## RESEARCH ARTICLE

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# Force path curvature and conserved features of muscle activation

Received: 13 January 1995 / Accepted: 21 November 1995

Abstract This study examined the patterns of muscle activity that subserve the production of dynamic isometric forces in various directions. The isometric condition provided a test for basic features of neuromuscular control, since the task was analogous to reaching movement, but the behavior was not necessarily shaped by the anisotropy of inertial and viscoelastic resistance to movement. Electromyographic (EMG) activity was simultaneously recorded from nine elbow and/or shoulder muscles, and force pulses, steps, and ramps were monitored using a transducer fixed to the constrained wrists of human subjects. The force responses were produced by activating shoulder and elbow muscles; response direction was controlled by the relative intensity of activity in muscles with different mechanical actions. The primary objective was to characterize the EMG temporal pattern. Ideally, synchronous patterns of phasic muscle activation (and synchronous dynamic elbow and shoulder torques) would result in a straight force path; asynchronous muscle activation could result in substantial force path curvature. For both pulses and steps, asynchronous muscle activation was observed and was accompanied by substantial force path curvature. A second objective was to compare phasic and tonic EMG activity. The spatial tuning of EMG intensity was similar for the phasic and tonic activities of each muscle and also similar to the spatial tuning of tonic activity in a previous study where the arm was stationary but unconstrained.

Key words Isometric force  $\cdot$  Muscle force  $\cdot$  EMG  $\cdot$  Directional tuning  $\cdot$  Path curvature  $\cdot$  Human

### Introduction

Regarding the control of arm movement, two phenomena have received a great deal of recent research interest:

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hand path curvature and the anisotropy in movement duration. The hand paths of point-to-point arm movement are slightly curved, and this has been attributed to a variety of different factors ranging from a distorted perception of the desired straight path (Wolpert et al. 1994, 1995) to a need to minimize the first derivative of torque (Uno et al. 1989). One explanation is that a straight hand path is specified by a "virtual trajectory" and curvature results from the nonuniform inertial and viscoelastic resistive forces encountered during the movement (Flash 1987). By the same token, Gordon and colleagues (1994) have postulated that arm movements in different directions are initially planned without accounting for the anisotropy in inertial resistance to acceleration, and that initial errors in acceleration are then compensated by complementary adjustments to movement duration (see also Ghez et al. 1990). We will show that under isometric conditions, where inertia does not contribute to the dynamics, path curvature and directional variations in duration are just as prominent as during the analogous point-to-point arm movements. Under isometric conditions these phenomena are due to muscle activation patterns, rather than mechanical resistance to an idealized control signal.

In the preceding paper (Flanders et al. 1996) and in previous work from our laboratory, we have sought to identify and describe the basic features of the motor pattern for two-joint reaching movements of the human arm (Flanders 1991; Flanders and Herrmann 1992; Buneo et al. 1994; Flanders et al. 1994). In the course of these studies, we have noticed that hand paths in vertical planes exhibit systematic curvature and that movement duration varies with movement direction in a manner analogous to the reports of these phenomena cited above, for movements in the horizontal plane. We have also noticed that the timing of phasic muscle activation varies gradually, as a systematic function of movement direction. Although the mechanical implications are not obvious, this temporal staggering of EMG bursts appears to constitute a robust feature of the motor pattern for reaching.

Whereas a directionally dependent phasing of EMG bursts may be important for dealing with the evolving dynamics of the moving arm, a simpler control scheme should work better for the task of generating dynamic forces in various directions, under isometric conditions. When the wrist is fixed to a force transducer and the goal is to produce a pulse or a step of force in a particular direction, one might predict that synergistic muscles would be synchronously activated with the proper relative intensity to produce the desired force direction. The force path displayed to the subject on an oscilloscope screen would then be a straight line to the target. For force pulses and steps, asynchronous EMG bursts could promote a curvature in the force path; for steps, differences in the directional tuning of phasic (early) and tonic (later) EMG intensity could also contribute to force path curvature. We will show that, despite the many differences in the control of force responses and movements, the general tendency to use asynchronous EMG bursts is a feature that is conserved across conditions. We will also give evidence for a conservation of phasic and tonic spatial tuning.

# **Materials and methods**

#### Experimental design

The experimental and analytical methods were the same as in the preceding study (Flanders et al. 1996) except that subjects were asked to make isometric force pulses, steps, or ramps instead of reaching movements. Force directions were arranged in the sagittal plane of the arm or the frontal plane passing through the wrist. Each subject stood (or sat on a tall stool) with the upper arm vertical and the forearm horizontal and actively supported the weight of the arm against gravity at the start of each trial (to produce initial EMG levels comparable with those in other studies). The wrist was neutral with respect to pronation/supination and was placed in a stiff leather cuff (reinforced with a sheet of aluminum) that was mechanically coupled to a two-dimensional force transducer. Although an apparatus such as this is never completely isometric, the amount of movement was negligible when compared with reaching movements.

