Spatial/Temporal Characteristics of a Motor Pattern for Reaching

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SUMMARY AND CONCLUSIONS

1. Temporal patterns of electromyographic (EMG) activity were related to the direction of fast reaching movements. Reaches were to 20 targets in the sagittal plane of the human arm.

2. The subtraction of EMG levels recorded during very slow movements to each target allowed this study to focus on the phasic aspects of complex EMGs.

3. General features of the phasic spatial/temporal patterns differed across muscles, even across muscles at the same joint. This indicates that future models of cortical to motoneuronal processing must include nonuniform space-time transformations.

INTRODUCTION

The temporal structure of the motor pattern for reaching is just beginning to receive attention. The current concept of the transformation between motor cortical activity and motoneuronal activity is that of a weighted mapping of activation levels, such that a particular pattern of cortical activity corresponds to a particular spatial pattern of muscle activity (Kalaska and Crammond 1992). It previously seemed possible that reaching movements might be subserved by simple (triphasic) temporal patterns of muscle activity that are exactly opposite (reciprocal) for movements in opposite ranges of directions (Hoffman and Strick 1986; Wadman et al. 1980). We will show that this simplifying assumption must now be replaced by more precise information.

Muscle activity for fast movement of a single joint can be quantified as a series of three phasic bursts (Gottlieb et al. 1989). However, the muscle activity associated with slower movement and movement involving more than one joint can be more complex and difficult to quantify. We recently showed that the complex electromyographic (EMG) waveforms associated with reaching movements can be analytically decomposed into two waveforms: one representing the control of the quasi-static series of postures traversed by the moving arm, and one representing the control of movement dynamics (Flanders and Herrmann 1992). This led to our use of a procedure by which the dynamic (or phasic) component of a complex EMG waveform is obtained by subtraction of EMG data from very slow movements (Buneo et al. 1994).

METHODS

In the present study, we used this subtraction procedure to reveal the spatial/temporal structure of phasic muscle activation for reaching. Four human subjects stood with the right arm in the initial posture shown in Fig. 1. On each trial the subject reached to a target in the sagittal plane of the arm, and the hand moved along one of the 20 paths shown. We recorded the hand trajectory and the activity of several arm muscles using previously described techniques (Flanders 1991; Flanders and Soechting 1990). On alternate trials, subjects were instructed to move fast or slow. Target directions were presented in pseudo-random order. For each muscle, EMG recordings from like trials (same movement time and same direction) were full-wave rectified, aligned according to movement onset, averaged, and then smoothed. Movement onset was measured from the velocity profile using an interactive cursor program. Only movements with a unimodal velocity profile were used. EMG averages were from 5 to 10 trials and were smoothed digitally, using a two-sided exponential. Phasic EMG traces were obtained by normalizing the time base of averages from slow movements to the time base of averages from fast movements, and then subtracting these posture-related waveforms from the corresponding waveforms from the faster movements. A computer algorithm was used to scale the time base of the slow trace to the appropriate time base for subtraction. For the subject whose data are shown, the average slow and fast movement times were 1,050 and 415 ms. Human subjects gave informed consent.

RESULTS

Figure 2 depicts the phasic activity of anterior deltoid (AD) and latissimus dorsi (LaD) for reaches in four downward directions (arrows). As a result of the subtraction procedure, the AD waveform showed negative epochs, indicating a decrease in the ongoing postural activation. As movement direction changed in 18° intervals (from down and forward to down and back) the positive burst moved gradually in its relation to movement onset. In contrast to this gradual shift, the timing of the LaD burst switched abruptly from the timing of an antagonist (*top two panels*) to the timing of an agonist (*bottom panel*).

In Fig. 3 we show polar intensity plots of phasic EMG amplitude for LaD, AD, long head of triceps (LoT) and biceps (BI). All data are from the same subject as the data in Figs. 1 and 2, but the overall patterns of all four subjects were very similar (see cover). On these intensity plots, time progresses outward, such that the perimeter of the small central circle marks 200 ms before movement onset, the next larger circle represents movement onset (0 ms), the next larger circle approximates the end of the movement (400 ms after onset), and the outer perimeter approximates 200 ms after the movement had stopped. [The SD of the movement time (415 ms) across the 20 directions was 36 ms.] The polar directions are oriented in the same way as the hand paths shown in Fig. 1.

