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Initial Muscle Activity in Planar Ballistic Arm Movements With Varying External Force Directions

Tom G. Welter and Maarten F. Bobbert

We have investigated, in fast movements, the hypothesis that bi-articular muscles are preferentially selected to control the direction of force exerted on the environment, while mono-articular muscles are selected to control both this exerted force direction as well as the movement direction. Fourteen subjects performed ballistic arm movements involving shoulder and elbow rotations in the horizontal plane, either with or without an external force applied at the wrist. Joint torques required to counteract the external force were in the same order of magnitude as those required to overcome the inertial load during movements. EMG was recorded from mono- and bi-articular flexors and extensors of the elbow and shoulder. Signals were rectified and integrated (IREMG) over 100 ms following the first detected activity. MANOVA revealed that, contrary to the hypothesis, IREMG of bi-articular muscles varied with movement direction just as that of the mono-articular muscles. It was concluded that the present data do not support the hypothesis mentioned above. A second finding was that movement effects on IREMG were much stronger than external force effects. This could not be explained using Hill's force-velocity relationship. It may be an indication that in the initiation of fast movements, IREMG is not only tuned to movement dynamics and muscle contractile properties, but also to the dynamics of the build up of an active state of the muscle.

Key Words: motor control, EMG, arm movements, bi-articular muscles, activation dynamics

Introduction

Humans perform a large variety of purposeful arm tasks, which involve movements of the hand in various directions and with varying external forces. Which rules are used by the central nervous system in the selection of muscles and the generation of the time-varying muscle activation levels? In search of an answer to this question, van Ingen Schenau and colleagues (van Bolhuis, Gielen, & van Ingen

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Schenau, 1998; van Ingen Schenau, 1989; van Ingen Schenau, Pratt, & Macpherson, 1994) realized that the desired movement of the wrist and the external force acting during the movement are two independent variables to be controlled. They hypothesized that bi-articular muscles could be exploited to simplify control and increase efficiency (van Ingen Schenau, 1989; van Ingen Schenau et al., 1994). According to the hypothesis, bi-articular muscles were preferentially selected to control the direction of force exerted on the environment without regard to muscle shortening. Mono-articular muscles would be selected to control both the exerted force direction as well as the movement direction; they would be preferentially activated if the required movement direction involved their shortening.

The organizational principle proposed by van Ingen Schenau, to divide muscles in two groups that are dealt with separately in the nervous system, could provide at least part of the answer to the question of how the nervous system selects muscles to perform a given task. EMG data from human arm movements by van Bolhuis et al. (1998) seemed to confirm the hypothesis. Slow linear horizontal wrist movements (1.5 cm/s) involving shoulder and elbow rotations were performed with external forces applied at the wrist. Measurements were done around a test position of 90° abduction in the shoulder, with the upper arm in line with the shoulders, and 90° elbow flexion. It was found that muscle activation varied as hypothesized. The movement direction for which the mono-articular muscles showed highest EMG activity was termed the preferred movement direction (PMD) and seemed to be the direction with the largest muscle shortening velocity at the given linear wrist velocity. Van Bolhuis et al. (1998) interpreted the results as evidence that different rules are used for the activation of mono- and bi-articular muscles. However, Welter et al. (Welter & Bobbert, 2001; Welter et al., 2000) showed that at least qualitatively, the variations in EMG could also be interpreted as compensations for the effects of shortening velocity and shortening distance on the force generating capacity of muscles. This lack of clarity, whether EMG changes were a reflection of an activation rule or a reflection of adaptations to contractile properties, may be related to the use of slow movements by both van Bolhuis et al. and Welter et al. In these movements there may be no need for a specific activation rule, because activation can be corrected on the basis of, for example, visual feedback. Furthermore, it does not seem appropriate to investigate the relation between EMG and movement direction in slow movements, where the joint torques required to accelerate the segments are negligible compared to those required to counteract the external force. After all, the hypothesis was initially formulated on the basis of fast movements (van Ingen Schenau, 1989; van Ingen Schenau, Boots, de Groot, Snackers, & Woensel, 1992). Therefore, we felt that the hypothesis should be tested further using fast movements.

The aim of the present study was to investigate the variation of mono- and bi-articular muscle activation with movement- and force direction in fast movements, where joint torques required to overcome inertial load are in the same order of magnitude as those required to counteract the external force. Ballistic arm movements in the horizontal plane, involving shoulder and elbow rotations, were made in various directions, either with or without an external force applied at the wrist. The setup used was comparable to the one used previously with slow movements (Welter & Bobbert, 2001; Welter et al., 2000). To keep the EMG interpretation from being complicated by the need to terminate the movement, which demands tri-phasic activation patterns of agonists and antagonists (Cooke & Brown, 1990),

mechanically braked movements were used in this study: punches towards a cushion. In such movements, the antagonist bursts are delayed (Marsden, Obeso, & Rothwell, 1983; Waters & Strick, 1981). Based on the hypothesis of van Ingen Schenau et al. (see van Bolhuis et al., 1998), activation for mono-articular muscles was expected to vary with force and movement direction, and bi-articular muscle activation was expected to vary only with force direction.

