

CONTROL OF AN EXTERNAL FORCE IN LEG EXTENSIONS IN HUMANS

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SUMMARY

1. We investigated the hypothesis that mono- and bi-articular muscles perform different functions: the former are chiefly dependent on their mechanical advantage, while the latter are considered to be mainly concerned with controlling the direction of an external force.

2. Seven subjects were asked to exert a constant external force in various directions from three different positions. Feedback was given on the amplitude (300 and 600 N) and direction of the force vector.

3. During each trial the position of the subject was registered. Ground reaction force and muscle activity (EMG) from the main mono- and bi-articular upper leg muscles were recorded. Link segment modelling was used to obtain net moments about the knee and hip joints. For each muscle the mechanical advantage was calculated in each force direction.

4. The task of controlling the ground reaction force was performed with little interindividual variation as reflected by the variability of the different force and EMG variables.

5. A linear relationship between the difference in activity of rectus femoris and hamstrings and the difference in net moment around the knee and hip was found. This relationship showed very high correlation coefficients of 0.96 (300 N) and 0.97 (600 N) and was independent of position. Mean correlations between this activity difference and the angle of the force vector were also high: -0.95 (300 N) and -0.94 (600 N).

6. The mono- as well as the bi-articular muscles increased in activity when a larger mechanical advantage could be obtained from them, except for the biceps femoris (short head).

7. The results support the hypothesis that bi-articular muscles have a unique role in controlling the distribution of net moments about the joints and, as a consequence, in controlling the direction of the external force exerted on the environment.

INTRODUCTION

The control of multi-joint movements involves a system which is redundant from a mechanical point of view. Theoretically, various sets of muscle activation patterns are possible for a specific movement. However, despite this redundancy, activation

patterns acquired in the same experimental task are rather stereotyped across subjects, for elbow movements (Zuylen, Gielen & Denier van der Gon, 1988) and for more complex tasks such as jumping (Bobbert & van Ingen Schenau, 1988), speed skating (de Koning, de Groot & van Ingen Schenau, 1991), and a sprinting task

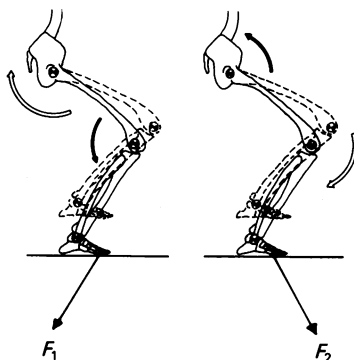


Fig. 1. This figure shows that for the same position changes of the foot in a downward direction but a distinct direction of the reaction force (F_1 or F_2) a different combination of net moments (arrows) about the hip and knee is required.

(Jacobs & van Ingen Schenau, 1992). Obviously, anatomical, neuronal or biomechanical constraints impose restrictions on the possible muscle actions. Such constraints constitute the basis for models of movement control.

Most current theories of movement control are formulated in terms of position control of a joint or an endpoint of a limb, e.g. servo-control theories (e.g. Loeb, 1984) and in particular the equilibrium point hypothesis (Vincken & Denier van der Gon, 1985; Feldman, 1986; Hogan, Bizzi, Mussa-Ivaldi & Flash, 1987). Support for these theories has been mainly obtained from single joint experiments. Loeb (1987) stated that extrapolation of such theories to more complex movements is difficult. For example, in the field of robotics, the control of idealized robotic systems, accomplished by torque motors which are merely position encoders, is difficult and inefficient (Loeb, 1987; Gielen & van Ingen Schenau, 1992).

Recently, we realized in analyses of multi-articular movements that not only the position of a limb has to be controlled, but also the distribution of net moments about the joints necessary to control the direction of an external force (van Ingen Schenau, Boots, de Groot, Snackers & van Woenzel, 1992). For example, for the same change of joint position, different distributions of net moments about the hip and knee joints may be required to control different directions of the external force (F_1 or F_2 , Fig. 1). The force vector F_1 requires a unique combination of net hip extension and net knee flexion moments, while F_2 requires a reversed sign of net moments about the hip and knee compared to F_1 . This means that the necessary net moments to do work, as in the case of a net hip and knee extension moment illustrated in Fig. 1, can be entirely different from the net moments which are actually applied since they are required to control the external force.

Based on an analysis of cycling, a hypothesis was formulated that mono- and bi-

articular leg muscles may have different roles (van Ingen Schenau *et al.* 1992). The activation of mono-articular muscles appeared to be dependent on position changes and more or less independent of the required moment about the joint that is crossed, while the bi-articular hamstrings and rectus femoris muscles seemed to control the distribution of net moments over the hip and knee joints. To accomplish a force vector comparable to F_1 during cycling, the vasti and hamstring muscles apparently need to be co-activated, while a vector comparable to F_2 appeared to be realized through a co-activation between the gluteus maximus and rectus femoris (van Ingen Schenau *et al.* 1992).

