The control of mono-articular muscles in multijoint leg extensions in man

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1. Movements often require control of direction and a magnitude of force exerted externally on the environment. Bi-articular upper leg muscles appear to play a unique role in the regulation of the net torques about the hip and knee joints, necessary for the control of this external force.
2. The aim of this study was to test the hypothesis that the mono-articular muscles act as work generators in powerful dynamic leg extensions, which means that they should be activated primarily in the phases during which they can contribute to work, irrespective of the net joint torques required to control the external force.
3. Cycling movements of six trained subjects were analysed by means of inverse dynamics, yielding net joint torques as well as activity patterns and shortening velocities of four mono- and four bi-articular leg muscles.
4. The results show that the mono-articular muscles exert force only in the phase in which these muscles shorten, whereas this appears not to be the case for the bi-articular muscles.
5. Reciprocal patterns of activation of the rectus femoris and hamstring muscles appear to tune the distribution of net joint torques about the hip and knee joints, necessary to control the (changing) direction of the force on the pedal.
6. An analysis of running in man and additional related literature based on animal studies appears to provide further support for the hypothesis that mono- and bi-articular muscles have essentially different roles in these powerful multijoint leg extension tasks.

Both neurophysiological and biomechanical literature provide increasing evidence that the mono- and bi-articular upper leg muscles can have essentially different roles and that the organization of their neural control is based on different but parallel processes. As recently emphasized by Pratt & Macpherson (1992), knowledge about these differential roles in multijoint movements is essential for understanding the general principles of movement control.

Many studies of leg and arm movements of both animals and man have revealed that bi-articular muscles show complicated and task-dependent behaviour during multijoint movements, whereas mono-articular muscles seem to be organized into basic flexor–extensor synergies (Walmsley, Hodgson & Burke, 1978; Perret & Cabelguen, 1980; Loeb, Hoffer & Marks, 1985; Smith & Zernicke, 1987; Bekoff, Nusbaum, Sabichi & Clifford, 1987; van Ingen Schenau, 1989; Buford & Smith, 1990; Pratt, Chanaud & Loeb, 1991).

Intracellular studies of motoneuron responses evoked through stimulation of hindlimb afferents, particularly cutaneous, demonstrated that motoneurons of mono-articular muscles show either excitatory or inhibitory responses. Motoneurons which innervate bi-articular muscles, however, appear to receive complex mixtures of multimodal inputs leading to task-dependent responses which can even reverse in sign from excitatory to inhibitory or vice versa during the different phases of a movement (e.g. Eccles & Lundberg, 1959; Schomberg & Behrends, 1978; Vidal, Viala & Buser, 1979; Aniss, Gandevia & Burke, 1988; Nichols, 1989; Pratt *et al.* 1991; Pratt & Macpherson, 1992).

Biomechanical analyses of various powerful leg extension tasks in man led us to the hypothesis that bi-articular muscles are particularly involved in the fine regulation of the distribution of net torques over the two joints crossed whereas mono-articular muscles seem to act mainly as force or work generators (van Ingen Schenau, 1989; van Ingen Schenau, Boots, de Groot, Snackers & van Woenzel, 1992; van Ingen Schenau & Bobbert, 1993). The regulation of net joint torques appears especially relevant in the control of tasks which require that the hand or foot exerts a force on the environment in a prescribed direction; for example, in posture control or in order to move an object or one's own body in a particular direction (van Ingen Schenau *et al.* 1992). This is also true when accounting for the dynamics of the body segments (van Ingen Schenau, Pratt & Macpherson, 1994).

Recent experiments, in which subjects had to exert a force on a force plate in various prescribed directions from three different static leg positions, provide strong evidence in favour of the hypothesized role of bi-articular muscles (Jacobs & van Ingen Schenau, 1992). The difference in (normalized) activity between hamstrings and rectus femoris appeared to be strongly correlated with the difference in net joint moments about the hip and knee (mean correlation coefficient, $r = 0{\cdot}97$; $n = 7$). Even when calculated over all three leg positions, 90% of the variation in the prescribed directions of the external force appeared to be explained by shifts in reciprocal activation of these bi-articular antagonists. The role of mono-articular muscles, however, appeared to be less clear in these static experiments. From a mechanical perspective it was suggested that mono-articular muscle activation would depend on their mechanical advantage, that is, on the extent to which they can contribute to virtual external work (see Jacobs & van Ingen Schenau, 1992, for details of the virtual work concept). It was argued that the lack of a clear relation with virtual work might be a result of the absence of actual movements and, as a consequence, the absence of proprioceptive information about the (virtual) muscle shortening. Moreover, the tasks were rather unfamiliar to the subjects, which led us to the expectation that the hypothesized action of mono-articular muscles would be more obvious in dynamic leg tasks which are more common.

