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ELSEVIER

THE RELATIVE ACTIVATION OF ELBOW-FLEXOR MUSCLES IN ISOMETRIC FLEXION AND IN FLEXION/EXTENSION MOVEMENTS

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Abstract—Coordination studies of multi-joint movements suggest that the central nervous system uses some constraints to reduce the large number of degrees of freedom of the arm. To gain insight into how the net joint torque is distributed among the muscles, intramuscular EMG recordings were made to determine the relative activation of five major elbow-flexor muscles during isometric, shortening, and lengthening contractions at three elbow joint angles. A regularization procedure was used to evaluate the effect of two different approaches used to calculate the relative contribution of elbow-flexor muscles to joint torque from intramuscular EMG recordings. The results demonstrate a significant increase of the relative contribution of the biarticular muscles for more extended elbow joint angles and for isotonic tasks relative to isometric tasks. © 1997 Elsevier Science Ltd

Keywords: Intramuscular EMG; Muscle activation; Elbow joint.

NOTATION

CNS	central nervous system
EMG	electromyogram
EFR	EMG–force relation (factor)
FLR	force–length relation (factor)
LA	lever arm of the muscle with respect to the elbow
VCSA	cross-sectional area of effective recording volume
PCSA	physiological cross-sectional area of the muscle
CF	correction factor

INTRODUCTION

Due to the number of degrees of freedom in joints and the number of muscles acting across these joints, multijoint movements can be performed in numerous ways. Most movements, however, reveal some stereotypical properties (Soechting and Flanders, 1991, 1992; Theeuwen *et al.*, 1994a). This has been interpreted as evidence for the hypothesis that the central nervous system (CNS) uses some constraints to reduce the number of degrees of freedom (Berthoz, 1993; van Ingen Schenau, 1989). In the past a number of possible constraints have been suggested (e.g. Gielen and van Ingen Schenau, 1992). Finding out which of these constraints are used by the CNS in coordinating multijoint movements requires information on the relative activation and on the relative contribution to joint torque of the muscles contributing to the movement.

To determine the contribution of muscles to joint torque previous studies have relied on optimization procedures, such as minimizing total muscle force (Yeo, 1976) or minimization of muscle stress (Cholewicki *et al.*, 1995), and on EMG-assisted approaches. In general, EMG-assisted approaches appear to give better results than the optimization procedures, which do not take EMG activity in account. EMG-based methods used thus far to obtain the relative activation can be divided into two groups. The first relates the magnitude of the recorded EMG activity directly to the actual force delivered by a muscle (Buchanan *et al.*, 1989). The second only considers the relative changes in the magnitude of EMG activity between the muscles (Buchanan *et al.*, 1993; Cnockaert *et al.*, 1975; Theeuwen *et al.*, 1995).

In this paper we present a regularization technique (Morozov, 1984; Tikhonov and Arsenin, 1977) which combines the two methods. Since surface EMG recordings are highly dependent on physiological factors we intramuscularly recorded the EMG activity of the five most powerful elbow-flexor muscles during the performance of isometric and isotonic force tasks at three elbow angles.

METHODS

The experimental procedures used in this study have been approved by the medical/ethical committee of the University of Nijmegen and were set up in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. The data were collected from three male subjects (one subject was recorded twice) ranging in age from 24 to 41. No subject had any known history of neurological or musculoskeletal disorder and all gave their informed consent prior to each experiment.

Experimental setup

The subject was seated with his right arm in a horizontal plane through the shoulder joint. The forearm was supported by a sling attached to the ceiling. A force transducer in the sling confirmed that the vertical force was constant within 2 N. The right shoulder was securely strapped to the chair. A lightweight aluminum bracelet was fixed around the wrist of the subject and was connected via a cable to a torque motor in such a way that the torque motor could pull in various directions. A force transducer in the cable was used to measure the horizontal force produced at the wrist (Fig. 1).

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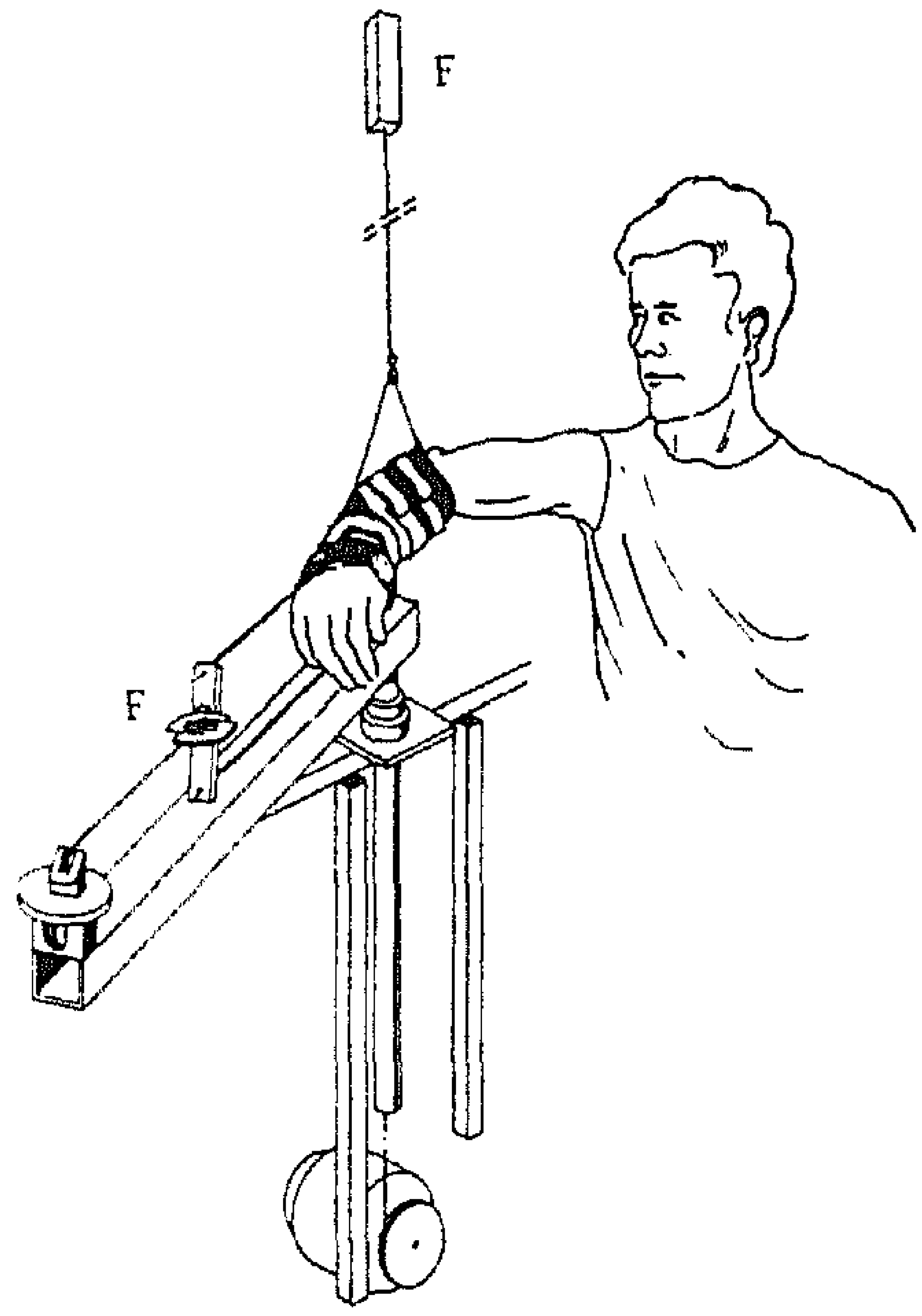

