Control Strategies for the Transition From Multijoint to Single-Joint Arm Movements Studied Using a Simple Mechanical Constraint

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Scheidt, Robert A. and W. Zev Rymer. Control strategies for the transition from multijoint to single-joint arm movements studied using a simple mechanical constraint. J. Neurophysiol. 83: 1–12, 2000. Changes were studied in neuromotor control that were evoked by constraining the motion of the elbow joint during planar, supported movements of the dominant arm in eight normal human subjects. Electromyograph (EMG) recordings from shoulder and arm muscles were used to determine whether the normal multijoint muscle activity patterns associated with reaching to a visual target were modified when the movement was reduced to a single-joint task, by pinning the elbow to a particular location in the planar work space. Three blocks of 150 movements each were used in the experiments. Subjects were presented with the unconstrained task in the first and third blocks with an intervening block of constrained trials. Kinematic, dynamic, and EMG measures of performance were compared across blocks. The imposition of the pin constraint caused predictable changes in kinematic performance, in that near-linear motions of the hand became curved. This was followed by changes in limb dynamic performance at the elbow. However, changes in EMG activity at the shoulder lagged the kinematic changes substantially (by about 15 trials). The gradual character of the changes in EMG timing does not support a primary role for segmental reflex action in mediating the transition between multijoint and single-joint control strategies. Furthermore, the scope and magnitude of these changes argues against the notion that human motor performance is driven by the optimization of muscle- or joint-related criteria alone. The findings are best described as reflecting the actions of a feedforward adaptive controller that has properties that are modified progressively according to the environmental state.

INTRODUCTION

Several earlier studies have suggested that there are broad similarities in the neuromotor control of single and multijoint movements (Accornero et al. 1984; Hong et al. 1994; Wadman et al. 1980; although see Kaminski and Gentile 1989). However, the relationship between the multijoint movement strategies and constrained single-joint strategies remains unclear. For example, it is not clear whether these strategies are distinct and separate. If they are distinct, we do not know the characteristics of the transition between them when environmental constraints are changed. Our objective, then, was to explore neural control of arm motion in the transition from multi- to single-joint movements, by determining whether the motor plan is modified to allow for substantial differences in load experienced when motion at one joint is constrained.

The experiments we describe probed the relative contributions of feedback and “adaptive feedforward” mechanisms in the generation of planar, voluntary arm movements by examining the transition from multijoint to single-joint limb motion, implemented by “pinning” the elbow. This mechanical constraint at the elbow allowed free rotation of that joint while restricting motion at the shoulder. Subjects performed supported reaching movements in the horizontal plane between two targets that could be reached either with the upper arm free or with upper arm motion constrained. Current hypotheses of motor control provide conflicting predictions regarding subject behavior in such constrained and unconstrained movements. For example, if limb trajectory formation depends on feedback regulation for detailed pathway control (Cooke 1980; Cordo 1990; Feldman et al. 1990; Marsden et al. 1972; McIntyre and Bizzi 1993; Merton 1953; Weeks et al. 1996), then the changes in behavior (reflected in electromyogram [EMG] output of arm muscles) should be evident immediately after imposition of the constraint, because afferent pathways would detect changes in limb kinematics immediately. On the other hand, if subjects use a feedforward strategy during single- and multijoint movements (Flanagan and Wing 1997; Ghez et al. 1990; Gordon and Ghez 1992; Gottlieb et al. 1996; Kawato 1991; Sainburg et al. 1995; Schmidt 1988), then changes elicited by the imposition of our mechanical constraint should be more gradual and may not even be evident at all immediately after onset of the constraint.

Our data reveal that imposition of the constraint caused changes in shoulder EMG activity that developed quite gradually as the block of trials progressed. Furthermore, the timing of the observed EMG changes does not support a strong feedback-regulatory effect attributable to peripheral afferent pathways. Ultimately, these results show that single-joint arm movements are not simply constrained multijoint arm movements but reflect a different neuromotor strategy, which is implemented progressively with time and repeated exposure to a predictable mechanical environment. Portions of this work have appeared in abstract form (Scheidt and Rymer 1996a, 1996b).

METHODS

Eight subjects with no known neuromotor disorders, ranging from 28 to 38 yr of age, consented to participate in this study. Five of the eight subjects were men and seven of the eight were right-handed. In all cases, the dominant arm was used in the reaching tasks we studied. We investigated the changes in movement strategy in response to the imposition of a mechanical constraint at the elbow. Three blocks...
of 150 movements each were required during the experimental session. The subjects were presented with the unconstrained (i.e., two-joint) task in the first and third blocks with an intervening block of constrained (i.e., one-joint) trials. The blocking of trials in this manner was designed to reveal the presence of nonstationarities in subject performance, if any existed.

**Experimental setup**

Subjects made reaching movements in the horizontal plane with the test arm supported against gravity by an air-bearing system (Fig. 1A). This system consisted of a light-weight, air-driven arm-support riding over a smooth table surface in the horizontal plane. High-pressure air (80–120 psi) was forced into the support and was then vented through an array of exit ports on the underside of the device. Wrist rotation was minimized by fixing the hand and forearm with a light-weight fiberglass casting material into a semipronated position. Shoulder translation was minimized using a torso restraint fixed to the subject’s high-backed chair. The height of the chair was adjusted to ensure that the shoulder was adducted 90° when the subject was resting on the air-bearing surface.

