Neuromuscular Adaptation During Skill Acquisition on a Two Degree-of-Freedom Target-Acquisition Task: Dynamic Movement

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INTRODUCTION

When we first perform a novel movement, the pattern of muscle activation we use to achieve the goal of the action does not typically use the muscles available in the most effective manner (Carson and Riek 2001; Kotke et al. 1978). As skill is acquired through practice, however, the CNS modifies the pattern of muscle activity to make optimal use of the effector system (Carson and Riek 2001). Stated another way, we can say that the potential of the structures that constitute the musculoskeletal system to contribute to the desired movement inevitably constrains the extent to which skill can be acquired through practice. Most movements are generated through the combined action of many muscles within a highly redundant musculoskeletal system. It has been proposed that the CNS reduces the dimensionality of control by activating functionally cooperative muscles as a group (referred to as a synergy) rather than individually (Bernstein 1967). Thus it is the potential for adaptation of synergistic muscle groups that ultimately constrains the extent to which task performance may be altered. It may be surmised that, in the context of skill acquisition, the goal of the CNS is to converge on the set of motor commands that best exploit the mechanical properties of synergistic muscle groups to achieve the primary goal of a task.

The results of a recent study conducted in our laboratory (Shemmell et al. 2005) demonstrated that practice of a goal-directed isometric torque production task produced improvements in performance that were mediated primarily by increases in the rate of agonist muscle recruitment. We concluded that, in the isometric task context at least, increasing the rate of agonist muscle recruitment represented the most effective means by which the CNS could exploit the intrinsic properties of the musculoskeletal system. Tasks performed in an isometric context, however, necessarily represent a constrained expression of muscular dynamics. It is thus possible that the scope for modification of the spatiotemporal properties of muscle synergies is similarly constrained. In contrast, tasks in which the limb is free to move may provide a context in which the distribution of activity across muscles within a synergistic group (the spatial organization of a muscle synergy) or the relative phasing of muscle activations (the temporal organization of a synergy) represents a more effective method of improving performance.

The acquisition of skill is necessarily defined in relation to the primary goals of a task. For example, for tasks in which the primary goal is to reach a destination in the minimum possible time, adaptations effected through practice may be deemed successful only to the extent to which they contribute to this goal. It is possible to conceive of a number of aspects of performance that might be altered to reduce the overall duration of a movement. One possibility would be to increase the overall speed with which the movement is executed. This is the aspect of performance that changes most appreciably in isometric conditions (Shemmell et al. 2005). A reduction of the extent to which the path of the end effector (e.g., the hand) deviates from the direct path to the target might also be expected to reduce overall movement time. Indeed systematic changes in this aspect of performance have been demonstrated when reaching movements are performed under altered dynamic conditions (Flanagan and Rao 1995; Lackner and Dizio 1994; Shadmehr and Mussa-Ivaldi 1994). In circumstances in which movements of the hand are disturbed by the imposition...
of a novel external force field, a straight trajectory of the effector toward the target is resumed after many practice trials. It seems reasonable to suppose that the process of skill acquisition will be associated with concurrent changes in a number of performance variables. It might also be assumed that the nature of the overall adaptive “strategy” that is implemented, will be such as to exploit most effectively the mechanical properties of the muscles involved.

The selection by the CNS of the most effective pattern of muscle activity is based on the facility for individual muscles and muscle compartments to produce the desired joint torque without the simultaneous production of unnecessary torque (MacConaill and Basmajian 1977; Macpherson 1991). During elbow flexion, for example, the monofunctional flexors, brachialis and brachioradialis, are always recruited because they produce torque exclusively in the desired direction (MacConaill and Basmajian 1977). The bifunctional biceps brachii is recruited only if the torque demands of the task are sufficient to require it because the activation of this muscle in this situation produces undesired supination torque. It may be anticipated therefore that the acquisition of skill in single-df movements will be associated with an attenuation of activity in bifunctional muscles.

