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Activation patterns of mono- and bi-articular arm muscles as a function of force and movement direction of the wrist in humans

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1. In order to explain the task-dependent activation of muscles, we have investigated the hypothesis that mono- and bi-articular muscles have a different functional role in the control of multijoint movements. According to this hypothesis, bi-articular muscles are activated in a way to control the direction of external force. The mono-articular muscles are thought to be activated to contribute to joint torque mainly during shortening movements.
2. To investigate this hypothesis, surface electromyographic (EMG) recordings were obtained from several mono- and bi-articular arm muscles during voluntary slow movements of the wrist in a horizontal plane against an external force. The direction of force produced at the wrist and the direction of movement of the wrist were varied independently.
3. The results revealed distinct differences between the activation patterns of mono- and bi-articular muscles. The activation of the bi-articular muscles was not affected by movement direction, but appeared to vary exclusively with the direction of force.
4. The mono-articular muscles showed significantly more EMG activity for movements in a specific direction, which equalled the movement direction corresponding to the largest shortening velocity of the muscle. The EMG activity decreased gradually for movements in other directions. This direction-dependent activation appeared to be independent of the direction of the external force.

One of the central problems in movement control is related to the fact that for most joints several muscles can contribute to joint torque. For example, five muscles can contribute to flexion torque in the elbow. As a consequence, the same joint torque can be the result of multiple muscle activation patterns. Studies on activation patterns of muscles have shown that for a given motor task more or less the same relative activation of the muscles exists across subjects (e.g. Cnockaert, Linsel & Pertuzon, 1975; Buchanan, Moniz, Dewald & Rymer, 1993; Theeuwes, Gielen & van Bolhuis, 1996; van Bolhuis & Gielen, 1997). The fact that a more or less unique activation pattern is observed for each motor task suggests the existence of underlying constraints, reducing the number of possible muscle activation patterns for each task. These constraints have been attributed in the past to a minimization principle, for example minimization of total muscle force (Yeo, 1976) or muscle fatigue (Dul, Johnson, Shiavi & Townsend, 1984). However, no convincing evidence in favour of one of these minimization principles could be found, although some minimization principles seem to give qualitatively good fits (Prilutsky & Gregor, 1997).

Another possible explanation for the reduction of the number of degrees of freedom is related to a particular role of mono- and bi-articular muscles (van Ingen Schenau, Boots, de Groot, Snackers & van Woensel, 1992; Gielen & van Ingen Schenau, 1992). Based on the fact that movement trajectories of an end-effector (e.g. the hand or foot) have to be made by well co-ordinated rotations in multiple joints, van Ingen Schenau (1989) proposed that the activation of bi-articular muscles might be related to the direction of force exerted by the end-effector, whereas the activation of the mono-articular muscles might be related to the movement direction of the end-effector (related to whether a mono-articular muscle is shortening or lengthening). This hypothesis was supported by experimental observations by Jacobs & van Ingen Schenau (1992*a, b*) and van Ingen Schenau, Dorssers, Welter, Beelen, de Groot & Jacobs (1995), which suggested that the mono-articular muscles are primarily responsible for the generation of force and work, whereas the activation of the bi-articular muscles was compatible with the notion that they control the direction of external forces by regulating the distribution of the net

moments across the joints. Additional support for the hypothesis that bi-articular muscles control the direction of force at the end-effector was provided by Doorenbosch & van Ingen Schenau (1997), who reported a strong linear relationship between the difference in the electromyographic (EMG) activity of the antagonistic bi-articular m. rectus femoris and hamstrings and the difference in hip and knee joint torque, and thus with the direction of the external force at the foot. The activation of the mono-articular muscles, however, appeared to be influenced by the desired force direction as well. However, since the dynamometer used in that study allowed movements in a few directions only, the role of mono-articular muscles in controlling movement direction could not be tested explicitly.

In another study, Theeuwes, Gielen & Miller (1994) investigated the activation patterns of elbow and shoulder flexor muscles during isometric contractions as a function of the direction of force produced at the wrist and during voluntary arm movements against external forces in a horizontal plane. This study showed that each muscle has a unique 'preferred' direction in which the muscle produces the largest amount of EMG activity. It also showed that a different relative activation pattern of the muscles exists for force and movement tasks. These results were in agreement with the notion of a different functional role of mono- and bi-articular muscles. Since, in that study (Theeuwes *et al.* 1994), the movement direction of the wrist was always parallel to the direction of the force produced at the wrist, it was not possible to make a distinction between the dependence of the activation patterns on the force and the movement direction separately.

Evidence for a different role of mono- and bi-articular muscles also comes from animal studies. Experiments analysing postural control in cat (Macpherson, 1988*a,b*) indicate that bi-articular muscles play an important role in determining the direction of ground reaction force. Such a relationship was not found for mono-articular muscles.

Most of the evidence described above was obtained from experiments in which the direction of force and displacement covaried in a very systematic way. A conclusive test for a different role of mono- and bi-articular muscles requires at least the study of EMG activity of these muscles in movements in which movement direction and force direction are varied independently.

The purpose of this study was to record EMG activity in human arm movements in various directions against forces in various (mostly different) directions. The direction of force at the wrist and movement of the hand were varied independently. In a first experiment the EMG activity of the bi-articular m. biceps brachii caput breve (BIB) and the mono-articular m. brachioradialis (BRD) was measured for arm movements in a horizontal plane.

Since the amount of change of elbow joint angle for a movement of the wrist in a specific direction is different for different arm postures, the amount of shortening of the

muscles crossing the elbow joint also changes for the same movement directions at different arm postures. Therefore, by testing muscle activation for the same movement direction for various arm postures it is possible to investigate the effect of variations of muscle shortening under the same external conditions (i.e. the same direction of force at the wrist and the same movement direction of the hand). To investigate the effect of the amount of shortening of a muscle on its activation, the EMG activity of the BIB and the BRD was recorded during voluntary slow movements of the wrist against external forces at several arm postures. Finally, to see whether the differences in the activation patterns of the BIB and the BRD as a function of force and movement direction could be generalized to other mono- and bi-articular muscles, the experiments were repeated while recording the activation patterns of three other mono- or bi-articular arm muscles.

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. All subjects tested ($n = 13$) gave their informed consent prior to each experiment. None of the subjects had any known history of neurological or musculoskeletal disorder.