The aim of the present study is to provide a thorough test of the hypothesis that mono- and bi-articular muscles perform different roles. To this end, static experiments were performed in which subjects were asked to exert a force of constant magnitude, but varying direction, from three different leg positions. Although there are no displacements, it can be shown that under isometric conditions, the same principles will hold. This follows from an application of the concept of virtual work (cf. Andrews, 1985) to these static movements. This concept, identified in the engineering sciences (e.g. Mach, 1974), is based on the assumption of an infinitely small displacement (dS_e) of the point of application of the external force, which results in an infinitely small amount of external work (dA). By calculating the changes in muscle length (dS_m), which are the result of the displacement dS_e , one can determine to what extent each muscle is able to contribute to the external work in each task. The same principle underlies the hypothesis for the role of mono-articular muscles in dynamic experiments. So, from a mechanical point of view, there is in this respect, no essential difference between static and dynamic movements. Muscles showing a relatively large (virtual) shortening, at given (virtual) displacement dS_e , can contribute more easily to the external work than muscles which shorten to a lesser extent because the transfer of muscle force to external force is larger. For this reason, the concept of virtual muscle shortening in static tasks has essentially the same meaning as the actual muscle shortening in dynamic tasks. This is comparable to the way in which pulley systems work. In pulley systems, one can also obtain different external forces both in dynamic as well as static situations, dependent on the same type of transfer of internal forces to the external force. In this study, this transfer is referred to as mechanical advantage. When ignoring frictional losses this mechanical advantage can easily be deduced by stating that the external work should equal the internal work:

$$F_e dS_e = \sum_{i=1}^n F_{m,i} dS_{m,i},$$

or

$$F_e = \sum_{i=1}^n F_{m,i} (dS_{m,i}/dS_e),$$

which implicates that a muscle i with a high mechanical advantage, dS_m/dS_e , has a larger transfer of muscle force (F_m) to the force on the environment (F_e) than a muscle with a low mechanical advantage.

When reformulating the above mentioned hypothesis on the role of mono- and bi-articular muscles, it is expected that the activation of the mono-articular muscles is

related to their mechanical advantage, while the activation of the bi-articular muscles should be related to the distribution of net moments over the joints, irrespective of their mechanical advantage.

METHODS

Subjects and experimental procedure

Seven healthy male subjects (age, 25 ± 5 years; height, 1.86 ± 0.04 m; body mass, 81.3 ± 5.1 kg) participated in this study. Informed consent was obtained from all of them. After a warm-up the subjects performed standard isometric contractions (SIC) and were asked to exert static forces in various directions while sitting on a chair. The magnitude of the required force was 300 and 600 N and the direction varied from an oblique anterior direction (60 deg) to an oblique posterior direction (120 deg) in steps of 15 deg (Fig. 2). The two different force amplitudes were examined to investigate their respective influences on the activation patterns. Each trial lasted for 6 s. After a start signal the subjects had to generate the correct amount of force in a specific direction within 4 s. Subsequently, for 2 s both the magnitude and the direction of the force were held constant during the experiment. Visual feedback of these two parameters was given. Computer-generated audible cues indicated the start signal and the holding period. The sequence in which the different force directions were accomplished was first the 300 N and then the 600 N series, whereas the succession of directions was chosen randomly.

In order to realize various combinations of net moments in the joints and mechanical advantages of the muscles, the subjects had to repeat all these trials in three different positions. These positions were chosen in such a way that the line-of-pull of the force pointed posterior to the hip joint as well as anterior to the knee joint, and that they corresponded with body positions adopted in natural movements like cycling, running, jumping and sprinting (Bobbert & van Ingen Schenau, 1988; Putnam & Kozey, 1989; van Ingen Schenau *et al.* 1992; Jacobs & van Ingen Schenau, 1992). The height of the hip joint was adjusted so that the knee angle was 100 deg in each position. The three positions were defined as (see Fig. 2): position I, lateral malleolus lies at the same horizontal position as the major trochanter; position II, the horizontal distance between the major trochanter and the lateral malleolus is 15% of the total leg length; position III, the horizontal distance between the major trochanter and the lateral malleolus is 30% of the total leg length.

A static position was achieved by belting the subjects to the backrest as well as to the seat of the chair which they sat on during the experiment. They were allowed to hold the chair with their hands. The right foot was placed at a marked position on a force plate. A pilot study showed that the task of directing an external force was rather difficult, therefore several training sessions preceded the actual experiments. Each subject trained for 1 h a day for a period of 3 days. The experimental procedure consisted of a short training trial followed by the 300 and 600 N trials. For each subject, one measurement was made for each combination of force amplitude and direction and leg position. During each trial the position of the subject was recorded during the fifth second. The ground reaction force and muscle activities were recorded for the entire period of each trial.

Position and force

For the registration of the body position, landmarks were placed on the skin corresponding to the following anatomical points: the fifth metatarsophalangeal joint, the heel, the lateral malleolus, the knee joint (lateral collateral ligament at the height of the joint cleft), the major trochanter, spina iliaca anterior superior and the neck (at the height of the fifth cervical vertebra). During each trial a slide was taken of the right side of the subject with a camera (Canon T90, 100 mm). With the aid of a digitizer (Grafbair, Scientific Accessory Corporation, Southport, CT, USA; resolution, 0.01 mm), the following information was extracted twice from each slide: co-ordinates of the anatomical landmarks, of the marker placed on the force plate (used as a point of reference), of two markers with a known distance in a horizontal plane and of two markers placed vertically. After proper scaling the co-ordinates were averaged. The co-ordinates defined five body segments: the foot, lower leg, upper leg and two parts of the upper body. The angles of each segment were calculated relative to the horizontal; joint angles were defined as the angles between adjacent body segments. The co-ordinates and measured anthropometric data were used, in combination with data from Clauser, McConville & Young (1969), to calculate the positions of the mass centres of the different body segments.