Methods

Outline of the Experimental Set-Up

Fourteen healthy subjects (18–36 years of age; 4 female, 10 male) with no known neurological disorders, participated in the experiments after giving informed consent. The experimental setup was the same as in a previous study (Welter et al., 2000) except for the way external force was generated. Subjects were seated at a table with markers indicating the initial and target positions. The arm was abducted 90° so that the upper arm was in line with the shoulders (Figure 1). The elbow was flexed 90° in the horizontal plane. The forearm was in a position half-way between full supination and full pronation. This was the reference position in which muscle activity was investigated. To avoid fatigue, the forearm was suspended from the ceiling. The shoulder was prevented from moving back and forth by a brace mounted on the back of the chair. Movement and force directions in the horizontal plane were defined relative to a sagittal axis through the forearm in the reference position: 0° was along the sagittal axis in the direction of the elbow, 90° was perpendicular to the sagittal axis in the direction of elbow extension, and so on (see Figure 1). A horizontal force of 30 N could be applied at the wrist so that, in order to hold the reference position, a flexion torque (condition F270, see Figure 1) or an extension torque (condition F90) at the elbow was required. The force directions F90 and F270 were selected because in slow movements they provoked large EMG differences between flexor and extensor muscles in the elbow and provided a clear example of the proposed difference in activation of mono- and bi-articular muscles (van Bolhuis et al., 1998). The force magnitude of 30 N was chosen after pilot experiments had shown that it required joint torques of the same magnitude as the torques in the unloaded condition (i.e., the torques needed to overcome inertia). The force was generated by an elastic band attached to the wrist (see Figure 1). Movements were made in the horizontal plane towards seven targets (M45, M90 . . . M315; see Figure 1) either with external force (loaded conditions) or without (unloaded condition). The subjects were instructed to hit, as hard as possible, a cushion that was positioned in the requested movement direction. At the start of the trial, the arm was positioned such that the wrist would have to travel 3 cm to reach the reference position. The distance to the cushion was 20 cm. Infrared markers on the shoulder, elbow, and wrist joints were used to obtain positional data allowing for calculations of net joint torques in the shoulder and elbow using standard inverse dynamics (Elftman, 1939). EMG was recorded from brachioradialis (BRD, mono-articular elbow flexor), triceps caput lateralis (TLA, mono-articular elbow extensor), biceps caput breve (BIB) and biceps caput longum (BLO, two bi-articular elbow-shoulder flexors), triceps caput longum (TLO, bi-articular elbow-shoulder extensor), deltoideus pars clavicularis (DPC, the mono articular shoulder flexor), and deltoideus pars spinalis (DPS, extensor). Integrated rectified EMG

Figure 1 — Schematic drawing, top view, of the experimental setup. Force and movement directions in the horizontal plane are defined relative to the sagittal axis through the forearm. A movement direction of 90° is indicated by M90. The black arrow indicates a force direction exerted by the subject of 270° counteracting an external force generated by an elastic rubber band. EMG was recorded from: BRD, brachioradialis; TLA, triceps caput lateralis; BIB, biceps caput breve; BLO, biceps caput longum; TLO, triceps caput longum; DPC, deltoideus pars clavicularis; DPS, deltoideus pars spinalis.

(IREMG) for all muscles was calculated over 100 ms following the start of the activity burst of the first muscle.

External Force

An almost constant force of 30 N on the wrist was generated by an elastic rubber band of 9 m stretched to 12 m. Only slight variations in force were present. A maximum force change of 1 N occurred over the movement range due to the length changes of the rubber band. A maximum force deviation of 2 N occurred at the highest acceleration and deceleration of the wrist during the trials due to inertia of the elastic band itself. The wrist was strapped in an elastic brace to support the joint and to provide a connection site for the rubber band.