The purpose of the present study was to discover the extent to which mono-articular muscles act as ideal work generators in a task which requires considerable external work and which is highly familiar to experienced subjects, in this case, cycling. As in many other leg extensions, such as those occurring in jumping and running, optimal work generation of mono-articular muscles requires an overlap between the phases of muscle shortening and the phases in which the muscles deliver force. From various experiments, however, it is known that there is a considerable time delay (EMD, electromechanical delay) between muscle activation as measured electromyographically and the force response measured externally. This means that the control signals relative to the expected periods of muscle shortening must be anticipated by the CNS. For cycling this means that one would expect the CNS to activate the mono-articular muscles in such a way that the period in which their force response can contribute to the pedal force coincides with the period during which the muscle can shorten. Cross-correlation techniques are used to test this. EMD was measured in the cycling position and was compared with the time shift (T) between EMG and muscle shortening velocity for a number of mono- and bi-articular muscles measured during cycling. In the light of the proposed differential roles of the two muscle types, the EMD should equal T for all mono-articular muscles whereas this should not necessarily be true for the bi-articular muscles.

METHODS

Six well-trained cyclists consented to participate in the experiments. After warming up, the subjects cycled on a bicycle ergometer at a pedal frequency of 80 r.p.m. The subjects wore cleated shoes and used toe clips. The load setting was chosen so that the power output was approximately 450 W. This high load setting was chosen in order to achieve relatively large signal-to-noise ratios. The experiments were approved by the local ethical committee. The bicycle ergometer was equipped with pedals which measured forces along and perpendicular to the pedal surface. Incremental encoders (model 63; Leine and Linde AB, Strångnås, Sweden) were used to measure the angle of the crank relative to the vertical, and the angle between the pedal and the crank. The movements of the right leg were filmed with a 16 mm high-speed camera (Teledyne DBM 55, Teledyne Camera Systems, Arcadia, CA, USA). The camera was positioned perpendicular to the sagittal plane and operated at 104 frames per second. Markers were placed on the top of the iliac crest, the greater trochanter, the estimated centre of rotation of the knee, the lateral malleolus, the fifth metatarsophalangeal joint, the pedal axes and on a fixed reference point. A vertical and a horizontal bar, placed in the same plane as the bicycle, were used to reconstruct the 2-D co-ordinates of the markers. The films were analysed using a (NAC) motion analyser. The co-ordinates of the markers were filtered with a Butterworth fourth-order low-pass filter (zero lag; cut-off frequency, 17 Hz). Joint positions, joint angles and positions of the mass centres of pedal/foot, lower leg and upper leg were calculated from these markers. Segmental masses and moments of inertia were estimated on the bases of body mass and segmental lengths using data of Dempster (1955) and Winter (1979).

EMG activity was measured from the gluteus maximus (GM), rectus femoris (RF), vastus lateralis (VL), vastus medialis (VM), biceps femoris caput longum (BF), semitendinosus (ST), gastrocnemius medialis (GA) and soleus (SOL) muscles. Surface electrodes (silver–silver chloride; Sentry Medical Products, CA, USA) were positioned at the approximated geometrical centre of the muscle belly with an interelectrode distance of 2 cm. From previous experiences with the analyses of different leg movements (vertical jumping, speed skating, running, walking, lifting) which revealed quite large differences in muscle activation patterns (both with respect to amplitudes and to relative timing), it can be concluded that cross-talk between these muscles must be small. This suggests that the same must also be true for the cross-talk of other muscles. Raw EMG was filtered (bandpass, 25–200 Hz), rectified and A/D converted (12 bit; sample frequency, 400 Hz) into a microcomputer. To obtain patterns of muscle activity, the rectified EMGs were low-pass filtered (fourth-order Butterworth; zero phase lag; cut-off frequency, 13 Hz).