Fig. 1. Schematic representation of the experimental setup.

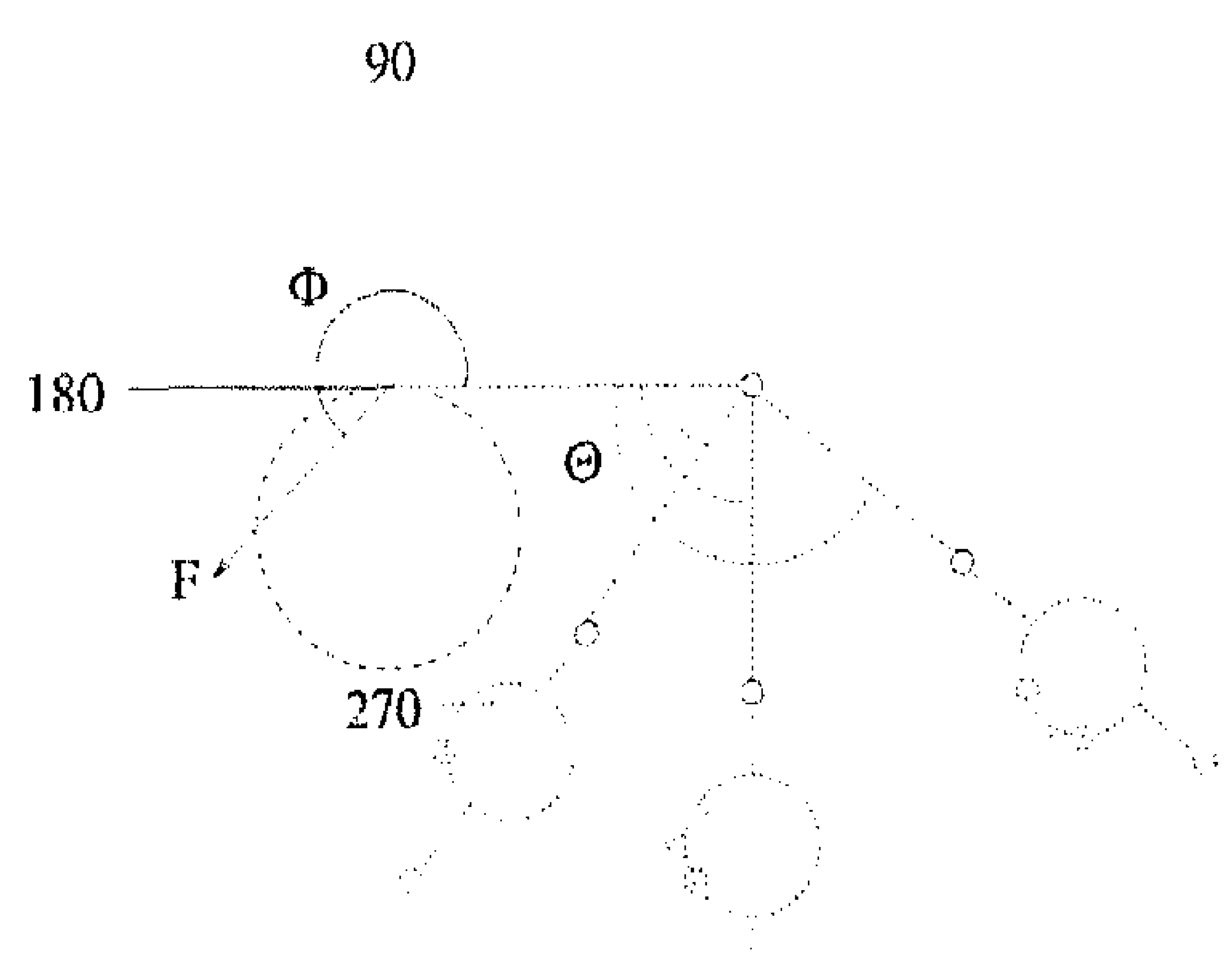

Fig. 2. Schematic representation of the subject in the setup (top-view; dotted line) for the three different positions in which subjects were tested ($\Theta = 55, 90$ and $135°$). The dashed circle represents the torque in the elbow as a function of the direction Φ of force F with constant amplitude.