A critical aspect of muscle synergy organization is the relative timing of individual muscle recruitment. In the execution of rapid motor acts, it is likely that the most effective pattern of muscle activity is that in which all contributing agonist muscles are recruited synchronously because this leads to the most effective summation of muscle forces. Indeed, it has been demonstrated that both single- and dual-df movements are normally characterized by the relatively synchronous recruitment of agonist muscles before the commencement of movement, followed toward the end of the movement by a similarly synchronous recruitment of antagonist muscles (Hoffman and Strick 1990, 1999; Sergio and Ostry 1995). It is therefore reasonable to suppose that if the temporal organization of muscle synergies is amenable to adaptation, the recruitment of muscles that act together to achieve a common goal (e.g., the acceleration of a limb segment in the case of agonist muscles) will occur more synchronously after practice. It is anticipated, however, that the latency of activation onset for some muscles will vary as a function of movement direction (Hoffman and Strick 1999; Pfann et al. 1998). It has been hypothesized that such temporal shifting represents an attempt by the CNS to minimize the curvature of the endpoint movement (Hoffman and Strick 1999). It is thus possible that the latency of activation onset in muscles that demonstrate this phenomenon will not be modified to synchronize their activation with that of other agonist or antagonist muscles.

The likely nature of changes in the contribution and timing of mono- and bifunctional muscle recruitment is less clear in the context of movements that require motion in two mechanical dfs. Achieving the most effective pattern of muscle activity in dual-df tasks may not necessarily be associated with minimizing the extent to which bifunctional muscles are activated. On the contrary, in many cases bifunctional muscles produce the least unnecessary torque because their direction of action is closely aligned with that of the intended action, although a growing body of evidence suggests that the motor commands generated by the CNS to control dual-df actions may be vectorial summations of those used to drive actions in each component df (Bizzi 1993; Mussa-Ivaldi and Giszter 1992; Sergio and Ostry 1995). If the CNS simplifies the control of dual-df actions in this manner, it is likely that the nature of spatiotemporal neuromuscular adaptations would be similar in both single- and dual-df tasks. We would therefore anticipate that an attenuation of bifunctional muscle activity will accompany skill acquisition in both single- and dual-df movements.

The purpose of this study is to determine the nature and efficacy of kinematic and neuromuscular adaptations that mediate the acquisition of skill on a discrete target-acquisition task set involving joint rotations in two skeletal dfs. We hypothesize that these adaptations will primarily consist of modifications of the spatiotemporal characteristics of muscle synergies rather than the increases in the rate of muscle recruitment that we have observed in an isometric context (Shemmell et al. 2005). Specifically, we anticipate that the contribution of bifunctional muscles will be reduced after practice on both single- and dual-df movement tasks. We also expect that the timing of muscle recruitment within agonist and antagonist groups will become increasingly synchronous with practice in both types of movement.

**Methods**

**Participants**

Eight right-hand–dominant (Oldfield 1971) participants between the ages of 20 and 36 yr (six males and two females) were involved in this experiment. Participants gave their informed consent before involvement in the study. All experimental procedures were approved by the Medical Research Ethics Committee of The University of Queensland, and conformed with the Declaration of Helsinki.

**Apparatus**

Participants were seated in a height-adjustable chair 1 m from a computer display positioned at eye level. The dominant arm was placed in a manipulandum that permitted movement in elbow flexion/extension and forearm pronation/supination (Fig. 1). The upper arm...
was held stationary and adjacent to the torso by a Velcro strap. A handle was fitted to the manipulandum, and padded clamps were located above and below the hand to minimize the required grip force. All adjustable elements of the apparatus were positioned to ensure that the upper arm was aligned vertically and that the centers of rotation of the elbow and the flexion/extension axis of the manipulandum coincided precisely. The positions of all adjustable elements of the apparatus were recorded for all participants during their first experimental session and remained constant for all subsequent sessions. Torque was applied to the manipulandum by a servocontrolled torque motor (AC Brushless Servo Motor; Baldor Electric) in the flexion/extension df to eliminate the effect of gravity on the manipulandum.

Kinematic recordings

The manipulandum was instrumented with two potentiometers that provided real-time feedback as to the angular position of the limb in flexion/extension and pronation/supination. Joint angular positions were sampled at 2,000 Hz at an analog-to-digital interface (AT-890, National Intruments, Austin, TX) and stored on a personal computer. Labview (v. 5.0, National Instruments) was used to write the custom experimental control and data-acquisition routines.

Position feedback

The visual feedback cursor moved 1 cm on the display for every 10° of joint rotation in either df. Flexion of the elbow resulted in a cursor movement vertically upward; pronation of the forearm moved the cursor to the left of the participants and supination to their right.