The axes of the transducer were positioned in the sagittal plane for the first part of the experiment and in the frontal plane for the second part of the experiment. Subjects were instructed to confine their force responses to these planes, and previous studies using a three-axis transducer have indicated that human subjects should be able to follow this instruction within  $5^{\circ}$  "degrees" (Massey et al. 1991). The subject viewed the transducer output as a cursor movement on an x-y oscilloscope screen. The scope was arranged so that the cursor movement direction was consistent with the voluntary force response: the screen was in a parasagittal plane to the left of the subject for sagittal force directions and directly facing the subject for directions in the frontal plane. In each case the scope (with its 12-cm screen) was about  $30^{\circ}$  down from eye level and about 80 cm distant to the eyes. The targets were 3-mm-diameter circles, arranged in a circle with a 3-cm radius. Subjects were instructed to move the cursor to the target without making corrections.

Each recording session consisted of 600 trials. Force directions were randomized. A block of 400 trials with steps and ramps (on alternate trials), was followed by a block of 200 trials requiring force pulses (see Fig. 1). Timing cues were given using computer-generated tones (e.g., start, fast, slow). The sagittal and frontal planes were covered on separate days.



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**Fig. 1** Force trajectories and force paths for targets in the sagittal plane of the arm. Data corresponding to force pulses are shown in the *top panel;* fast sustained responses (steps) are shown in the *middle panel;* slow responses (ramps) are shown in the *bottom panel.* Tangential force trajectories for the 20 targets are superimposed to show the range of response duration. Target directions are numbered for reference. All data are means of five to ten trials, from subject D

To permit as direct a comparison as possible between mechanical conditions, we used the same four subjects in this study as in the preceding study (with informed consent and Institutional Review Board approval). As explained in the preceding paper (Flanders et al. 1996), however, a force response in a specific direction is not directly comparable with a movement in the same direction, due to the inertial anisotropy of the arm, i.e., a force in a particular direction will generally not produce an acceleration in exactly that direction (see Fig. 13 of Flanders et al. 1996). Therefore, although we used the same 40 directions for the movement and force experiments, the EMG patterns under these two conditions cannot be exactly the same. We can, however, compare general features of the EMG patterns across the two conditions, and the analysis was designed to make such comparisons.

#### Data acquisition and analysis

We used small bipolar surface electrodes to record from the same nine muscles as in our previous studies: brachioradialis (BR, elbow flexor), biceps (BI, elbow and shoulder flexor), medial head of triceps (MT, elbow extensor), long head of triceps (LoT, elbow and shoulder extensor), pectoralis (Pec, shoulder adductor and medial rotator), anterior deltoid (AD, shoulder flexor and adductor), medial deltoid (MD, shoulder abductor), posterior deltoid (PD, shoulder extensor and adductor), and latissimus dorsi (LaD, shoulder extensor and medial rotator).

Processing of EMG data was identical to previous procedures. Briefly, force and EMG were digitized at 500 Hz. A computer cursor program was used to mark the onset of the first derivative of tangential force for each trial, and these data were used to align rectified EMG traces for averaging. EMG means from 5–10 trials were smoothed. For step responses, smoothed EMG means from ramp responses were time-scaled and subtracted away, to isolate the phasic component (Buneo et al. 1994). Burst timing was quantified by finding the point in time (10 ms resolution) at the center of the most intense 100-ms epoch; burst intensity was defined as the mean amplitude of this 100-ms epoch (Flanders et al. 1996).

For one subject (probably our strongest subject) we increased the amount of force required for responses in the sagittal plane. Whereas in all other experiments subjects produced 8 N of steadystate force at the target, for this one experiment the target level of force was 16 N. This modification put the stronger subject's response duration (time to target) into the same range as the other subjects. When we combined EMG intensity levels across subjects we normalized by equating the mean burst intensity across all directions for each muscle and each subject.

We used a standard index of path curvature (Atkeson and Hollerbach 1985). Thus, curvature was quantified using a dimensionless index defined as the maximum normal distance from the actual path to a straight-line path, divided by the length of the straightline path (from the actual start to end). The "duration" of individual force responses was measured using the first derivative of force data from individual trials, with duration defined as the time between the first two zero crossings.