EMG activity was measured in three conditions: isometric contractions, isotonic shortening (concentric) and isotonic lengthening (eccentric) contractions. The subjects were tested in each of these conditions for three elbow joint angles: $\Theta = 55$, 90 and 135°. Full extension corresponds to an angle of 180° (Fig. 2). The shoulder joint angle was always the same (0° anteflexion) and the hand was always in the middle between full supination and pronation.

For isometric contractions the wrist of the subject was fixated. Subjects were instructed to exert a prescribed horizontal force of 30 N at the wrist in 13 different equidistant directions (Φ_i) in the range between 180 and 360° (Fig. 2). Feedback about the force at the wrist was provided on an oscilloscope in front of the subject.

For lengthening (shortening) contractions the wrist of the subject was pulled back (released) by the torque motor with a constant speed of $1.5\,\mathrm{cm\,s^{-1}}$, corresponding to angular velocities in the elbow between 0 and $3.7°\,\mathrm{s^{-1}}$, depending on the movement direction and the elbow angle. Subjects had to keep the magnitude of the force at 30 N, while the hand moved in one of the 13 different directions. The movement was made over a range of about 20 cm centered at the position in which the isometric contraction was performed. EMG activity was recorded, however, only in a range of 6 cm centered around the isometric test position to prevent any effects of the force–length relation. Each trial was repeated three times. Movements were made in the same 13 directions as the isometric contractions. For each direction, task and elbow angle EMG activity was averaged over the three signals obtained in the three trials. For each trial the EMG activity at rest was subtracted from the mean EMG signal.

The elbow angle Θ and the direction of force Φ were defined as in Fig. 2. The dashed circle in Fig. 2 represents the torque in the elbow joint when the direction Φ of a force with constant amplitude is varied in a range between $180 \leqslant \Phi_i \leqslant 360$. The torque is plotted in polar coordinates.

Intramuscular EMG

We intramuscularly recorded the EMG activity of m. biceps breve, m. biceps longum, m. brachioradialis, m. brachialis and m. pronator teres. Fine-wire nylon-coated karma electrodes with a diameter of 25 μm were used. The wires were inserted by means of a hypodermic needle in the middle of the muscle belly. The insulation of the wire was removed at the electrode tip over a length of about 1 mm to record an EMG activity which was an integrated value obtained over a particular effective volume around the electrode tip ('depth EMG'). The length over which the insulation was removed was the same for all electrodes. This was verified by careful preparation and inspection of the electrode under a microscope. The impedance of the various electrodes was the same within 5% (approximately 0.7 MΩ). This means that the effective pick-up volume for the various muscles can be considered to be of the same size.

After amplification and filtering (with a fourth-order Bessel filter; 3 dB high-pass frequency at 3 Hz and 3 dB low-pass frequency at 150 Hz) the EMG signals were sampled at a rate of 500 Hz. The mean amplitude of the rectified EMG activity was taken as the amplitude of EMG activity in each trial.

THEORY

The electromyographic activity $\mathrm{EMG}_{m,t}(\Phi_i, \Theta)$ of a muscle m measured with intramuscular fine-wire electrodes during the production of a force of 30 N at the wrist in a direction Φ_i can be expressed by the following equation:

$$\mathrm{EMG}_{m,t}(\Phi_i, \Theta) = \mathrm{EFR}_{m,t}(\Theta) \cdot F_{m,t}(\Phi_i, \Theta) \cdot \mathrm{FLR}_m(\Theta) \left(\frac{\mathrm{VCSA}}{\mathrm{PCSA}}\right)_m \mathrm{CF}_m, \tag{1}$$

where $\mathrm{EFR}_{m,t}(\Theta)$ is the amplitude of EMG activity which a muscle m produces when it delivers a force of 1 N

Table 1. Literature values used in the calculations

Elbow angle	M. biceps breve	M. biceps longum	M. brachio-radialis	M. brachialis lower/upper head	M. pronator teres
Physiological cross-sectional areas (PCSA) in cm²*					
	2.4	2.7	1.6	4.5/4.5	3.1
Muscle length in cm†					
	33.3	31.2	28.7	7.6/15.0	14.0
Lever arms with respect to the elbow joint (LA) in cm‡					
55	4.0	4.0	7.7	3.3	2.1
90	4.8	4.8	7.3	3.0	2.1
135	3.2	3.2	4.3	1.7	1.1
Correction factor for the force-length relation (FLR)§					
55	1.0445	1.0479	1.0890	1.2367/1.5574	1.0851
90	1.0	1.0	1.0	1.0/1.0	1.0
135	1.0499	1.0003	1.1224	1.0969/1.1612	1.0974

Note: Each value is the average of the literature values.
* Data obtained from An *et al.* (1981) and Lehmkuhl and Smith (1983).
† From Wood *et al.* (1989) and Kleweno (1987).
‡ From Winters and Kleweno (1993) and Van Zuylen *et al.* (1988b).
§ From Kleweno (1987), Van Zuylen *et al.* (1988b) and Murray *et al.* (1994).

at an angle Θ between the upper arm and forearm. The index t refers to a particular motor task (isometric contraction, flexion movement, etc.). Therefore, $\mathrm{EFR}_{m,t}(\Theta)$ can be considered as the constant in the EMG–force relation which relates the force delivered by muscle m to the EMG activity of that muscle. $F_{m,t}(\Phi_i,\Theta)$ is the force delivered by muscle m when a force of 30 N at the wrist is produced in direction Φ_i at an elbow angle of $\Theta°$. $\mathrm{FLR}_m(\Theta)$ is a factor accounting for the force–length relation, which was necessary since we have been recording at various elbow angles Θ. $(\mathrm{VCSA/PCSA})_m$ is the ratio between the cross-sectional area of the effective volume from which the activity is actually recorded with the intramuscular wires (VCSA) and the total physiological cross-sectional area of the corresponding muscle (PCSA). Finally, CF_m is a correction factor which accounts for several other factors possibly giving rise to a difference in the recorded activity between the various electrodes. For example, CF may depend on the ratio of the number of muscle fibers of various subpopulations of motor units in the effective recording volume of the muscle. The factor CF_m is similar to the G-factor used by Cholewicki *et al.* (1995) who had to account for the difference in gain between muscles.