Shoulder and elbow muscle EMGs and kinematics were captured with an OPTOTRAK 3010 system. Three OPTOTRAK markers were placed on each of the relevant limb segments and were sampled 300 samples/s. Marker position data were filtered digitally (cutoff frequency of 20 Hz), preamplified (gain = 1,000), low-pass filtered (cutoff frequency of 500 Hz), postamplified (with a variable gain dependent on electrode placement, typically between 2 and 10), and sampled at 1,500 samples/sec. Further processing, including rectification and low-pass filtering ($f_c = 25$ Hz), was performed off-line within the MATLAB computing environment.

EMGs during a series of isometric, maximum voluntary contractions (MVCs) were collected after every experimental session to allow comparison of EMG activity across subjects. The series consisted of three elbow flexions, three elbow extensions, three shoulder flexions, and three shoulder extensions. After signal conditioning as described, the peak EMG value observed for each muscle in any isometric trial was taken to be the maximal EMG for that muscle. EMGs recorded from the movement trials were normalized in relation to these maximal, isometric EMG values according to the equation: $\text{EMG}_{\text{norm}}(t) = \frac{\text{EMG}(t)}{\text{EMG}_{\text{max}}}$. The mechanical constraint consisted of a removable pin joint that was collinear with the elbow’s center of rotation. The constraint was implemented by fitting oilite bushings into the table and the arm support underneath the elbow’s center of rotation. A 1/4-in. diameter steel shaft was then inserted into both bushings to complete the pin joint. In conjunction with the shoulder harness used to constrain trunk motion, the elbow pin provided an effective constraint on shoulder rotation. With the pin removed, the arm was free to rotate in the horizontal plane at both the shoulder and elbow joints.

**Experimental design**

The experiment compared two types of movements: 1) point-to-point, two-joint arm movements requiring 50° elbow flexion with minimal shoulder rotation, and 2) movements between the same initial and final targets as in 1, but in the presence of a pin constraint that prevented any translation of the elbow.

With the pin in place, arm movements were restricted to elbow rotations in the horizontal plane. Subjects were instructed to make movements “from point A (the starting target) to point B (the final target) as accurately as possible in 200 ms.” The linear separation of the targets was dependent on the subject’s forearm and hand lengths, and consequently ranged from 36 to 42 cm. One subject was unable to perform the movements comfortably at this speed and was asked to make movements of 300-ms duration. Although both task requirements allowed minimal reaction-time correction of the movements while in progress. Subjects were provided feedback of movement duration after every trial by a photodiode timing device that sensed the passage of the hand over the targets.

Differences in steady-state subject performance for kinematic, dynamic, and EMG measures were evaluated using a repeated-measures, two-factor (subject × treatment) ANOVA technique. For those measures exhibiting significant differences between blocks of trials (i.e., treatments), Tukey’s multiple-paired $t$-test ($P \leq 0.05$) was invoked to determine which blocks of trials did not differ one from the other.

**Quantification of kinematic performance**

Kinematic behavior was quantified using several indices of performance. We used a curvature index (CI) to quantify the linearity of the endpoint path during the movements. The curvature index for a reaching movement is determined by calculating the ratio of maxi-
Quantification of dynamic performance

Dynamic behavior was quantified by calculating the accelerative and decelerative torque impulses and the peak accelerative torque at the elbow. The accelerative torque impulse (ATI) is defined as the time integral of the elbow torque profile from movement onset to the time of the first sign change in torque. The decelerative torque impulse (DTI) is calculated by integrating elbow torque from the time of the first sign change to the end of movement or the time of the second sign change, whichever comes first. Peak accelerative elbow torque ($pK_T$) was calculated using the equations of motion presented in Eq. 1, where $i = 1$ corresponds to the shoulder joint parameters and $i = 2$ corresponds to the elbow joint parameters.

\[
\begin{aligned}
\tau_1 &= I_1 + I_2 + 2I_1 m_1 r_2 \cos(q_2) + r_1^2 m_1 q_1 + r_2^2 m_2 + I_2 + r_2^2 m_2 + l_1 m_1 r_2 \cos(q_2), \\
\tau_2 &= I_2 + r_2^2 m_2 + l_1 m_1 r_2 \cos(q_2) + \begin{bmatrix}
0 \\
l_1 m_1 r_2 \sin(q_2)
\end{bmatrix},
\end{aligned}
\]

where $\tau$ is joint torque (Nm), $q$ is joint angle (rad), $m$ is segment mass (kg), $r$ is distance from joint to segment center of mass (m), $I$ is segment moment of inertia about its center of mass (kg/m$^2$), and $B_{ij}$ is joint viscosity (N s/\text{rad}).

Quantification of EMG behavior

The relative strength of EMG activity was compared across constraint conditions. EMG onsets were determined visually for all muscles and every trial. The EMG parameters we considered included (1) time integral of rectified elbow agonist (antagonist) activity, $Q_{Eag}$ ($Q_{Eant}$), (2) time integral of rectified shoulder agonist (antagonist) activity, $Q_{Sag}$ ($Q_{Sant}$), and (3) time integral of rectified biarticular agonist (antagonist) activity, $Q_{Bag}$ ($Q_{Bant}$). Two distinct integration windows were applied to the rectified EMGs to distinguish between changes in EMG behavior due to the action of short- to medium-latency autogenic reflex pathways and those due to voluntary changes in behavior.