Experimental set-up

EMG activity was measured with surface electrodes from the mono-articular elbow flexor m. brachioradialis (BRD), m. biceps brachii caput breve (BIB; bi-articular elbow and shoulder flexor muscle), m. deltoideus pars spinalis (DPS; mono-articular shoulder extensor muscle), the mono-articular elbow extensor m. triceps caput lateralis (TLA), and m. triceps caput longum (TLO; bi-articular elbow and shoulder extensor muscle) during voluntary slow movements of the wrist. The EMG signals were bandpass filtered (3–150 Hz) and subsequently sampled at 500 Hz.

Subjects were seated with their right arm in the horizontal plane at shoulder height (Fig. 1). The shoulder was strapped tightly to the back of a chair in order to keep the shoulder fixed in space during the experiment. The position of the shoulder was measured several times by means of an OPTOTRAK (Northern Digital) system, demonstrating that the amplitude of movements of the shoulder was typically less than 2 mm. Supporting the forearm relieved the subject from keeping the arm in the horizontal plane by activating the shoulder muscles which contribute to elevation of the humerus. The forearm was in a semi-prone position. A force transducer mounted between the sling and the ceiling during several experiments showed that variations in vertical forces produced by the subject during the experiments were typically smaller than 2 N.

By means of a cable, fixed to a bracelet around the subject's wrist, the position of the wrist in the direction of the cable was measured and fed back to an oscilloscope in front of the subject. Subjects were instructed to move the wrist in the direction of the cable at a speed of 1.5 cm s^{-1} , which was done by tracking a target signal also shown on the oscilloscope. The cable was connected, via several pulleys, to a torque motor which produced a constant force of 6 N in order to keep the cable at tension. By changing the direction of the cable with respect to the wrist, which could be done by rotation of the bar supporting the pulleys and the cable around a vertical axis,

movements in various directions could be tested. Each direction was tested twice and the data obtained in the two tests were averaged for further analysis. Due to friction in the set-up the force at the wrist in the direction of the movement increased or decreased by 1 N, depending on whether the cable was pulled at or released, respectively. By hanging a weight (3 kg) over a pulley, fixed to the side of the table (see Fig. 1), a constant force of 30 N was applied to the wrist. By changing the position of this pulley the direction of force could be varied independently of the movement direction.

Movements were made over a range of approximately 15 cm. In order to exclude any effects of the force-length relationship of muscles, only the EMG recordings for wrist positions within a range of 3 cm centred around the rest position were used for further analysis. With this restriction the joint angles did not change more than 9 deg for the elbow and 5 deg for the shoulder joint centred at the rest position (at an elbow joint angle of 90 deg). The movement velocity of the wrist of 1.5 cm s^{-1} corresponds, for this rest position, to angular velocities smaller than 2.3 deg s^{-1} for the elbow and 1.3 deg s^{-1} for the shoulder joint.

Data analysis

All rectified and averaged EMG signals were normalized with respect to the maximal amount of EMG activity (100%) measured from each muscle in the entire experiment. The normalized amount of EMG activity was plotted as a function of the movement direction of the wrist in polar co-ordinates for each direction of the preload (Figs 4, 5 and 6). All polar representations for each muscle

have the same scale with the outer circle representing 100%. When the EMG activity of a muscle shows no dependence on the movement direction, one should expect a more or less circular distribution of the data centred around the origin in this representation. On the other hand, when the distribution of the data in this representation is not shaped as a circle or when the centre of the distribution is not located at the origin, this implies that the amount of EMG activity depends on the movement direction. To analyse the dependence of the EMG activity on the movement direction, an ellipse with the smallest sum of squared radial distances of the data points to the ellipse (see Fig. 2) was fitted to these polar data representations with a gradient descent method (Press, Flannery, Teukolsky & Vetterling, 1992), using eqn (1) to describe the ellipse:

$$\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} x_0 \\ y_0 \end{pmatrix} + \begin{pmatrix} \cos\Theta & -\sin\Theta \\ \sin\Theta & \cos\Theta \end{pmatrix} \begin{pmatrix} a\cos\Phi \\ b\sin\Phi \end{pmatrix}. \quad (1)$$

Here (x_0, y_0) represent the co-ordinates of the centre of the ellipse; a and b are the long and short axis of the ellipse, respectively; Θ gives the orientation of the ellipse; and Φ is the running parameter ($0 \leq \Phi < 2\pi$).

Experimental protocols

Subjects were tested using three different experimental protocols.

Protocol I. For five subjects the EMG activity of the BIB and BRD was measured for movements in twelve different directions (0, 25, 60, 90, 120, 150, 180, 205, 240, 270, 300 and 330 deg), for five

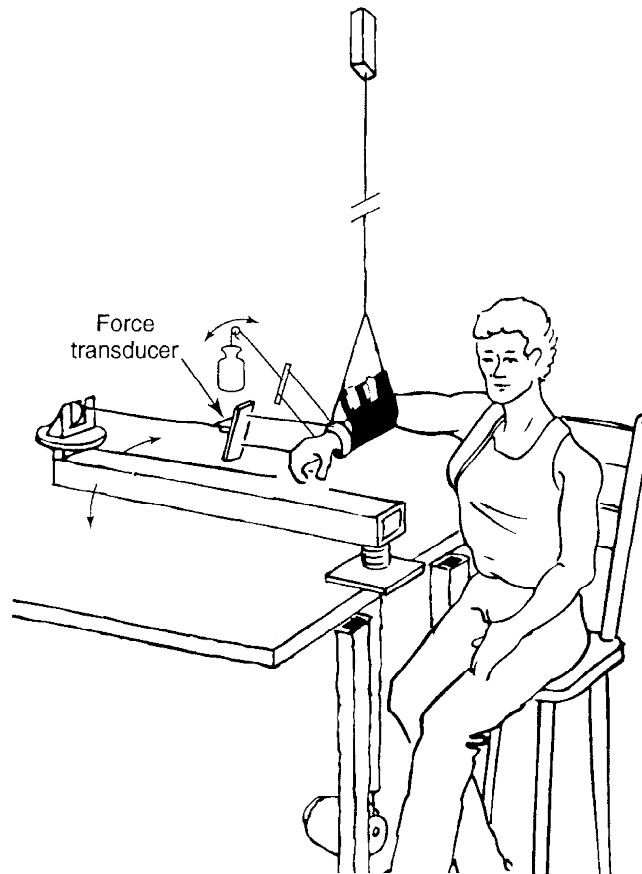


Figure 1. Schematic drawing of the set-up

The upper arm is in the direction of 0 deg anteflexion. The arm is supported near the elbow joint by a cloth sling attached to the ceiling.

different force directions (210, 235, 260, 285 and 315 deg) for each movement direction (0 deg corresponds to the direction from the wrist to the elbow joint, see Fig. 4). Movement directions and force directions were tested in a random order. The rest position during these experiments was at an elbow flexion angle of 90 deg (Fig. 4).