Muscle contraction velocities were calculated from the angular velocity and angle at the joint(s) crossed by the muscle. Using the methods introduced by Grieve, Pheasant & Cavanagh (1978), various authors have measured muscle length changes as a function of changing joint angles and expressed these relationships in second-order polynomes (Grieve *et al.* 1978; Hawkins, 1989; Visser, Hoogkamer, Bobbert & Huijing, 1990). For bi-articular muscles this was done for both joints separately. By taking the time derivative of these functions, the muscle contraction velocities were expressed in joint angular velocities and joint angles. These velocities represent the contraction velocities of the entire musle–tendon complexes. No reliable study was found which contained a complete set of data. Therefore it was necessary to choose the coefficients of the polynomes for the muscles from different studies. The coefficients for the RF, VL and VM were taken from Visser *et al.* (1990), those for BF and ST from Hawkins (1989) and those for GA and SOL from Grieve *et al.* (1978). For GM we took the results of Nemeth & Ohlsen (1985), who used a tomographic scanning technique. Joint torques were calculated on the basis of inverse dynamics: Newtonian equations of motion were applied to three segments (foot/pedal, lower leg and upper leg), yielding the net torques and forces in the ankle, knee and hip joint. A five-point numerical differentiating filter was applied to obtain the acceleration of the segmental centres of mass and the angular accelerations of these segments which are required for these equations. For each subject, five successive pedal revolutions were analysed.

To obtain a measure for the delay between the muscle activity patterns obtained from the EMGs of the muscles and the force on the pedal, the subjects were asked to push on the pedal in a static position (crank was fixed at an angle of 90 deg from the vertical). During approximately 10 s, the subjects pushed and relaxed with a frequency of about one contraction per second at a (pedal) force level comparable to that found during cycling. The muscle activity patterns were cross-correlated with the pedal force. This is a signal-processing technique in which the correlation between two signals is calculated as a function of a phase shift in time (τ) between the two signals. Electromechanical delay was defined as the phase shift $\mathrm{EMD} = \tau$ which yielded the highest correlation coefficient (Vos *et al.* 1991). Clearly, this does not lead to the actual EMD for each separate muscle, since the force on the pedal is the result of the additional activity of other muscles. However, since we did not observe significant differences in the timing of the onsets of muscle activity in this static task, we assumed that the error associated with this phenomenon is limited.

The possible relationship between muscle activity and muscle shortening was investigated by cross-correlating the activity pattern of the muscle with the contraction velocity data of the same muscle, as obtained during the five successive cycles. The phase shift $\tau = T$ between these two signals was defined as the time shift which yielded the highest correlation coefficient.

For all muscles, Student's paired t tests were used to determine the significance of the differences between EMD and T ($P < 0{\cdot}05$).

In addition to the data based on this analysis of cycling, some comparable data based on running are presented.

RESULTS

Cycling

The mean EMDs, calculated from the static experiments, and the phase shifts, T, between muscle activity and the mean muscle shortening velocity of the subjects are presented in Table 1 for the four mono- and the four bi-articular muscles analysed. Note that values of T for the mono-articular muscles do not differ from the EMDs measured for these muscles, while for the bi-articular muscles this is only the case for the gastrocnemius muscle. The mean EMD for all mono-articular muscles is 93 ± 30 ms and is not significantly different from the mean value for the bi-articular muscles (95 ± 35 ms). The mean value for all muscles is 94 ± 34 ms.

Typical examples of the net joint torques are presented in Fig. 1. Note that the hip torque increases during the first part of the downstroke (between 0 and 90 deg) and remains relatively high during the second part (between 90 and 180 deg), while the torque about the knee decreases to negative values (which means flexing torque) well before bottom dead centre (180 deg) and thus in a period in which the knee is still extending.

Figure 2 shows a number of successive leg and pedal positions and the vectors of the force on the pedal taken from the same cycles as the data presented in Fig. 1. Note the change in direction of the force on the pedal.

Typical examples of muscle activity and the shortening velocity of the muscles are presented in Fig. 3. The reason for presenting typical examples rather than mean curves is that temporal aspects are easily obscured by averaging these results.