#### Results

Force path curvature and force duration

Figures 1–3 show the mechanical characteristics of subjects' responses. We illustrated the forces in the sagittal plane (and not the frontal plane) because mechanics in the sagittal plane are simpler, more comparable with the horizontal plane, and potentially of greater interest for future simulation studies. We should note, however, that force responses in the frontal plane exhibited comparable trajectories and the force paths exhibited comparable amounts of curvature. Figure 1 illustrates the three types of force response, using data from a representative subject. The line representing each trajectory or path is a mean of five to ten trials. On the left, trajectories from the 20 directions are superimposed for each condition: pulses (top), steps (middle), and ramps (bottom). For both pulses and steps, there was some variability (across directions) in the time to reach the target or the "duration" of the response.

The force paths show a distinct curvature for some response directions (Fig. 1, right). In the top panel, target force end-points are labeled 1–20 for reference. As indicated by the labels in the middle panel, the force paths are in the sagittal plane, with forward (F) to the right. The paths are as they would have appeared on the oscilloscope screen if we had set the scope for storage mode. (The subject, however, saw only the current position of the force cursor and the target position.) Figure 1 shows that the path curvature was similar for pulses and steps but was reduced for the slower ramp responses (e.g., compare the path in direction 9 across conditions).

In Fig. 2 we compare force path curvature during isometric conditions (open symbols) to hand path curvature during reaching movements (filled symbols). Path curvature was quantified such that a straight line has zero curvature and a semicircle has a curvature of 0.5. We defined a counterclockwise curvature (as for direction 9) to be positive and a clockwise curvature (as for direction 13) to be negative.

For isometric conditions, most subjects appeared to exhibit two full cycles of variation in curvature across direction. For example, in subject A, a peak clockwise curvature occurred for forward directions, a peak counter-

Fig. 2 Force path curvature (open symbols) and hand path curvature (filled symbols), plotted against target direction for the sagittal plane. The basic pattern was similar across the four subjects (A-D). Counterclockwise (CCW) curvature is positive; clockwise (CW) curvature is negative. Each data point represents a mean ( $\pm$ SE) of values calculated from five to ten individual trials.





Fig. 3 Response duration (time to target) plotted against target direction for the sagittal plane. *Filled symbols* represent grand mean movement times for five to ten trials in each of the four subjects. *Open symbols* represent the corresponding grand means for force steps and pulses. Duration was normalized by equating the mean values for each subject and each condition: 100% represents 461 ms for movement time, 182 ms for pulses, and 267 ms for steps

clockwise curvature occurred for downward directions, and then the cycle repeated with a clockwise peak for "back" and a counterclockwise peak for "up." Subjects B and C exhibited peaks in slightly different directions from subject A, but the same general trend was apparent. For subject D, the trend was more apparent for pulses than for steps (this was the subject used for Fig. 1).

We also computed hand path curvature for the fast movements (30-cm hand paths) described in the preceding paper (Flanders et al. 1996). The filled symbols in Fig. 2 reveal that movements and forces had a different relation between curvature and direction. For each subject the variation in hand path curvature went through only one cycle: peak clockwise curvature was for downward directions and peak counterclockwise curvature was for upward directions.

Although the spatial distribution was quite different, the *amount* of curvature exhibited under isometric conditions was similar to the amount of curvature exhibited during movement. For each of the three conditions shown in Fig. 2 (movements, pulses, steps) we summed the absolute value of curvature across the 20 directions. A one-way ANOVA indicated that there was no significant difference in this sum, across conditions (F=1.47; df=2.9; P=0.28). Combining the values from the four subjects, the grand mean absolute value of curvature was 0.058 for movement, 0.062 for pulses, and 0.052 for steps.

The amount of time to reach the target also varied with direction. This is displayed in Fig. 3, where for each direction we show the grand means across the four subjects. Time to reach a force target was typically shorter than movement time (about 130-300 ms compared with 400–500 ms). To facilitate comparison across conditions, duration was normalized as percentage of the mean duration for each subject and each condition. Movement times (filled symbols) varied with direction in a consistent fashion, exhibiting two full cycles, with peaks aligned to the inertial anisotropy of the initial posture (see Fig. 13 of Flanders et al. 1996). Force pulse and step durations, however, were more variable and appeared to exhibit only one cycle. An ANOVA similar to the one described above revealed no significant difference in the total variation in duration (absolute difference from 100%), compared across the three conditions (F=2.18; *df*=2,9; *P*=0.17).

