $-0.77$  N/%, Low;  $-1.01$  N/%, Mean; and  $-1.17$  N/%, High; Fig. 3A) and plantaris ( $-0.66$  N/%, Low;  $-0.76$  N/%, Mean; and  $-0.82$  N/%, High; Fig. 3C),

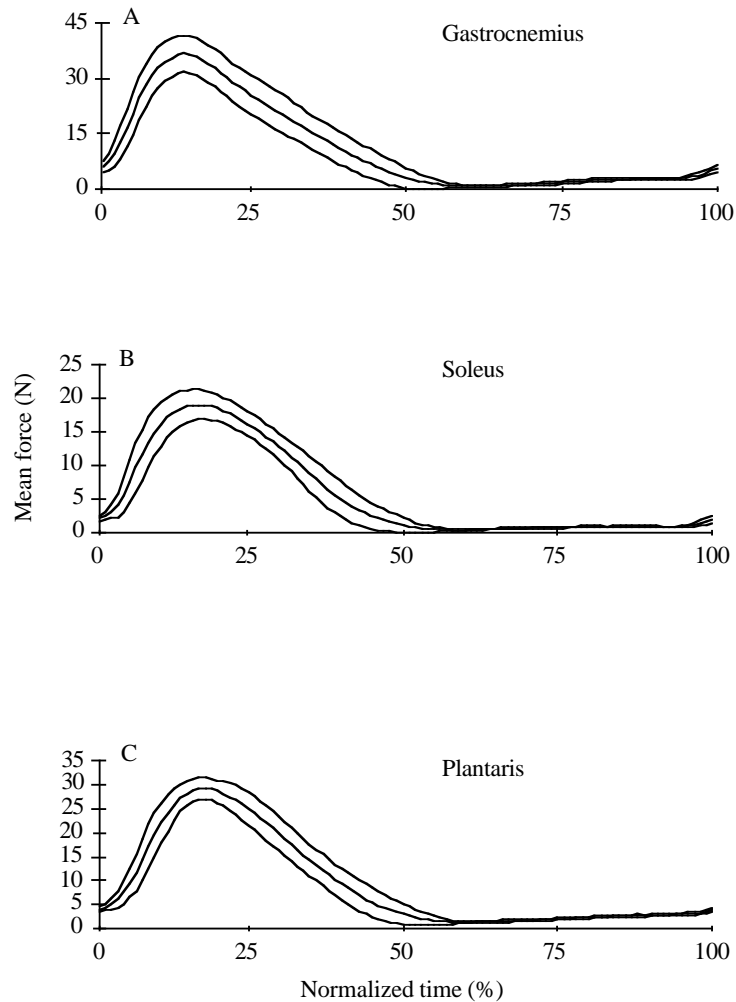


Fig. 2. Mean force–time histories ( $\pm 1$  S.D.) of gastrocnemius (A), soleus (B) and plantaris (C) muscles for animal 1 walking at a constant nominal speed of  $1.2 \text{ m s}^{-1}$ . Mean forces were calculated from 43 step cycles. Times were normalized relative to step-cycle durations. Paw contact occurs at time 0% and is followed by the stance (approximately 0–60%) and swing (approximately 60–100%) phases.

these slopes tend to be steeper for the ‘high’-force steps than for the ‘low’-force steps. During the swing phase of the step cycle, there are no visible differences between the forces for the three conditions shown, possibly with the exception of the last part of the swing phase for the soleus muscle.

In the preceding figures, it was shown that there are considerable differences in the time histories of the muscular forces obtained from a given animal walking at a constant nominal speed. If force-sharing among muscles occurs in a systematic and unique way (as is implicitly assumed in the theoretical approaches aimed at addressing force-sharing