The main hypothesis tested in this study is that the mechanical output of the mono-articular muscles coincides with the periods of muscle shortening, irrespective of the required torques about the joints that are crossed. When comparing Fig. 1 with Fig. 3 it is clear that at the knee, a

Table 1. Electromechanical delay (EMD) and phase shift (T) between muscle activity and muscle shortening velocity of the six subjects

	Mono-articular muscles				Bi-articular muscles			
	GM	VL	VM	SO	RF	BF	ST	GA
T (ms)	84 ± 9	94 ± 8	92 ± 23	116 ± 27	144 ± 24	177 ± 45	159 ± 53	140 ± 49
EMD (ms)	91 ± 36	89 ± 29	92 ± 24	99 ± 26	85 ± 30*	96 ± 49*	91 ± 41*	108 ± 43

Values are means ± S.D. * Significant difference between EMD and T.

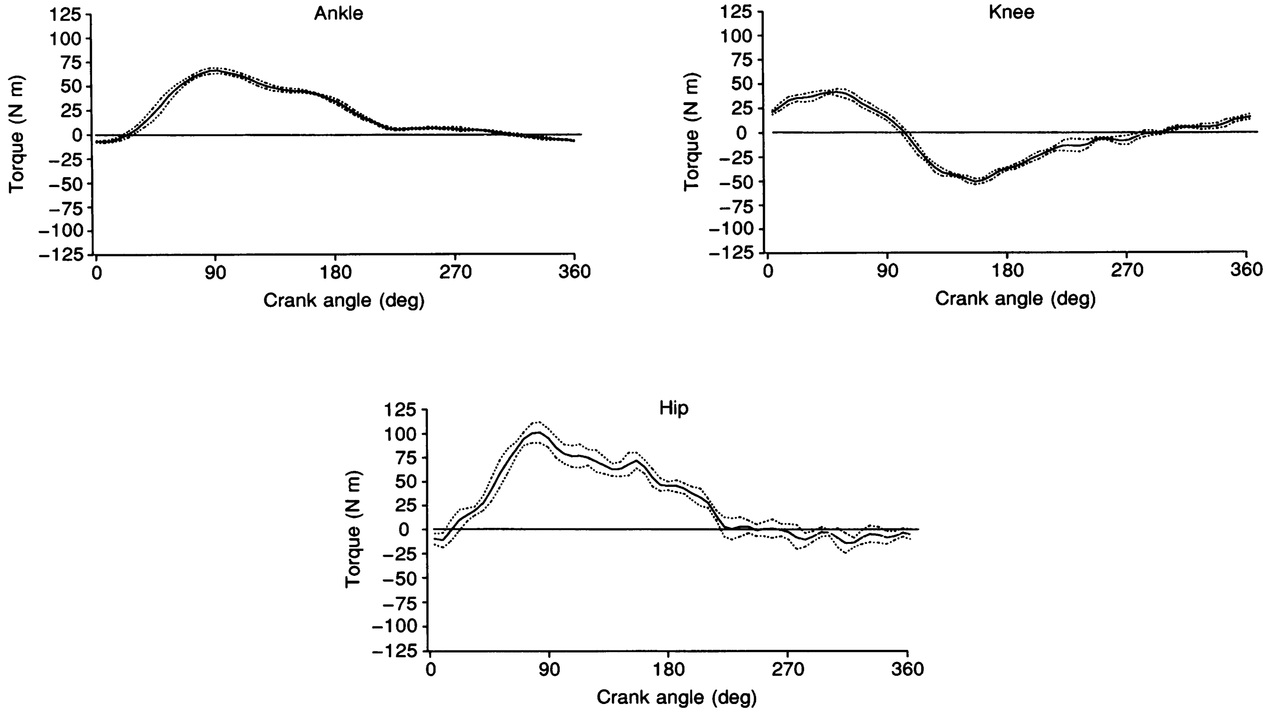

Figure 1. Net joint torques during cycling

Typical examples of the net torques in hip, knee and ankle as a function of crank angle, where the top dead centre of the pedal position is 0 deg. The means and standard deviations of 5 consecutive cycles of one subject are presented.

distinct difference appears to exist between the period of shortening of the mono-articular vasti and the period in which the net torque is extensor. The correlations found between the activity patterns of the mono-articular muscles and the torques about the joints crossed, yielded optimal time shifts of 81 ± 23 ms between hip joint torque and GM activity, −6 ± 27 ms between knee joint torque and vasti and 65 ± 25 ms between ankle joint torque and SOL, the second value being significantly different from the EMD of the vasti.