An “early” time window was chosen to accentuate features of the EMG likely to be influenced primarily by short and medium-latency autogenic reflex contributions (0–80 ms after movement onset). This reflex activity is expected to arise from differences in muscle stretch experienced in the constrained and unconstrained movements. A “late” integration window (50–150 ms after movement onset) was chosen to accentuate changes in EMG behavior that were likely to be the result of long-latency (reaction time) responses to the constraint (cf. Evans and Vaughn 1978; Soechting 1988).

Trial-selection procedure for steady-state analysis

Even though we provided feedback of movement duration, subjects had difficulty producing movements of similar duration as measured objectively using a photodiode timer circuit. The standard deviation of movement duration was generally $>10\%$ of the total movement time and sometimes exhibited a distinct trend on a trial-to-trial basis. To remove any possible influence of nonstationarities from our statistical analyses, we selected from each subject’s set of movements only those movements that were kinematically similar for further study. We used our measure of peak endpoint tangential velocity ($MV$) to assess kinematic similarity. For each subject, there was substantial overlap in the peak hand speeds calculated across constraint conditions. An “inclusion window,” optimally chosen according to each subject’s movements, was applied to insure that only similar movements were compared. The window was selected to maximize the number of trials whose peak velocity fell within a 0.2-m/s-wide window across all conditions. This was accomplished by minimizing the cost function of Eq. 2

\[
F(v_c) = -N_c(v_c) N_o(v_c) N_r(v_c)
\]

where $N_c$, $N_o$, and $N_r$ refer to the number of included trials from blocks 1, 2, and 3 respectively, and $v_c$ is the center velocity of the inclusion window. $F(v_c)$ was optimized using a simplex search algorithm (Press et al. 1988). For each subject and each constraint condition, the number of trials selected for further analysis fell between 18 and 55.

Transient analysis

To allow comparisons across subjects, each performance measure for each subject was normalized by the median value of that measure from the first block of selected, unconstrained movements. This normalization procedure was designed to accentuate motor strategies held common across subjects in response to the constraint perturbation. As described earlier, ANOVA and Tukey’s $t$-tests (i.e., multiple, paired, group comparisons; $P \leq 0.05$) were performed to test the null hypothesis that the constraint had no effect on subject performance (as quantified by the measures: $CI$, $MD$, $NJ/C$, $OS$, $\Delta \theta_5$, $ATI$, $DTI$, $pK_T$, $Q_{Eag}$, $Q_{Eant}$, $Q_{Sag}$, $Q_{Sant}$, or $Q_{Bag}$).

\[
\begin{bmatrix}
\tau_1 \\
\tau_2
\end{bmatrix} = \begin{bmatrix}
I_1 + I_2 + 2I_1 m_1 r_2 \cos(q_2) + r_1^2 m_1 + r_2^2 m_2 \\
I_2 + r_2^2 m_2 + l_1 m_1 r_2 \cos(q_2)
\end{bmatrix},
\]

\[
\begin{bmatrix}
\dot{q}_1 \\
\dot{q}_2
\end{bmatrix} = \begin{bmatrix}
0 \\
l_1 m_1 r_2 \sin(q_2)
\end{bmatrix},
\]

\[
\begin{bmatrix}
\ddot{q}_1 \\
\ddot{q}_2
\end{bmatrix} = \begin{bmatrix}
q_1^2 \\
q_2^2
\end{bmatrix} + \begin{bmatrix}
B_{11} & B_{12} \\
B_{21} & B_{22}
\end{bmatrix} \begin{bmatrix}
\dot{q}_1 \\
\dot{q}_2
\end{bmatrix}.
\]
initially centered on the first trial after imposition of the constraint and was moved forward, trial by trial, until the windowed mean deviated from the steady-state, unconstrained mean ($P \leq 0.05$). The trial number at which the window stopped sliding was taken as the point at which subject performance in the constrained environment diverged observably from that established in the unconstrained environment. We refer to this analysis as a “departure” metric, because we are quantifying the number of trials necessary for a subject’s performance in the constrained case to depart observably ($P \leq 0.05$) from that established in the first unconstrained case.

**Measurements of limb mechanical properties**

We performed a simple pendulum test on three subjects, to estimate passive joint-damping for use in simulations and inverse dynamics calculations. The methods used were modeled after those of Stein et al. (1996) except that we did not attempt to separate mechanical contributions of passive joint stiffness from those of gravity, because the movements studied here were small. Within this range, passive stiffness is expected to be quite small (Audu and Davy 1985; cf. Stein et al. 1996).

Briefly, subjects lay prone on an examining table with their upper arm supported by the table (Fig. 1B). The hand was cast as described earlier. Shoulder and elbow EMGs as well as limb kinematics were captured with the OPTOTRAK 3010 system. Subjects were instructed to remain relaxed with eyes closed during the entire experimental session. Periodically, the experimenter elevated the subject’s forearm $\sim 30^\circ$ using a string attached to the wrist. At a time unknown to the subject, the string was released and the forearm was allowed to rotate about the elbow under the influence of gravity. Five trials were collected from each of the three subjects. EMGs were examined for evidence of reflex activation (none was found).

A linear, second-order pendulum model was then fit to the elbow joint motion data to derive lumped parameter estimates of inertial and passive linear damping parameters of the subject’s forearm-hand-cast and elbow system. The damping parameters estimated in this fashion were pooled across subjects and trials to derive the estimate of passive damping used in the inverse and forward dynamic calculations pertaining to the constraint study ($B = 0.073 \pm 0.005$ kg m$^2$s$^{-2}$; mean $\pm$ SE; $n = 3$). Similarly, the inertia of the forearm-hand-cast system was estimated to be $I = 0.050 + 0.001$ kg m$^2$ (mean $\pm$ SE; $n = 3$).