In summary, despite the dramatic differences in the overall pattern, amounts of curvature and directional variation in duration (percentage mean) were comparable for arm movement in a sagittal plane and for the analogous isometric force responses in the sagittal plane. Curvature data and percentage duration trends were similar for isometric pulses and steps. Comparable amounts of curvature and variation in duration were apparent in the force data from the frontal plane (data not shown).

#### Timing of phasic muscle activation

Force path curvature was accompanied by asynchronous phasic muscle activation. If EMG bursts occurred synchronously amongst synergists (and produced synchronous shoulder and elbow torques), the resulting force direction would be constant throughout the force rise. In contrast, temporal offsets between the activities of various muscles could promote a gradual change in force direction during the response, e.g., force might initially be in the direction corresponding to shoulder torque and then curve toward the direction corresponding to elbow torque. For forces in the sagittal plane, a staggering of activity in shoulder and elbow muscles would produce curvature, because these muscles have different mechanical actions. Furthermore, asynchrony amongst shoulder muscles would produce force path curvature in the frontal plane. This is because shoulder muscles exhibit a range of actions in the frontal plane, owing to the additional degrees of freedom (see Fig. 14 of Flanders and Soechting 1990).

The phase plots in Fig. 4 afford the possibility of viewing temporal relations between muscles, for individual target directions. In each panel, MT EMG values are plotted on the abscissa and EMG values from another muscle are plotted on the ordinate. The data for each muscle are the smoothed EMG means from subject D,



**Fig. 4** Smoothed medial triceps (MT) EMGs from force pulses or movements (subject D) are plotted against the simultaneously recorded EMGs from other muscles (long head of triceps, LoT, biceps, BI, or posterior deltoid, PD). Records begin 200 ms prior to force or movement onset; *points* along the curves are points in time; the *arrows* indicate the progression of time. For example, in the *top right plot*, PD activity led MT activity for direction 13, and MT activity led PD activity for direction 9. EMG is in arbitrary units (0–100)

for force pulses (top four panels) and movements (bottom two panels) in the sagittal plane. In the middle left panel, the activity of the long head of triceps is plotted with the simultaneously recorded activity of the medial head. The EMG waveforms of these two parts of the triceps rose and fell together, creating a nearly straight line on the plot. The top left panel compares biceps activity to the same MT trace (from direction 9). Initially biceps activity decreased as MT activity remained nearly constant, and later the relation had a negative slope. This early phasic decrease in biceps activity was as prominent under isometric conditions as it was for movement (cf. Flanders et al. 1994).

The top two panels on the left of Fig. 4 show the simplest types of relations across muscles: LoT and MT were nearly synchronously activated or "in phase" (positive slope), whereas BI and MT were reciprocally activated (beyond the earliest period), or approximately "180° out of phase" (negative slope). In terminology borrowed from the analysis of sinusoidal oscillations, a counterclockwise circle on these plots would represent a 90° phase lag for the signal on the ordinate; a clockwise circle would represent a 90° phase lead for the signal on the ordinate (if amplitude is scaled to fill a square plot). A slanted ellipse would represent an intermediate phase relation (such as  $45^{\circ}$ ). In terms of EMG waveforms, a circular or elliptical phase relation represents a temporal staggering of muscle activation, neither synchronous nor reciprocal.

The top right panel shows that phase relations between synergists can be different for different directions. Posterior deltoid and MT changed their temporal relation between direction 9 (down and forward) and direction 13 (down and back). In agreement with the results of Karst and Hasan (1991b), we found distal to proximal sequencing in directions where the intensity of the proximal muscle was relatively low. Thus for direction 9, MT led and PD intensity was low, whereas for direction 13, PD led and exhibited more intense activation. We will show in the next section that direction 9 was a transitional region of the intensity tuning curve of PD (Fig. 8). For pairs of elbow and shoulders muscles, phase relations generally flipped from clockwise to counterclockwise at boundary regions of the spatial tuning curve for EMG intensity.

For direction 9, MT led LoT only slightly (see arrow): the activities of the two muscles were almost completely in phase (Fig. 4, middle left panel). For the next clockwise direction (direction 10) however, LoT led MT and was close to "45° out of phase" (Fig. 4, middle right panel). These two muscles have different mechanical actions due to the fact that LoT crosses both the shoulder and the elbow, whereas MT crosses only the elbow. Although it is impossible to predict the relation between EMG and force without a complete musculoskeletal model of the arm, one can conclude that this asynchrony in direction 10 can potentially contribute to force path curvature.