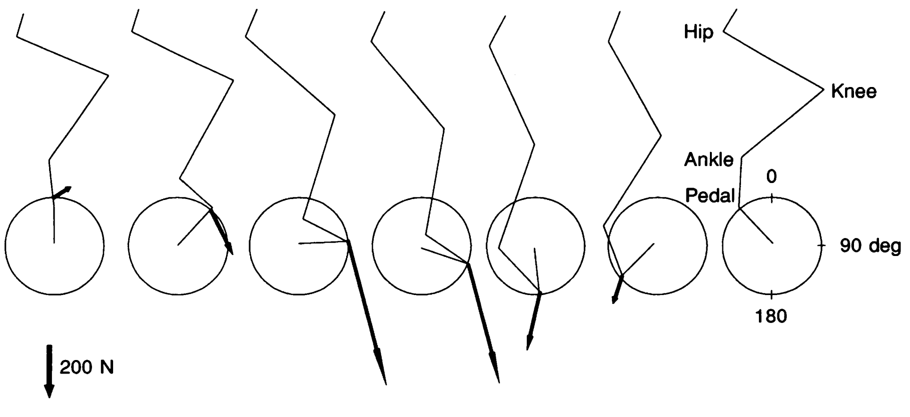

Figure 2. The orientation of the pedal force

The force vector is presented at different pedal positions. Note that the lowest segment of the stick figure does not represent the foot but the connection between ankle and point of application of the pedal force.