**RESULTS**

To explore the relative contributions of reflex feedback and adaptive, feedforward control mechanisms to the generation of arm movements, we compared supported, two-joint, unconstrained reaching movements with similar, constrained movements for the same subject within a given experimental setting. The constraint consisted of a pin placed at the elbow, and it prevented translation of the elbow joint. It could be inserted in the course of the experiment, and it allowed the subjects to generate hand trajectories similar (but not identical) to the unconstrained trajectories. The pin transformed two-joint motions performed by coordinated movements of both the shoulder and elbow joints, into one-joint movements performed exclusively at the elbow. Although it limited the endpoint path between the two targets, the pin allowed for an increased range of shoulder joint torques during the constrained movement.

If subjects were to capitalize on the constraint, they might be expected to decrease shoulder muscle activity, because the pin stabilized the location of the elbow in space, limiting the need for shoulder muscle activity. Alternately, subjects could have persisted with the unconstrained joint torque profiles in the constrained case without detriment to task performance, because elbow torques required in the two cases were evidently very similar (based on computer simulations; see description later). Alternately, responses to the pin also could be mediated by reflex action (because joint kinematics were significantly different in the two cases). In the following paragraphs we show that adaptive mechanisms influenced subject motor behavior to a much greater extent than did feedback from autogenetic reflex pathways during the performance of our reaching tasks.

**Steady-state analysis**

The addition and removal of the pin constraint are interventions that may initiate both transient and sustained behavioral changes. Preliminary experiments have shown that because of the simple nature of the required task, changes in behavior stabilize within the passage of $\sim 50$ movements (Scheidt and Rymer 1996a,b). Consequently, the steady-state, statistical analysis of kinematic, dynamic, and EMG performance (described in the next section) considered only the last 100 movements in each block of 150 for study.

**Kinematic and dynamic behavior**

Figure 2 presents the steady-state, kinematic, and dynamic performance features of a single subject (S8), highlighting differences between constrained and unconstrained movements. Figure 2A depicts an overhead view of the horizontal plane movements. Although the unconstrained movements for this subject were definitely straighter than the constrained movements, they were clearly not linear. Figure 2B presents histograms of peak tangential velocities showing the location of the trial selection window used to generate the remaining graphs in this figure. The figure shows that both the unconstrained and the constrained movements had endpoint tangential and elbow angular velocity profiles that were roughly bell-shaped (Fig. 2, C and D). Figure 2E presents the shoulder joint angle profiles for the three sets of movements. Clearly, the pin acted to constrain shoulder joint rotation (thin dashed line). Figure 2F shows the estimated elbow joint torques for the constrained (shaded) and unconstrained (unshaded) movements. The leftmost, positive, lightly shaded region under the constrained elbow joint torque profile indicates the area integrated to calculate the accelerative elbow torque impulse ($ATI$). The decelerative elbow torque impulse ($DTI$) was calculated in a similar manner by integrating the heavily shaded area above the constrained elbow joint torque profile in the decelerative phase of the movement. Taken together, Fig. 2, A–F reveals that this subject’s kinematic and dynamic behavior was substantially altered in the presence of the constraint and that this behavioral alteration was, in large part, reversed after removal of the constraint.

Table 1 presents a summary of the steady-state, kinematic and dynamic performance statistics gathered from our eight subjects, whose data, on the whole, were broadly comparable to those of the subject presented in Fig. 2. Each subject’s data were normalized in relation to the median value in the first block of constrained trials to facilitate comparison across subjects. The major kinematic finding is that imposition of the constraint clearly reduced shoulder rotation, whereas it increased the curvature of the endpoint path. These were the only
two consistent kinematic outcomes across subjects ($P \leq 0.05$; Table 1, *). Table 1 also reveals that the decrease in peak elbow torque described for subject S8 was replicated across subjects. Although the accelerative torque impulse exhibited a decrease on imposition of the constraint, performance in the second block of trials was not significantly different from that in the third block of movements ($P > 0.05$; Table 1, †).

We performed computer simulations of the movements we required of the subjects in an attempt to understand the dynamic requirements of the tasks (Fig. 3A). We estimated the torque requirements of two-joint and single-joint movements using Eq. 1 and the limb mechanical properties derived from the pendulum test data and anthropometric measurements of a typical subject. Figure 3B depicts the normalized velocity profile that was integrated and scaled to generate the elbow angle profile for the curved movement and the endpoint displacement profile for the linear movement. Figure 3E shows the tangential endpoint velocity profile for these two movements. The peak tangential endpoint velocity was only 4.5% greater in the constrained case than in the unconstrained case. In contrast, Fig. 3D reveals that the elbow velocities required for these two movements were quite different. The peak elbow velocity required of the constrained movement is 7.5% lower than that of the straight movement and occurs $\sim 30$ ms later. The onset of elbow rotation (as estimated by angular velocity exceeding 0.5 rad/s) of the linear movement is also delayed relative to the unconstrained movement by $\sim 15$ ms. Although elbow kinematics are clearly different for the two movements, Fig. 3E reveals that the torques required about the elbow were quite similar. These simulated results contrast with the observation...
EMG activity

We investigated each subject’s EMG response to both the imposition and removal of the constraint to assess how the observed changes in kinematic and dynamic performance were mediated. In particular, we recorded EMG magnitude within two time windows of functional importance. An “early” window (0–80 ms after EMG onset) quantified EMG activity during the time when monosynaptic (and other short-latency) reflex modulation of EMG activity was likely to occur in response to the limb’s altered mechanical environment. A “late” window (50–150 ms after movement onset) quantified EMG activity, allowing sufficient time for state-dependent feedback and long-loop responses to modulate EMG activity. Although some subjects exhibited modest modulation of EMG activity, we found that none turned off shoulder muscle activity to capitalize fully on the constraint.