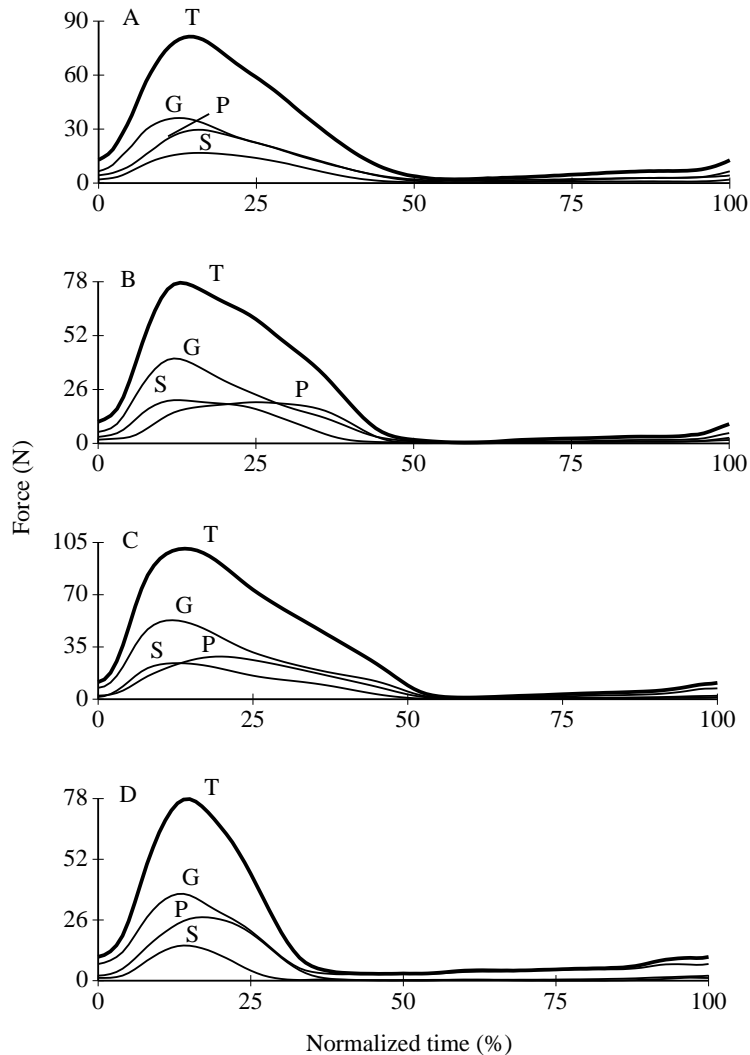


Fig. 3. Mean force–time histories of cat gastrocnemius (G), soleus (S) and plantaris (P) muscles (as shown in Fig. 2), plus the sum of these three forces (T), representing an estimate of the total Achilles tendon force, for animals 1–4 (A–D), respectively, walking at a constant nominal speed of  $1.2 \text{ m s}^{-1}$ . The contribution of soleus forces to the total Achilles tendon force tended to be smallest throughout the step cycle. Gastrocnemius forces were largest for about the first 25% of the step cycle and then became about equal to plantaris forces for the remaining 75% of the step. Peak forces tended to occur first in the gastrocnemius muscle, followed by the soleus and then the plantaris.

questions), it must be possible to relate the variations shown above to corresponding changes in dynamic variables. This comparison has been attempted in Fig. 5A–C, where the forces of the three steps with the third, fourth and fifth longest and the third, fourth and fifth shortest step-cycle time (thick and thin lines, respectively) of animal 1 are plotted as

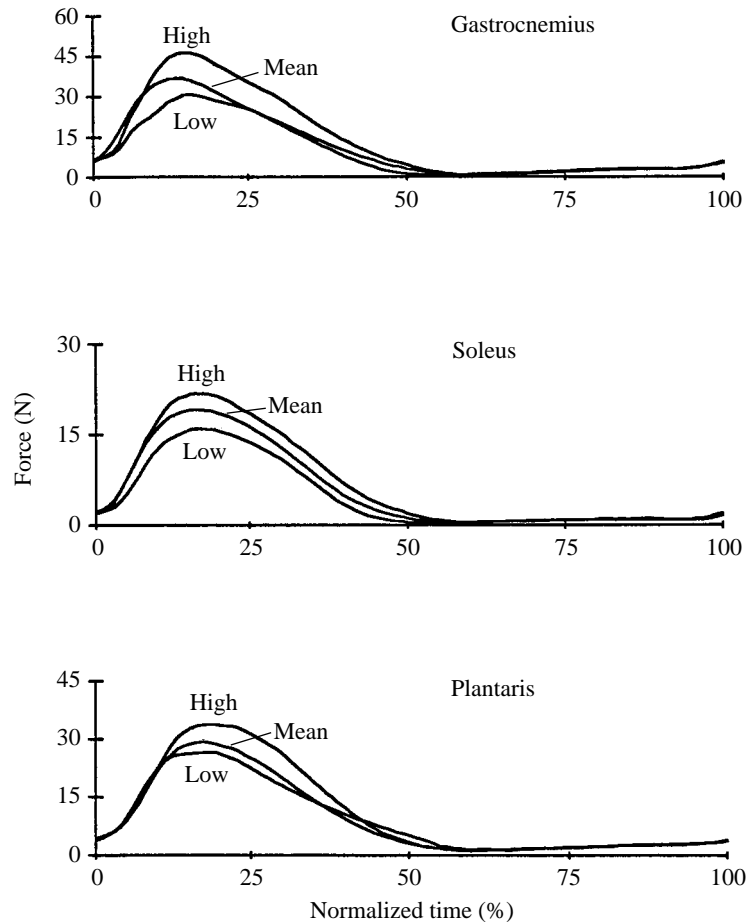


Fig. 4. Mean force–time histories (Mean) of gastrocnemius (A), soleus (B) and plantaris (C) muscles, plus corresponding means of the three steps, yielding the highest (High) and lowest (Low) peak forces for animal 1 walking at a constant nominal speed of  $1.2 \text{ m s}^{-1}$ . Note that the step cycles in which one muscle achieved the highest (or lowest) peak force values are not necessarily the same step cycles in which the remaining muscles reached their highest (or lowest) values.

a function of absolute step-cycle time. Although step-cycle time is only one of many possible variables that were used to describe the kinematics of a step, it appeared to be systematically related to changes in muscular forces.