Vertical (F_y) and fore-aft (F_x) components of the ground reaction forces were recorded by means of a force platform (Kistler, type 9281B, Switzerland). The analog force signals were amplified, low-pass filtered (75 Hz, fourth order and 24 dB octave⁻¹), sampled (500 Hz, 12 bits) and stored in a computer. Simultaneously the F_y and F_x signals were connected with a *XY*-writer (Kipp, BD90, The

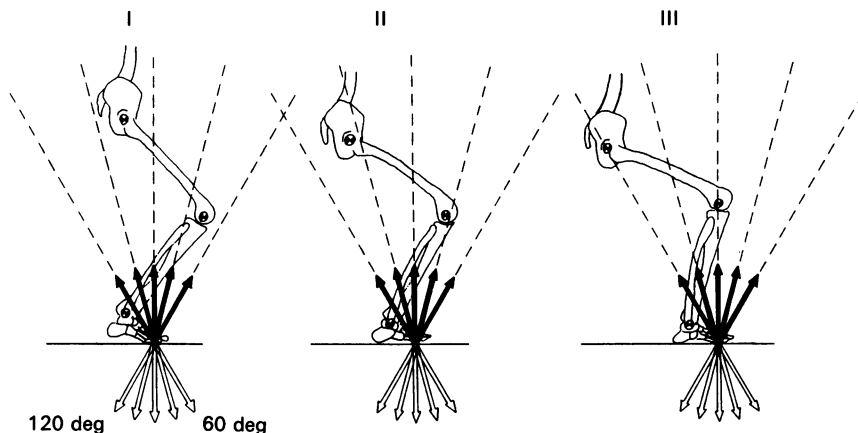


Fig. 2. In three positions (I, II and III) the subjects were asked to exert five different force directions from 60 to 120 deg. Postural changes effect the direction of the force with respect to the joints.

Netherlands) to obtain on-line visual feedback of the force vector. Force directions and magnitudes were indicated on a stencil with deviation margins of $\pm 2.5\%$; the size of the force vector was 12 cm for both force amplitudes. The subjects were asked to direct the force so that the deviation from the intended end-point of the force vector was within the 2.5% margins.

From the distribution of the force plate components, the centre of pressure of the force vector was calculated. Combined with the point of reference on the slide, the centre of pressure was related to the position of the foot.

A model of link segments was used to calculate net moments about a joint (Elftman, 1939). Inputs of the model were the positions of the segments, positions of the mass centres of the segments, the force vector and its point of application. Moments involving extensions of the hip and knee and plantar flexion were given a positive sign.

Electromyography and virtual muscle shortening

The electromyographic activity (EMG) of seven upper leg muscles was obtained telemetrically (Biomes 80, Glonner, Germany) from the following mono-articular muscles: gluteus maximus, biceps femoris (short head), vastus medialis and lateralis and from the bi-articular muscles: semitendinosus, biceps femoris (long head) and rectus femoris (RF). Pairs of Ag-AgCl surface electrodes (Sentry Medical Products, CA, USA; lead-off area 1 cm², centre-to-centre electrode distance, 4.5 cm) were applied to the muscles after standard skin preparation (Basmajian, 1978). The positions of the electrodes are described by Gregoire, Veeger, Huijing & van Ingen Schenau (1984). The subjects put on a skin suit to reduce movement artifacts arising from swinging cables. Openings in the suit allowed the markers to be placed on the skin.

Standard isometric contractions (SIC) for each muscle group were determined with a method described by Gregoire *et al.* (1984). The subjects were asked to perform three maximal contractions for 3 s under five standardized conditions specifically developed for each muscle group. SIC 1: for gluteus maximus, maximal hip extension against external resistance (hip joint, 180 deg). SIC 2: for biceps femoris (long and short head) and semitendinosus, maximal knee flexion against external

resistance (hip joint, 90 deg and knee joint, 90 deg). SIC 3: for rectus femoris and vasti, maximal knee extension against external resistance (hip joint, 90 deg and knee joint, 90 deg).

The EMG signals were bandpass filtered (25–200 Hz) and on-line sampled with a sampling rate of 500 Hz. The EMG signals were plotted on a writer (Gould ES 1000, France) for visual inspection during the experiment. To obtain a linear envelope, the signals were rectified and low-pass filtered

TABLE 1. The coefficients derived from different authors for the determination of muscle length (L_{oi} (expressed in % of segment length))

Muscle	Joint	A_0	A_1	A_2	A_3	Joint	B_0	B_1	B_2	B_3	Author
Gluteus maximus	Hip	—	13.99	-8.50	0.68	—	—	—	—	—	1
Biceps femoris	Hip	101.00	-4.35	-2.58	—	Knee	101.00	24.41	-3.58	—	2
Semitendinosus	Hip	103.90	-1.82	-3.24	—	Knee	103.90	10.94	-0.17	—	2
Vastus medialis	Knee	14.65	1.84	-2.12	—	—	—	—	—	—	3
Vastus lateralis	Knee	18.24	-2.33	-0.99	—	—	—	—	—	—	3
Rectus femoris	Hip	-12.84	-0.46	-2.69	—	Knee	24.46	-1.71	-1.54	—	3

All coefficients were recalculated to our definition: enclosed joint angle in radians and percentage of segment length. Data are used from: (1) Nemeth & Ohlsen (1985), (2) Hawkins & Hull (1990), and (3) Visser, Hoogkamer, Bobbert & Huijing, 1990). Calculations were done with the following formula: $L_{oi} = A_{0,i} + A_{1,i} \Theta_i + A_{2,i} \Theta_i^2 + A_{3,i} \Theta_i^3 + B_{0,j} + B_{1,j} \Theta_j + B_{2,j} \Theta_j^2 + B_{3,j} \Theta_j^3$, with Θ the joint angle and i and j representing two different joints.