Protocol

For practical reasons related to the length of the elastic rubber band, a given subject was measured in the unloaded condition and only one of the external force

directions. Subjects were randomly assigned to a group performing either the unloaded and F90 or the unloaded and F270 conditions. This design obstructed the opportunity to make intra-individual comparisons between the conditions F90 and F270. However, comparisons between F90 and F270 could still be made because the statistical analyses showed that both groups had the same performance in the unloaded condition (see Results section). Prior to the movement trials, resting EMG was obtained from an unloaded static measurement, with the subjects holding the arm in the reference position. Standard isometric contraction (SIC) EMG was recorded in the reference position while the subject exerted maximal force in the direction of elbow flexion (F270 for BRD, BIB, BLO), elbow extension (F90 for TLA and TLO), and shoulder anteflexion and retroflexion (F180 and F0 for DPC and DPS, respectively). For the movement trials, the wrist was positioned at the starting position, 3 cm before the wrist reference position in the direction 180° opposite to the requested movement direction. This starting position was used because it resulted in maximum wrist acceleration at the instant that the wrist passed the reference position. After positioning, the force was applied at the wrist over a period of 2 s, the subject made a fist, the EMG and position recording was started and, finally, on command, the subject tried to hit the cushion as hard as possible after which the recording was stopped. After each trial, the external force was released to avoid fatigue.

Joint Torques and Kinematics

Infrared markers (SELSHOT) were placed on the acromio-clavicular joint, epicondylus lateralis humeri, and halfway between the processus styloideus of radius and that of ulna. Positional data were collected at 100 Hz and synchronized with EMG using a common pulse on both signals. Net joint shoulder and elbow torques were calculated using standard inverse dynamics (Elftman, 1939). Segment inertial parameters were calculated according to Winter (1979). Elbow flexion and shoulder flexion (anteflexion) torques in the horizontal plane were defined positive. In the unloaded condition, the net joint torques are responsible for the segmental accelerations only. In the loaded conditions, the net joint torques are responsible for both the segmental accelerations and for counteracting the external force. These two components can be calculated separately as kinematic joint torques, required for the acceleration of the segments, and quasistatic joint torques, required to counteract the external force (Hull & Jorge, 1985). Kinematic joint torques were calculated by setting the external forces to zero. Quasistatic joint torques were not used in the present study.

Initial wrist movement directions were calculated as the direction of the line between wrist marker position at the instant of the first burst start and the position that was reached after 100 ms.

EMG Measurements

Electrodes (Ag/AgCl electrodes, Medi-Trace, Pellet 1801, diameter = 1 cm, inter-electrode distance = 2.5 cm) were placed on the muscle belly parallel to the direction of the muscle fibers. EMG was amplified (20×), low pass filtered (270 Hz), and AD converted (delta sigma AD converter, 22 bits, 5.752 MHz per channel), after which it was band pass filtered (20–200 Hz) and stored at 1000 Hz (Porti-17, Twente Medical Systems, Enschede, the Netherlands). Offline, the EMG signal of

each muscle was rectified (yielding REMG), and the average level of 3 s of resting REMG was subtracted. For each muscle in every trial, the start of REMG bursts was calculated by a computer algorithm. Burst start was defined 25 ms before the instant that REMG reached 50% of the value obtained during the SIC trials. The 25-ms adjustment was used to incorporate the build up of EMG just before the signal reached the threshold. This method was selected because the initial muscle EMG differed in each external force condition so that more common burst detection algorithms using a threshold value for the EMG, could not be used. The results were displayed on screen for visual inspection and manual correction of possible detection errors. Muscle activation was quantified by calculating the integrated rectified EMG (IREMG) following the start of the activity burst of the first muscle. IREMG values were normalized to the highest value reached in the unloaded condition. Integration was performed over 100 and 300 ms. These two integration periods gave almost identical results. To avoid an excessive number of graphs and tables, only the results of the 100-ms IREMGs are presented.

Statistical Analyses

To investigate the effects of external force- and movement direction on IREMG, MANOVA for repeated measures was performed using the SPSS statistical software (SPSS, Inc.). Data were organized as shown in Table 1. From two groups of subjects (rows), seven muscles (seven variables) were analyzed for seven different directions (Factor 1 : movement direction was the repeated measures factor) in either an unloaded or loaded situation (Factor 2 : *load* in the columns of Table 1). Thus, each cell in the table contains IREMG values for 7 subjects for seven muscles for seven movement directions. Overall effects of the presence of an external force on IREMG were investigated by MANOVA of the data in all four cells of the table. Post hoc analyses of differences between groups in the unloaded or loaded condition were done by MANOVA of the data of the first and second column, respectively. Post hoc analyses of differences between the unloaded condition and F90, and between the unloaded condition and F270, were done by MANOVA on the

Table 1 Overview of Experimental Subject Groups and Load Conditions

Group		Load 0	Load 1
Group 1	F90	Unloaded	F90
Group 2	F270	Unloaded	F270

Note. Two groups of seven subjects performed arm movements in the unloaded and either the F90 or F270 loaded condition. Each cell contains data for seven movement directions, seven muscles, and seven subjects. Overall MANOVAs (Wilks' Lambda) were performed on data in all 4 cells. Differences between the unloaded conditions of the two groups were tested with data from the cells in the left column; differences between F90 and F270 were tested with data in the right column. Differences between unloaded and either F90 or F270 were tested using data from the first or second row, respectively.

data in the first and second row of the table, respectively. Post hoc testing of effects on IREMG for each muscle separately was also done with a MANOVA for repeated measures using the data from one muscle in the appropriate cells. Differences in movement direction and velocity between load conditions for each movement direction were tested with MANOVA. For all MANOVAs, Wilks' lambda was used as the multivariate test statistic. For all tests, $p = .05$ was used as the level of statistical significance.