The results shown in Fig. 5A–C suggest that, compared with steps of short duration, steps of long duration (thick lines) are associated with somewhat smaller peak forces for gastrocnemius and plantaris muscles and with larger peak forces for soleus muscle. When tested statistically, this trend was supported for soleus and plantaris muscles (Fig. 6B,C); however, the relationship between peak forces of the gastrocnemius muscle and corresponding step-cycle times failed to reach statistical significance for this animal (Fig. 6A) and for all the remaining animals tested. Statistically significant relationships



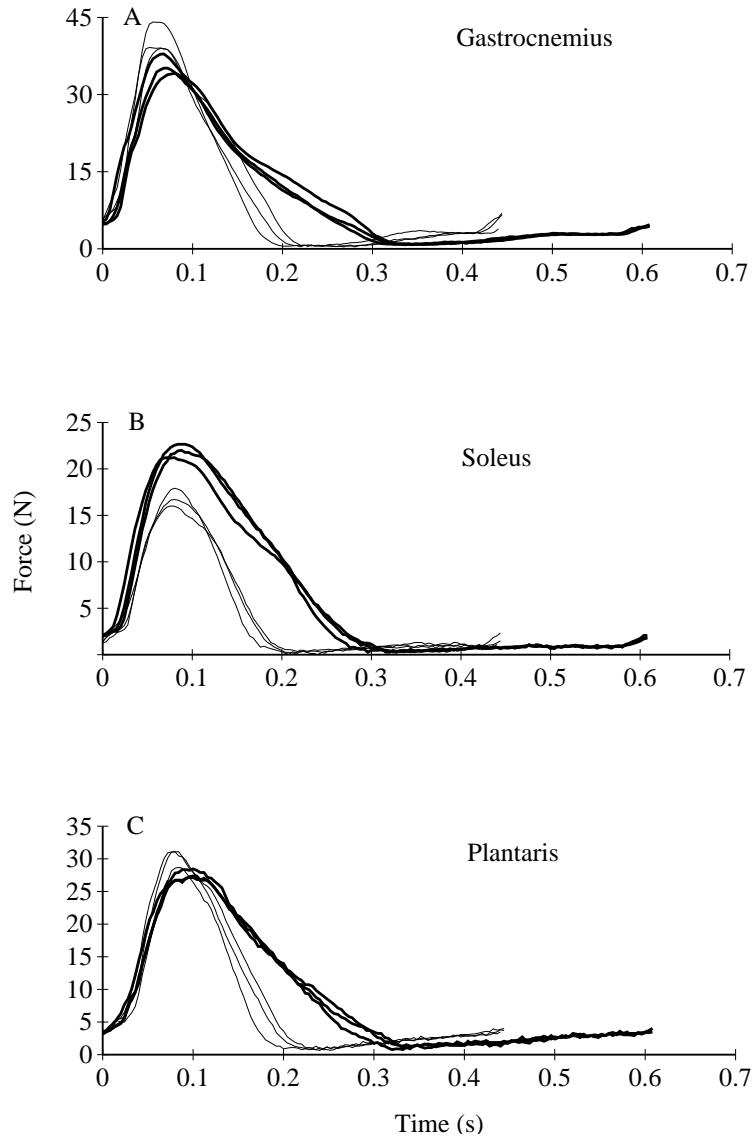


Fig. 5. Selected force–time histories of gastrocnemius (A), soleus (B) and plantaris (C) muscles for animal 1 walking at a constant nominal speed of  $1.2 \text{ m s}^{-1}$ . The thick traces correspond to the steps of third, fourth and fifth longest, and the thin traces to the steps of third, fourth and fifth shortest, step-cycle duration among all 43 steps analyzed for this animal. The force–time histories of all three muscles appear to be systematically related to step duration, although not necessarily in the same way.

between peak soleus and peak plantaris forces and step-cycle times were found in two out of four animals. The statistical analysis, therefore, does not support any significant relationship between muscle force and step duration for the conditions studied here.