(zero phase lag through a bi-directional application of a fifth approximation, second order Butterworth filter) with a net cut-off frequency of 13 Hz. The SIC values for each muscle were determined by taking the mean of the curve for a period of 1 s in which the activation level remained constant. The EMGs were normalized to 100 % SIC level.

Muscle mechanical advantage dS_m/dS_e (see Introduction), was obtained by taking a virtual displacement (10 mm) of the ankle from its original position in the direction of the exerted force. Note that the mechanical advantage of a muscle was calculated in each direction of the force and position of the limb (positions I, II and III). Alterations of joint angles, together with information of total muscle length (L_{oi} , the length between origin and insertion) as a function of joint angle(s), made it possible to calculate the associated virtual muscle shortening. We constructed a database from different studies to calculate L_{oi} for the seven muscles (Table 1). Because various authors have expressed the coefficients differently, we recalculated these coefficients in accordance with our definition: enclosed joint angles (180 deg is full extension) in radians and percentage of segment length. The results and their origins are presented in Table 1. In the Results and Discussion section, we will take the virtual changes in muscle length dL_{oi} as a representation of the mechanical advantage, since dS_e was taken as equal in all experiments.

Treatment of data

Force and EMG data were synchronized on the basis of computer-generated pulses which controlled the experiment. This output channel was sampled simultaneously with the EMG signals as well as with the force signals. To eliminate the phase lag between EMG and force response, the linear envelopes were shifted 90 ms relative to the other signals (van Ingen Schenau, 1989). For a period of 1 s (4.5th–5.5th s), the mean values of the force, net moments and EMG signals were obtained. These values were combined with the position data obtained at the fifth second. Trials were accepted if position and force were stable in the holding period.

RESULTS

Directing the ground reaction force was performed with little interindividual variation, as indicated by the magnitude of the standard deviations of the force vector characteristics presented in Table 2. All subjects achieved the end-point of the

force vector very accurately, particularly during the 300 N trials. However, during the 600 N trials a decrease of the mean force amplitude was present from 105 to 120 deg. The means and the increased standard deviations indicate that some subjects were not able to realize 600 N from these two positions.

The mean EMG values of the muscles expressed as a percentage of SIC values are shown in Fig. 3. A value of more than 100% means a higher activity of that

TABLE 2. Mean values (\pm S.D.) of the angles (α) and amplitudes (F) of the ground reaction forces obtained during the 300 and 600 N trials in the three different positions

		Direction of exerted force (deg)						
		60	75	90	105	120		
α (deg)	300	I	60.6 \pm 0.4	75.4 \pm 0.4	90.0 \pm 0.4	104.6 \pm 0.3	119.5 \pm 0.5	
		II	60.6 \pm 0.4	75.0 \pm 0.6	89.7 \pm 0.3	104.7 \pm 0.4	119.5 \pm 0.1	
		III	60.4 \pm 0.3	75.1 \pm 0.3	89.9 \pm 0.4	104.5 \pm 0.2	119.6 \pm 0.3	
	600	I	61.6 \pm 2.3	75.4 \pm 0.5	89.8 \pm 0.4	104.3 \pm 0.3	118.7 \pm 1.7	
		II	60.9 \pm 0.8	75.0 \pm 0.4	90.0 \pm 0.3	104.4 \pm 0.5	117.8 \pm 3.3	
		III	60.6 \pm 0.5	75.1 \pm 0.3	89.9 \pm 0.5	104.6 \pm 0.9	119.2 \pm 1.9	
	F (N)	300	I	300.1 \pm 2.7	300.5 \pm 4.5	302.5 \pm 3.1	299.5 \pm 4.4	300.1 \pm 4.5
			II	299.6 \pm 2.7	301.5 \pm 1.6	300.1 \pm 4.0	299.5 \pm 2.1	299.6 \pm 3.1
			III	300.7 \pm 3.2	303.1 \pm 2.6	300.6 \pm 3.9	299.3 \pm 3.1	298.8 \pm 3.0
600		I	598.0 \pm 8.3	600.7 \pm 7.8	600.9 \pm 5.5	570.5 \pm 79.0	465.8 \pm 110.4	
		II	599.1 \pm 9.6	598.4 \pm 5.4	599.2 \pm 8.0	573.7 \pm 53.2	421.1 \pm 123.7	
		III	599.7 \pm 4.2	600.6 \pm 4.2	605.0 \pm 4.6	548.4 \pm 65.2	424.7 \pm 51.6	

particular muscle during the experiment relative to that attained during the standard contractions. The EMGs are plotted as a function of the net moment about the joint that is crossed by the muscle. For the bi-articular muscles the moments about both joints crossed by these muscles are subtracted where $M_k - M_h$ is knee moment minus hip moment. A combination of hip extension and knee flexion results in a negative $M_k - M_h$ difference, while the opposite combination, hip flexion and knee extension leads to a positive difference.