Protocol II. Small rotations around the shoulder ($\delta\Phi_1$) and elbow ($\delta\Phi_2$) joint resulting in displacements of the wrist over a distance ($\delta x, \delta y$) are related as in eqn (2):

$$\begin{pmatrix} \delta x \\ \delta y \end{pmatrix} = J(\Phi_1, \Phi_2) \begin{pmatrix} \delta\Phi_1 \\ \delta\Phi_2 \end{pmatrix}, \tag{2}$$

where $J(\Phi_1, \Phi_2)$ is the Jacobian matrix, given by:

$$J(\Phi_1, \Phi_2) = \begin{pmatrix} -l_1 \sin\Phi_1 - l_2 \sin(\Phi_1 + \Phi_2) & -l_2 \sin(\Phi_1 + \Phi_2) \\ l_1 \cos\Phi_1 + l_2 \cos(\Phi_1 + \Phi_2) & l_2 \cos(\Phi_1 + \Phi_2) \end{pmatrix}. \tag{3}$$

Here l_1 and l_2 are the length of the upper arm and forearm, and Φ_1 and Φ_2 are the joint angles in shoulder and elbow, respectively. The change in the joint angles as a function of the displacement of the wrist can, therefore, be written as in eqn (4):

$$\begin{pmatrix} \delta\Phi_1 \\ \delta\Phi_2 \end{pmatrix} = J^{-1}(\Phi_1, \Phi_2) \begin{pmatrix} \delta x \\ \delta y \end{pmatrix}. \tag{4}$$

Thus, the amount of change of the joint angles ($\delta\Phi_1, \delta\Phi_2$) depends on displacements δx and δy of the wrist (i.e. on the movement direction, since the ratio $\delta y/\delta x$ gives the tangent of the movement direction) as well as on the Jacobian matrix. Since the Jacobian is a function of the joint angles Φ_1 and Φ_2 , the amount of change of the joint angles for a displacement ($\delta x, \delta y$) of the wrist also depends on the geometry of the arm (Φ_1, Φ_2).

To investigate the effect of the relative changes of the joint angles in elbow and shoulder, and therefore the effect of the relative changes of the lengths of the muscles crossing the joints, on the EMG activity, the EMG activity of the BIB and the BRD was measured at three different rest positions with elbow angles of 55, 90 and 135 deg (full extension corresponds to an elbow angle of 180 deg) (Fig. 5). The shoulder angle at the rest position was 0 deg ante flexion in all experiments. Voluntary slow movements were performed by four subjects in sixteen different movement directions (0, 20, 40, 60, 90, 120, 140, 160, 180, 200, 220, 240, 270, 300, 320

and 340 deg) for one force direction (260 deg). One of the subjects was also tested using protocol I.

In our experiments, data were collected for wrist positions within 3 cm of the rest position ($\sqrt{(\delta x)^2 + (\delta y)^2} < 3$ cm). With this restriction, the amount of change of the joint angles can be calculated as a function of the movement direction of the wrist for each rest position. For an elbow joint angle of 90 deg, displacements of equal amplitude give the largest decrease of elbow joint angle for movements of the wrist in a direction of 305 deg. This means that the mono-articular elbow flexor muscles will show maximal shortening for movements of the wrist in this direction. For arm postures with elbow angles of 55 and 135 deg, the maximal decrease in elbow joint angle occurs for movements of the wrist in directions of approximately 279 and 333 deg, respectively.

During experimental protocols I and II, the subjects had to produce a force of 6 N in or opposite to the movement direction to counteract the force generated by the torque motor in order to keep the cable at tension. Also an increment (decrement) of 1 N, to overcome the friction in the set-up, had to be produced for movements in the 'pulling' ('release') direction. The total force exerted at the wrist was therefore the sum of these two forces and the force counteracting the gravitational force of the weight. As a consequence, the total force exerted at the wrist was not entirely constant for the various movement directions, but varied by about 10–15%.

Protocol III. To investigate whether other mono- and bi-articular muscles show similar activation patterns as the BIB and BRD, the EMG activity was measured in BIB, BRD, TLO, TLA and DPS for five subjects. Voluntary slow movements in twelve different movement directions (the same as tested in protocol I) were investigated for six different force directions (10, 40, 70, 195, 235 and 260 deg). The rest position was at 90 deg elbow flexion (see Fig. 6). The position of the wrist during these experiments was not recorded by means of a torque motor, but instead by using an OPTOTRAK system. The advantage of this set-up was that no forces, other than that to counteract the force exerted by the weight, had to be produced at the wrist. In the directions 10, 40 and 70 deg a force of 20 N was produced, since a force of 30 N in these directions was too large for some subjects to perform the constant velocity movements.

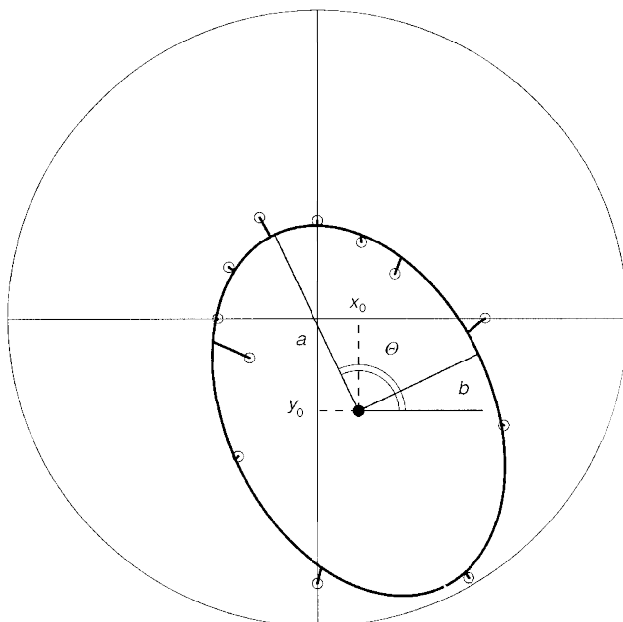


Figure 2. Typical example of an ellipse fitted to the data

The sum of the squared radial distances of the data points (open circles) to the ellipse was minimized. The location of the centre point (filled circle) was calculated to obtain a measure for the dependence of the EMG activity on the movement direction. See eqn (1).