Electromyographic recordings

The electromyographic (EMG) activity of eight muscles was recorded during the pre- and posttests as well as during the first, third, and fifth days of training. Bipolar (AgCl) surface electrodes (5 mm diameter) were used to obtain recordings from 1) brachioradialis (BRAD), 2) triceps brachii (lateral head) (TRI), 3) pronator teres (PT), 4) flexor carpi radialis (FCR), and 5) extensor carpi radialis (ECR). The placement of electrodes was verified with test movements and isometric tasks as defined by Delagi and Perotto (1980). The electrodes were placed 2 cm apart on the muscle belly, parallel to muscle fibers. The EMG activity of the 6) long [BB(L)] and 7) short head [BB(S)] of biceps brachii and 8) brachialis (BRA) was recorded using fine-wire (75 micron) bipolar hook electrodes, inserted into the muscle 2 cm apart by 27-gauge needles. The needles were removed before recording. The EMG signals were amplified (250–10,000 times; PS111 amplifiers, Grass Instruments, Berkshire, UK), band-pass filtered (30–1,000 Hz), sampled at 2,000 Hz, and stored in the manner described previously.

To provide a means of normalizing the amplitude of the EMG signals across the experimental sessions, maximal M-waves were evoked in all muscles by electrical stimulation (Digitimer DS7A: pulse width 0.5 ms) of the brachial plexus at Erb’s point, before the commencement of each session. The stimulation intensity was increased in steps from an imperceptible level until the magnitude of the EMG responses no longer increased. The intensity of stimulation was then increased by a further 20%, and the responses to eight supramaximal stimuli recorded at intervals varying randomly between 6 and 8 s.

Familiarization

Before the commencement of training, all participants completed a familiarization session. This consisted of eight trials in each of the eight joint rotation combinations that were to be used during the practice session. Unlike the experimental task (described below), the joint rotation produced in each df was presented as a bar graph. The target position for each df was indicated by a line superimposed on the graph. When the joint positions fell within the target area (target position ± 4°) there occurred a change in the color of the bar.

Target-acquisition task

Targets representing dual-df movements (flexion/pronation [FLX/PRO], flexion/supination [FLX/SUP], extension/pronation [EXT/PRO], extension/supination [EXT/SUP]) were positioned such that a constant visual distance was maintained between the center of the screen and each target. The vertical (S\textsubscript{FE}) and horizontal (S\textsubscript{PS}) joint displacements required to reach each target (both single- and dual-df targets) were calculated as

\[ S_{FE} = 9 \text{ cm} \times M_{PROP} \times \sin(\theta) \]

\[ S_{PS} = 9 \text{ cm} \times M_{PROP} \times \cos(\theta) \]

where \(M_{PROP}\) is the proportional multiplier for each target distance (0.2 and 0.4 for pre- and posttests; 0.3 for practice sessions) and \(\theta\) is the visual angle between the target and the positive horizontal visual axis (Fig. 2). For single-df movements this equated to joint displacements of 36 and 72° in the pre- and posttests and 54° during practice sessions.

At the start of each trial, a yellow dot was displayed in the middle of the computer screen, corresponding to an elbow angle of 90° and a midprone forearm position. When the cursor indicating the current limb position fell within this “home” zone, the color of the dot changed from yellow to red. After a random foreperiod (1–3 s) a target was then presented, accompanied by an auditory cue (370 ms, 1.2-kHz square wave). The target was also displayed as a yellow dot, which changed to red whenever the limb position fell within target zone (defined as ± 4.5 mm on the display). Once the target limb position was maintained in the target zone for a continuous period of 0.1 s, a second auditory cue was generated to signify the end of the trial.

The practice period consisted of five sessions on consecutive days during which the participants completed 16 trials moving to each of the eight targets (defined at a visual distance of 5.4 cm from the “home” position: 128 trials in total). During the practice sessions, the targets were presented in a block-randomized order such that all target positions were

![FIG. 2](http://jn.physiology.org/Downloaded from http://jn.physiology.org/)
presented before any were repeated. During the pre- and postpractice sessions the participants completed 16 trials moving in each of the eight target directions (targets were defined at visual distances of 3.6 and 7.2 cm from the “home” position: 256 trials in total; Fig. 3). The presentation of targets during these sessions was counterbalanced such that the order of presentation within each of 16 blocks of 16 targets (eight target positions at two levels of torque) was unique and adjacent blocks did not result in the consecutive presentation of the same target. Periods of rest were granted at any time during a session if required by a participant, although no such requests were made because the nature of the task was such that it did not result in significant fatigue.

Data reduction

All position data were digitally low-pass filtered by dual pass through a 15-Hz second-order, Butterworth filter. Movement onset was determined for each trial as the point at which the joint rotation produced in either df first exceeded 4.5° after presentation of the target. All trials were visually inspected to ensure that this criterion eliminated false onset identification. All kinematic-dependent variables were calculated between movement onset and the time of target acquisition, excluding the 100-ms hold time. EMG-dependent variables were calculated between the instant of target presentation and target acquisition, again excluding the 100-ms hold time.