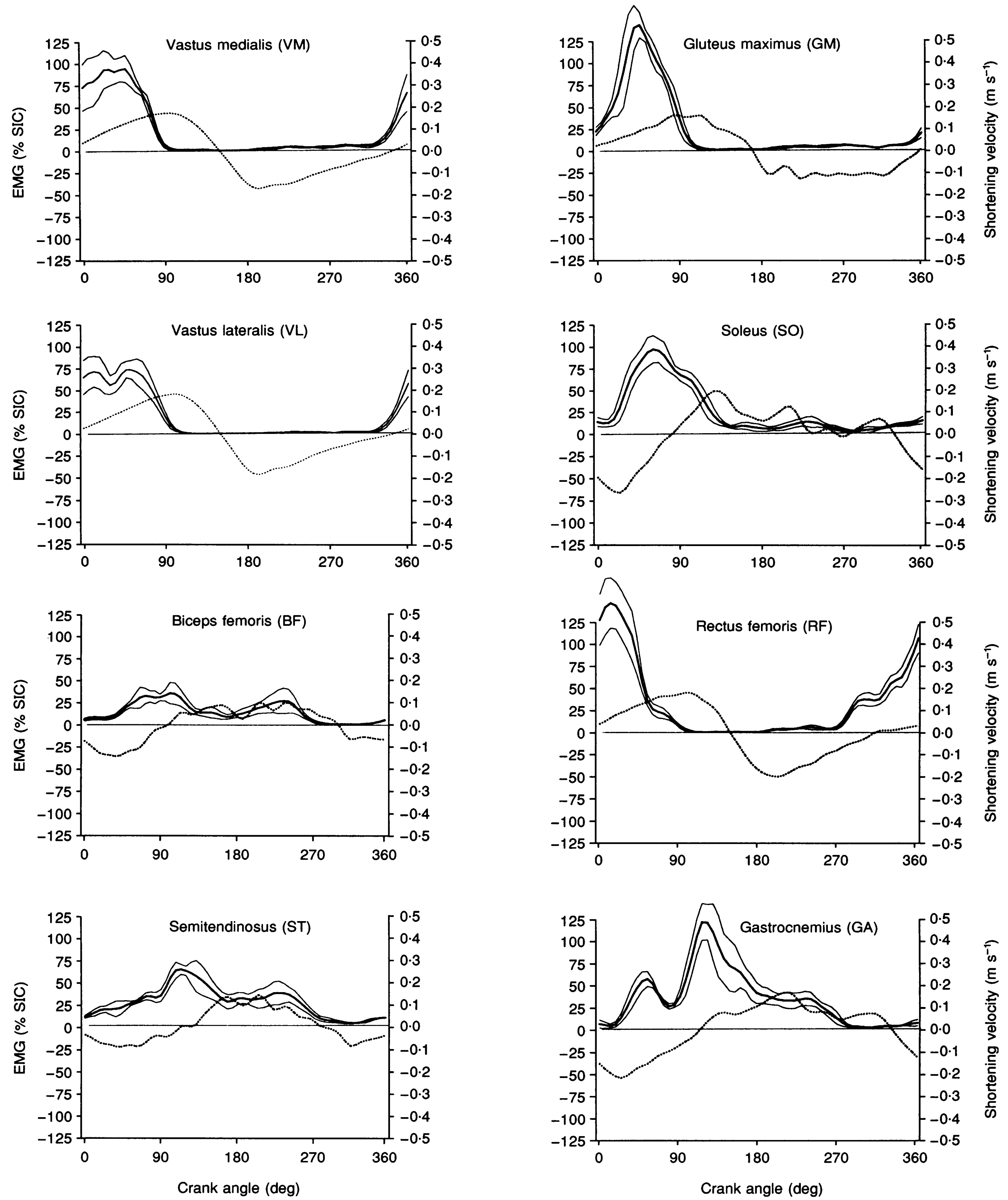

Figure 3. Muscle activity and muscle shortening velocity in cycling

Typical examples from one subject of means and standard deviations of 5 consecutive cycles of muscle activity (continuous lines) and muscle shortening velocities (dotted lines) for four mono- and four bi-articular muscles as a function of crank angle, where top dead centre pedal position is 0 deg (standard deviations of the shortening velocities are too small to indicate). EMGs are normalized to the values measured during standard isometric contractions (SIC). Note that the electromechanical delay (corresponding to a phase shift of 45 deg) is not incorporated in the activity patterns.

Running

In another study, with different aims, (Jacobs, Bobbert & van Ingen Schenau, 1993), we performed an analysis of the stance phase in running using a similar method to that used here. This work contains data on muscle activation patterns and muscle shortening velocities which also appear to support the differential role of mono- and bi-articular upper leg muscles in powerful leg extensions. Since the analysis did not include the swing phase, however, it is not possible to apply a comparable cross-correlation technique to those data. We therefore show the muscle activity patterns including an EMD of 90 ms (Vos *et al.* 1991). The mean activity patterns of the eight runners analysed are shown in Fig. 4, together with the mean muscle shortening velocities. Again a striking correspondence appears to exist between the phases of muscle shortening of the mono-articular muscles and their mechanical output with the exception of the tibialis anterior (TA). For the bi-articular hamstring and gastrocnemius muscles in particular, this correspondence is absent.

DISCUSSION

The patterns of muscle activity (Fig. 3), the joint torques (Fig. 1) and the direction of the pedal forces (Fig. 2) described here are in close agreement with those found in other studies (Suzuki, Watanabe & Saburo, 1982; Gregor, Cavanagh & Lafortune, 1985; Ericson, Bratt, Nisell, Arborelius & Ekholm, 1986; van Ingen Schenau *et al.* 1992). Despite the fact that the EMDs measured in the present study are based on pedal force responses, which are the result of muscle forces of several muscles crossing over different joints, the mean value of 94 ms is close to the value of 86–90 ms found with the same cross-correlation technique during both static and dynamic (fast and slow) mono-articular dynamometer experiments (Vos *et al.* 1991) and those found with other techniques (Inman, Ralston, Saunders, Feinstein & Wright, 1952). With respect to muscle shortening velocities, it can be noted that Hull & Hawkins (1990) reported patterns of the bi-articular RF, ST and BF muscles, which show a close agreement with those found in the present study.