Joint torque versus force direction

When a force of constant amplitude is produced at the wrist, the corresponding joint torques will depend on the direction of the force. A force in a direction of 270 deg, for instance, will cause maximal elbow flexion torque and a force in the opposite direction (90 deg) maximal elbow extension torque (Fig. 3). Torque in the shoulder joint also depends on the elbow joint angle (rest position). For an elbow angle of 90 deg the directions of maximal flexion and extension torque in the shoulder, respectively, are approximately 220 and 40 deg (depending on the ratio of the distance from shoulder to elbow and from elbow to the position of the bracelet at the wrist; see Fig. 3 and van Bolhuis & Gielen, 1997). The joint torque amplitude changes as a cosine function with force direction. Shoulder torque is zero for force directions of approximately 130 and 310 deg.

Statistics

In order to obtain a measure of the dependence of the EMG activity of a muscle on movement direction, the vector pointing to the location of the centre (x_0, y_0) of the ellipse fitted to the data was calculated. From the direction Θ of the centre with respect to the origin (see Fig. 2) as well as from the distance of the centre from the origin, information about the movement direction dependence could be obtained. The intra-subject variability in the location of the centre of the ellipse appeared to be much smaller than the inter-subject variability (about 100 times). Therefore, only the inter-subject variability was used to calculate the significance levels presented in Table 1.

To investigate whether for all subjects the centres of the ellipses for one muscle and one specific task were all oriented in the same direction with respect to the origin, the set of inner products between all possible pairs of vectors, pointing to the centres, was calculated. For N subjects this gives $N(N - 1)/2$ inner products. A positive inner product of two vectors indicates that the vectors are oriented within an angle smaller than 90 deg. When all vectors are distributed randomly in all directions an equal number of positive and negative inner products is expected. The null hypothesis, assuming a randomly distributed set of vectors, therefore, is that the probability distribution of obtaining a specific set of inner products is binomial, centred around an equal number of positive and negative values. From the set of inner products calculated for a

certain muscle or task compared with the binomial probability distribution a confidence level for rejecting the null hypothesis, and therefore implying that all vectors tend to be oriented in a specific direction, could be obtained. The direction of the centre of the polar EMG plot for a muscle for a certain task is called the 'preferred movement direction' (PMD).

In this way we could obtain a confidence level for the occurrence of a PMD. To investigate whether the PMDs differed significantly between muscles or tasks a one-sided Fisher–Pitman randomization test (FP-test; Krauth, 1988) was used. The same test was used to investigate whether a set of centres differed significantly with respect to the mean distance from the origin between muscles or tasks. This non-parametric test investigates whether two distributions of values of a one-dimensional variable (in this case distance from the origin or direction of the centres) differ significantly, without assuming a specific probability distribution of the variable.

RESULTS

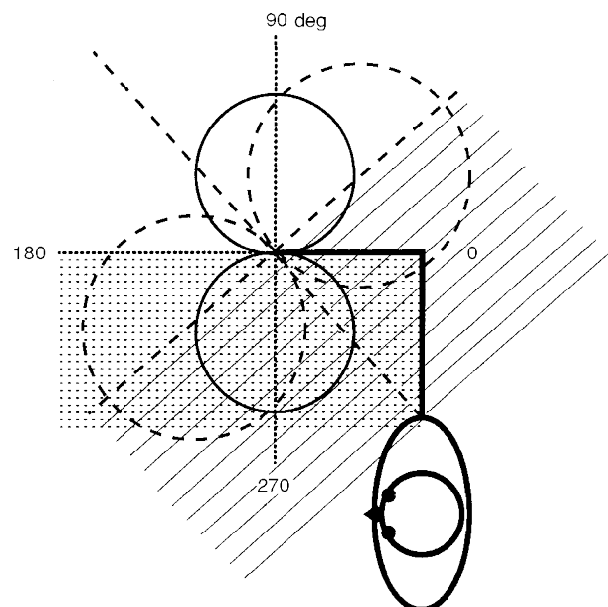
Protocol I

Figure 4 shows polar plots of the averaged amount of EMG activity as a function of movement direction and force direction. Each circle gives a polar representation (thick continuous lines) of the average EMG value as a function of the movement direction for a particular force direction. The schematic drawing in the centre of the figure shows the subject in the rest position. Data obtained for the BRD and the BIB during protocol III were added to the data obtained for the BRD and the BIB during protocol I. This will be discussed in more detail later. In this way nine different force directions were tested, from which two force directions (235 and 260 deg) were tested in protocol I as well as in protocol II.

Force direction dependence. Figure 4 shows that the amount of EMG activity depended on the direction of force exerted at the wrist. Although the size of the polar plots of EMG activity as a function of movement direction differed

Figure 3. Top view of a subject in the rest position

Polar representation of the elbow (continuous circles) and shoulder (dashed circles) torques as a function of the direction of force (with constant amplitude) produced at the wrist for an arm posture at 90 deg elbow flexion. The dotted area indicates the region of force directions at the wrist resulting in a flexion elbow torque and the dashed area indicates the region of movement directions of the wrist corresponding to flexion of the elbow.



for different directions of force, the shape of the polar plots of the EMG activity was more or less the same for all force directions. The thick dashed lines indicate the mean PMDs, which were more or less the same for the various force directions. For the BRD (Fig. 4A), the largest amplitudes of EMG activity were found for a force direction near 285 deg. The size of the polar plots, representing the amount of EMG activity, decreased gradually for other force directions. For the BIB (Fig. 4B), a similar dependence of the amplitude of the polar plots of EMG activity on force direction was observed. However, it was not tuned as sharply as for the BRD.