Because participants were instructed to acquire targets as rapidly as possible, target-acquisition time (the time in seconds from movement onset to target acquisition) was the primary measure of performance. The peak speed of the resultant movement was calculated to determine whether variations in acquisition time could be directly attributed to differences in the rapidity of movement. A time-normalized measure of the extent to which trajectories deviated from straight paths to each target was determined by calculating the root mean squared (rms) error between the normalized movement trajectory, and the vector defined between the start position (the initial condition) and the target. A measure of target overshoot was obtained as the difference between the peak of the resultant position trace and the location of the target, and was as a percentage of the distance between the start position and the target. A normalized jerk value (unitless) was also calculated for each trial using the algorithm detailed below (Teulings et al. 1997). The normalized jerk value serves as a measure of the smoothness of the movement trajectories

\[
Jerk_N = \left( \frac{1}{2} \int \left( \frac{d^2r(t)}{dt^2} \right)^2 \right) \times \frac{\text{duration}}{\text{length}}
\]

where \( j \) is a vector containing the third derivative of the resultant position at each time point, “duration” is the duration of each movement measured in seconds, and “length” is the length of the movement trajectory measured in degrees.

The EMG recordings obtained from each muscle were full-wave rectified and enveloped (low-pass Butterworth dual pass) at 40 Hz. A measure of EMG amplitude was obtained as the rms for a time window defined from the onset of muscle activity to the point at which the level of muscle activity dropped below a selected threshold (see definition below). The values obtained for each muscle were subsequently normalized with respect to the amplitude of the corresponding maximal M-wave recorded before the session. The onset of muscle activity was defined as the time at which the rectified, enveloped EMG data either first exceeded a value equal to a baseline mean (calculated from a window of data before the presentation of the target) plus 2.5 SDs, or exceeded a value equal to 20% of the maximum recorded for that trial. The offset of each burst of muscle activity was determined based on identical parameters with the additional constraint that the level of activity had to remain below the threshold level for a minimum of 50 ms between bursts. The onset times were expressed relative to the presentation of the target.

The peak rate of muscle activation was determined for the first burst of activity in each muscle, from the first derivative of (rectified) EMG data low-pass filtered at 6 Hz. The mean burst onset rate was defined as the mean slope of the EMG. In the region about the peak rate of rise of the EMG, for which the magnitude of the signal was increasing (i.e., the average of the segment between zero crossings of the differentiated time series that contained the largest positive value).

Statistical analysis

The median values of the 16 trials performed in each condition were used as the basis of all statistical analyses. Each dependent measure was analyzed separately using a repeated-measures time (pre- and postpractice) \times target position ANOVA design. Planned comparisons were used to assess whether the outcome measures obtained after practice differed from those recorded before practice. In assessing the changes that occurred during the practice period, the outcome measures obtained during sessions two to five were compared individually to the values obtained during the first practice session. Because EMG data were not recorded in the second and fourth practice sessions, the corresponding analyses of EMG-derived variables involved only the first, third, and fifth practice sessions. To assist in the interpretation of the tests of significance, the effect size index for ANOVA (\( f \)) was calculated following Cohen (1969). A small effect size is considered by convention to be indicated by an \( f \) value of <0.25, a medium effect size by an \( f \) value between 0.25 and 0.4, and a large effect size by an \( f \) value of >0.4. In the text, all data are presented as means \( \pm SD \).

RESULTS

Although decreases in target-acquisition time were observed in trials to all eight of the targets presented after practice, the nature of kinematic and electromyographic changes underlying these decreases varied across the target directions. In Fig. 4, mean data for a single participant are presented to demonstrate the typical patterns of adaptation. It is evident from the top of this figure that greater changes were made to the cursor trajectory (representing relative motions in each skeletal df) during movements in which motion in two dfs was required to reach the target position than those in which movement in a single df was sufficient. Increases in the level of muscle activity are also observable, primarily for monofunctional muscles that act to flex and extend the elbow joint (BRA, BRAD, and TRI). Practice-related changes in the patterns of movement and muscular activity that were robust across par-
of the dimensions of the manipulandum, a far greater inertia was encountered during flexion and extension movements than during pronation and supination movements. After the practice period, targets in pronation (3.6 cm: 0.31 ± 0.07 s; 7.2 cm: 0.48 ± 0.1 s) and supination (3.6 cm: 0.27 ± 0.07 s; 7.2 cm: 0.47 ± 0.08 s) remained those most rapidly acquired, whereas dual-df movements requiring elbow extension remained the least rapidly executed (Ext/Sup [3.6 cm: 0.43 ± 0.07 s; 7.2 cm: 0.64 ± 0.09 s], Ext/Pro [3.6 cm: 0.42 ± 0.08 s; 7.2 cm: 0.59 ± 0.07 s]).