Since the total elbow torque $\mathrm{T}(\Phi_i,\Theta)$ must be equal to the sum of the torque contributions delivered by each single muscle, we obtain

$$\mathbf{T}_t(\Phi_i,\Theta)=\sum_m \mathbf{T}_{m,t}(\Phi_i,\Theta)$$

$$=\sum_m \{\mathbf{F}_{m,t}(\Phi_i,\Theta)\cdot \mathrm{LA}_m(\Theta)\}, \tag{2}$$

where $\mathrm{LA}_m(\Theta)$ represents the lever arm of muscle m at the elbow joint at an elbow angle Θ. Since in our experiments all forces and positions of the arm were in a horizontal plane through the shoulder joint (see the Methods section), the direction of the torque was always perpendicular to this plane ($\mathbf{T}=\mathbf{r}\times\mathbf{F}$, where $\times$ represents the vector crossproduct). This allowed us to replace the vector $\mathbf{T}(\Phi_i,\Theta)$ by the scalar $T(\Phi_i,\Theta)$. Combining equations (1) and (2) we obtain

$$T_t(\Phi_i,\Theta)=\sum_m\left\{\mathrm{EMG}_{m,t}(\Phi_i,\Theta)\left(\frac{\mathrm{LA}}{\mathrm{FLR}}\right)_m(\Theta)\mathrm{PCSA}_m \times\frac{1}{\mathrm{VCSA}_m\cdot \mathrm{EFR}_{m,t}\cdot \mathrm{CF}_m}\right\}. \tag{3}$$

The values for $(\mathrm{LA/FLR})_m(\Theta)$ at various elbow angles and the values for PCSA were obtained from literature. Table 1 gives the literature values which have been used in this study.

We define $S_m=(\mathrm{VCSA\cdot EFR\cdot CF})_m^{-1}$. The first approach to determine the contribution of the various muscles to elbow torque estimated the value of S_m for every muscle from the set of 13 equations (3) using a least-squares method. The second approach used the same least-squares method, but now we imposed the constraint that S_m had to be the same for every muscle. This assumption implies that every muscle produces the same amount of EMG activity intramuscularly recorded per unit volume for a certain activation (EFR) and that the product of the effective volume (VCSA) with the correction factor (CF_m) is the same for all muscles.

Since the first approach allows more variables to be fit, the fit obtained with the first approach should always be better than or equal to that obtained by the second approach. The first approach is the same as that followed by Buchanan *et al.* (1993), Cnockaert *et al.* (1975) and by Theeuwen *et al.* (1995). However, a disadvantage of this approach is that when the preferred direction of a muscle is near 270° (i.e. in the direction of force which causes the largest elbow torque; Fig. 4), only the activation of this particular muscle is taken to fit the total torque produced. The contribution of the other muscles is then set to zero, even when these muscles reveal significant EMG activity (Theeuwen *et al.*, 1995). This would imply that the force produced by these other muscles is zero, irrespective of the amount of EMG activity of these muscles. Also, when two muscles have more or less the same preferred direction, this approach only uses the activation of one of these muscles to fit the elbow torque and the activation of the others is set to zero.

We now used a regularization procedure to see how the error in the fit changes when we gradually go from the first to the second approach. This is done by introducing a parameter λ $(0 \leqslant \lambda \leqslant 1)$ such that when $\lambda = 0$ the solution was the least-squares solution without any constraints on S_m (first approach) and such that when $\lambda = 1$ the solution was the one which was found when S_m was required to be the same for all muscles ($S_m = S$, second approach). So λ can be seen as the weight factor by which the constraint of S_m being the same for all muscles was applied to the least-squares method used to solve the 13 equations. Equation (4) describes the error E as a function of λ:

$$E(\lambda) = (1-\lambda)\sum_i \left(\frac{T(\Phi_i) - \sum_m T_m(\Phi_i, S_m)}{T(\Phi_i)}\right)^2 + \lambda \sum_i \left(\frac{T(\Phi_i) - \sum_m T_m(\Phi_i, S)}{T(\Phi_i)}\right)^2. \tag{4}$$

Note that in the first term the factor S_m can be different for each of the various muscles and that in the second term the factor S is the same for all muscles.

RESULTS

Figure 3 shows the amplitude of the EMG activity for various elbow-flexor muscles as a function of the direction of isometric force at the wrist. For each elbow angle the data points lie more or less on a circle, which is in agreement with earlier reports (Theeuwen *et al.*, 1994b). The direction which corresponds to the direction of the center of a circle fitted to the data will be referred to as the 'preferred direction' of that muscle. Table 2 lists the mean values of the preferred directions, as well as the mean of the radii of the circle fits averaged over all subjects for all muscles and for all test conditions. The data in Fig. 3 illustrates that the amount of EMG activity for the same force vector is different for different elbow joint angles for each muscle. One-way ANOVA tests revealed significant differences between the various tasks and elbow angles. All significance levels are listed in Table 3.

Since, the monoarticular muscles (M. brachioradialis, M. brachialis and M. pronator teres) have approximately the same preferred directions, the relative change in activation, for various directions of force, between these muscles is not very large. The same is true for the biarticular muscles. Hence, the first approach to find the relative activation of the flexor muscles could not distinguish between the contribution from brachioradialis and brachialis. Neither was it possible to distinguish between the long and short head of m. biceps. Moreover, since the preferred direction of m. brachialis and m. brachioradialis was close to the direction of 270°, the first procedure many times attributed all torque contributions to the brachialis and brachioradialis and, therefore, resulted in torque contributions of value zero for the biarticular muscles which reveal significant amplitudes of EMG activity (see Theory). It is obvious that this solution ($\lambda = 0$ solution) cannot be a good estimate for the actual relative activation of the muscles since it frequently ignores the activation of the biarticular muscles.