Movement direction dependence. A comparison of Fig. 4A and B reveals that the EMG activity of the BIB did not depend on the movement direction in the same way as did the EMG activity of the BRD. The BIB showed more or less the same amount of EMG activity for all movement directions for each direction of force. In contrast, the BRD clearly showed more EMG activity for movements in directions of approximately 300 deg for each direction of force. Table 1 shows the locations (distance from the origin (fourth column) and orientation (fifth column) of the mean of the centres of ellipses fitted to the data (averaged over five subjects) for the BRD and the BIB for various force

directions (third column). Data are shown only for the force directions in which the PMDs of the subjects were significantly oriented in one direction. The sixth column gives the upper limits of the probability that all of the centre points (all subjects) were randomly oriented (see Methods).

Table 1 shows that the means of the centres of the ellipses fitted to the BRD data were located approximately 5 times as far from the origin as the means of the centres of the ellipses fitted to the BIB data. The difference is significant ($P < 0.001$; FP-test) when the data of all force directions are grouped together.

For the BRD the PMDs were oriented in approximately the same direction (near 300 deg) for each force direction. This clustering of the PMDs was significant ($P < 0.001$) for each force direction listed in Table 1. The small differences between the mean PMDs for each force direction were not significant (FP-test). For the BIB the clustering of the PMDs was significant ($P < 0.005$, $P < 0.001$) for only two force directions (235 and 260 deg, respectively). Combining this result with the fact that the mean centres of the BRD were located significantly further from the origin than the mean centres of the BIB, demonstrates that the activation patterns of the BRD and the BIB as a function of the

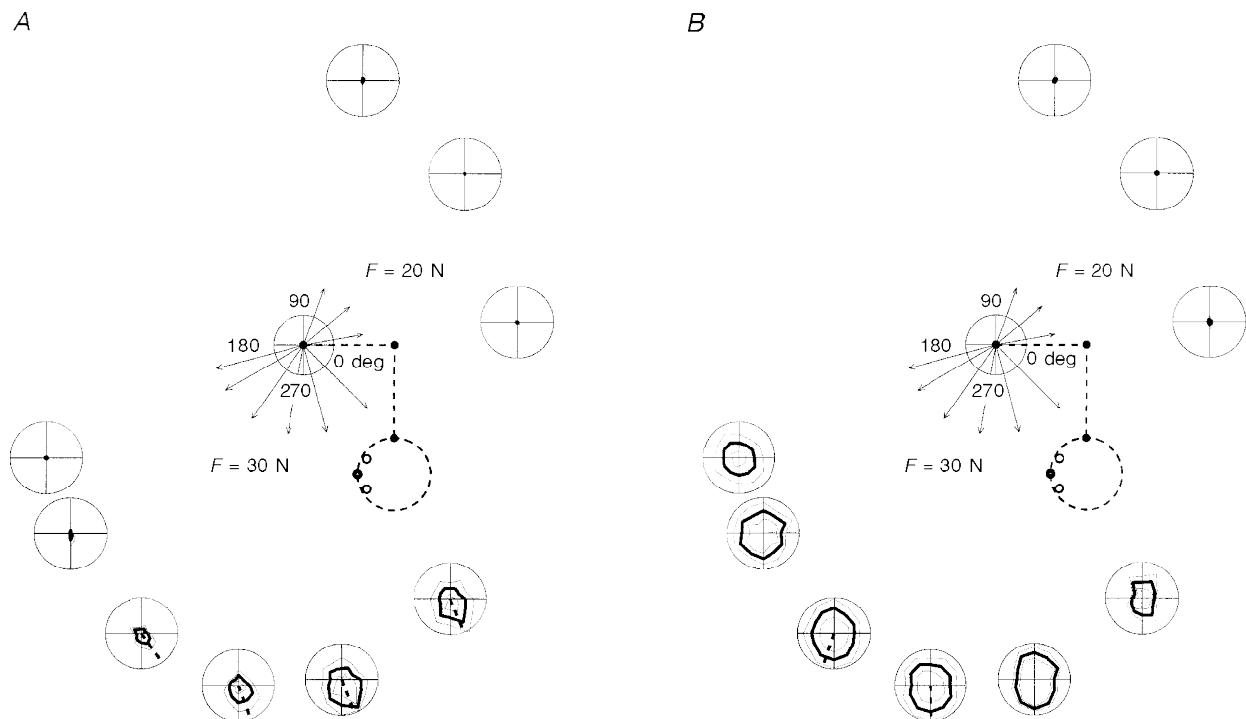


Figure 4. Muscle activity as a function of the force and the movement direction

Polar plots of the averaged amount of EMG activity (thick continuous lines) of the BRD (A) and BIB (B) as a function of movement direction for various force directions. The thick dashed lines indicate the mean PMDs. Data for force directions of 10, 40, 70 and 195 deg were averaged over 5 subjects (protocol III), data for force directions of 210, 285 and 315 deg were averaged over 5 other subjects (protocol I) and data for force directions of 235 and 260 deg were averaged over 10 subjects (protocols I and III). The standard deviation is indicated by the thin continuous lines. The arrows pointing from the wrist of the subject to the polar plots represent the force directions during the movements for each polar plot. F , force.

Table 1. The locations of the mean of the centre points of the ellipses fitted to the data of each muscle averaged over the subjects

Figure	Muscle	Force direction (deg)	Distance (%)	PMD (deg)	<i>P</i>
4A	BRD	235	21.1	305	0.001
		260	25.0	290	0.001
		285	27.1	291	0.001
		315	25.2	293	0.001
4B	BIB	195	3.6	260	n.s.
		210	4.1	226	n.s.
		235	5.0	252	0.005
		260	8.3	271	0.001
		285	5.3	321	n.s.
		315	5.1	349	n.s.
5D	BRD	260	28.2	280	0.002
5E		260	23.5	292	0.002
5F		260	25.7	313	0.002
5G	BIB	260	7.6	270	0.002
5H		260	10.3	265	0.002
5I		260	17.2	256	0.002
6A	TLO	10	3.4	94	n.s.
		40	1.8	73	n.s.
		70	7.2	113	0.007
6B	TLA	10	8.6	66	0.001
		40	14.3	110	0.001
		70	17.6	119	0.001
6C	DPS	10	18.1	7	0.001
		40	16.8	15	0.001
		70	15.5	8	0.001

n.s., not significant ($P > 0.05$).

movement direction are significantly different. The BIB shows no clear movement direction dependence, whereas the BRD does show a distinct movement direction dependence. Moreover, the movement direction dependence of the BRD appears to be independent of the force direction.