The gluteus maximus activity was low in the period of hip flexion moments, while it showed an increasing activity when hip extension moment increased. The knee flexor biceps femoris (short head) was active during flexion moments, while less activity was present during knee extension moments. The vasti muscles showed a more or less linear activity pattern with increasing activity towards greater knee extension moments. Note that these muscles are also active during negative (flexion) moments about the knee. The bi-articular biceps femoris (long head), semitendinosus and rectus femoris are plotted against $M_k - M_h$. It can be seen that these muscles revealed a reverse pattern when compared with each other. The biceps femoris (long head) and semitendinosus were silent in the positive range while the activity of the rectus femoris was rather small in the negative range. The activity of the biceps femoris (long head) and semitendinosus increased if the hip extensor and knee flexion moment become prominent. This pattern was exactly opposite for the rectus femoris; its activity enlarges by increasing hip flexor and knee extensor moments.

To address the first question of this study as to the extent to which the bi-articular

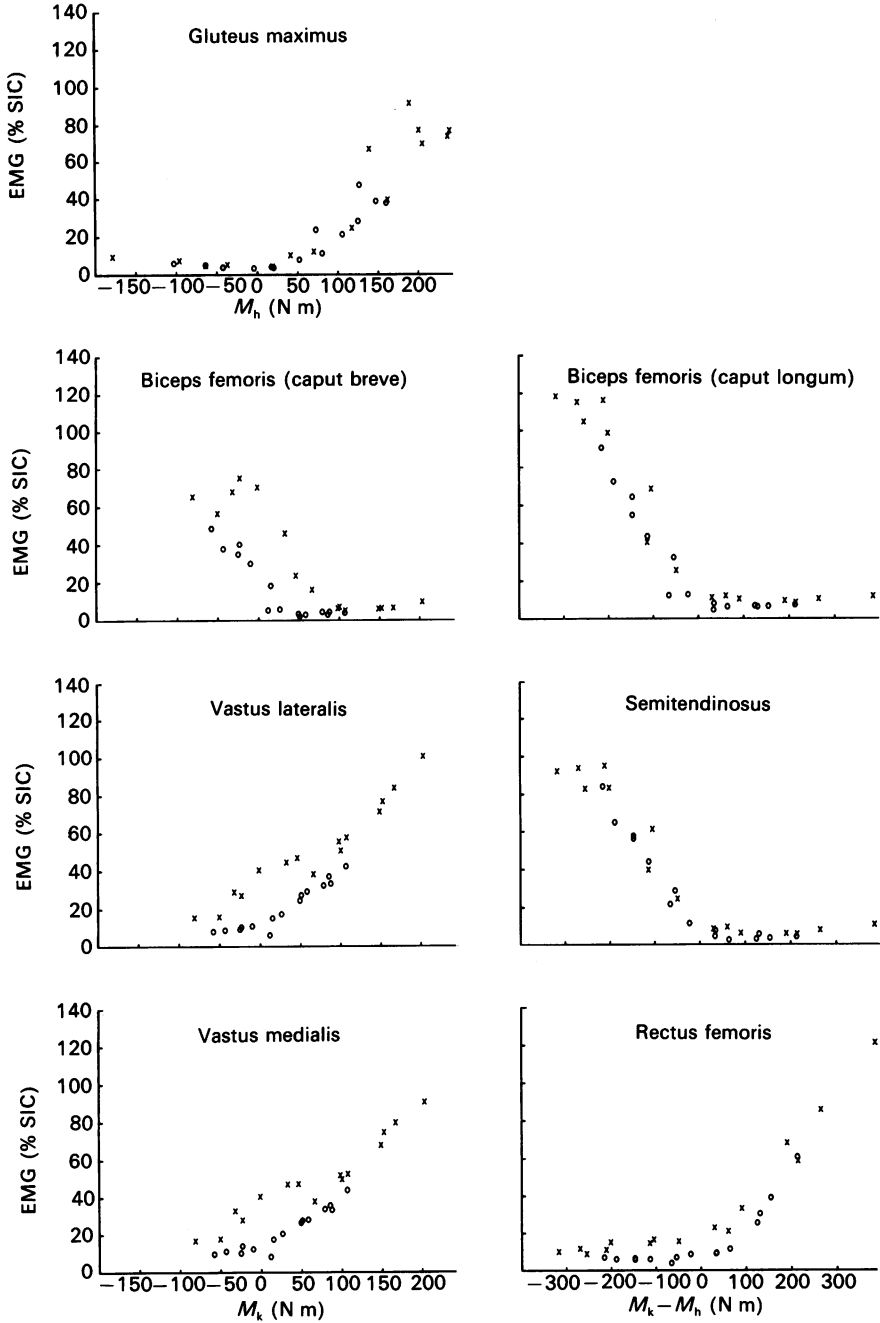


Fig. 3. Mean EMG values obtained from the 300 (○) and 600 N (×) trials of five representative muscles as a function of net moments (M_k , M_h or $M_k - M_h$).

muscles determine the distribution of the net moments, we subtracted the rectus femoris activity from the averaged activity of the semitendinosus and biceps femoris (long head), denoted by hamstring activity (HAM) (Fig. 4). A linear relationship