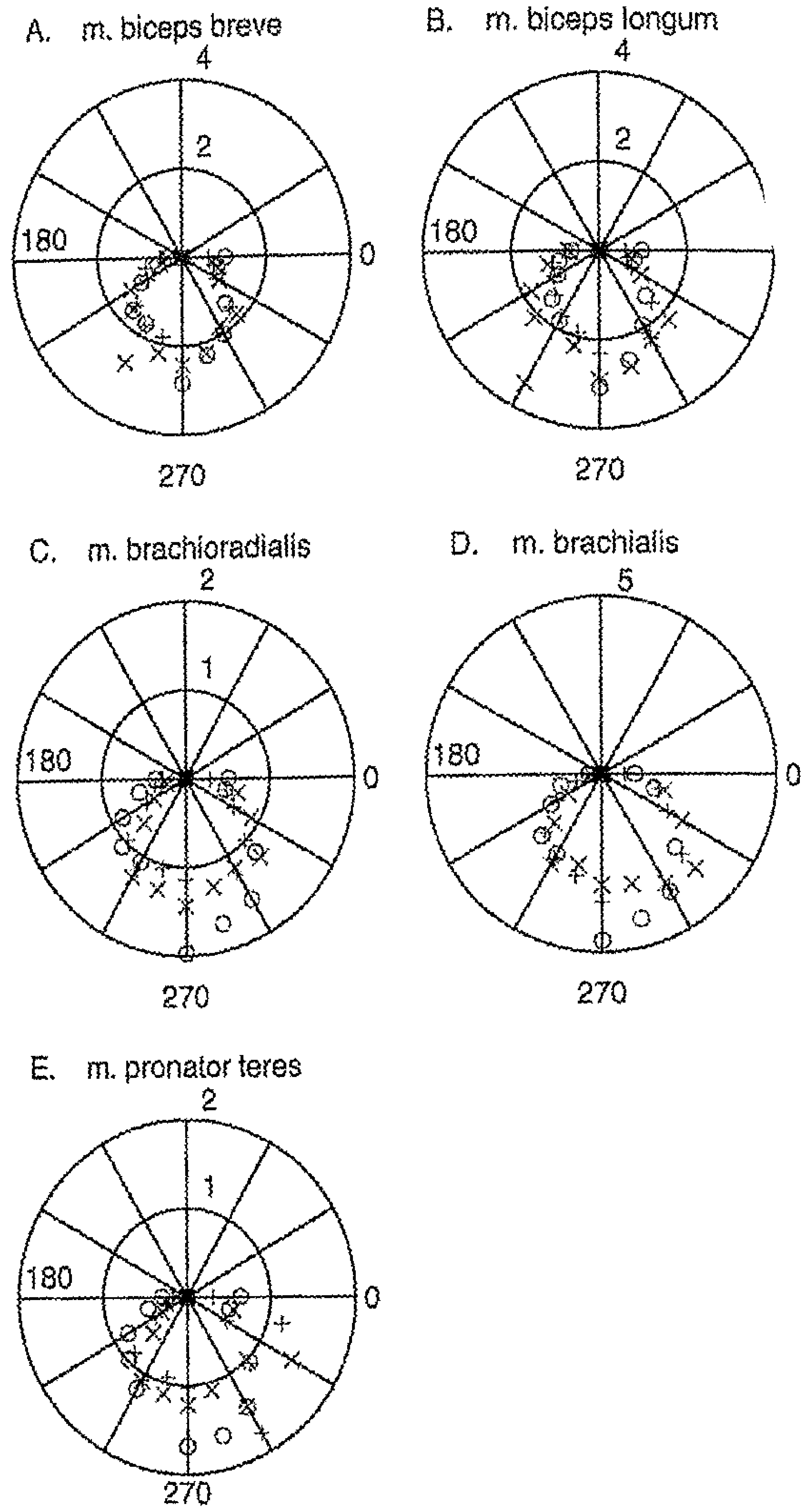

Fig. 3. EMG activity of several muscles for subject CG for an isometric force production of 30 N in different directions with respect to the forearm for elbow angles of 55 (+), 90 (O) and 135° (×). (A) m. biceps breve; (B) m. biceps longum; (C) m. brachioradialis; (D) m. brachialis; (E) m. pronator teres.

When, on the other hand, we assume that S_m is the same for all muscles, we only have to find the optimal value of S_m in order to calculate the relative torque contributions to the total elbow torque from the recorded EMG values ($\lambda = 1$ solution). S_m being equal for all muscles means that the EMG muscle–force relation per unit volume for intramuscular EMG activity (EFR_m) is the same for all muscles.

In Fig. 4 we have plotted the sum of the torque contributions calculated for $\lambda = 0$ (×) and $\lambda = 1$ (O). Figure 4 clearly shows that the data for $\lambda = 1$ and for $\lambda = 0$ both are similar to the total elbow torque. This was the case for all other experimental paradigms and for all other subjects. The mean error over all experimental paradigms in the

Table 2. Mean (averaged over all four subjects) of the preferred directions and radii of the circle fits for all experimental paradigms

Task	Elbow angle	M. biceps breve	M. biceps longum	M. brachio-radialis	M. brachialis	M. pronator teres
Mean preferred direction (deg)						
Isometric	55	274(10)	269(13)	276(5)	281(5)	271(7)
	90	275(11)	272(9)	284(12)	276(7)	277(8)
	135	261(8)	269(11)	289(9)	294(5)	281(7)
Isotonic shortening	55	267(18)	264(10)	272(7)	279(2)	270(6)
	90	271(3)	268(10)	281(10)	284(12)	276(5)
	135	261(9)	267(6)	291(13)	290(5)	286(8)
Isotonic lengthening	55	265(15)	268(9)	266(14)	283(5)	275(11)
	90	265(7)	269(9)	283(14)	288(11)	281(5)
	135	262(6)	269(6)	276(11)	286(6)	280(9)
Mean radii						
Isometric	55	37(5)	59(22)	24(11)	55(26)	18(11)
	90	36(17)	48(10)	25(11)	58(31)	18(13)
	135	61(24)	69(20)	25(9)	57(21)	20(12)
Isotonic shortening	55	62(26)	73(27)	33(7)	66(31)	24(12)
	90	60(24)	64(12)	33(12)	64(33)	24(18)
	135	77(25)	81(20)	26(9)	58(22)	20(13)
Isotonic lengthening	55	58(16)	75(22)	28(7)	52(22)	24(14)
	90	57(24)	67(11)	32(8)	52(27)	21(14)
	135	75(24)	85(18)	27(7)	54(23)	19(12)

Note: The standard deviations between subjects are given in parentheses.