The bottom two panels in Fig. 4 show the analogous LoT/MT plots for two clockwise consecutive movement directions (directions 10 and 11) using data from the preceding study (Flanders et al. 1996). The EMG bursts of these two synergists were in phase for one direction but slightly out of phase for the next. In contrast to the isometric condition, here MT activation slightly leads LoT activation. In comparing force responses and movements, there is a conserved general tendency for synchrony in some directions and asynchrony in others. However, the relation between phasing and target direction is not necessarily conserved across conditions.

As explained in the preceding paper (Flanders et al. 1996), an exact comparison between movement and isometric conditions is impossible, and directional differences are to be expected. Nevertheless, it is of interest to compare general features of the patterns, and therefore we have quantified the EMG burst timing in the same way for movements and forces. We will now illustrate these features using two examples (Figs. 5, 6).

In Fig. 5, we show an example where the directional pattern in a shoulder muscle was quite different from the

Fig. 5 Anterior deltoid phasic EMG timing for force pulses (open circles) and movements (filled squares) in the sagittal plane. For force pulses, rectified EMG data (averaged across five to ten trials) are shown on the left for directions 4, 6, 8, and 10 (as defined in Fig. 1). Estimates of the time of the largest burst are shown in the right panel for these and other force directions. In the right panel, the timing scales on the left (movement) and the right (force) are adjusted to equate the approximate time of the antagonist burst (50% for movement, 100% for force). All data are from subject C



pattern exhibited by this same muscle during movement. These data are from the AD of one representative subject. As described in the preceding paper (Fig. 6 of Flanders et al. 1996), the filled symbols show the gradual shift of peak activity in this muscle, as the burst timing changes with movement direction. The open symbols exhibit the corresponding data for force pulses, and in the left panel are four of the EMG means from which these timing estimates were derived (forward and downward directions). The thick black bar represents the time to peak force, which in each case was about 140 ms. According to Ghez and Gordon (1987, their Fig. 3A), the antagonist burst for a force (F) pulse would be expected to begin at peak dF/dt and to be centered near the largest negative value of  $dF^2/dt^2$  (which is equivalent to the time of occurrence of peak force). Therefore, the second burst for directions 6 and 8 and the largest burst for direction 10 had the timing of an "antagonist burst." As direction changed, this burst gradually increased in intensity, as the intensity of the first agonist burst declined. Thus, for force pulses (open symbols) the main trend exhibited by this muscle was a discontinuity in the timing data due to the change in relative amplitudes of the agonist and antagonist bursts (directions 8-10). However, the force data also revealed a gradual shift in the timing of the agonist activity across directions 4-8.

Examples of an abrupt transition from agonist to antagonist timing were more commonly observed for isometric conditions than for movement (cf. Hoffman and Strick 1986). However, there were also several clear examples of a gradual temporal shift of agonist activity for isometric force pulses and steps. Figure 6 exhibits data from MD for steps of force in lateral directions (frontal plane). The data in the top panel are from the subject used to illustrate a temporal shift for movement, in the preceding paper (cf. Figs. 4–6 by Flanders et al. 1996). The intensity of the ag-

onist burst became gradually smaller and its timing (onset as well as peak) became gradually later as movement direction changed from lateral (direction 6) to downward (direction 9). The bottom panel shows the timing estimates from all four subjects for this muscle over this range of directions. All subjects exhibited this tendency.

Spatial tuning of phasic and tonic activation

In the preceding section, we described the asynchronous activation that can contribute to force path curvature. For force pulses this is probably the major contributor. For force steps, another possible component would be a change in the relative intensity of activity across the various muscles as the force increase progresses. This could be manifested as a dissociation between the phasic and tonic spatial tuning curves of EMG intensity. If phasic activation were synchronous and the spatial tuning of EMG intensity was always identical for phasic (early) and tonic (later) activity, it would imply that the net force direction was the same throughout the response. Alternatively, if phasic and tonic spatial tuning differs for some muscles, this could promote a gradual change in force direction.

In Fig. 7 we show an example from the two muscles with the most pronounced difference between phasic and tonic spatial tuning. For forces in the sagittal plane, the directions for high levels of phasic activity were close to straight up for BI and straight down for LoT. Phasic spatial tuning is indicated by the solid line, which is a spline fit to the data. These phasic data were from the step responses of one representative subject. The corresponding tonic data, derived from the same trials, exhibited a somewhat different spatial tuning (circular symbols).



**Fig. 6** Temporal shift of medial deltoid (*MD*) across the agonist range (frontal plane). The *top panel* shows the phasic portions of smoothed EMG means from the step responses of subject B; the force response began at 0 ms. The *bottom panel* shows timing estimates for all four subjects (*square symbols*).