The extent of the improvement in each movement direction was such that the variation across target positions was not substantially altered after practice, although some differences between the two target amplitudes were evident in terms of the extent of the decreases in acquisition times that occurred after practice. For example, target-acquisition times for movements in pronation and supination were reduced to a greater extent after practice when targets were presented at a distance of 3.6 cm (Pro [0.31 ± 0.07 s], Sup [0.27 ± 0.07 s], decreases respectively of 27 and 36%) than at a distance of 7.2 cm (Pro [0.48 ± 0.1 s], Sup [0.47 ± 0.08 s], decreases of 19% in each case). In contrast, for flexion targets, the decrease in the time required to acquire the target was greater when targets were displaced 7.2 cm from the start position (Flx [0.55 ± 0.17 s], Flx/Sup [0.65 ± 0.09 s], Flx/Pro [0.58 ± 0.15 s], decreases respectively of 25, 25, and 28%) than when they were displaced by 3.6 cm. The amount of improvement observed in dual-df extension and supination movements was similar at both target distances, whereas acquisition times in dual-df extension and pronation were decreased to a greater extent when the target distance was 7.2 cm (0.59 ± 0.07 s, a decrease of 35%) than 3.6 cm (0.42 ± 0.08 s, a decrease of 21%).

Participants are described below in terms of changes in selected dependent variables.

**Kinematic variables**

Before practice, the targets acquired most rapidly by participants at both target amplitudes were those that required movements in pronation and supination (Pro [3.6 cm: 0.42 ± 0.08 s; 7.2 cm: 0.60 ± 0.16 s], Sup [3.6 cm: 0.43 ± 0.11 s; 7.2 cm: 0.58 ± 0.09 s]; Fig. 5). Targets requiring movements in pure flexion (3.6 cm: 0.49 ± 0.1 s; 7.2 cm: 0.73 ± 0.25 s) and extension (3.6 cm: 0.47 ± 0.11 s; 7.2 cm: 0.72 ± 0.16 s) were acquired more slowly than those demanding pure pronation or supination, although they were acquired more rapidly than any targets requiring movements in two dfs (Flx/Sup [3.6 cm: 0.52 ± 0.08 s; 7.2 cm: 0.87 ± 0.13 s], Ext/Sup [3.6 cm: 0.55 ± 0.13 s; 7.2 cm: 0.84 ± 0.12 s], Ext/Pro [3.6 cm: 0.53 ± 0.1 s; 7.2 cm: 0.91 ± 0.22 s], Flx/Pro [3.6 cm: 0.56 ± 0.07 s; 7.2 cm: 0.80 ± 0.19 s]). The variation in acquisition times across target positions observed before practice was similar for each of the two target distances. The fact that pronation and supination targets were acquired more rapidly than those in flexion and extension is likely explained by the relatively large difference in inertia evident between the two dfs. Specifically, as a result

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**FIG. 4.** Joint angular displacements and electromyographic (EMG) data displayed for one subject (in each case the data represented the mean of 16 trials) before (gray, solid lines) and after (black, dashed lines) practice. Top: angular displacements at each joint plotted against each other (the same method used to provide real-time visual feedback to participants during the experiment). Bottom: time series data for joint angular displacements and EMG for the 8 muscles recorded. Units for each trace have been removed to improve the clarity of the figure.
Peak movement speeds before practice were greatest during the acquisition of pronation and supination targets (3.6 cm: Pro [245 ± 72°/s], Sup [251 ± 75°/s]; 7.2 cm: Pro [339 ± 87°/s], Sup [337 ± 88°/s]; Fig. 6). Peak speeds in the other six directions were significantly lower (3.6 cm: 150 ± 20°/s; 7.2 cm: 193 ± 19°/s; mean ± SD across target positions). Reliable increases in this measure were observed after practice at both target distances when target acquisition required elbow extension in isolation ($P < 0.05$, $f > 0.4$). The acquisition of targets that required either pure flexion or a combination of extension and pronation, were performed with higher peak speeds after practice only when targets were presented 7.2 cm from the start position (Flx [222 ± 65°/s], Ext/Pro [245 ± 82°/s]; respective increases of 23 and 27%; $P < 0.05$, $f > 0.4$). Single-df pronation movements of 36° were performed with lower peak speeds after practice ($P < 0.04$, $f > 0.4$). Overall, increases in the peak speed of movement most pronounced for single-df elbow flexion or extension movements.