Figure 4 depicts steady-state, trial-averaged EMGs from a single subject (S8). Each panel presents the mean, rectified, and filtered EMG activity (EMG-onset aligned) for the velocity-selected movements from the three blocks of trials. This subject, whose kinematic and dynamic data are presented in Fig. 2, showed constrained elbow muscle activities that were of greater duration (BRA and BICL) and of lower amplitude (BRA) than those observed in the unconstrained case (Fig. 4, C and E). These findings are also consistent with the estimated joint torques presented in Fig. 2F. This subject’s ADL activity (Fig. 4A) exhibited an early decrement in the constrained trials (within the early, [0–80-ms] time window), which disappeared as the constrained ADL activity became indistinguishable from the unconstrained activity toward the end of the movement. Finally, this subject exhibited a slight decrement in two-joint antagonist activity (TRILG; Fig. 4F) in the constrained trials, which presented itself within the early time window and was sustained (at least in comparison with the first block of unconstrained trials) throughout much of the movement. A decrease in two-joint antagonist activity within the late time window was, in fact, observed in all subjects (Table 2), whereas a decrease in early two-joint antagonist activity was not. As with the other subjects, this subject’s muscle activities were significantly greater than baseline levels established 100 ms before movement ($P < 0.0005$ for each muscle); the peak values ranged from 10 to 50% MVC at the shoulder to >80% MVC at the elbow. If shoulder muscle activity were being modulated in accordance with the minimization of joint torque-change, muscle strain, energetics, or effort, we would expect shoulder muscle activity to be rapidly downregulated to a much larger extent than was observed in the presence of the constraint.

Table 2 summarizes, for all eight subjects, the EMG signal power contained within the two time windows: early (0–80 ms), and late (50–150 ms). As in Table 1, each subject’s performance statistics were normalized in relation to the median value in the first block of unconstrained trials to facilitate comparisons of performance across subjects. Our findings are that there was no consistent difference in early EMG activity across constraint conditions and subjects. The decrement in subject S8’s early ADL activity observed in Fig. 4 was not seen in other subjects. However, because of the variable nature of EMG activity, our failure to observe significant modulation of EMG activity within the early window does not mean that there are no short-latency autogenic reflex contributions to movement. Rather, such contributions must be relatively weak. A test of statistical power found that for six of eight subjects, our tests had the capacity to detect a decrease of shoulder muscle activity of 30% or less ($b \leq 0.20$; cf. Hogg and Ledolter 1987). In contrast, the late, two-joint antagonist activity exhibited a change in performance across subjects that was significant ($P < 0.05$), symmetric and reciprocal (TRILG).

The time course of this change will be described in the next section; however, it is important to note that the EMG reduction was not immediate, but developed progressively over many trials. This decrease in late TRILG activity in response to the imposition of the pin was reversed on removal of the constraint, again over several trials. Shoulder antagonist (PDL) also exhibited a decrement in late activity in response to the imposition of the constraint; however, this decrease was not consistently reversed after removal of the pin.

In summary, there was a small, but significant, reduction in shoulder EMG in response to the imposition of the pin constraint across subjects. This EMG response was evident later within a movement rather than earlier (i.e., between 50 and 150 ms after movement onset).

Transient analysis

An EMG response to an altered mechanical environment that occurs >100–120 ms after a change in movement kinematics could well be mediated by long-loop afferent pathways. If these pathways were involved in the feedback regulation of an ongoing movement, responses to the altered mechanical environment should be manifested immediately on imposition of the constraint (that is, on the first trial after constraint). Alternately, an altered mechanical environment may evoke
adaptive, feedforward changes in the EMG response that are cortical in origin. Accordingly, we evaluated evolution of long-latency responses after imposition of the constraint.

Table 3 summarizes the results of an analysis of transient behavior (based on Student's *t*-test) intended to determine when performance in the constrained movements deviated significantly from the initial behavior. We present the results of our “departure” analysis for those kinematic and EMG performance measures that exhibited a significant change on constraint imposition across subjects. Clearly, kinematic changes occurred immediately after pin insertion, as observed in the curvature of movement (\(\mu_{C} = 1.3\) trials; \(n = 8\)) and in the change in shoulder angle (\(\mu_{S} = 1.6\) trials; \(n = 7\)). Only subject 4 failed to show a change in shoulder angle rotation, because her initial block of unconstrained movements were performed almost exclusively at the elbow. Consequently, she exhibited little shoulder rotation in both the first unconstrained and the constrained blocks of trials. Such kinematic changes contrast sharply with the changes in late EMG activity of shoulder antagonists (TRILG and PDL). Changes in posterior deltoid behavior occur substantially later in the sequence of constrained trials with a time-to-departure measure of \(\mu_{PDL} = 13\) trials (\(n = 7\)). Similarly, changes in the behavior of the long head of the triceps became observable after 16 trials (\(n = 7\)). In the case of each muscle shown, one subject failed to exhibit a change in performance, and therefore did not contribute a meaningful observation to the calculation of these performance
statistics. This analysis clearly reveals that EMG adaptation lagged the imposition of the constraint by ~13–16 movements.