Protocol II

Figure 5 shows the EMG activity as a function of movement direction for experiments performed at three arm postures (elbow angles of 55 deg (*A*, *D* and *G*), 90 deg (*B*, *E* and *H*) and 135 deg (*C*, *F* and *I*). Figure 5*D–F* shows that the activation pattern of the BRD as a function of the movement direction changed with arm posture. A change of the PMD (dashed lines) to larger angles can be observed in Fig. 5*D*, *E* and *F*, respectively. Figure 5*G–I* shows that the activation patterns of the BIB for the three arm postures predominantly changed in size (Fig. 5*H* shows the smallest and Fig. 5*I* the largest EMG activity) but not in direction.

For both muscles the PMDs were oriented in approximately the same direction for all subjects for each arm posture. This clustering of the PMDs (over subjects) was significant ($P < 0.002$) for both muscles for each arm posture. The mean of the centres (averaged over four subjects) for the BRD and the BIB for each arm posture are shown in Table 1.

In contrast to the results obtained during protocol I the mean PMDs of the BRD were not in the same direction for every force direction. The mean PMDs of the BRD changed from 280 deg to 292 deg to 313 deg for arm postures with elbow angles of 55, 90 and 135 deg, respectively (Table 1). The mean PMD at elbow angles of 55 and 90 deg differed significantly from the mean PMD at an elbow angle of 135 deg (FP-test: $P_{55-135} < 0.020$ and $P_{90-135} < 0.018$). Moreover, the PMDs of the BRD data of the four subjects were significantly correlated (coefficient of 0.84) with the movement directions (279, 305 and 333 deg, respectively) at which maximal decrease of the elbow joint angle occurred (dashed lines in Fig. 5*A*, *B* and *C*, respectively; $P < 0.005$; $n = 12$). This means that the PMDs of the BRD show a significant correlation with the direction of maximal shortening of the mono-articular elbow flexor muscles (see Methods).

For the BIB a similar shift of the PMD with arm posture was not observed. Moreover, the mean distance of the centres to the origin was significantly smaller for the BIB than for the BRD (FP-test: $P < 0.001$). This means that the activation of the BIB does not show a clear dependence on arm posture.

The results obtained during the experiments of protocols I and II lead to the conclusion that the mono-articular BRD shows more EMG activity during movements at which the shortening of the muscle is largest. This effect does not depend on the force direction. The activation of the bi-articular BIB does not show a clear movement direction dependence, and is determined by the force direction only.

Protocol III

To investigate whether the activation of other mono- and bi-articular arm muscles show a similar dependence on the force and the movement direction as the BRD and the BIB, respectively, five subjects were tested using protocol III. We have added the data of the BRD and the BIB obtained in protocol III to the data obtained in protocol I. These data were shown in Fig. 4. The results for the other four muscles are plotted in Fig. 6.

Force direction dependence. Figure 6 shows that the amount of EMG activity was determined by the force direction, in a similar way as shown in protocol I for the BRD and BIB. The amplitude of the polar plots of EMG activity as a function of movement direction was tuned by the force direction. Figures 4 and 6 show that the force direction at which the maximal amplitude of the polar plots

of EMG activity was recorded was different for the different muscles. For instance, the BIB showed large amounts of EMG activity for force directions producing large flexion torques in the elbow and the shoulder joint, whereas the TLO showed large amounts of EMG activity for force directions producing large extension torques in the elbow and the shoulder joint. Correlating the difference of the amount of EMG activity of the BIB and the TLO to the sum of the elbow and shoulder torque resulted in a high correlation with a coefficient of 0.97.

Movement direction dependence. Table 1 shows that for the bi-articular TLO there was only one force direction (70 deg) for which the vectors, pointing to the centres of the ellipses fitted to the data of the five subjects, were significantly oriented in one direction ($P < 0.007$). For the mono-articular TLA and DPS all force directions (from which the amount of EMG activity recorded was large enough to determine a PMD) resulted in a PMD with vectors, pointing to the centres of the ellipses fitted to the data of the three mono-articular muscles (BRD, TLA and DPS) relative to the origin was significantly larger (FP-test: $P < 0.001$) than that of

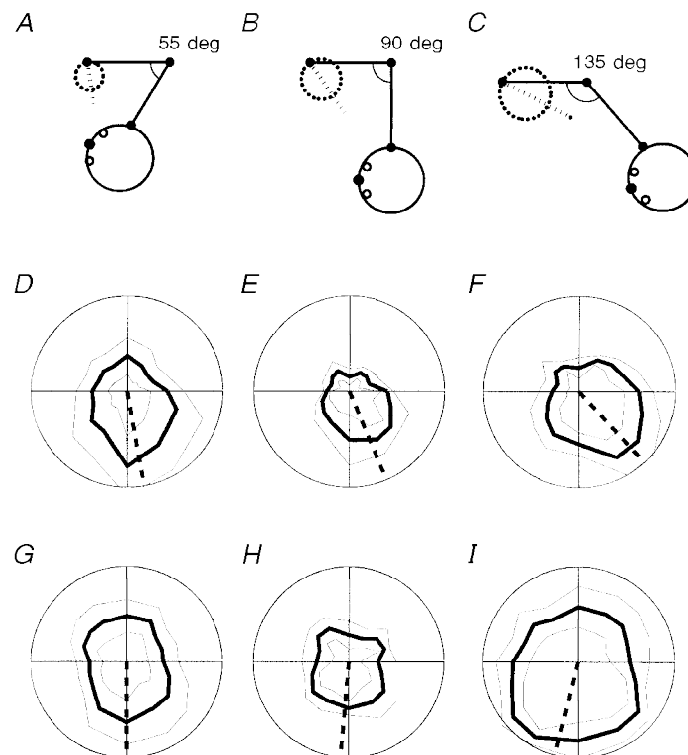


Figure 5. Muscle activity as a function of the rest position

Polar plots of the average amount of EMG activity (thick continuous lines) of the BRD (*D–F*) and the BIB (*G–I*) as a function of movement direction for three different rest positions (*A–C*), respectively. The standard deviation is indicated by the thin continuous lines. The dotted circles in *A–C* are polar representations of the amount of decrease of the elbow angle (see Methods) as a function of the movement direction of the wrist. The dashed lines in *A–C* indicate the directions of maximal decrease of elbow angle. The dashed lines in *D–I* indicate the mean PMDs. The force direction was 260 deg.