Whereas single-df movements were performed with little deviation from straight paths to each target (mean ± SD across single-df targets: 3.6 cm: 0.90 ± 0.12°; 7.2 cm: 1.28 ± 0.12°), substantial deviation was demonstrated during dual-df movements, particularly before practice (mean ± SD across dual-df targets: 3.6 cm: 6.04 ± 0.38°; 7.2 cm: 6.68 ± 1.03°; Fig. 7). Decreases in directional deviation were subsequently observed after practice in each of the dual-df movements at both target distances (all $P < 0.05$, $f > 0.4$). The amount of directional deviation produced in each of the single-df movements was not different after practice.

Before practice, pronation (3.6 cm: 1376 ± 884; 7.2 cm: 1568 ± 1395) and supination (3.6 cm: 1378 ± 768; 7.2 cm: 1420 ± 696) movements were associated with the largest normalized jerk values. Elbow flexion (3.6 cm: 607 ± 441; 7.2 cm: 691 ± 278) and extension (3.6 cm: 485 ± 353; 7.2 cm: 547 ± 239; Fig. 8) movements were associated with the smallest jerk values. Dual-df movements produced jerk values between these two extremes when targets were presented at
displacements of 3.6 cm, whereas the jerk values associated with these movements during larger joint excursions were similar to those observed in pronation and supination movements. Normalized jerk values associated with movements produced when targets were presented at a distance of 3.6 cm were reduced to the greatest extent after practice during pronation and supination movements, although significant decreases were also observed when these movements were combined with elbow extension (all \( P < 0.05 \), \( f > 0.4 \)). When targets were presented at a distance of 7.2 cm, the greatest reductions in jerk were observed for dual-df movements (all \( P < 0.05 \), \( f > 0.4 \)), whereas smaller decreases were evident for pronation (\( P = 0.09 \), \( f > 0.4 \)) and supination movements (\( P < 0.05 \), \( f > 0.4 \)).

Electromyographic variables

Consistent with expectations, the greatest levels of activity in both agonist and antagonist muscles were observed when the joint rotations required for target acquisition corresponded to the principal moment of each muscle (Fig. 9). For example, the monofunctional elbow flexors brachialis (3.6 cm: 10.48 ± 7.4%; 7.2 cm: 16.83 ± 11.04%) and brachioradialis (3.6 cm: 12.19 ± 5.18%; 7.2 cm: 14.22 ± 5.6%; Fig. 9) were most active during single-df flexion movements. The level of activity in both of these muscles was appreciably lower during movements in which elbow flexion was combined with pronation (3.6 cm: 7.37 ± 2.79%; 7.2 cm: 10.3 ± 3.81%) or supination (3.6 cm: 7.51 ± 2.78%; 7.2 cm: 10.27 ± 3.97%). This consistency with the fact that neither muscle has a line of action that allows it to contribute as an agonist to rotations about the radioulnar joint away from the neutral start position, despite their insertions on the radius (brachioradialis) and ulna (brachialis) (Ettema et al. 1998).

Increases in activity levels after practice were expressed primarily in the monofunctional muscles (TRI, BRA, and BRAD), whereas the level of activity in bifunctional muscles either remained at prepractice levels (ECR, FCR, biceps brachii) or decreased (PT). Increases were observed, however, in the contribution of both heads of the biceps brachii during large-amplitude movements (72°) to flexion (Flx) targets (pretest: BB(L) [6.04 ± 6.76%], BB(S) [8.20 ± 9.26%]; posttest: BB(L) [8.05 ± 5.53%], BB(S) [12.05 ± 15.59%]). The amount of activity in the long head also increased during movements to large-amplitude targets requiring combinations of flexion and supination (pretest: 5.66 ± 5.11%; posttest: 7.59 ± 6.11%; all \( P < 0.05 \), \( f > 0.4 \)). Decreases in the contribution of PT were observed after practice in all small-amplitude (36°) movements for which it acted as an agonist (pretest: Pro [12.88 ± 16.42%], Flx/Pro [11.18 ± 12.61%], Ext/Pro [8.54 ± 9.46%]; posttest: Pro [6.58 ± 4.66%], Flx/Pro [7.29 ± 4.71%], Ext/Pro [5.46 ± 4.44%]). A decrease in the contribution of PT was also observed for pure pronation movements of large amplitude (pretest: 23.93 ± 29.80%; posttest: 14.95 ± 10.28%). A reliable practice-related increase in ECR activation was evident during combinations of flexion and supination when targets were presented 7.2 cm from the start position (pretest: 7.10 ± 5.72%; posttest: 8.33 ± 7.33%).