Variations in the force–time histories of all muscles between steps of long and short

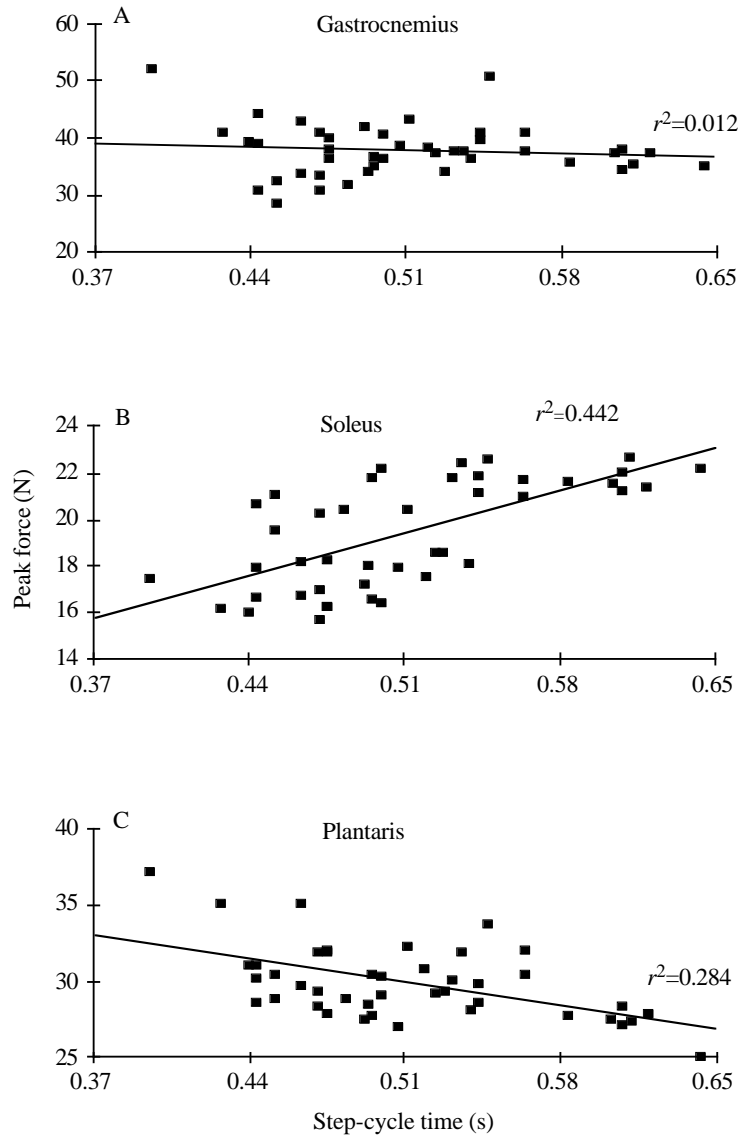


Fig. 6. Least-squares linear regression analysis between peak forces and step-cycle times for gastrocnemius (A), soleus (B) and plantaris (C) muscles of animal 1.

duration appeared to be associated primarily with the second part of the stance phase (i.e. at or after reaching peak forces) rather than with the initial part of the stance phase immediately following paw contact (Fig. 5A–C). This observation was quantified statistically by relating the force-relaxation time (i.e. the period from the instant of peak force to the instant of minimal force) to the step-cycle time. There was a significant correlation between the force-relaxation time and the step-cycle time for all muscles tested in each animal (Fig. 7A–C).