The tonic levels of activity were computed as the absolute value of the difference between the initial EMG level and the steady-state level at the end of each step increase in force. Thus the *change* in tonic EMG level is represented by the circular symbols: black symbols stand for increases in EMG, and white symbols stand for decreases in EMG. For BI, there was a decrease in tonic activity for downward movements. (In this downward range, the phasic activity had the timing appropriate for an antagonist burst.) LoT exhibited increases in tonic activity in the upward range (coactivation with BI).

In Figs. 8 and 9 we compare phasic and tonic spatial tuning using data from all four subjects and all nine muscles. As in the preceding paper (Flanders et al. 1996), we excluded Pec for the sagittal plane (Fig. 8) and LoT for the frontal plane (Fig. 9). The phasic tuning curves were derived from combined pulse and step data (shaded areas). The tonic tuning curves were derived from combined step and ramp data (circular symbols). Areas of consistent decreases in tonic activity (white circles) were especially prominent in BI and AD, the two muscles that were most active to support the weight of the arm in the initial posture. MT showed an upward region of tonic coactivation for both planes, as did LoT for the sagittal plane and LaD for the frontal plane. For PD activation for forces in the sagittal plane, the intensity of tonic activity was just as great in the region where this muscle acts as an antagonist (up and forward) as in the region where it acts as an agonist (down and back).

As illustrated in Fig. 7 (using data from one subject), in the BI and LoT data in Fig. 8 (four subjects), the pha-



Fig. 7 Spatial tuning of EMG intensity for the biceps and long head of triceps of subject C: EMG intensity on polar plot of force direction for steps in the sagittal plane. Phasic intensity values are from the largest amplitude 100-ms epochs (*solid back lines*); tonic intensity values are from the 100-ms epoch, 100 ms after the end of the step (*circular symbols*). Black symbols represent an EMG increase and *white symbols* represent an EMG decrease, from the initial EMG level

sic spatial tuning was directed more vertically than was the tonic spatial tuning. MT data for the sagittal plane suggest the same tendency. However, for most other muscles, phasic and tonic spatial tuning was closely aligned. This was especially striking in the full set of data from the frontal plane (Fig. 9).

In Figs. 8 and 9, we have also given an indication (arrows) of how well these present results agree with data from the previous study of Flanders and Soechting (1990). In the previous study, subjects' arms were unsupported and the task was to hold the arm in a certain posture while a pulley system was used to apply loads in various direction. We will refer to this as the "unconstrained isometric condition," in contrast to the present study where subjects were "constrained" by a stationary wrist cuff. The longer arrow on each plot represents the direction of the largest intensity of tonic activity (the center of the cosine fit of Flanders and Soechting 1990). When a smaller arrow is also present, it indicates the direction of a smaller activation lobe. For forces in the sagittal plane, there were some small (about 20°) discrepancies between the best directions for constrained and unconstrained conditions, but the overall pattern across muscles was comparable. For forces in the frontal plane the agreement was remarkable (considering that the data represent a different group of subjects and were obtained in a different laboratory, under different conditions). This suggests that out-of-plane forces were minimal in the present, constrained situation, since there was no global



Fig. 8 Spatial tuning of EMG intensity for phasic and tonic muscle activity (sagittal plane, four subjects). *Shaded areas* represent the phasic values from pulses and steps; *circular symbols* represent tonic levels from steps and ramps. *Arrows* represent the best directions for tonic EMG from a previous study where the arm was unconstrained (*BR* brachioradialis, *AD* anterior deltoid, *LaD* latissimus dorsi)

difference in the EMG pattern when compared with a situation where out-of-plane forces would have resulted in movement. It also indicates that the EMG preferred directions tabulated by Flanders and Soechting (1990) might also apply to dynamic isometric forces.

# Discussion

We have demonstrated that, despite the differences in the overall pattern, the amounts of curvature and variation in percentage mean duration are comparable for reaching movements and isometric force responses. Since neither inertial nor viscoelastic anisotropy come into play during constrained isometric conditions, the curvature and variation in duration must be attributed to other factors. Although perception of path curvature might be involved in the control of horizontal reaching movements (Wolpert et al. 1994, 1995), it seems doubtful that it is an important factor either in the curvature of hand paths in the sagittal plane (where vision is often obscured) or in the curvature of force paths displayed on a small screen, placed beyond reach. Asynchronous patterns of muscle activation can contribute to force path curvature under isometric conditions, and it is reasonable to hypothesize



Fig. 9 Spatial tuning of EMG intensity for phasic and tonic muscle activity (frontal plane, four subjects). *Shaded areas* represent the phasic values from pulses and steps; *circular symbols* represent tonic levels from steps and ramps. *Arrows* represent the best directions for tonic EMG from a previous study where the arm was unconstrained (*Pec* pectoralis)

that this same feature may contribute to hand path curvature during reaching movements (see Flanders et al. 1996).