Before practice, muscles that acted as either partial or complete agonists were recruited around 200 ms before movement initiation (Fig. 10). This was true for both mono- and bifunctional muscles. Consistent with their role in movement deceleration, the recruitment of antagonist muscles generally occurred later than for agonist muscles, between 0 and 200 ms after movement onset. An exception to this was the triceps brachii, which was recruited concurrently with the agonist muscles during all movements in which elbow flexion was required (3.6 cm: Flx [−166 ± 76 ms], Flx/Sup [−124 ± 103 ms], Flx/Pro [−117 ± 99 ms]; 7.2 cm: Flx [−165 ± 63 ms], Flx/Sup [−152 ± 88 ms], Flx/Pro [−134 ± 82 ms]). After practice, decreases in recruitment latency were generally observed when muscles acted as a complete or partial antagonist such that recruitment occurred between 0 and 100 ms. No changes were observed, however, with respect to the latency of agonist muscle recruitment.

The rate of muscle activation was greatest during those movements in which the principal line of action of the muscle coincided with the required direction of movement. Changes in the rate of recruitment as a result of practice were primarily observed during tasks involving elbow flexion movements. The BRAD and the BB(L) exhibited increases in recruitment rate during single-df flexion movements of large amplitude (72°), whereas the rate of recruitment of BRA and ECR decreased in all flexion movements of the same magnitude. Single-df elbow flexion was the only movement direction for which there were increases in the maximum speed attained after practice (Fig. 6), suggesting that the rate of recruitment of BRAD and the BB(L) may have been instrumental in governing the rate at which flexion movements were performed. The rate of triceps recruitment decreased after practice in combinations of extension with both pronation and supination when targets were presented at a distance of 3.6 cm.

Adaptations exhibited during practice

Target-acquisition times were significantly lower in seven of the eight target directions (Flx, Flx/Sup, Ext/Sup, Ext, Ext/Pro, Pro, and Flx/Pro) during the final practice session than during the initial practice session (Fig. 11A). These performance improvements were associated with reliable increases in peak movement speed in each target direction (Fig. 11B). Participants also decreased the extent to which cursor trajectories deviated from a straight path in all dual-df movements (Fig. 11C). Reliable decreases in the jerk values over the practice period were evident only in Flx/Sup and Ext/Pro, the target directions initially associated with the longest target-acquisition times (Fig. 11D). These results demonstrate that practice-related performance improvements in all movements were associated with an increase in movement speed. Skill acquisition in dual-df movements was also associated with decreases in the extent to which cursor trajectories deviated from a direct path to each target.

Discussion

In each of the eight movements examined in the present study, both the spatial and temporal characteristics of the associated muscle synergies were altered after practice. Although the nature of changes in movement kinematics varied between the eight movements, the neuromuscular adaptations were similar in each case. In general, the contribution of bifunctional muscles to each action was maintained after prac-
practice, whereas the contribution of monofunctional agonist and antagonist muscles was increased. The increase in activation of monofunctional muscles may allow each skeletal degree of freedom to be controlled with greater independence after practice. This idea is consistent with previous suggestions that muscle coactivation is decreased and skeletal degrees of free-
dom released as skill is acquired to simplify the problem of control (Bernstein 1967; Spencer and Thelen 1999). The activation of bifunctional muscles during single-df movements would produce unnecessary torque about the stationary axis of rotation and would thus require additional muscle activation to avoid undesired elbow or forearm rotation (Basmajian 1977). Although the primary task goal was to decrease the time required to move the cursor to each target, the pattern of