**DISCUSSION**

This study was designed to present subjects with a mechanical environment that would allow them either to maintain an established, multijoint motor strategy or to express some other potentially more desirable motor strategy. We sought to do this by introducing a mechanical constraint that would restrict motion at one joint while allowing natural motion at a second joint. The data reveal that the changes in motion after imposition of the mechanical constraint were accompanied by rather gradual and progressive changes in EMG behavior. The slow time course of these EMG changes does not support a strong reflex regulatory effect; rather, these data reveal that imposition of the constraint was handled adaptively.

**Reflex contributions to the generation of voluntary movements**

Although recent evidence provides support for the notion that movements are conducted in a feedforward manner (Flanagan and Wing 1997; Ghez et al. 1990; Gordon and Ghez 1992; Gottlieb et al. 1996; Kawato 1991; Sainburg et al. 1995; Schmidt 1988), autogenic reflex modulation of descending commands are not excluded by such observations. If reflex modulation of descending commands contributes substantially to the ongoing control of reaching movements, then we would predict that this modulation should be observable during our constrained task. The change in shoulder joint rotation imposed...
TABLE 2. Electromyographic steady-state analysis results

<table>
<thead>
<tr>
<th>EMG Source</th>
<th>Time Window (ms)</th>
<th>Unconstrained (Set 1)</th>
<th>Constrained (Set 2)</th>
<th>Unconstrained (Set 3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anterior deltoid</td>
<td>0–80</td>
<td>1.096 ± 0.062</td>
<td>0.774 ± 0.177</td>
<td>1.126 ± 0.195</td>
</tr>
<tr>
<td></td>
<td>50–150</td>
<td>1.058 ± 0.025</td>
<td>0.846 ± 0.133</td>
<td>1.035 ± 0.108</td>
</tr>
<tr>
<td>Posterior deltoid</td>
<td>0–80</td>
<td>1.069 ± 0.032</td>
<td>0.865 ± 0.053</td>
<td>1.070 ± 0.076</td>
</tr>
<tr>
<td></td>
<td>50–150</td>
<td>1.010 ± 0.009†</td>
<td>0.762 ± 0.062†</td>
<td>0.945 ± 0.060</td>
</tr>
<tr>
<td>Brachialis</td>
<td>0–80</td>
<td>1.023 ± 0.026</td>
<td>0.833 ± 0.070</td>
<td>0.909 ± 0.037</td>
</tr>
<tr>
<td></td>
<td>50–150</td>
<td>1.055 ± 0.019</td>
<td>1.079 ± 0.094</td>
<td>1.015 ± 0.056</td>
</tr>
<tr>
<td>Lateral triceps</td>
<td>0–80</td>
<td>1.052 ± 0.038</td>
<td>0.924 ± 0.100</td>
<td>0.968 ± 0.093</td>
</tr>
<tr>
<td></td>
<td>50–150</td>
<td>1.038 ± 0.009</td>
<td>0.934 ± 0.123</td>
<td>1.078 ± 0.093</td>
</tr>
<tr>
<td>Long head of biceps</td>
<td>0–80</td>
<td>1.069 ± 0.030</td>
<td>0.946 ± 0.087</td>
<td>0.911 ± 0.092</td>
</tr>
<tr>
<td></td>
<td>50–150</td>
<td>1.059 ± 0.012</td>
<td>1.026 ± 0.114</td>
<td>0.938 ± 0.068</td>
</tr>
<tr>
<td>Long head of triceps</td>
<td>0–80</td>
<td>1.146 ± 0.057</td>
<td>0.903 ± 0.104</td>
<td>1.087 ± 0.086</td>
</tr>
<tr>
<td></td>
<td>50–150</td>
<td>0.999 ± 0.026*</td>
<td>0.624 ± 0.060*</td>
<td>1.008 ± 0.078*</td>
</tr>
</tbody>
</table>

Values are means ± SE. *† Performance measures as described in Table 1.

by our constraint due to the reduction in shoulder joint rotation was appreciable, ~6–8° in magnitude (Fig. 2). Because EMG activity at the shoulder was substantial (10–50% maximum voluntary contraction; Fig. 4), decreases in shoulder rotation caused by the constraint should have influenced shoulder muscle activity if reflex contributions were substantial. This is because increasing the activation of a muscle increases the fraction of motoneurons that are close enough to threshold to be activated by a stretch (Stein and Kearney 1995). Because reflex pathways are hardwired, changes in EMG activity due to reflex activity were expected to start with the trial immediately after constraint imposition and could be expected to occur as early as 20 ms after a detectable kinesthetic stimulus (Evarts and Vaughan 1978). However, the data provide little evidence for continuous-time reflex regulation of ongoing movements, because the constrained and unconstrained shoulder EMG activities were similar immediately after imposition of the constraint and required 13–16 trials for late EMG changes to become observable (Table 3). These results provide further support for the notion that reflex contributions to the generation of an ongoing movement are small.