Muscle synergies, motor primitives, rules, and basic features

Historically the discussion of patterns of muscle activation was centered around the concept of "muscle synergy" (reviewed by Macpherson 1991). While some envisioned a need to reduce the number of muscles independently controlled by the central nervous system, others viewed the concept as a way to describe neuromuscular control strategies. In their studies of isometric force production at the human elbow, Buchanan and colleagues (1986, 1989) concluded that, with the possible exceptions of BR/brachialis and the LoT and MT, the synergistic actions of most muscles vary with each task performed. Although this group of investigators did not see a large distinction between the heads of triceps, we now show that their temporal activation can be synchronous for some force directions and asynchronous for others (Fig. 4). We have also shown that the spatial tuning of these two muscles is consistently different (Fig. 8; see also Flanders and Soechting 1990; Flanders et al. 1996).

Currently the discussion of muscle synergies has shifted toward the theme of "motor primitives" (see Giszter et al. 1993). As the name implies, these are natural patterns of muscle activity that may underlie a whole range of movements. In contrast to muscle synergies, which are thought to be flexible to modification by task demands, motor primitives are thought to be sets of motor patterns that can be combined in various ways for various tasks. Theoretically, the elements of the set can be combined to produce a certain movement and recombined in a different way to produce a different movement, in the same way that "primitive" object attributes are thought to be used to "build up" a visual perception (Marr 1982). This is a somewhat different way to describe motor patterns than the approach taken here.

Another conceptual approach is used by investigators who seek to describe the process of motor pattern generation by identifying the algorithms or "rules" that relate EMG parameters to the characteristics of the movement task (see Hasan and Karst 1989). Karst and Hasan (1991a, b) have shown that, for a wide range of two-joint horizontal arm movements, EMG onset is related to the direction of the target from the line of the forearm: neither a rule based on initial force nor a rule based on initial acceleration described the data as well as these geometric parameters.

Our conceptual approach is very similar to that of describing the rules of the process of motor pattern generation. We have sought to identify "basic features" of this process in the hope that these features will provide insight to neural control mechanisms. In the sections below we will discuss what we consider to be the two most important *basic features*, and we will speculate as to the mechanisms of neural control.

#### Neural control of timing and duration

The discovery of asynchronous agonist activation under isometric conditions is compelling evidence for the generality of this type of control. Although we showed only a few examples of this phenomenon, the eminence of force path curvature for pulse responses (Fig. 2) is not readily explained by any other mechanism. As discussed in the preceding paper, the implications of asynchronous agonist activation may remain unclear until a more complete musculoskeletal model can be developed, to simultaneously consider joint moments in all degree of freedom. However, as described below, it may be easier to interpret the implications of a control mechanism for agonist burst duration and antagonist burst latency.

Gordon and colleagues (1994) have shown that, for reaching movements in the horizontal plane, peak acceleration varies with movement direction in a manner consistent with the inertial anisotropy of the arm: directions perpendicular to the forearm possess the least inertial resistance and therefore the highest acceleration. Interestingly, incumbent errors in movement extent are minimized by changing movement duration as needed (as also seen in Fig. 3, filled symbols). Although these authors give evidence for a proprioceptive feedforward mechanism (Ghez et al. 1990, 1995), proprioceptive feedback is also potentially useful in adjusting the duration of muscle activation as needed to reach the target. During movement, this proprioceptive information could stem from a variety of receptors, including muscle spindles, and feedback could also adjust EMG levels to automatically compensate for changes in tension due to changes in muscle length.

During isometric force responses, the milieu of kinesthetic information is undoubtedly different, but nonetheless present. Tactile information may be of increased importance in providing feedback concerning the force trajectory (Edin and Abbs 1991). The pattern of variation in duration differed between force responses and movements (Fig. 3). This goes along with the fact that force responses do not require compensation for inertial resistance. For force responses the area associated with the longest duration was directed backward and upward. One can speculate that this direction is difficult due to a lack of muscles with pulling directions in this area (see Fig. 13 of Flanders and Soechting 1990). The directional pattern did not follow an elliptical or bimodal function, as might be required for an explanation invoking a twodimensional mechanical anisotropy. Instead the variation in duration seems to result from a nonuniformity in the ability of the muscles of the arm to generate forces in various directions.