Results

Task Execution

Figure 2 shows typical time histories of biomechanical parameters and EMG from one subject in one of his two unloaded trials in movement direction M90. The curves show that the REMG integration period captured the initial muscle activity at the start of the movement at 90° elbow extension when torque builds up to its peak value.

Figure 3A and 3B show net and kinematic elbow joint torques averaged over all subjects for the unloaded, F90, and F270 condition in movement direction M90 (elbow extension). Figure 3C shows corresponding net shoulder torques. Joint torques were synchronized at the start of the first EMG burst. The curves vary systematically with each movement direction, similar to, but with shorter duration and higher amplitude, the variations reported by Koshland et al. (1999). Net elbow torques in the unloaded condition (solid line) are zero until the detected start of the first EMG burst at $t = 0$, the subsequent downward deviation marks angular acceleration in extensor direction, and the final upward deviation marks angular deceleration. As intended, the torque fluctuations in the unloaded condition were of the same order of magnitude as those required to counteract the external force prior to the movement in F90 (Figure 3A, dotted line, -9 Nm) and F270 (dashed line, 9 Nm). Apart from the offset in the flexion or extension direction, the net torque development for the three conditions seems unchanged by the external load. This is also the case for the other movement directions. Since the external force was constant, this means that the kinematic torques, and therefore the movement kinematics in the elbow, were relatively unchanged by the external force which had to be counteracted by the subject (Figure 3B).

Figure 3D shows the average REMG of TLA, which was one of the main muscles that contributed to the torque fluctuation in Figure 3A and 3B. At the end of the integration period (the period indicated by the two vertical lines), an extension torque of approximately -20 Nm was present in F90 (Figure 3A) but torque was approximately zero in F270. Despite this difference in extensor joint torques, TLA EMG did not change much. IREMG differences in other muscles were even smaller (see also Figure 5 below).

Figure 4 shows average wrist paths over the first 200 ms for each movement direction (defined in Figure 1) and load condition. Lengths of the curves are an indication of the average wrist movement velocity. It can be seen that differences in movement direction occurred due to force direction. (Differences in movement direction between F90 and F270 after 100 ms were significant for all movement directions except M180 and M225.) The only significant difference in movement velocity after $t = 100$ ms was found for movement direction M315, where F90 was performed faster than F270.

Figure 2 — Results from one of the unloaded M90 trials of one subject. From top to bottom: wrist displacement from initial position, wrist velocity, acceleration, net elbow torque, TLA and DPS REMG (scaled to the highest IREMG value in the unloaded condition). Solid vertical lines mark the REMG integration period of 100 ms. The dashed vertical line (top panel) indicates 3-cm wrist displacement (i.e., the instant that the reference position was reached). Arrows indicate the start of individual muscle activity bursts. Note that the integration period captures the initial muscle activity until the instant that elbow torque reaches its peak extensor value.

Figure 3 — A: Average net elbow torque (14 subjects) for movement direction M90 in the unloaded, F90, and F270 conditions. Vertical lines mark the REMG integration period. Flexor torque was defined as positive. Note that, although their shape remains relatively constant throughout the movement, the offset in the net torque curves ranges from 10 to -10 Nm, which is in the same order of magnitude as the variation in each net torque curve (i.e., torques related to inertial load and external force were in the same order of magnitude). B: Corresponding average kinematic torques. C: Corresponding average net shoulder torques. D: Corresponding mean rectified EMG of TLA. Note that EMG remains relatively unchanged considering that the differences in net torque ranged from extension to flexion.

Figure 4 — Average wrist paths over 200 ms for all movement directions and force directions. Movement directions are marked and correspond to the definition in Figure 1.

Initial EMG

Figure 5 shows averaged normalized IREMG values as a function of movement direction for each muscle. The first column shows comparisons between group 1 (solid line) and group 2 (dotted line) for the unloaded condition, the second column compares the unloaded (solid) and F90 (dotted) condition of group 1, the third column compares the unloaded (solid) and F270 (dotted) condition of group 2, and the fourth column compares the F90 condition of group 1 (solid) with the F270 condition of group 2 (dotted). In MANOVA terminology, lines at different vertical positions indicate a main effect of force direction on IREMG, lines that vary in a similar fashion as a function of movement direction indicate a main effect of movement direction, and crossing or diverging lines indicate interaction effects.