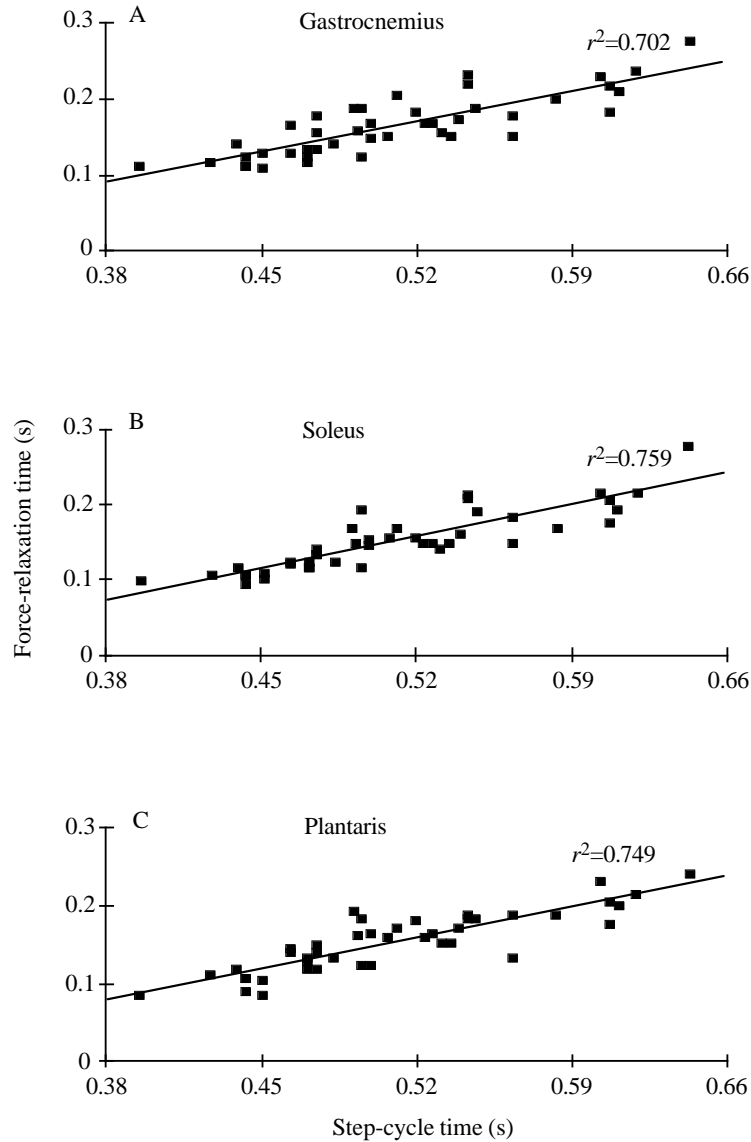


Fig. 7. Least-squares linear regression analysis between the force-relaxation times and step-cycle times for gastrocnemius (A), soleus (B) and plantaris (C) muscles of animal 1. Force-relaxation time was defined as the period from the instant of occurrence of peak force to the instant of occurrence of minimal force.

The corresponding relationships between the time of force development (i.e. the period from the instant of paw contact to the instant of peak force) and the step-cycle times were not significant for gastrocnemius and soleus in any of the animals tested, suggesting that the achievement of peak force of these muscles occurs within the same approximate time period after paw contact, regardless of the slight variations in the step-cycle times. The

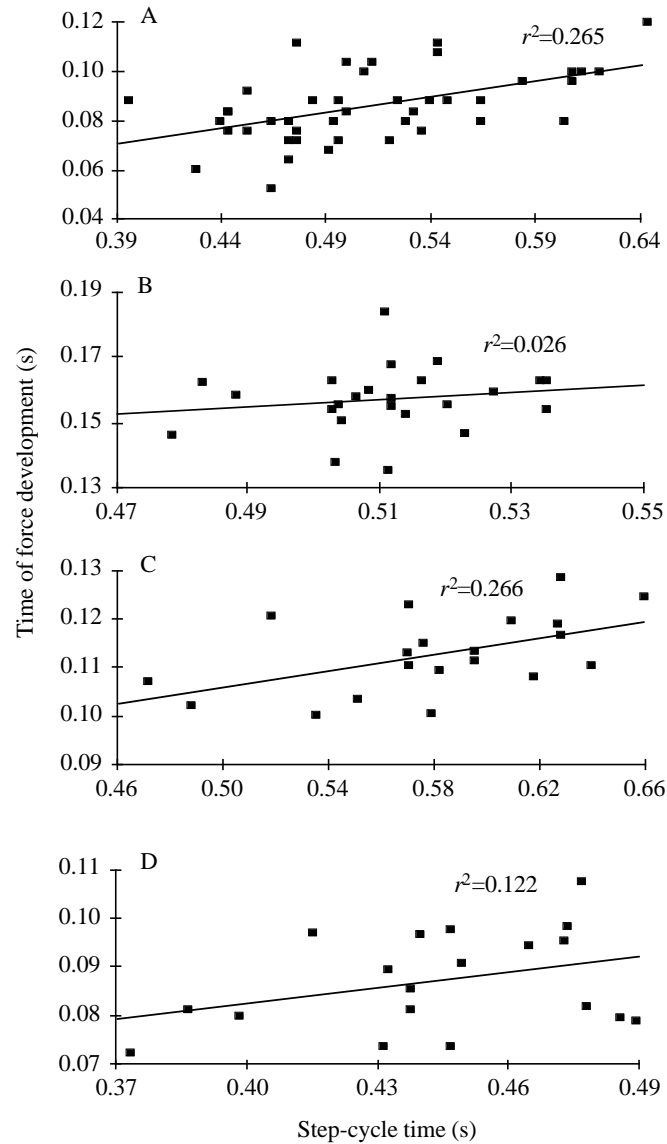


Fig. 8. Least-squares linear regression analysis between times of force development and step-cycle times for plantaris muscles of animals 1–4 (A–D), respectively. Time of force development was defined as the period from the instant of occurrence of paw contact to the instant of occurrence of peak force.

relationship between the time of force development and the step-cycle time for plantaris was significant for animals 1 and 3, but not for animals 2 and 4, although these latter animals showed the same trend as animals 1 and 3 (Fig. 8A–D). The significant correlations were obtained for the two animals with the largest difference in step-cycle times (i.e. 24 ms, cat 1, and 19 ms, cat 3; *versus* 6 ms, cat 2, and 12 ms, cat 4), suggesting