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**FIG. 10.** Onset of the initial burst of muscle activity is shown relative to the time at which movement commenced. Data are mean values calculated across the 8 participants. Muscles are labeled according to the conventions given in the text. *A, left column:* data obtained when target acquisition required joint excursions of 36°. *B, right column:* data for targets that required joint excursions of 72°. Dashed lines and diamond-shaped symbols represent data obtained during pretest sessions; solid lines with square symbols represent data obtained during posttest sessions. Filled symbols represent differences between pre- and posttest values that were both statistically reliable ($P < 0.05$) and associated with a large effect size ($f > 0.4$).
neuromuscular adaptation observed was also consistent with the proposal that a secondary goal of the CNS during task practice is to improve the economy with which actions are carried out (Basmajian 1977; MacConaill and Basmajian 1977). In single-df movements, the activation of bifunctional muscles necessarily requires the simultaneous recruitment of at least one other muscle to counteract the undesired joint torque generated. The observed increase in the contribution of monofunctional muscles therefore represents a more economical strategy in single-df movements than increases in the activity of the bifunctional muscles. Increases in bifunctional muscle activity were observed, however, during single-df flexion and dual-df flexion and supination movements (BB(S) in both directions and FCR in Flx/Sup). Because these muscles, in particular the biceps brachii, provide a substantial contribution to the joint torque produced during these movements (Ettema et al. 1998), the increase in activation suggests that improvements in muscular economy are expressed only in situations where the associated neuromuscular adaptations do not have a deleterious effect on performance.

When the results of the current experiment are considered in relation to those of a previous study of isometric target acquisition conducted in our laboratory (Shemmell et al. 2005), they suggest that the context in which a task is performed (i.e., with constrained or unconstrained muscle length) requires the simultaneous recruitment of at least one other muscle to counteract the undesired joint torque generated. The observed increase in the contribution of monofunctional muscles therefore represents a more economical strategy in single-df movements than increases in the activity of the bifunctional muscles. Increases in bifunctional muscle activity were observed, however, during single-df flexion and dual-df flexion and supination movements (BB(S) in both directions and FCR in Flx/Sup). Because these muscles, in particular the biceps brachii, provide a substantial contribution to the joint torque produced during these movements (Ettema et al. 1998), the increase in activation suggests that improvements in muscular economy are expressed only in situations where the associated neuromuscular adaptations do not have a deleterious effect on performance.

Although the timing of agonist muscle recruitment remained largely invariant in the current experiment, the latency of recruitment of some antagonist muscles was reduced such that their recruitment was more synchronous with that of other antagonists after practice. The synchronous recruitment of antagonist muscles may reduce the force demands on individual muscles during movement deceleration by allowing the force from each muscle to be summed from the instant of recruitment. Although synchronous recruitment is a feature of agonist muscle activation even during the performance of novel tasks (Hoffman and Strick 1990, 1999), these results suggest that the timing of activity in individual antagonist muscles may be modulated independently in response to practice to increase the effectiveness of antagonist muscle actions.

The success with which performance gains achieved during practice are transferred to different targets appears to be dependent on the type of performance changes that occurred during practice. For example, the generalization of flexion movements (Flx, Flx/Pro, Flx/Sup) was more successful to targets more distant than those practiced to targets closer to the start position. The relative success of generalization to flexion movements of larger amplitude may be explained by the fact that practice-related adaptations in these directions (Flx, Flx/Pro, Flx/Sup) involved increases in the peak speed of movement. In contrast, the generalization of skill acquired in pure pronation and supination movements was more successful when the transfer was to movements of smaller amplitude than...
to larger-amplitude movements. The extent of performance improvement in these movements (Pro and Sup) during practice was closely related to the smoothness of movement. Adaptations that increase the peak speed of movements therefore appear to generalize better to larger movements, whereas those that decrease the variability (both spatial and temporal variability) of the endpoint trajectory appear to generalize more successfully to smaller movements than those practiced.

In summary, the extent to which performance improved in the experimental tasks was not dependent on the specific combination of joint rotations required. However, kinematic adaptations associated with practice-related performance gains differed significantly between movements in each skeletal df and also between the single- and dual-df tasks. Specifically, improvements in the performance of elbow flexion and extension movements after practice were associated primarily with increases in peak movement speed after practice, whereas pronation and supination movements were associated with increases in the smoothness of movement trajectories. Performance improvements in dual-df movements were primarily associated with reductions in the extent to which the movement trajectories deviated from a direct path to the target. The kinematic adaptations observed in each variant of the task were mediated by substantial reorganization of the spatial and temporal characteristics of the muscle synergies involved. In every instance this reorganization involved increases in monofunctional muscle activity, whereas bifunctional muscle activity was generally retained at prepractice levels. Although this pattern of neuromuscular adaptation primarily serves to reduce the extent associated with target acquisition, it may also reduce the energetic cost of muscular actions by reducing the extent to which antagonistic muscle action is required.

REFERENCES