According to the hypothesis of van Ingen Schenau (see van Bolhuis et al., 1998), bi-articular muscle activity should vary with force direction but not with movement direction. Therefore, in the bi-articular muscle plots, one would expect horizontal lines (no movement direction effect) at different vertical positions (force direction effect), and the MANOVA should support this with significant main effects of force direction. Mono-articular muscle activation should vary with both force and movement direction. In the plots, one would expect fluctuating (movement direction effect) and diverging (interaction effect) lines at different vertical

Figure 5 — IREMG of all muscles scaled to the maximum reached in the unloaded condition as a function of movement direction. Each column shows one of the four comparisons that were made. The respective comparisons are named in the column header. Solid line: first condition; dotted line: second condition. For example: In the second column, IREMG from group 1 in the unloaded condition is compared to that of the same group in the F90 condition (dotted lines). Error bars indicate standard errors of the mean. The relative positions of two curves in a panel gives an indication of MANOVA outcomes. See text for explanation.

positions (force direction effect), and the MANOVA should give a significant main effect for movement and force direction and a significant interaction effect. The MANOVA results are summarized in Table 2. In the next paragraphs, we will use Figure 5 and Table 2 to show whether these predictions were supported.

The two groups had comparable activation levels for all muscles in the unloaded condition (Figure 5, column 1), but activation levels were different in the loaded conditions (Figure 5, column 4). This was confirmed by the overall test of the MANOVA using all data in the four cells of Table 1: Differences between IREMG of the two groups depended on whether a load was present (Table 2, test 1, interaction effect between load and group). Post hoc testing showed that groups did not differ in IREMG in the unloaded condition (Figure 5 column 1, all curves are overlapping; Table 2, test 2: no interaction effects between group and movement direction, no group effects). However, in the loaded condition, the groups were different in the way that IREMG depended on movement direction (Figure 5, column 4, curves are diverging; Table 2, test 3, interaction effect between movement direction and group). Since the groups were comparable in the unloaded condition, we conclude that group differences in IREMG in the loaded condition (i.e., the differences that can be seen in column 4 of Figure 5) were actually force direction effects.

Further post hoc testing shows the contributions of the individual muscles to the overall effects between F90 and F270 (Figure 5, column 4 all panels; Table 2, test 3.1 to 3.7). The results did not support the hypothesis: (a) From the four mono-articular muscles, only one showed IREMG that varied with both force and movement direction (Figure 5, column 4: only TLA showed diverging curves; Table 2, test 3.5: interaction effect for TLA). (b) From the three bi-articular muscles, only one showed significantly different IREMG depending on force direction (Figure 5, column 4: only TLO showed different vertical curve positions; Table 2, test 3.4: group main effect for TLO). (c) From the four mono-articular muscles, only two showed significantly different IREMG depending on force direction (Figure 5, column 4: only TLA and DPS showed different vertical curve positions; Table 2, test 3.5 and 3.6: group main effects for TLA and DPS). (d) All muscles, including the bi-articular muscles, showed IREMG that was dependent on movement direction, whereas this was only predicted for mono-articular muscles (Figure 5, column 4: bi-articular BIB, BLO, and TLO showed changes as a function of movement direction; Table 2, test 3.1 to 7: main effect of movement direction).

Post hoc testing for differences within each group between the unloaded condition and either F90 (Figure 5, column 2) or F270 (column 3), showed that these differences between unloaded and loaded conditions were significant (Table 2, test 4 and 5: interaction effects between movement direction and load). Individual muscle IREMG showed a similar (or even larger) lack of agreement with the hypothesis as was found between F90 and F270: (a) In neither of the two groups, any of the four mono-articular muscles showed the predicted IREMG dependence on movement and force direction (Figure 5, column 2 and 3: muscles did not show significantly diverging lines; Table 2, test 4.1–7 and test 5.1–7). (b) In both groups, only one of the three bi-articular muscles showed significant dependence on force direction (Figure 5: TLO in column 2 and BLO in column 3 had significantly different vertical positions; Table 2, test 4.4 and 5.3, main effect of load for TLO and BLO). (c) In both groups, only one of the four mono-articular muscles showed significantly different IREMG depending on force direction (Figure 5: TLA in column 2 and DPS in column 3 had different vertical positions;

Table 2 *P* Values for the Main and Interaction Effects of the MANOVA Between Loaded and Unloaded Conditions