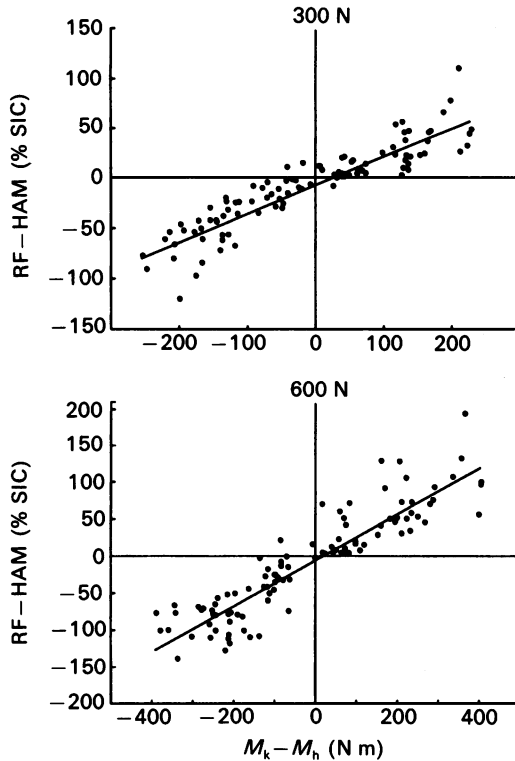


Fig. 4. The activity difference between the hamstrings and rectus femoris muscles (RF-HAM) during the 300 and 600 N trials as a function of the net moment difference ($M_k - M_h$). All individual data are shown.

TABLE 3. Individual and mean (\pm s.d.) correlation coefficients of the relationship between the activity difference of rectus femoris and hamstrings muscles (RF-HAM) and the difference between net knee and hip moment ($M_k - M_h$).

		Subject							
		1	2	3	4	5	6	7	Mean
300	All	0.97	0.95	0.95	0.96	0.97	0.96	0.97	0.96 \pm 0.01
	I	0.98	0.97	0.97	0.99	0.99	0.97	0.99	0.98 \pm 0.01
	II	0.98	0.97	0.97	0.99	0.99	0.97	0.99	0.98 \pm 0.01
	III	0.98	0.76	0.90	0.98	0.99	0.91	0.99	0.93 \pm 0.08
600	All	0.96	0.98	0.98	0.97	0.98	0.96	0.98	0.97 \pm 0.01
	I	0.99	1.00	0.99	0.98	1.00	0.99	0.99	0.99 \pm 0.01
	II	0.91	1.00	0.98	0.97	0.98	1.00	0.99	0.98 \pm 0.03
	III	1.00	0.99	0.98	1.00	0.99	0.99	0.98	0.99 \pm 0.01

The correlations were calculated for the 300 and 600 N trials and also for separate positions (I, II and III) or taking the positions together (all).

between the activity difference, RF-HAM, and moment difference, $M_k - M_h$, was demonstrated for each individual (Table 3). The individual correlation values were very high with mean coefficients of 0.96 and 0.97 in 300 and 600 N trials, respectively,

for all positions together. As can be observed from Table 3, the influence of position changes was negligible. Table 4 shows the correlation between the activities of the individual muscles and M_k , M_h and $M_k - M_h$ respectively. It can be seen that the individual correlations of RF and HAM activity with M_k , M_h or $M_k - M_h$ are considerably lower than those for the RF-HAM correlations in the previous table.

TABLE 4. Mean correlation coefficients (\pm s.d.) of the relationship between the activity of rectus femoris (RF) and hamstring (HAM) muscles and the separate net knee (M_k), hip (M_h) moment and net moment difference ($M_k - M_h$)

	300 N			600 N		
	M_k	M_h	$M_k - M_h$	M_k	M_h	$M_k - M_h$
RF	0.74 ± 0.07	-0.81 ± 0.07	0.78 ± 0.07	0.80 ± 0.04	-0.88 ± 0.04	0.86 ± 0.05
HAM	-0.87 ± 0.03	0.83 ± 0.03	-0.85 ± 0.03	-0.89 ± 0.06	0.83 ± 0.08	-0.87 ± 0.07

The correlations were calculated for the 300 and 600 N trials for all positions.

Figure 5 shows the same curves as in Fig. 3, but now related to the virtual muscle shortening (dL_{oi}), resulting in three dimensional plots. The mono-articular muscles, gluteus maximus and vastus lateralis, increased in activity with both the net moment and the virtual muscle shortening. However, the biceps femoris (short head) was active in periods of virtual muscle lengthening. The shortening range of the bi-articular muscles was much smaller than for the mono-articular muscles. Nevertheless, these muscles also increased in activity if a larger mechanical advantage could be obtained from them.

DISCUSSION

Variability

The human body is supplied with a large number of muscles of different types. This study was designed to provide a detailed examination of the hypothesis that mono- and bi-articular muscles have different roles. To answer the questions posed in the introduction, the first step is to find out if different subjects perform the task involved in a stereotyped manner. The subjects were asked to direct the ground reaction force at various angles. From Table 2 it can be deduced that in general these force vectors were achieved with a high degree of accuracy, a conclusion that is also supported by the low variability of the required net moments (Fig. 3). The responsible muscles were activated in a similar way by all subjects as reflected by the high correlations and low standard deviations between the subjects (Tables 3 and 4, Fig. 4). It can be concluded that different subjects perform the complex task of controlling an external force in the same way despite the mechanical redundancies inherent in the action system. In addition, the activation patterns identified by Wells & Evans (1987), who measured EMG patterns of mono- and bi-articular leg muscles as a function of both pushing and pulling force directions, are comparable to our patterns despite their use of the lower force level of 63 N.