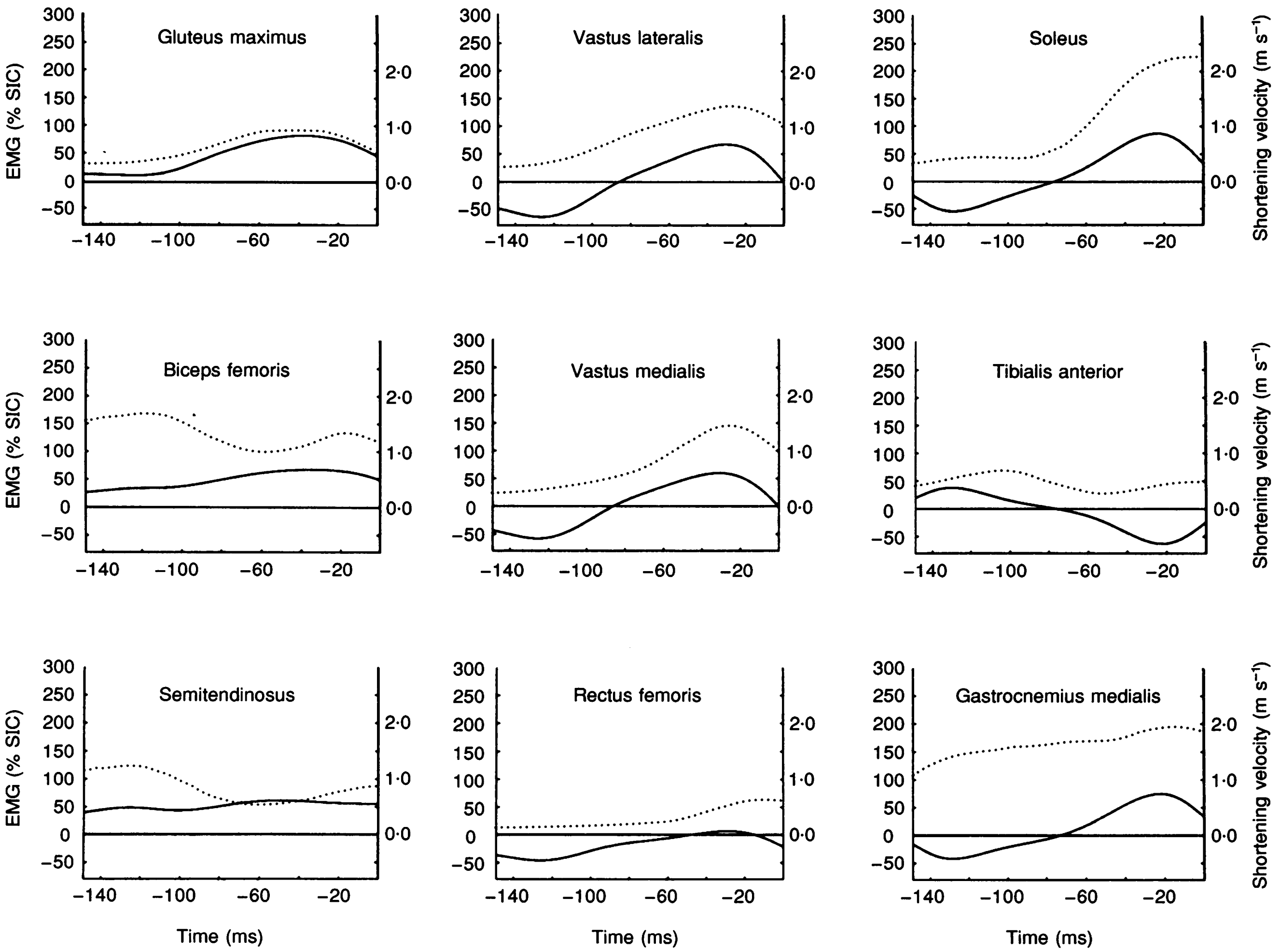

Figure 4. Muscle activity and muscle shortening velocity in running

Mean muscle activity patterns (EMG, including an EMD of 90 ms; dotted lines) and muscle shortening velocities (continuous lines) of eight subjects during the stance phase in running. The EMGs are normalized to the values measured during standard isometric contractions (SIC).

The major finding of this study is that in cycling, the phase shift between activity and shortening of mono-articular muscles appears not to differ from the EMDs of these muscles, which means that the periods of muscle force production coincide with the periods of muscle shortening. At the knee, in particular, there is no such relation between joint torque and muscle activity, since the phase shift between muscle activity of the vasti and net torque about the knee is significantly different from the EMD of these muscles. The results therefore support the hypothesis that mono-articular muscles are activated in this task in such a way that they contribute to positive work, while eccentric contractions of these muscles are avoided, irrespective of the required distribution of net torques about the joints that are crossed. This behaviour is to be expected for work generators. The results found for running largely support these observations.