Test	Group	Group $\times$ Load	Load
Test 1 Overall	.074	.003*	.043*
	Movement	Movement $\times$ Group	Group (equal to load)
Test 2 (unloaded-unloaded)			
Overall	<.001*	.846	.599
Test 3 (F90-F270)			
Overall	<.001*	<.001*	.009*
3.1 BRD	<.001*	.428	.383
3.2 BIB	<.001*	.183	.126
3.3 BLO	<.001*	.022*	.087
3.4 TLO	<.001*	.039*	.003*
3.5 TLA	<.001*	<.001*	<.001*
3.6 DPS	<.001*	.141	.011*
3.7 DPC	<.001*	.125	.958
	Movement	Movement $\times$ Load	Load
Test 4 (unloaded-F90)			
Overall	<.001*	<.001*	.206
4.1 BRD	.043*	.829	.644
4.2 BIB	.047*	.252	.569
4.3 BLO	.010*	.792	.173
4.4 TLO	.002*	.319	.008*
4.5 TLA	.070	.074	<.001*
4.6 DPS	.055	.179	.275
4.7 DPC	.085	.375	.453
Test 5 (unloaded-F270)			
Overall	<.001*	.004*	.421
5.1 BRD	.055	.940	.940
5.2 BIB	.083	.741	.165
5.3 BLO	.073	.131	.006*
5.4 TLO	.089	.070	.195
5.5 TLA	.003*	.752	.564
5.6 DPS	<.001*	.234	.021*
5.7 DPC	.164	.511	.272

Note. This table shows whether IREMG varies with movement direction, external force, or whether interaction between these two factors occurs. Overall, Test 1 (interaction effects) shows that the two groups had significantly different IREMGs, which was the basis for further post hoc testing. The overall post hoc tests showed that the two groups did not differ in the execution of the unloaded trials (Test 2, no significant interaction or group effects), but

Table 2, test 4.5 and 5.6: main effect of load for TLA and DPS). The fact that the main effect of movement direction that seems present in all muscles in Figure 5, columns 2 and 3 (Table 2, tests 4 and 5) did not reach the same level of significance as in column 4 (Table 2, test 3) is most likely due to the number of subjects in the test (14 subjects in column 4 [test 3] vs. 7 subjects in column 2 and 3 [test 4 and 5]).

The plateaus in the curves of the elbow muscles (Figure 5) show that, as intended, we succeeded in avoiding co-contractions due to tri-phasic muscle activation in the first 100 ms. Roughly, the flexor curves show no IREMG for the first four movement directions, and the extensor muscles show no IREMG in the last three directions. In pointing movements of such short duration as in the present experiment, antagonist muscle activity would have been expected as early as 35 ms after movement onset (see Gottlieb et al., 1992)—that is, well within 100 ms after the first initial muscle activity. In addition, the plateaus are an indication that stretch reflexes due to the sudden stretch of muscles in some movement directions play no role in the reported IREMG values.

Two Main Observations

The first general observation that can be made is that the initial EMG for the movement and force directions studied did not show the characteristic separation of mono- and bi-articular muscles as suggested by van Ingen Schenau et al. (van Bolhuis et al., 1998). The two muscles, BIB and BRD, that demonstrated this separation most clearly in slow movements (van Bolhuis et al., 1998) never showed significant force direction effects in the present study. In agreement with the MANOVA results, examining the graphs for a possible non-significant separation of mono- and bi-articular muscles does not reveal such tendencies either. The only tendency that may be noted is that IREMG is increased only when a muscle was already active before the movement started. For instance, flexor muscles, except BRD, increased IREMG in F270 but not in F90. Extensor muscles increased IREMG in F90 but not in F270 (compare Figure 5, column 2 and 3). This tendency is stronger, and also present in BRD, when the integration period is extended to 300 ms (results not shown).

The second observation is that initial IREMG from all muscles varied more with movement direction than with force direction. We already mentioned that despite differences in net joint torques between the load conditions, REMG amplitude in TLA was relatively unaffected at a given movement direction (Figure 3). The MANOVA showed that, in general, the movement effects seemed stronger (lower *p* values) than the load effects (Table 2). A further illustration of this point is given in Figure 6, which shows mean IREMG of BRD (same data as in Figure 5)

only in the loaded trials (Test 3, interaction effects). Further post hoc testing (Test 3.1–3.7) showed no separation between mono- and bi-articular muscles as proposed by Van Ingen Schenau. For example: All muscles showed movement direction effects (column 2), whereas this was only predicted for the mono-articular muscles; load effects were present only in some muscles, whereas these were predicted for all, specifically the bi-articular, muscles. The same tendency was found when IREMG was compared in loaded and unloaded trials (Test 4.1–4.7 and 5.1–5.7). See text for further details.

*Statistical significance.