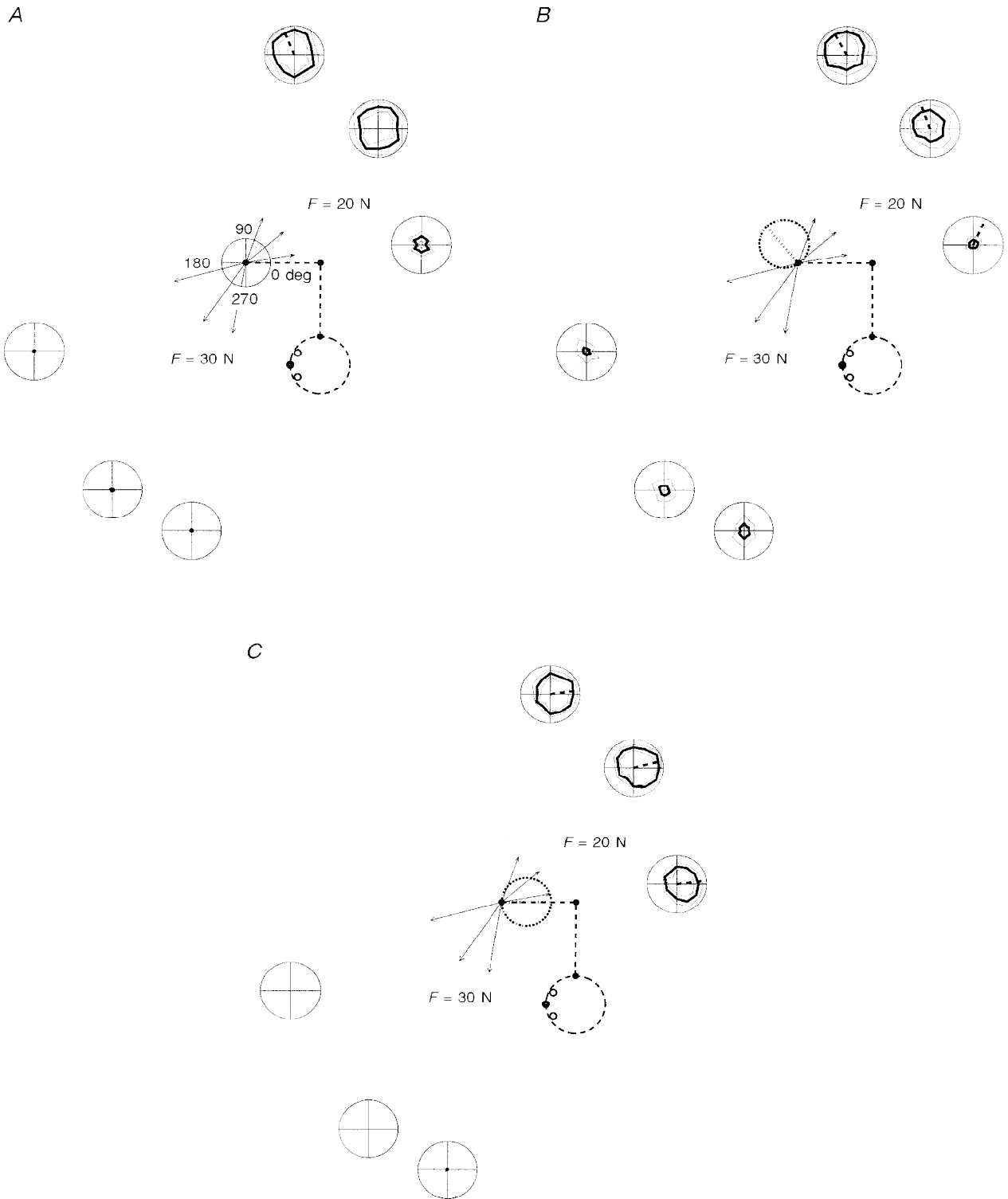


Figure 6. Muscle activity as a function of the force and the movement direction

Polar plots of the average amount of EMG activity (thick continuous lines) of the TLO (A), TLA (B) and DPS (C) as a function of movement direction for six (10, 40, 70, 195, 235 and 260 deg) force directions. The thick dashed lines indicate the mean PMD. The standard deviation is indicated by the thin continuous lines. The dotted circles in the centre of B and C are polar representations of the approximate amount of shortening of the corresponding muscle as a function of movement direction of the wrist (movements within the 3 cm range centred around the rest position). The dashed lines represent the directions of maximal shortening. For the bi-articular TLO (A) this circle was not plotted, since the direction of this circle depends critically on personal parameters, such as the ratio of the moment arms of the muscle with respect to both joints. The arrows pointing from the wrist of the subject to the polar plots represent the six force directions during the movements for each polar plot.

the two bi-articular muscles (BIB and TLO), which were recorded during protocol III.

This leads to the conclusion that the TLO does not show a clear movement direction dependence (Fig. 6*A*), whereas the mono-articular TLA and DPS do show a clear movement direction dependence (Fig. 6*B* and *C*).

DISCUSSION

The main aim of this study was to determine the EMG activity of mono- and bi-articular muscles under conditions in which the direction of force and the direction of movement were varied independently. The results reveal a clear difference in the activation of mono- and bi-articular muscles as a function of force and movement direction, suggesting differences in the organizational processes which underly the activation of these two types of muscles.

Figure 4 shows that there exists a clear difference in the activation of the mono-articular BRD and the bi-articular BIB, in such a way that the BRD shows a clear movement direction dependence, whereas the activation of the BIB does not show a dependence on the movement direction. The size of the distribution of the EMG activity as a function of the movement direction is tuned as a function of the direction of force. The PMD of the BRD is, however, unaffected by the force direction. In contrast, the PMD of the BRD changes with arm geometry. In the Results section we have shown a significant correlation between the PMD of the BRD and the movement direction corresponding to the largest amount of shortening. The BIB did not show such a correlation. The results obtained during protocol III showed that similar results were observed for other mono- and bi-articular muscles. Also, a high correlation was found between the difference of the amount of EMG activity of the bi-articular BIB and TLO and the sum of the elbow and shoulder torque.

Therefore, the present and previous results demonstrate that for bi-articular muscles the amount of EMG activity is exclusively a function of the force direction. For the mono-articular muscles the amount of EMG activity depends both on the direction of force, as well as on the movement direction. The mono-articular muscles show the largest amounts of EMG activity for movements at which they shorten. Remarkably, this movement direction dependence (PMD) does not depend on the force direction.