In Fig. 3, EMG values are binned and bin boundaries form contours of equal EMG amplitude. The medium gray background represents no difference between slow and fast movements; the lighter gray represents a phasic decrease in postural activation; the darker gray represents agonist and antagonist bursts. For LaD (*top left*), movements down and 18° forward exhibited an antagonist burst, and move-
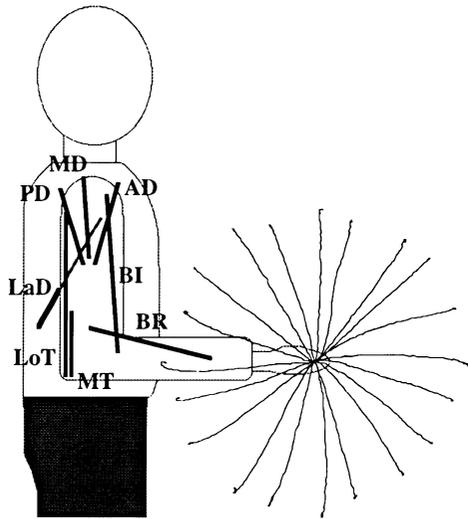
FIG. 1. Experimental design. Pictured are the averaged, 30-cm, hand paths from 10 fast movements in each of 20 directions in the sagittal plane of the arm. We used surface electrodes to record from posterior deltoid (PD), medial deltoid (MD), anterior deltoid (AD), latissimus dorsi (LaD), long head of triceps (LoT), biceps (BI), medial head of triceps (MT), and brachioradialis (BR).

ments down and 18° back exhibited the classic agonist pattern of burst-pause-burst (cf. Fig. 2).

The overall pattern for LaD conforms to expectations based on previous studies (Hoffman and Strick 1986; Wadman et al. 1980), except that the second agonist burst was sometimes more intense than the first agonist burst. The polar pattern for LaD was "circumferential" (fixed in time) and was reciprocally organized for movements in opposite directions. The spatial/temporal pattern for AD, however, was fundamentally different, indicating a nonuniform patterning of central motor commands to different muscles at the same joint.

In contrast to the circumferential pattern of LaD, the AD shows a gradual outward spiraling of temporal variation. The *top right panel* in Fig. 3 shows that during upward movements AD exhibited an early agonist burst (dark gray) followed by a negative dip (light gray) and then a second agonist burst (dark gray). Going clockwise on the plot, for progressively more forward movements, the first agonist burst was longer in duration such that the burst ended gradually later in time. Then, as the direction changed from forward to downward, the burst gradually changed to the timing of an antagonist burst (as also shown in Fig. 2).

The biarticular muscles (LoT and BI) also exhibited patterns that were distinctly different from each other (Fig. 3, *bottom*). Biceps exhibited a circumferential pattern in the downward range, where the antagonist burst maintained a relatively constant temporal relationship to movement onset. In contrast, LoT activity became gradually earlier in this downward range.

DISCUSSION

Despite the differences across muscles, the results highlight several organizational principles.

1) There is a generally reciprocal organization for opposite ranges of movement directions, such that a given mus-

cle exhibits agonist-like activity in one range and antagonist-like activity in the opposite range. This is consistent with classic concepts dating back to Sherrington and has been previously demonstrated by other investigators.

2) After subtraction of postural activity, the classic triphasic pattern was seen in these data from multijoint reaching movements, but it was modified to include instances where the second agonist burst was more intense than the first (LaD and LoT) and instances of phasic inactivation of postural activity. Early antagonist inactivation has been previously reported, but the implication of this mechanism for controlling movement in a gravitational field has not been fully explored (Gottlieb et al. 1970; Hallet et al. 1975; Hufschmidt and Hufschmidt 1954).

3) On the basis of the work of Wadman and colleagues (1980) and Karst and Hasan (1991), one might expect the time between the *onset* of shoulder muscle activation and the *onset* of elbow muscle activation to be a continuous function of movement direction. A previous study in our laboratory (Flanders 1991) showed that for several muscles, the timing of EMG *waveforms* gradually shifted in parts of a range of 10 directions. In the present study, the use of 20 directions and the subtraction of postural activity has allowed us to view this temporal variation more clearly. We have demonstrated that the "temporal shift" in the AD waveform is due to an increase in agonist burst duration for upward directions and a delay of the entire waveform for downward directions. We have also demonstrated that
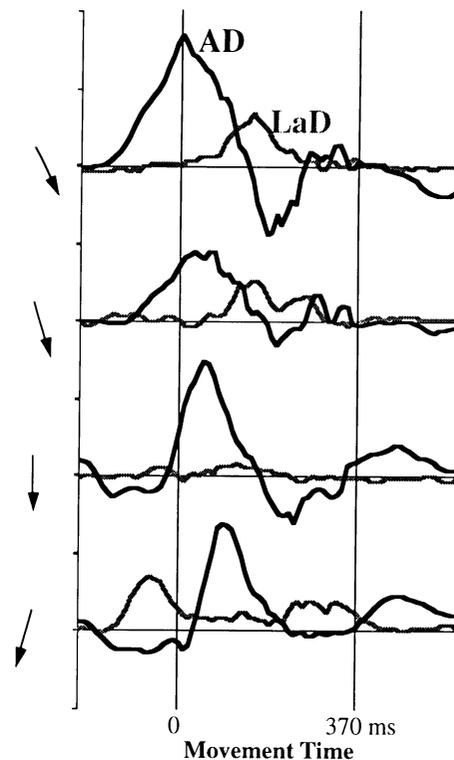