Figure 6 — A: average BRD IREMG per movement direction per external force condition over all subjects as a function of the corresponding average joint torques in the elbow at the end of the integration period. **B:** Same for kinematic joint torques. The IREMG data are the same data as in Figure 5—the average of 7 (F90 / F270) or 14 (unloaded) subjects. Note that the scatter of data points for IREMG as a function of net joint torques is larger than for IREMG as a function of kinematic joint torques.

for each force condition and movement direction plotted against the corresponding average net joint torque (Figure 6A) and kinematic torque (Figure 6B) in the elbow at the end of the integration period. The smaller horizontal scatter of data points in Figure 6B compared to Figure 6A was found for all muscles except TLO and shows that IREMG varied mainly with kinematic torques (movement direction), not with net torque (influenced by external force).

Discussion

We investigated, in fast arm movements, the hypothesis that bi-articular muscles are preferentially selected to control the direction of force exerted on the environment, while mono-articular muscles are selected to control both this exerted force direction as well as the movement direction (see van Bolhuis et al., 1998). If this hypothesis is true, bi-articular IREMG should vary with force direction only, and mono-articular IREMG should vary with both force and movement direction. The two main results are (a) there is no support for a differential control of mono- and bi-articular muscles, and (b) IREMG varies more with movement direction than with force direction.

No Support for Separate Control of Mono- and Bi-Articular Muscles

The first result was that there was no difference between mono- and bi-articular muscles in the variation of IREMG with movement and force direction. The

presence and the direction of an external force had a limited effect on the initial EMG of both mono- and bi-articular muscles. Considering the grouping of muscles in Figure 5, it seemed that if any separation between groups of muscles existed, it was based on anatomical location and not on the number of spanned joints.

Part of the variation of IREMG with movement direction may have been caused by changes in the timing of activity bursts with movement direction (Flanders, Pellegrini, & Geisler, 1996; Hoffman & Strick, 1999). For instance, a delayed burst timing could have caused the activity burst to shift out of the 100-ms time window, causing a decrease in IREMG when in fact the burst itself remained unchanged. The influence of this effect can be examined by making the integration period longer so that it captures the entire activity burst. A 300-ms integration period produced almost the same curves as in Figure 5. The flat parts in the curves were somewhat rounded, indicating that very small antagonist EMG occurred after 100 ms, but it appeared that no large activity bursts were shifted in or out the 100-ms time window with changing movement direction. It can be concluded that changes in burst timing did not influence IREMG outcomes in this study.

Based on the present results, we must conclude that in fast arm tasks, the nervous system does not coordinate mono- and bi-articular muscles differently in the manner proposed by van Ingen Schenau (see van Bolhuis et al., 1998).

Recently, Prilutsky (2000) proposed general rules for the coordination of mono- and bi-articular muscles in multi-joint movements. Force would preferentially be allocated to muscles with larger mechanical advantage and larger physiological cross-sectional area (PCSA), and all muscles would exhibit synergistic action to reduce the stress per unit PCSA. For the interpretation of experimental data in this context, Prilutsky (2000) assumes that the relationship between EMG and muscle force is not markedly affected by the force-length and force-velocity relationship.

The present data do not support these proposed rules. First, on the basis of these rules, it would be expected that IREMG of both mono- and bi-articular muscles varied with external force direction because joint torques differed considerably between external force direction conditions. However, as mentioned above, this was not the case (Figure 3 & 5). Second, bi-articular EMG should be highest when a particular bi-articular muscle's action is agonistic in both spanned joints. When it is agonistic in only one of the joints, the muscle should become less active, and when it is antagonistic in both joints the EMG should vanish. Thus, when EMG of a bi-articular muscle is plotted as a function of the torque difference between the joints spanned, a linear relationship would be expected. Such a linear relationship has indeed been found (Jacobs & van Ingen Schenau, 1992; Prilutsky, 2000; note that these authors defined hip and knee extension torque positive). In the present study, however, no linear relationship was found when IREMG of the bi-articular muscle BLO was plotted against the difference between elbow and shoulder torque (Figure 7). Instead, the horizontal scatter of data points (i.e., the different torques belonging to one IREMG level) was comparable to that of the mono-articular BRD in Figure 6A. This is a logical consequence of the fact that differences in torque offset due to differences in external force direction (Figure 3A) were not accompanied by differences in IREMG. A third prediction of Prilutsky's rules is that mono- and bi-articular muscles that cross the same joint should show activation in different movement directions because of the relation of the bi-articular muscle with the second joint. However, despite their identical moment arm at the elbow and the

Figure 7 — Average BLO IREMG per movement direction per external force condition over all subjects as a function of the corresponding average elbow-shoulder torque difference. Numbers 1 to 7 correspond with M45 to M315. To calculate the torque difference, the sign of the elbow torque was reversed in accordance with the definition by Jacobs and van Ingen Schenau (1992). Note the horizontal scatter of data points (i.e., the horizontal displacement of points belonging to different external force conditions) that is also present in Figure 6.

additional moment arm of TLO around the shoulder, both TLA and TLO had their maximum IREMG around M90 (Figure 5).