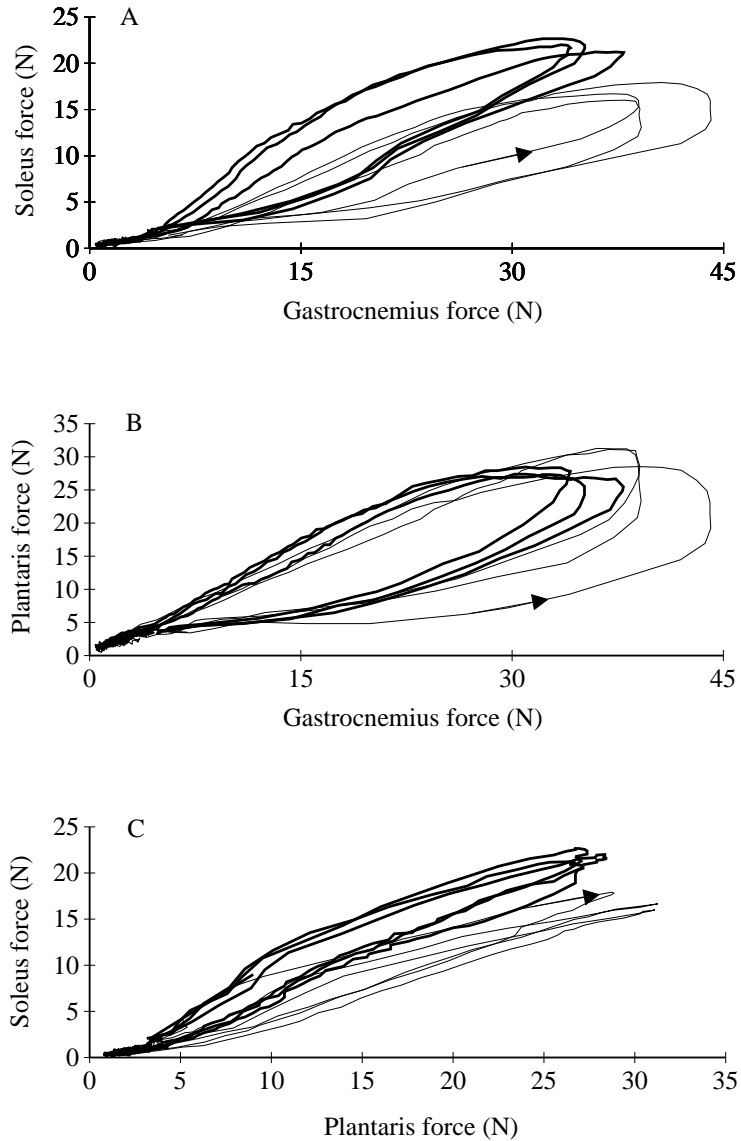


Fig. 9. Force-sharing between soleus/gastrocnemius (A), plantaris/gastrocnemius (B) and soleus/plantaris (C) muscles for animal 1 walking at a constant nominal speed of  $1.2 \text{ m s}^{-1}$ . Thick force-sharing curves represent the trials of third, fourth and fifth longest step-cycle duration, and thin curves those of third, fourth and fifth shortest step-cycle duration, among all 43 steps analyzed for this animal.

that plantaris peak forces are reached significantly later in the step cycle if step-cycle times are increased sufficiently.

Fig. 9A–C shows force-sharing plots between soleus/gastrocnemius, plantaris/gastrocnemius and soleus/plantaris, respectively, for the six steps presented in Fig. 5 for

animal 1. Each 'loop' corresponds to the stance phase of one step, whereas the dense accumulation of lines towards the origin of the graphs corresponds to the swing phase. Direction of force build-up and decay is indicated by the arrow and is counter-clockwise for all force-sharing plots between soleus/gastrocnemius and plantaris/gastrocnemius (Fig. 9A,B) and is clockwise for all plots of soleus/plantaris (Fig. 9C). The force-sharing 'loops' between soleus and gastrocnemius have similar shapes for all six steps shown; however, they tend to be shifted from soleus towards gastrocnemius as step-cycle durations become shorter (Fig. 9A). The same observation may be made for the force-sharing between soleus and plantaris (Fig. 9C). Force-sharing between plantaris and gastrocnemius appears to be associated with a change in the shape of the force-sharing 'loops' as step-cycle duration varies. Steps of short duration tend to have a faster increase in force in gastrocnemius relative to plantaris, which results in a wider 'loop' for these steps compared to steps of long duration (Fig. 9B).