Similar conclusions were drawn by Almeida et al. (1995). In that study, EMG recordings were made during reaching movements in both the horizontal and sagittal planes. Subjects performed elbow flexions “as fast as possible” in a horizontal, single-degree-of-freedom manipulandum and in the sagittal plane with the limb unconstrained. Shoulder flexions were only performed in the sagittal plane by the unconstrained limb. In the case of unconstrained, single-joint shoulder or elbow flexions (with principal movement at the “focal” joint), the subjects were explicitly instructed not to move the “nonfocal” joint. Almeida et al. (1995) found that agonist bursts increase at distance-independent rates and have distance-proportional durations under constrained and unconstrained conditions, at both elbow and shoulder joints, and over three movement distances. In fact, the patterns of EMG behavior were similar in both the unconstrained elbow and unconstrained shoulder tasks, even though the subjects were explicitly instructed not to move one or the other of the joints during each task. Based on these observations, Almeida et al. (1995) conclude that centrally specified patterns of motoneuron excitation play the dominant, but not necessarily exclusive, role in producing the observed EMGs and joint torques. Modification of muscle activation by reflex actions is not the primary patterning mechanism, although they state that it almost certainly is a factor. Furthermore, they conclude that the same motor command rules apply to constrained and unconstrained movement.

Whereas Almeida et al. (1995) studied EMG behavior with constrained and unconstrained tasks requiring very different kinematic solutions, we studied subject behavior while making constrained and unconstrained movements having similar kinematic solutions and identical initial and final postures. Our experimental task minimized the degree to which subjects were required to alter their constrained motor command strategies with respect to the unconstrained strategies. Rather, our constraint largely decoupled the control of the single-joint shoulder musculature from kinematic consequence at the endpoint. The present results support and extend those of Almeida et al. (1995) in that we also find little evidence for reflex regulation of ongoing movements. Furthermore, our results show that environmental constraints are indeed exploited as the human neuromotor controller adapts from an unconstrained to a constrained motor command strategy.

For example, the imposition of our pin constraint may be interpreted as providing a virtual unloading perturbation to the shoulder, because subjects were no longer required to compensate for interaction torques caused by rotation of the elbow. Sainburg and colleagues (1993, 1995) have provided strong evidence for the compensation of dynamic coupling torques in neurologically normal subjects. The magnitude of perturbation caused by unloading interaction torques at the shoulder would be equal to the torque represented in Fig. 3F by the dotted line. The virtual unloading of Fig. 3F peaks approximately halfway through the movement. An autogenic response to this pertur-
bation could be expected to fall within the “late” window of integration we applied to our EMGs. However, as argued earlier, reflex modulation of ongoing motor commands would be expected to begin with the first trial after imposition of the constraint. Our transient analysis showed that there was a significant lag in late EMG response after pinning the elbow. We therefore conclude that constrained and unconstrained movements are controlled in similar manners, at least initially, but that the motor strategies diverge as the neuromotor controller adapts to its new dynamic environment. By studying similar movements over an extended number of trials after the imposition of a constraint, we provide further evidence that adaptive, feedforward control mechanisms are dominant in the generation of goal-directed arm movements.

A very different interpretation of the role of reflexes during constrained motion has been forwarded by Weeks et al. (1996) who argue that reflexes contribute to the compensation of changing dynamic loads, although they note that this compensation appeared to be incomplete. In that study, subjects performed blocks of single joint movements both in the presence and absence of resistive and assistive spring-like loads. Using “correct as soon as possible” instructions to subjects, they found that subjects made errors in movement extent as well as secondary corrective movements in the trial immediately after the imposition or removal of a load. Weeks et al. (1996) observed alterations in secondary bursts of the elbow flexor brachioradialis that they interpreted as a reflex-mediated response to the perturbation. However, this change in EMG activity was insufficient to drive the limb back to its intended target.

Because of the gradual nature of the springlike load used by Weeks et al. (1996), it is difficult to interpret their EMG results in terms of reflex mediated responses because it is unclear when such a reflex response should have occurred. The earliest EMG changes they observed occurred \(\simeq 170\) ms after movement onset and need not have been of reflex origin. EMG changes may have been the result of intentional intervention by the subject in response to the generation of substantial kinematic errors. Kinesthetic reaction time responses can occur as soon as \(70–85\) ms after a forced displacement of the limb (Evarts and Vaughn 1978). Consequently, it is difficult to determine the extent to which short- (spinal) and medium-latency (supraspinal) autogenic reflex activity contributed to the changes in EMG behavior observed by Weeks et al. (1996). Although the absence of strong reflex regulation does not invalidate the hypothesis that the limb is controlled through sequentially programmed postural states coupled to a compliant musculoskeletal limb, the role of reflexes in the compensation of dynamic loads as proposed by Weeks et al. (1996) is not a requisite interpretation of the data they present.

Feedforward control of goal-directed arm movements

In general, a feedforward neuromotor controller generates motor command sequences in an open-loop fashion without using instantaneous feedback to shape those commands. It has been argued that a feedforward controller is, in and of itself, an internal model of the controlled system, because a desired movement is transformed into the neural commands necessary to perform that movement (Jordan 1993). However, some mechanism must exist by which a feedforward controller can determine which motor command sequences (of all possible command sequences) are appropriate for a given mechanical environment and a given task. This mechanism is commonly referred to as adaptation and/or motor learning.