Essentially, Prilutsky (2000) assumes that the relationship between EMG and muscle force (and consequently joint torque) is linear. This assumption may be true in static conditions, and even hold for movements that are executed with some speed (for more references, see Prilutsky, 2000; Prilutsky, Gregor, & Ryan, 1998). However, for maximally fast accelerated movements, such as the punching movements in the present experiment, this assumption may not be justified. This will be argued in the following paragraphs.

IREMG Varies More With Movement Direction Than With Force Direction

The interaction effects of movement and force direction on IREMG are a clear indication that factors other than torque magnitude influence IREMG. This may be related to the fact that muscle force (F) is not only a function of active state (q) but also of the length (l) and contraction velocity ($\dot{l}$) of the contractile element:

$$F = f(q, l, \dot{l}) \quad (1)$$

In the present study, EMG is taken to represent the neural input of the muscle. For the moment, active state is assumed to monotonically increase with EMG. At a

given linear wrist velocity, the variation of movement direction also affects muscle contraction velocities. Consequently, muscle activation needs to be changed to meet different torque requirements for each movement direction, but also to compensate for the effect of contraction velocity on muscle force (force-velocity relationship).

However, if IREM_G varies more with movement direction than with force direction because of the force-velocity relationship, either the movement-direction effects should have been much smaller or the force-direction effects should have been larger. This will be demonstrated with data from TLA which, for the sake of simplicity, we assume to be representative for all elbow extensors in the present experiment; the TLA results in Figure 5 are very similar to the TLO results. In the static situation, an elbow extension torque of -9 Nm is required prior to $t = 0$ to counteract the external force (Figure 3A), and a certain amount of EMG activity is found (Figure 3D). When in a dynamic situation (after $t = 0$) without external force, the same torque level (approximately -10 Nm) is required to make a fast elbow extension in direction M90 (Figure 3A), a higher EMG burst is found (Figure 3D). Using data from Welter et al. (2000), it can be estimated that after 100 ms, TLA contracts at ~30% of its maximum velocity in both external force conditions. According to Hill's force-velocity relationship, this reduces its force-generating capacity to ~30% of the isometric maximum. In order to generate the same torque, the active state in the dynamic situation would have to be increased by a factor of 3 compared to the level in the static situation. However, the magnitude of the burst in Figure 3D is about 10 times higher than the static IEMG level. Assuming that active state increases monotonically with IREM_G as in equation (1), this is clearly much higher than expected. If the force-velocity relationship were responsible for the IREM_G changes with contraction velocity (i.e., movement direction effects), the changes should have been smaller. In addition, adaptations in TLA burst height related to torque changes are much smaller than expected even though TLA had the largest difference in IREM_G between force conditions. Doubling the required elbow extension torque by adding an elbow flexing force leads to an increase of IREM_G of only 25% (Figure 3D, $t = 0.1$), whereas a doubling of IREM_G would be expected. Decreasing the elbow torque to zero in a condition where the initial torque is flexor (Figure 3A) leaves the IREM_G unchanged.

An alternative explanation for the present findings may be that in fast movements, the change in the active state in a muscle does not parallel the change in EMG as it does in slow movements. The change in the active state actually depends on the current active state and stimulation (neural input) to the muscle (Hatze, 1981). EMG gives an indication of the stimulation (*stim*) that is sent to the muscle by the nervous system, not of q .

$$\begin{aligned} F &= f(q, l, l) \\ q &= f(q, \text{stim}) \end{aligned} \quad (2)$$

where EMG is an estimation of *stim*.

To achieve the fast force build up necessary to generate a ballistic movement, the stimulation may be increased to a level that is disproportionate to the force level that is eventually reached. In other words, the dynamics related to the fast build up of the active state can no longer be ignored in the interpretation of EMG in movements, where segmental accelerations are maximized. Because the

movement in the present study lasted only 0.3 s, the entire EMG burst could have been dominated by stimulation that was necessary for the rapid build up of force. This idea is consistent with the observation of high firing frequencies in the initial phase of contraction (Sawczuk, Powers, & Binder, 1995), the increase of initial firing frequency, and the occurrence of doublets after the training of ballistic contractions in humans (van Cutsem, Duchateau, & Hainaut, 1998), and the conclusion by Zehr and Sale (1994) that these high initial firing frequencies may serve to markedly increase the rate of force development and maximal movement velocity.

Conclusions

The first conclusion is that the IREMG results of this study of fast movements does not confirm the hypothesis that the nervous system makes a distinction between the coordination of mono- and bi-articular muscles. The second conclusion is that IREMG levels in punching movements do not change in proportion to the changes in joint torques that are required to compensate for different external force directions at the wrist.

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