### Discussion

Force-time histories of cat gastrocnemius, soleus and plantaris muscles varied for consecutive step cycles during walking at a nominal speed of  $1.2 \text{ m s}^{-1}$  on a motor-driven treadmill (Figs 2A-C, 4A-C). The variations observed in this study were smaller than those typically shown in the literature (e.g. O'Donovan *et al.* 1983; Hodgson, 1983; Hoffer *et al.* 1989), probably because the step cycles were carefully selected from high-speed video records. Furthermore, the speed of walking chosen for this analysis ( $1.2 \text{ m s}^{-1}$ ) is fast enough to produce stable gait patterns in the cat. Standing or slow speeds of walking (approximately  $0.4\text{--}0.6 \text{ m s}^{-1}$ ) tend to produce force-time histories of muscles that are distinctly more variable than those observed here (e.g. Hodgson, 1983; Hoffer *et al.* 1989).

The variations observed in the force-time histories of the individual muscles were reflected by the corresponding changes in force-sharing among these muscles (Fig. 9A-C). The changes observed in the force-sharing 'loops' for steps of long and short duration were similar in tendency but much smaller in magnitude than corresponding changes observed for locomotor tasks performed at distinctly different speeds (Hodgson, 1983; Herzog and Leonard, 1991).

One of the purposes of this study was to evaluate whether variations in muscular force-time histories for a given cyclic movement were random or could be associated systematically with small variations in the execution of the movement. We found that selected variables describing the force-time histories of gastrocnemius, soleus and plantaris could be related systematically to corresponding variations in the kinematics of movement execution. Qualitatively, this finding is illustrated in Fig. 5A-C, where force-time histories of gastrocnemius, soleus and plantaris are plotted for three steps of short and three steps of long duration that were selected from 43 steps performed at a constant nominal speed. Quantitatively, this observation was described by relating selected variables of the force-time histories to step-cycle times (Figs 6-8).

When relating selected variables of the force-time histories of gastrocnemius, soleus and plantaris to step-cycle times, it was observed that certain variables of the three

muscles were related in the same way to step-cycle times, whereas other variables showed different or even opposite trends for one muscle compared with the others. For example, the force-relaxation time was positively correlated with step-cycle times for all muscles and each animal (Fig. 7A–C); whereas peak forces of gastrocnemius were not related to step-cycle times for any of the animals tested, while peak forces of soleus and plantaris tended to be positively and negatively correlated to step-cycle times, respectively (Fig. 6A–C).

The fact that selected variables of the force–time histories of gastrocnemius, soleus and plantaris were correlated to step-cycle time suggests that variations in force–time histories of muscles occur in a systematic rather than a random way and may be associated with variations in movement execution. Furthermore, the observation that correlations of a given variable of the force–time histories with step-cycle times may be different for gastrocnemius, soleus and plantaris suggests that these agonistic muscles in ankle plantar-flexion may have motoneuron pools that are, at least partly, independent of one another. This suggestion is further supported by the mean force–time histories of gastrocnemius, soleus and plantaris obtained for all experimental animals (Fig. 3A–D), which may be interpreted to show a distinctly different function for each muscle. For example, forces in gastrocnemius are always large early in the step cycle and reach a peak before those in soleus and plantaris, whereas plantaris forces tend to be small in the early stages of the stance phase, reaching a peak when gastrocnemius forces are already clearly decreasing and becoming relatively large in the latter part of the stance phase.

The hypothesis that the motoneuron pools of these muscles are at least partly independent of each other is further supported in the literature. For example, it has been shown that the soleus is active during quiet standing, whereas the medial gastrocnemius may be silent (Rasmussen *et al.* 1978; Hodgson, 1983). Furthermore, it has been demonstrated that there is a clear dissociation of the onset and finish of soleus, plantaris, lateral and medial gastrocnemius activity during normal cat locomotion (Rasmussen *et al.* 1978), whereas this dissociation appears to be lost for locomotion of the mesencephalic cat (Gambarjan *et al.* 1971). A partial independence of motoneuron pools has not only been demonstrated for individual synergistic muscles, but also for different compartments of the same muscle – for example, the lateral gastrocnemius of the cat (English and Letbetter, 1982*a,b*; English, 1984; English and Weeks, 1984).

A dissociation of the activation patterns of soleus, gastrocnemius and plantaris is probably quite useful, because these muscles span across different joints and, thus, the activity patterns can accommodate possible secondary functions (i.e. functions not directly related to ankle extension) of these muscles. Soleus acts only as a one-joint ankle extensor. However, gastrocnemius crosses the knee and the ankle, and plantaris crosses the knee and the ankle and has a partial, in-series, arrangement with the flexor digitorum brevis for flexing the toes late during the stance phase of walking (Goslow *et al.* 1972; Abraham and Loeb, 1985).