The fact that the mono-articular muscles show more EMG activity in the PMD, whereas the bi-articular muscles show a constant activation as a function of movement direction, may indicate a conflict with respect to the total sum of EMG activities of all muscles contributing to the task. For movements of the wrist in the PMD of the mono-articular elbow flexor muscles the total sum of EMG activities of the muscles will be higher than that during movements in the opposite direction. Part of this difference might be

explained by the force–velocity relationship of muscles. However, it is important to note here that the PMD observed for the mono-articular muscles cannot be explained by the force–velocity relationship of muscles. If this relationship would have caused the PMD observed for the mono-articular muscles, a similar movement direction dependence should have been observed for the bi-articular muscles as well. This was not observed. The fact that the total sum of EMG activities of all muscles contributing to a task varies for different tasks may be similar to previously reported differences in muscle activation for shortening and lengthening movements (Tax, Denier van der Gon, Gielen & Kleyne, 1990; Theeuwens *et al.* 1994). Recent data (van Bolhuis, Medendorp & Gielen, 1997) suggest that these differences may be attributed to a different force–EMG relationship for shortening and lengthening related to differences in recruitment and firing rate in shortening and lengthening contractions.

The data of the BRD and the BIB obtained during protocol III were added to the data obtained during protocol I in Fig. 4. Besides the fact that more muscles were studied using protocol III than protocol I, the only difference between protocols I and III was the force exerted at the wrist. Contrary to the forces exerted at the wrist in protocol I, which were not quite the same for each movement direction, the forces in protocol III were the same for each movement direction. However, since the BRD and the BIB were recorded simultaneously, the differences in the activation patterns of both muscles observed in protocol I (compare Fig. 4*A* and *B*) could not have been caused by the variations in the force exerted at the wrist. We were, therefore, able to add the data of the BRD and the BIB obtained in protocol III to those obtained in protocol I.

Figure 6*B* shows that the TLA shows a small amount of EMG activity for force directions of 195, 235 and 260 deg. Presumably this has to be attributed to cross-talk EMG from elbow flexor muscles. This effect was not observed in the other extensor muscles (TLO and DPS).

Theoretical implications of the results

It was hypothesized by van Ingen Schenau (1989) that mono- and bi-articular muscles had different functional roles. According to his ideas, the bi-articular muscles were thought to control the direction of force at the end-effector. Our data do support this hypothesis, since the activation of the bi-articular muscles did not depend on movement direction, but did depend on the direction of force at the wrist only.

Gielen & van Ingen Schenau (1992) explained that the bi-articular muscles also play an important role with regard to the efficiency of movements. There are several combinations of force and movement direction in which a joint torque may be opposite in sign to the change in joint angle which corresponds to the movement direction. This is illustrated in

Fig. 3. The dotted area shows the region with force vectors for which the elbow torque has a positive sign (i.e. torque in flexion direction). The dashed area shows the region with displacement vectors which require elbow flexion. In the region which is both dotted and dashed, the mono-articular elbow flexor muscles contribute positive work to the movement, since the direction of elbow torque and change in elbow joint angle have equal sign. In the regions which are either dotted or dashed, the direction of elbow torque and change in elbow joint angle have opposite sign. As explained by Gielen & van Ingen Schenau (1992), this implies that a mono-articular elbow flexor muscle would dissipate work, rather than contribute work to the movement. In order to improve the efficiency of the movement, the mono-articular elbow muscles should be activated only in the dotted-dashed area.

In a later study (van Ingen Schenau *et al.* 1995), this interpretation seemed to be quantitatively supported both for cycling and for running by a striking correspondence between the phases of shortening of the mono-articular muscles and their phases of force production. Though the present observations are completely consistent with those data since, indeed, mono-articular muscles do show little activity in the direction of muscle lengthening, these cycling and running data led the previous authors to the wrong conclusion that the activation of mono-articular muscles is exclusively based on position information.

In experiments on a dynamometer which was especially designed to allow an independent variation of force and movement direction, Doorenbosch & van Ingen Schenau (1997) failed to confirm this interpretation (van Ingen Schenau *et al.* 1995). Entirely consistent with the present arm data, however, they found that the activity of the mono-articular muscles is not only determined by the extent to which they shorten but also by the direction of the external force. This led them to the suggestion that the central nervous system might use different strategies, possibly guided by differences in feedback about the desired external force.

However, in the light of the present data, the interpretation of the hypothesis can be reformulated in a much more convincing (and testable) form than the more qualitative previous descriptions. The present data convincingly show that there does indeed exist a fundamental difference in the organizational processes which underly the activation of mono- and bi-articular muscles. This conclusion is based upon the observations that: (1) the activation of the bi-articular antagonists appears to be exclusively based on the required force direction, irrespective of whether these muscles lengthen or shorten, and (2) the preferred movement direction of the mono-articular muscles appears to be exclusively based on information of movement direction and appears entirely independent of force direction.

Due to the limited range of movement directions which could be realised during leg extensions on the dynamometer by Doorenbosch & van Ingen Schenau (1997), the concept of a PMD could not be demonstrated in the leg movements. Nevertheless, this reformulation is entirely applicable for previous arm and leg data (Jacobs & van Ingen Schenau, 1992*a,b*; Theeuwes *et al.* 1994; van Ingen Schenau *et al.* 1995; Doorenbosch & van Ingen Schenau, 1997).

Clearly, this does not mean that we know how the magnitude of the ellipses, which represent the activity of the mono-articular muscles, is modulated on the basis of force direction information. However, what is already important for theories on motor control is that this hypothesis is largely consistent with the idea of Bernstein (1967) and more recent authors (e.g. Georgopoulos, Schwartz & Kettner, 1986; Karst & Hasan, 1990; Bizzi, Hogan, Mussa-Ivaldi & Gisser, 1992; Feldman & Levin, 1995) that a single control vector of desired movement direction (or its derivative) in the external space might be used in the organization of muscle activation, in our case to specify the PMD of the mono-articular muscles. In addition to those studies, however, we have to conclude that one needs at least one second independent control vector (the external force) in order to explain the observed activity patterns of the bi-articular muscles and the modulation of the magnitude of the ellipses of activation of the mono-articular muscles. This second control vector is not compatible with any theory based on point attractor dynamics.

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