Control of force direction

Control of the ground reaction force results from a combination of net moments about the joints which are a function of muscle activation. From an analysis of cycling it was hypothesized that the bi-articular rectus femoris and hamstring

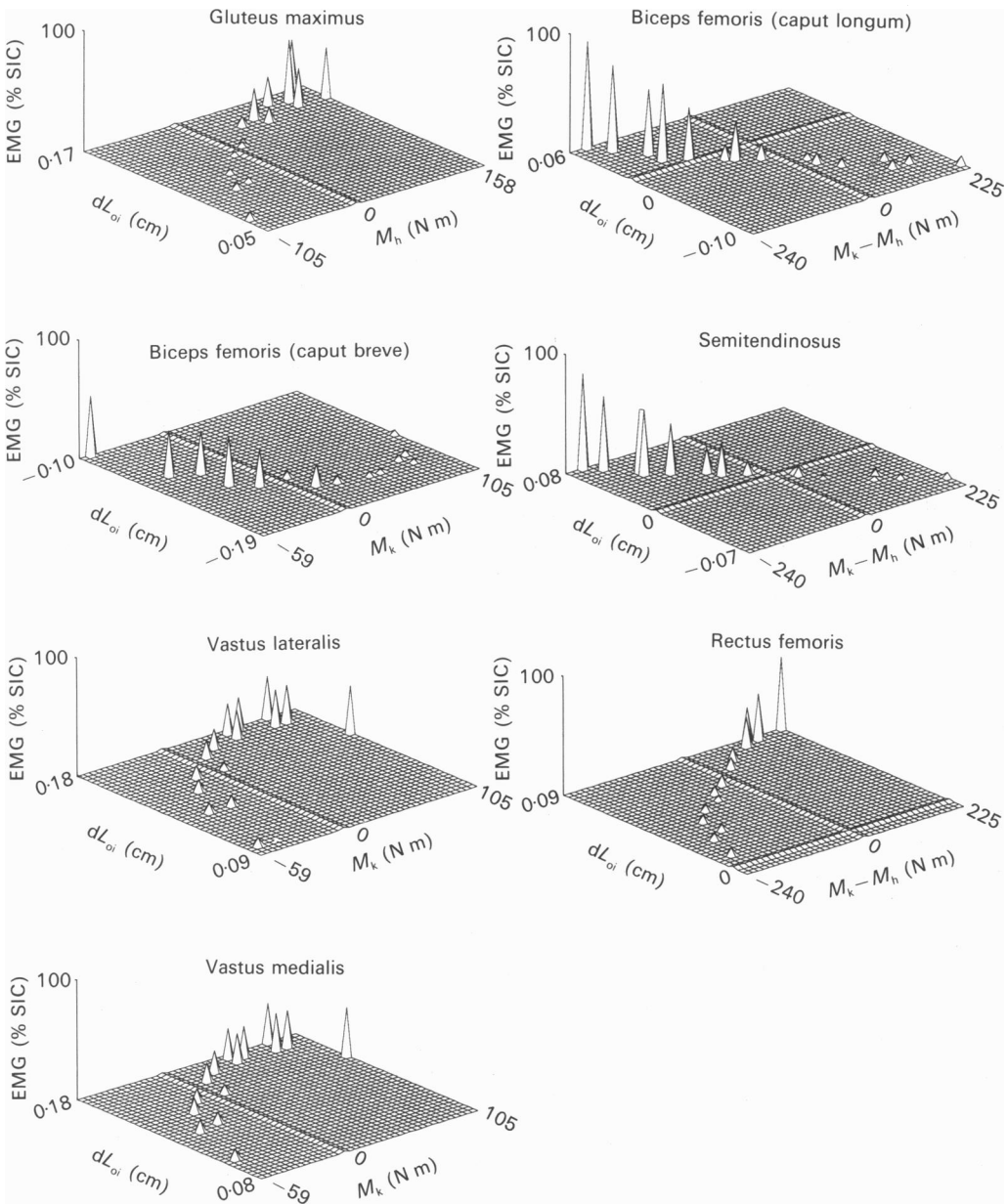


Fig. 5. Mean EMGs obtained during the 300 N trials as a function of net moment (M_k , M_h or $M_k - M_h$) and virtual muscle shortening. Positive values of dL_{oi} means virtual muscle shortening.

muscles distribute the net moments about the joints in order to control the force on the pedal so that it is comparable with the goal of the moment (van Ingen Schenau *et al.* 1992).

In the present study, high correlation coefficients of 0.96 (300 N) and 0.97 (600 N) were found between the activity difference (RF–HAM) and the difference in moments of the joints they cross ($M_k - M_h$) (Table 3 and Fig. 4). Separate correlations of RF or HAM with a single net moment or even with the net moments difference, as presented in Table 4, show very low correlations. Thus, it can be concluded that the bi-articular muscles, rectus femoris and hamstrings, play an important role in the distribution of the net moments of both joints they cross and thereby in the control of the direction of the ground reaction force. Mean correlation coefficients of the activity difference (RF–HAM) with the angle of the force were also high: -0.95 (300 N) and -0.94 (600 N).

The bi-articular rectus femoris and hamstrings function in a reciprocal manner so as to satisfy the main requirement of the task, the control of the external force vector. It is possible that a pattern of reciprocal inhibition exists between these muscles. Suzuki, Watanabe & Homma (1982) studied the muscle activation patterns of these bi-articular muscles during cycling at different pedalling rates. A pattern of reciprocal activation between the biceps femoris (long head) and rectus femoris muscles was generally observed at each velocity. Reciprocal EMG patterns between these bi-articular antagonists are also reported for other movements (e.g. Kumamoto, 1984; Nilsson, Thorstensson & Halbertsma, 1985; Wells & Evans, 1987; van Ingen Schenau, Bobbert & Soest, 1990; de Koning *et al.* 1991; Jacobs & van Ingen Schenau, 1992).