Variations in peak forces of soleus, observed in this study (i.e. with the animal walking at a constant nominal speed) were larger than the changes in mean peak forces of soleus observed for locomotor speeds ranging from  $0.4 \text{ m s}^{-1}$  (walking) to  $2.4 \text{ m s}^{-1}$  (trotting; Herzog and Leonard, 1991; Herzog *et al.* 1993). This finding suggests that forces of

soleus are very sensitive to small changes in walking kinematics, whereas they are virtually not influenced (on average) by large changes in the speed of walking or changes in the mode of locomotion [i.e. going from walking to a trotting mode (Herzog *et al.* 1993)]. In contrast, peak forces of gastrocnemius were not related to step-cycle times for walking at a nominal speed of  $1.2 \text{ m s}^{-1}$ , but increased 4–5 times from walking at  $0.4 \text{ m s}^{-1}$  to trotting at  $2.4 \text{ m s}^{-1}$  (Herzog and Leonard, 1991), suggesting that gastrocnemius is not sensitive to small changes in movement execution but adapts dramatically to large changes in locomotor speed and changes in the mode of locomotion. Peak forces of plantaris tend to be somewhere between the extremes found for gastrocnemius and soleus.

When studying control of muscular forces of agonistic muscles during locomotion, the typical approach has been to evaluate ‘representative’ or ‘typical’ step cycles (Walmsley *et al.* 1978; Hodgson, 1983; Abraham and Loeb, 1985; Hoffer *et al.* 1989; Herzog *et al.* 1992), or to analyze force–time histories or force-sharing of muscles for data ‘averaged’ over many step cycles (Herzog and Leonard, 1991; Herzog *et al.* 1993). The results of this study show that there are variations from one step cycle to the next and, further, that these variations may be systematically related to changes in the execution of a movement. Therefore, it appears that there may be considerable merit in analysing force-sharing behaviour among muscles for a series of individual step cycles and that conclusions based on a ‘representative’ or ‘averaged’ step must be considered with caution.

Theoretical approaches aimed at predicting individual muscle forces (e.g. Seireg and Arvikar, 1973; Penrod *et al.* 1974; Pedotti *et al.* 1978; Crowninshield, 1978; Crowninshield and Brand, 1981; Herzog, 1987*a,b*) or force-sharing among muscles (e.g. Dul *et al.* 1984*a,b*; Herzog and Leonard, 1991; Herzog, 1992; Herzog and Binding, 1992) were based (implicitly or explicitly) on the assumption that a given movement is executed with identical force–time histories of all muscles involved. Because of the redundant nature of the musculoskeletal system (Bernstein, 1947), this assumption is not necessarily correct; however, the results of this study support the notion that a given movement is executed with identical (or at least very similar) force–time histories of all muscles involved. This conclusion is based on the fact that selected variables of the force–time histories of gastrocnemius, soleus and plantaris could be associated systematically with a kinematic variable describing the small changes in the walking movement that occur for consecutive step cycles. If the redundant nature of the musculoskeletal system gave rise to randomly varying muscular force–time histories for executing a given movement, the systematic relationships between muscular forces and walking kinematics would not have been observed. Small variations in a given movement, which always exist and which may be associated with the concept of ‘facultative’ walking or stepping (Wetzel and Stuart, 1976), are therefore associated with systematic (and small) changes in muscular force–time histories.

Quantitatively, it appears that the initial part (about the first 50 ms) of the force–time histories of gastrocnemius, soleus and plantaris are virtually identical for consecutive step cycles executed at a given nominal speed of locomotion, whereas the latter part (after peak forces have been reached) differ substantially (Fig. 5A–C). This observation is supported by the lack of a statistical relationship between step-cycle duration and the



force at paw contact, or the average rate of increase in force in the first 50 ms of the stance phase (results not shown), and also by the strong relationship between the step-cycle duration and the force-relaxation times for gastrocnemius, soleus and plantaris in all animals (Fig. 7A–C). Therefore, the results of this study are in agreement with the idea of a pattern generator that may be modified through proprioceptive pathways. The pattern generator is responsible for the very consistent initial part of the force–time histories of gastrocnemius, soleus and plantaris during the stance phase of a step cycle; effective modulation of this pattern through cutaneous, spindle, Golgi tendon or other afferent pathways may occur only with a delay corresponding to the period from the stimulation of a proprioceptor until the effect may be seen in the muscle.

We found that there are considerable variations in the force–time histories of gastrocnemius, soleus and plantaris of cats walking at a constant nominal speed of  $1.2 \text{ m s}^{-1}$ . These variations appear to be systematically related to changes in movement kinematics, suggesting that motoneuron pools of cat gastrocnemius, soleus and plantaris may be partly independent of one another and, therefore, control of forces in one muscle may occur (at least partly) independently of the control of the remaining two muscles. On the basis of the results of this investigation, we believe that much insight may be gained into the mechanisms of control of muscular forces by analyzing large numbers of consecutive cycles of a given movement.

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