In the classic view, an adaptive controller requires three things: 1) an optimum condition or desired performance, 2) an objective means of comparing actual performance with the desired performance (i.e., a measure of performance), and 3) a mechanism to adjust system parameters to drive actual performance toward the desired performance (Gibson 1963). Historically, much effort has been expended studying the first aspect of adaptive control: What is optimized (or specified) in the generation of human movements? (Hogan 1984; Nelson 1983; Stein et al. 1985; Uno et al. 1989; Wolpert et al. 1995). A growing number of investigators are now beginning to study the second aspect of adaptive control: What information sources regarding limb state are used to guide motor adaptation and how do they interact? (Conditt et al. 1997; Horak and Kuo 1997; Johansson 1991; Wann and Ibrahim 1992). Few studies have addressed the third aspect of motor adaptation: What are the mechanisms by which limb state is used to alter neuromotor behavior? (Kawato et al. 1988; Newell et al. 1989; Spray and Newell 1986). The present study pertained to motor adaptation issues of the first kind.

Time course of adaptation

Although the current experiment was not designed to differentiate between trial and time dependence of adaptation, recent experimental evidence suggests that motor adaptation results as a consequence of motor memory formation—a process exhibiting substantial time dependence (Shadmehr and Brashers-Krug 1997). It is possible that the independent variable influencing the acquisition of a new adapted behavior is the amount of time spent exploring a new dynamic environment. Because the intertrial interval was \(~20–30\) s for each subject, the changes in EMG behavior only became observable after a period of \(~4–8\) min. This is well within the broad range of time shown to be critical to the formation of motor memories and to the learning of new motor skills through retrograde interference studies (\(<5.5–24\) h) (Shadmehr and Brashers-Krug 1997).

What performance criteria drive adaptive behavior?

Our pin constraint is unique in that it did not require that subjects modify their unconstrained neuromotor commands to accomplish the constrained task. By stabilizing the position of the elbow in space, the pin allowed subjects the option of optimizing motor performance at the shoulder without serious kinematic consequence. At least four interesting, hypothetical, control strategies can be postulated.

First, subjects may have attempted to minimize contact force at the pin. To do this, they would have had to modulate muscle activity substantially to compensate for the difference in shoulder torques required in the constrained and unconstrained tasks. This difference in shoulder joint torque is indicated by the thin, solid line in Fig. 3F. If this were so, then they should have generated the shoulder torques represented by the dashed line in Fig. 3F while in the presence of the constraint. These are the torques required at the shoulder to perform the “curved”
(constrained) movements in the absence of the constraint. We clearly did not observe such drastic behavioral changes (i.e., an overall increase in peak shoulder muscle activity). Our subjects were not trying to minimize contact forces with the constraint.

Second, subjects may have attempted to “play back” the unconstrained motor program, oblivious to the presence of the constraint. In this scenario the pin should have opposed all shoulder movement with a force large enough to generate approximately 50 Nm of torque about the shoulder (Fig. 3F; thin, solid line). Because our pin was not instrumented, we do not know for certain whether subjects generated close to 50 Nm of torque at the shoulder in opposition to the constraint. However, it is clear that persisting in multitask behavior in the presence of the pin is not consistent with motor strategies that attempt to minimize effort expended and/or joint-torque change (Nelson 1983; Stein et al. 1985; Uno et al. 1989).

Third, subjects may have attempted to maintain a straight endpoint path during movement (i.e., a minimum-jerk strategy). If this were so, subjects should have exploited unavoidable compliances in the coupling between the arm and its support to force the hand path to be as straight as possible. Such behavior would manifest itself as an dramatic increase in the activation of the shoulder muscles. The magnitude of this increase would be determined by the level of compliance in the constraint and by the maximum level of activation of the shoulder muscles. We observed no such increases in muscle activity at the shoulder and it seems improbable that the desire to maintain straight-line hand paths drove the adaptive behavior observed in this study.

Fourth and finally, subjects may have attempted to optimize some measure of dynamic or metabolic performance. We observed striking adaptive behavior of the late EMG response at the shoulder when our mechanical constraint maintained constant endpoint curvature. It is logically possible that the minimization of effort-, muscle- or joint-torque–related parameters contributed to the adaptation we observed. However, even after 150 movements in contact with the constraint, subjects generated substantial muscle activity about the shoulder (Fig. 4; Table 2). Given that the pin and torso restraints stabilized the upper arm in space (Fig. 2E), the minimization of metabolic energy consumption and/or joint-torque change must be regarded as incomplete.

CONCLUSIONS

This study shows that a mechanical constraint can invoke adaptive change in motor performance even when the kinematic consequence of its imposition is modest. Because the torque required at the elbow to perform the constrained and unconstrained tasks were quite similar, subjects could have chosen to perform the constrained movements in fashion identical to the unconstrained movements, leaving the pin to consume all unnecessary forces developed at the shoulder. Alternately, subjects could have chosen to terminate all muscle activity about the shoulder, relying on the pin and the torso restraint to stabilize the shoulder joint. However, they chose neither of these strategies, and consistently altered their behavior in an adaptive manner toward some intermediate strategy. The attenuation of shoulder EMG activity was significant, but moderate, even after 150 trials, suggesting that motor performance was not driven by the optimization of muscle-, joint-torque–, or effort-related criteria in isolation. Other factors, as yet undetermined, must be important in the generation of goal-directed reaching movements.

Further work is needed to advance our understanding of the factors motivating motor adaptation. The exploration of behavioral changes observed kinematically, dynamically, and electromyographically in response to manipulated mechanical environments promises to provide insight into the adaptive processes embedded within the human neuromuscular control system. Such insight into the motor adaptation process would provide bounds on the limits of human motor performance in rapidly changing dynamic environments. We find such prospects intriguing from the perspective of the robot-aided neurorehabilitation of the impaired neuromotor controller (Krebs et al. 1998; Rausch et al. 1997; Reinkensmeyer et al. 1996).

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