Table 3. Significant differences (*$p<0.05$, **$p<0.025$, ***$p<0.01$, ****$p<0.005$), calculated with a one-way ANOVA test, in the preferred direction and the mean radii of the EMG activity and the estimated torque contributions for forces at the wrist in direction 270 between the various tasks and positions

Muscle	55 vs 90	55 vs 135	90 vs 135	Isometric vs shortening	Isometric vs lengthening	Shortening vs lengthening
Significant differences in mean preferred direction of EMG activity						
M. biceps breve		****			**	
M. biceps longum				*		**
M. brachioradialis	*		****		**	*
M. brachialis		*	****			
M. pronator teres			**			
Significant differences in mean radii of EMG activity						
M. biceps breve	***	****	****	****	****	
M. biceps longum		****	*	****	****	
M. brachioradialis		****		****	****	
M. brachialis				***	**	****
M. pronator teres				***	*	
Significant differences in the estimated torque contributions for forces at the wrist in direction 270						
M. biceps breve	**	****	****	****	****	
M. biceps longum		****	****		****	****
M. brachioradialis		****	****			
M. brachialis	*	****	****	****	****	****
M. pronator teres		****	****			

Note: The significance levels between the various elbow angles were calculated with the data for the various tasks and subjects grouped together, while the significance levels between the various tasks were calculated with the data for the various elbow angles and subjects grouped together.

difference with the elbow torque (solid circle in Fig. 4) and the fitted torque was 5.2% for $\lambda=0$ and 8.1% for $\lambda=1$. As expected (see the Methods section) the fit was slightly better for $\lambda=0$, for which more free parameters were allowed to fit the total torque.

To get an idea of how good the fit was as a function of λ, we plotted in Fig. 5 the relative error of the sum of the torque contributions with respect to the total elbow torque [Equation (4)] (solid line). The error is near 4% for $\lambda=0$, it increases to about 5% for $\lambda=0.3$,

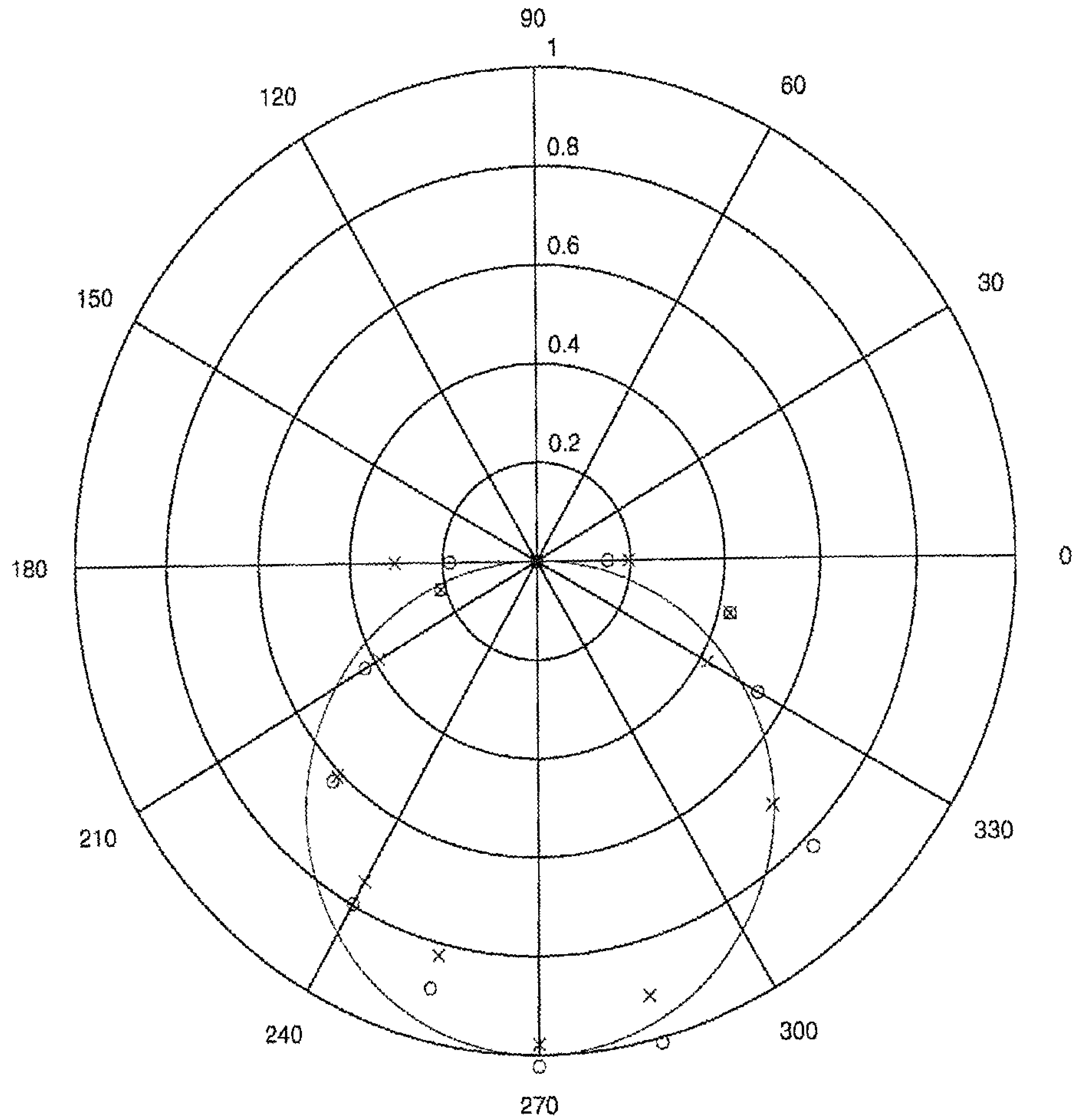

Fig. 4. Sum of the torque contributions calculated for $\lambda = O$ (×) and for $\lambda = 1$ (0) for subject CG, for an isometric task at an elbow angle of 55°. The solid line represents the actual torque amplitude in the elbow for forces in various directions.