Movement Time

FIG. 2. Phasic electromyographic (EMG) components for movements in 4 downward directions (arrows). Latissimus dorsi (LaD) activity switches abruptly from the timing of an antagonist (*top*) to the timing of an agonist (*bottom*). In contrast, the timing of the anterior deltoid (AD) burst shifts more gradually. The vertical lines show movement onset and the end of the movements (on average). The horizontal lines are at zero, or no difference between EMG levels for fast and slow movements.
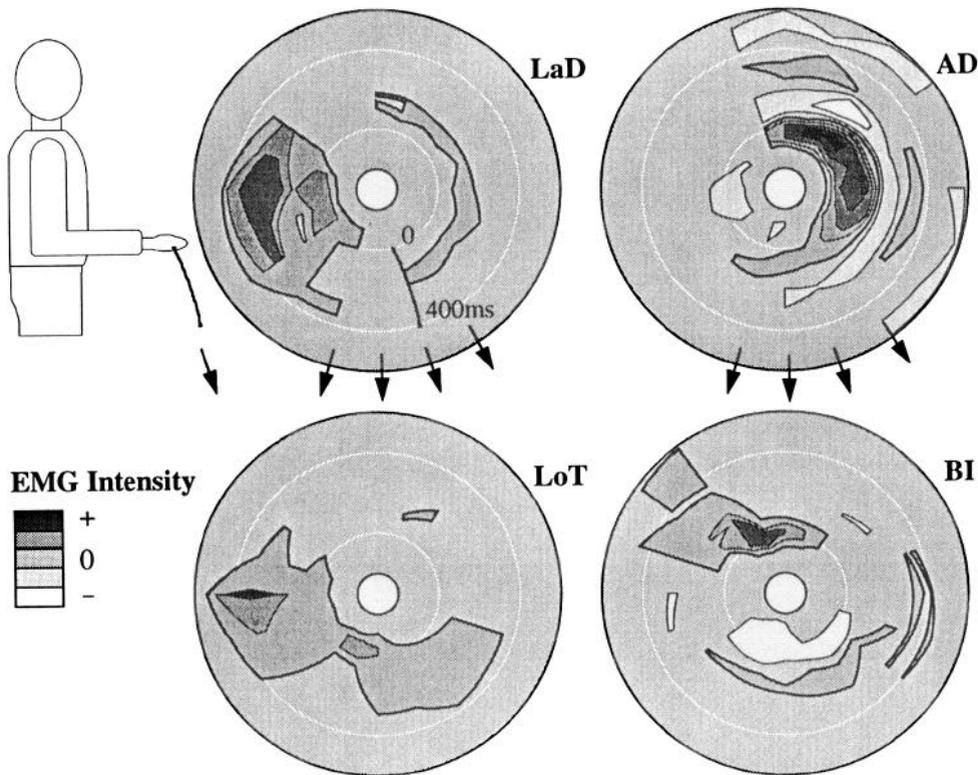
FIG. 3. Polar plots of phasic EMG intensity (gray scale) over time (radius) for 20 directions in the sagittal plane of the arm. The earliest time is the smallest circumference and directions are oriented as in Fig. 1. The arrows mark the data also shown in Fig. 2. The medium gray background indicates an EMG level close to zero; negative EMG levels are lighter gray; more positive EMG levels are darker gray. Bin widths are arbitrary but uniform within each muscle. These data were extracted from EMG waveforms recorded simultaneously from shoulder muscles (LaD and AD, *top*) and two-joint muscles (LoT and BI, *bottom*).

muscles crossing the same joint can have very different temporal patterns.

Studies of motor cortical activity have not yet begun to focus on temporal patterns. In both the modern and classic cortical literature (Evarts 1967; Georgopoulos et al. 1992), a distinction has been made between tonic neuronal activity (related to posture) and phasic neuronal activity (related to movement or force dynamics), but the temporal structure of the phasic activity has not been quantified. The current concept of a weighted mapping of cortical to motoneuronal activation levels needs to be expanded to include the relation of spatial direction to temporal characteristics of neuronal activity. It is now apparent that simple reaching movements are *not* subserved by simple, reciprocal, triphasic patterns that are uniform across muscles and fixed in relation to movement time. How motor cortical and related neuronal circuits generate precisely timed phasic muscle activations is an open question for future research.

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