From the findings of the present study it can be concluded that the hamstrings and rectus femoris show a reciprocal behaviour in order to control the direction of the force vector.

Different roles for mono- and bi-articular muscles?

From the analysis of cycling it was postulated that mono- and bi-articular muscles would have different functions. We have shown that the bi-articular rectus femoris and hamstring muscles control the distribution of the net moments. There remains the question of whether the activation patterns of the mono-articular muscles are determined by their changes in virtual muscle lengths (dL_{oi}) and whether they are more or less independent of the required moment. As can be seen from Fig. 5, the activity of the mono-articular muscles was not only dependent on dL_{oi} but also on the net moments. However, the vasti muscles were even active during negative moments about the knee. During these moments the vasti were shortening and in this way they were able to sustain the external force and the virtual work as long as the hamstrings provided the required flexion moment.

The biceps femoris (short head) was active in periods with virtual muscle lengthening. When activated it seems to be coupled to the alterations in the activity of the hamstrings (Figs 3 and 5). As stated before, the main function of the short head of the biceps appears to be one of stabilizing the knee joint (Gregoire, Veeger, Huijing & van Ingen Schenau, 1984; Baratta, Solomonow, Zhou, Letson, Chuinard & D'Ambrosia, 1988). The gluteus maximus is not active when the moment about the hip is flexion. This outcome is in contrast to cycling where a co-activation between

the gluteus maximus and rectus femoris was shown to be necessary in order to satisfy a net flexion moment and to allow the gluteus maximus to contribute to work.

On the basis of the present results it can be concluded that the differences in the role of mono- and bi-articular muscles are less pronounced than in the case of cycling. This conclusion is particularly relevant for the mono-articular muscles. Taking into consideration the concept of virtual work, this was not expected. However, from a mechanical point of view this is not really surprising since mono-articular muscles do contribute to the net joint moments while bi-articular muscles have an influence not only on the direction of the external force but also on its magnitude (and on external virtual work). Thus, a certain exchange of position and force information may be present in the control of both types of muscles. Evidence for such an exchange of information can be based on the existence of different motoneuron pools in both types of muscles, though more pronounced in the bi-articular muscles. In walking cats, for example, the sartorius muscle shows three different bursts of motor unit activity which are independently recruited to perform separate tasks in the step cycle (Hoffer, Loeb, Sugano, Marks, O'Donovan & Pratt, 1987). Such a segregation of motor unit activity was also identified for the semitendinosus (Perret & Cabelguen, 1980). For fast arm movements, Hasan & Karst (1989) found that elbow flexions involving arm and shoulder movements were not always initiated by EMG activity in the elbow flexor muscles, which might support our hypothesis on the different roles of mono- and bi-articular muscles. Even the results of Nardone, Romano & Schieppatti (1989), who pointed out that soleus and gastrocnemius muscles are selectively recruited depending on the type of contraction, appear to comply with this hypothesis.

Control of position and force

From this and previous studies (van Ingen Schenau, 1989; van Ingen Schenau *et al.* 1990, 1992; Jacobs & van Ingen Schenau, 1992) it is clear that the control of the distribution of net moments over the joints is required to direct an external force, which to a large extent is independent of the necessary changes in joint position or of the mechanical advantage of the muscles in static tasks (Fig. 4 and Table 3). Consequently, theories on movement control which do not account for this requirement will fail to predict patterns of intermuscular co-ordination, especially in multi-joint movements. It is likely, therefore, that previous studies (Buchanan, Rovai & Zev Rymer, 1989; Hasan & Karst, 1989; Flanders & Soechting, 1990; Lacquaniti & Soechting, 1986) might have provided a better understanding of the identified activation patterns of mono- and especially bi-articular muscles in the arm tasks if the direction of the external force was also included in their interpretations.

In this study the role of the mono-articular muscles was less clear than the one identified for the bi-articular muscles. However, it might be possible that if real position changes had been imposed under dynamic conditions, the activations of the mono-articular muscles would have shown a more positive relationship with muscle length alterations than in this isometric experiment. Therefore it seems likely that the global differences in the roles of mono- and bi-articular muscles will be more pronounced in dynamic movements. So, then, mono-articular muscles may be responsible for work, while the bi-articular muscles are the major instruments to meet specific task demands. Controlling (or learning to control) the mono-articulars

in such movements could be simply based on sensory information from muscle spindles. Achieving control over the bi-articular muscles is more difficult as information is not only required from the muscle spindles, but also input from golgi tendon organs and skin receptors (Nardone, Romano & Schieppati, 1988; Burke, Dickson & Skuse, 1991). As for the control of external force, information from the skin receptors can play a particularly important role. Additional evidence for the existence of different sources of information for position and force is derived from recordings of neural activity in the motor cortex of monkeys. It appears that in the motor cortex specific neurons are sensitive to movement direction (Georgopoulos, Schwartz & Kettner, 1986), while others code the direction of the force (Kalaska, Cohen, Hyde & Prud'homme, 1989).

Conclusions

It has been shown that the complex task of directing an external force was performed in a similar stereotyped manner by all different subjects. A pronounced role for the bi-articular muscles was identified in their co-regulation of the distribution of the net moments of the knee and hip which enabled the control of force direction. The role of the mono-articular muscles was less clear. Dynamic experiments are necessary so that real position changes are involved and thereby the relationship between activations and position changes could be more pronounced.

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