and remains more or less constant for larger values of λ. To illustrate how well the ratio between predicted muscle torque and the amplitude of the EMG activity varies for different values of λ, we calculated the ratio $\sum_m (S_m(\lambda) - S_m(\lambda=1))^2 / \sum_m S_m^2(\lambda=1)$ as a measure for the difference between the estimated coefficients $S_m(\lambda)$ for a particular value of λ. The result is shown by the dashed line in Fig. 5. It is obvious that for small values of λ this ratio increases, reflecting the fact that for small values of λ muscles were attributed a torque contribution of zero even when they revealed a considerable amount of EMG activity.

For all experimental paradigms the error functions had the same shape. This means that the solid line always increases by only a small amount as λ increases (on the average from 5.8 to 8.1%) and that the dashed line increases dramatically for every experimental paradigm when λ decreased to zero. The latter means that for $\lambda = 0$, S_m is very different for the various muscles.

Table 4 lists the mean of the estimated relative torque contribution of each muscle to the total elbow torque for force in direction 270 for all experimental paradigms. The standard deviations are rather small, indicating a consistent pattern of muscle torques over our subjects. The standard deviation reflects the variation between subjects and not the standard deviation in the data of one single subject. The latter is typically about 12% of the relative torque contribution. Significance levels for differences between the various tasks and elbow angles are listed in Table 3.

In a one-way ANOVA test the relative torque contribution of the m. biceps appeared to be significantly larger for an elbow angle of 135° relative to that at smaller elbow angles. Moreover, the torque contribution of m. brachioradialis, m. brachialis and m. pronator teres appeared to be significantly smaller for an elbow angle of 135° relative to smaller elbow angles.

DISCUSSION

This study shows that simply measuring EMG activity in several muscles with intramuscular electrodes with the same impedance as a direct measure of muscle force gives more plausible results for the relative torque contributions than previously used methods. Previous studies have reported difficulties (Buchanan, 1986) with methods to estimate the coefficients of a set of equations relating EMG activity of several muscles to muscle torque for a highly 'redundant' system as the elbow. The problems encountered with a similar method in this study are