Whether variation in duration is due to inertial and/or viscoelastic anisotropy (during movement) or a nonuniformity in muscular strength (expected during movement and during isometric responses) it seems clear that the neural control mechanism must include directional variations in the latency and duration of muscle activation. It has long been recognized in studies of single-joint movement, that changes in load or desired movement time are accomplished by changes in agonist burst duration and antagonist burst onset (for a recent review see Hoffman and Strick 1993). Perhaps the universality of the need to incorporate proprioceptive feedback to deal with changing force requirements has dictated a pattern of a modifiable asynchronous activation for flexibility in control over the time domain. It would be overly simplistic to suggest that EMG intensity and timing are controlled by distinct areas of the motor system, but one might note that research in motor cortex has focused on intensity, while the cerebellum and spinal pathways transmitting proprioceptive feedback are more often implicated in the control of temporal features.

# Control of phasic and tonic EMG intensities

The second basic feature of the motor pattern for reaching is the separation of phasic and tonic drives. Again, it does not seem feasible that these drives are controlled by completely distinct areas of the motor system, but it *has* been suggested that tonic activity is maintained downstream from motor cortex after phasic motor cortical activity initiates a movement (Georgopoulos et al. 1992). Phasic and tonic EMG activities are clearly separable based on their differential scaling with the speed of movement (Flanders and Herrmann 1992). This is due to mechanical needs: phasic propulsive and decelerative forces must increase to increase speed, whereas tonic forces that support the arm in a series of postures (against gravity) do not change with speed (Hollerbach and Flash 1982; Atkeson and Hollerbach 1985).

This separable modification of phasic and tonic EMG activities might be implemented by distinct neural subsystems or, alternatively, the differential control might instead reflect the phasic and tonic portions of the activities of individual neurons. (This states the two extremes - an intermediate is possible since neuronal types range on a continuum from phasic to phasic/tonic to tonic.) If the spatial tuning of phasic and tonic EMG intensity was identical in each muscle examined, it would tend to support the hypothesis that the two drives are linked, due to the neuronal substrate. For most muscles, spatial tuning was similar for phasic and tonic activities, both in terms of best direction and in terms of breadth of tuning. For BI and LoT, however, there was a small but consistent difference in best direction, demonstrating that the linkage is not obligatory.

Our most recent work suggests that a mechanical optimization of patterns of phasic muscle activation may influence the final pattern of tonic muscle activation when the arm is at the target (Soechting et al. 1995). This analysis was done on movement trajectories and final postures (rather than EMG patterns), since a complete model of the relation between EMG and movement is beyond our current capabilities. We found that, for a given spatial target, final posture at the end of a reaching movement differed so as to minimize the mechanical energy used to transport the arm from the various initial locations. Thus the pattern (across muscles) of tonic activation at the final posture was influenced by the movement dynamics and the corresponding patterns of phasic muscle activation.

#### Conclusions

It is interesting to note the similarities between the tonic spatial tuning under the present constrained isometric conditions and the unconstrained isometric conditions employed in our previous study (Flanders and Soechting 1990). With regard to the previous results, the frequency of occurrence of significant areas of agonist/antagonist coactivation has been a bit puzzling to others in the field, since it was not seen in the elbow studies of Buchanan et al. (1986, 1989) and was only observed for AD in the studies of Theeuwen et al. (1994). Previously, it seemed possible that this discrepancy was due to the fact that the other groups constrained the wrist in an apparatus similar to the one used in the present study. We now report significant areas of agonist/antagonist coactivation under constrained isometric conditions. In Figs. 7–9 we showed areas of tonic coactivation ("coactivation lobes") in LoT, MT, PD, and LaD. The coactivation lobe in PD was quite appreciable. The discrepancy amongst the laboratories could be due to the different postures used, since EMG patterns change rather dramatically with posture (Flanders and Soechting 1990).

For phasic EMG activity, the comparison between movements and isometric force responses leads us to conclude that an elaborate control of timing is a conserved feature of motor pattern generation. Although one must exercise caution in relating a force in a certain direction to a movement in that same direction, a more general comparison across conditions can be fruitful. This approach has previously been used by the Georgopoulos laboratory to show that velocity/curvature relations and segmentation of drawing movements are not simply due to mechanics (Pellizzer et al. 1992; Massey et al. 1992). We now use this approach to show that path curvature is not necessarily produced by mechanics and to strengthen our assertion that asynchronous muscle activation is a basic feature of the neural control of reaching.

Acknowledgements This work was supported by the National Institute of Neurological Disorders and Stroke, grant R01-NS27484. We thank C. A. Buneo for his insightful comments on the manuscript and J. F. Soechting for his enthusiasm. We also thank the reviewers, who provided constructive criticism.

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