During cycling, the vasti appear to exert force (and deliver work) even in the period when the required net knee torque is flexing (approximately between 100 and 170 deg). The negative (flexing) net torque about the knee is achieved through coactivation of the vasti with their bi-articular antagonists, ST and BF. This coactivation of mono-articular agonists and their bi-articular antagonists is often described in the literature and judged by most as uneconomical (e.g. Suzuki *et al.* 1982; Gregor *et al.* 1985; Ong, Hemani & Simon, 1990). However, as previously explained (van Ingen Schenau, 1989; van Ingen Schenau *et al.* 1992), such coactivations are highly effective in tasks which require a distinct, and often changing, distribution of net joint torques necessary to control the direction of the external force.

Figure 2 shows that the direction of the force on the pedal changes during leg extension. This ensures a propulsive force component in the direction of the pedal displacement. This change in pedal force orientation requires large changes both in net hip, and especially knee joint torques, as illustrated in Fig. 1. Without coactivations of mono- and bi-articular muscles, the requirements, with respect to joint torques, would strongly influence the ability of the mono-articular muscles to contribute to external work. In the last phase of a leg extension, it would be necessary to deactivate the vasti (despite the fact that they still shorten) and activate a knee flexor while the knee is still extending. Coactivation of the vasti and hamstrings solves this problem completely, since the vasti can continue to deliver work as long as the hamstrings can ensure the required net flexing torque. Work done by the vasti appears now computationally as extra work done in hip extension. A comparable type of co-ordination of gluteus maximus and rectus femoris muscles can be observed during the first part of the downstroke. The strong overlap between muscle force production and muscle shortening, as found for the mono-articular muscles in cycling (Table 1) and in running (Fig. 4), appears to support the statement made previously, that mono-articular muscles act as work generators in these types of leg extension, while the bi-articular upper leg muscles ensure that the work in this task is applied in the most effective way. When accounting for the EMD in Fig. 3 it can also be concluded that the coactivations of mono- and bi-articular muscles help to avoid wasteful eccentric contractions of the mono-articular muscles, although eccentric contractions of bi-articular muscles cannot be avoided entirely.

The avoidance of eccentric contractions of mono-articular leg extensors is not always possible, since the body weight is mostly not supported by a saddle. For example, in walking and running, one observes small but significant phases of knee flexion and dorsiflexion during the stance phase. The additional data of running, however, illustrate that even in such movements one can still observe a strong correlation between muscle activation and shortening velocity in the mono-articular muscles (Fig. 4). Moreover, it can be deduced from the literature that during running, it is unlikely that eccentric contractions of the knee extensors and plantar flexors occur at all at the level of the contractile machinery (Griffiths, 1991) as a consequence of the stretch of the series elastic components of these muscles. This means that these muscles are used in the flexion phase as actuators, which enable the organism to store energy (in the series elastic components), which can be expended during the subsequent joint extensions (see Jacobs *et al.* 1993, for more details and references).

In movements which show considerably larger hip and knee flexion angles while opposing an external force, such as gravity (e.g. when descending a slope), and in many arm (pointing, grasping, reaching, writing) movements, other types of intermuscular co-ordination may be found, like the one described above. However, as indicated in the Introduction, there is evidence that the organization of the control of mono- and bi-articular muscles (especially the upper leg) is based on different processes related to the co-ordination between mono- and bi-articular muscles described above. Moreover, as detailed by van Ingen Schenau *et al.* (1994), results obtained in cat studies suggest that the unique role of bi-articular muscles in the fine tuning of net joint torques seems related not only to the control of external forces but also to requirements associated with the dynamics of the limb segments. The nature of these different processes is still largely unclear. Based on the present results, however, it seems justifiable to advocate that the search for principles of motor control in neurophysiology (including the significance of spinal interneuronal networks; McCrea, 1992) requires explicit attention as to the possible differential (mechanical) roles of mono- and bi-articular muscles.

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