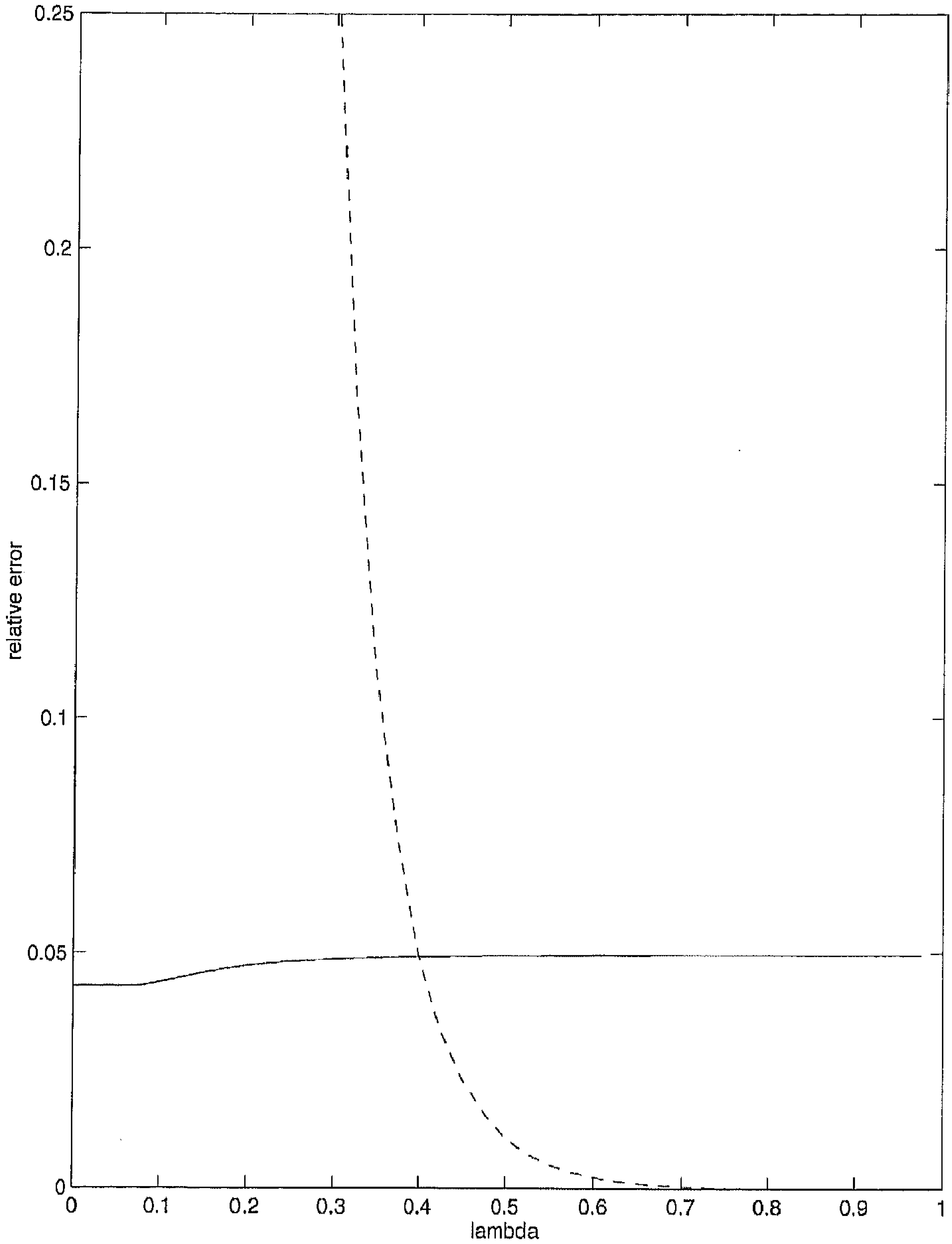

Fig. 5. The relative error as a function of λ of the sum of the torque contributions with the total torque produced with respect to the elbow (solid line). The relative error as a function of λ of the torque contributions, which were found by the least-squares method, with the torque contributions, which were found assuming S_m to be equal for all muscles ($\lambda = 1$) (dashed line) $\{\sum_m [S_m(\lambda) - S_m(\lambda = 1)]^2 / \sum_m S_m^2(\lambda = 1)\}$ (subject: BB; task: lengthening).

Table 4. Torque contributions (in percentages) (averaged over all subjects) of the various muscles for force at the wrist in direction 270 for all experimental paradigms

Task	Elbow angle	M. biceps breve	M. biceps longum	M. brachio-radialis	M. brachialis	M. pronator teres
Isometric	55	15.33(0.5)	27.35(2.4)	12.89(2.0)	40.43(3.6)	4.01(0.8)
	90	16.23(1.4)	26.59(2.4)	12.80(2.1)	40.73(3.7)	3.65(0.8)
	135	26.51(2.0)	36.34(2.5)	9.05(1.0)	25.31(2.5)	2.79(0.6)
Isotonic shortening	55	19.18(1.8)	25.51(1.8)	13.69(1.6)	37.76(3.4)	3.86(0.7)
	90	22.31(2.3)	26.83(1.9)	12.77(1.5)	34.49(3.7)	3.60(0.8)
	135	29.28(2.0)	37.36(2.2)	8.12(0.8)	22.82(2.3)	2.42(0.5)
Isotonic lengthening	55	20.12(1.1)	29.84(2.2)	12.65(1.3)	33.17(3.0)	4.21(0.8)
	90	22.45(1.7)	30.89(2.2)	13.27(1.4)	30.11(2.8)	3.27(0.7)
	135	28.59(1.7)	39.08(2.2)	8.65(0.5)	21.35(2.2)	2.32(0.5)

similar to the ones reported by Buchanan (1986). With regard to the first method (the method which relates the intramuscular EMG activity directly to muscle force) previous studies failed presumably because they used surface EMG rather than intramuscular EMG. Our method, which uses the same proportionality factor for all muscles, relies on several assumptions which were presumably not met in previous studies. For example, it assumes the same pick-up area for all electrodes. Also the possibility that fibers of motor units of non-activated subpopulations lie within the effective volume may influence the magnitude of the EMG activity recorded. In this study these external factors are included in the correction factor CF_m. The product of the effective cross-sectional area (VCSA) and CF_m is assumed to be the same for all muscles in the $\lambda = 1$ solution.

This study (see Table 4) demonstrates that for isometric contractions and for flexion movements the largest contribution to elbow joint torque is delivered by m. brachialis. This is in agreement with Bouisset *et al.* (1973).

Position dependency on the relative torque contributions

Our results (Table 2) reveal that the EMG activity of the biarticular m. biceps is increased for a more extended elbow. This can be understood from the fact that shoulder torques are larger when the elbow is more extended. When the m. biceps contributes more to the shoulder torque, it will also contribute more to the elbow torque. This is compatible with the smaller contribution of the monoarticular flexor muscles to elbow torque for the more extended arm.

Task dependency on the relative torque contributions

Our data show that all muscles are activated significantly more for the isotonic shortening than for the isometric condition. For all muscles, except for m. brachialis, the activation for the isotonic lengthening relative to the isometric condition was also larger. This indicates that the differences in activation between the conditions were not related to the force–velocity relation, since then the activation for the isotonic lengthening condition should have been smaller than that for the isometric condition for all muscles. A larger amount of EMG activity during movements was reported earlier (e.g. Bigland and Lippold, 1954; Theeuwen *et al.*, 1994a) and has to be attributed presumably to a different relative contribution of recruitment and firing rate to surface EMG.

Functional implications

The present results allow a quantitative comparison between the predictions of various hypotheses which have been put forward to explain the reduction of degrees of freedom in the motor system. If the purpose is to minimize fatigue, then the relative activation of muscles should be determined by the relative distribution of muscle fiber types in the elbow-flexor muscles Φ. In that case the same activation would have been expected in isometric contractions and in slow flexion movements. Another hypothesis, namely that energy wasting eccentric contractions are minimized, has been proposed by van Ingen Schenau (1989) and is based on the unique role of biarticular muscles. The larger contribution of the biarticular m. biceps during the concentric contractions in this study (relative to the contribution in isometric contractions) is in agreement with the predictions of that hypothesis (Gielen and van Ingen Schenau, 1992). However, this hypothesis would predict a much smaller contribution by the monoarticular muscles. Therefore, although the changes in the relative contribution of mono- and biarticular muscles are qualitatively in agreement, there is a disagreement quantitatively. One could argue that our results are a compromise between the two hypotheses. The changes in relative activation in isometric contractions and concentric/eccentric movements may then reflect a different weight of the constraints in the compromise. The hypothesis of minimal muscle force (Yeo, 1976) predicts that the biarticular muscles should be activated as much as possible. This hypothesis is falsified by the large contribution of brachialis. Summarizing, it seems that the data cannot be explained by any of the present hypotheses on the coordination of limbs with a large number of degrees of freedom.

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