CHANGES IN LIMB DYNAMICS DURING THE PRACTICE OF RAPID ARM MOVEMENTS

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Abstract—In our study we examined Bernstein’s hypothesis that practice alters the motor coordination among the muscular and passive joint moments. In particular, we conducted dynamical analyses of a human multisegmental movement during the practice of a task involving the upper extremity. Seven male human volunteers performed maximal-speed, unrestrained vertical arm movements whose upward and downward trajectories between two target endpoints required the hand to round a barrier, resulting in complex shoulder, elbow, and wrist joint movements. These movements were recorded by high-speed cine film, and myopotentials from selected upper-extremity muscles were recorded. The arm was modeled as interconnected rigid bodies, so that dynamical interactions among the upper arm, forearm, and hand could be calculated. With practice, subjects achieved significantly shorter movement times. As movement times decreased, all joint-moment components (except gravity) increased, and the moment-time and EMG profiles were changed significantly. Particularly during reversals in movement direction, the changes in moment-time and EMG profiles were consistent with Bernstein’s hypothesis relating practice effects and intralimb coordination: with practice, motor coordination was altered so that individuals employed reactive phenomena in such a way as to use muscular moments to counterbalance passive-interactive moments created by segment movements.

INTRODUCTION

Numerous studies spanning nearly a century have been directed at understanding problems of the acquisition of motor skills (see Adams, 1987, for a review). Traditionally, motor performance has been measured by one of a large number of possible outcome scores (e.g. errors, time on target, movement time) that have indicated the extent to which the subject achieved the task goal. Such movement performance data have been useful in revealing the effects of a multitude of experimental variables on performance and learning, such as variations in practice scheduling, the role of knowledge of results, or the influences of fatigue. These data, however, add comparatively little to our understanding of how movements are controlled, what processes underlie them, or how these control processes may change during practice (Schmidt, 1987). Although a few studies (Hobart et al., 1975; Marteniuk and Romanow, 1983; Vorro, 1973) have documented changes in movement patterns during practice, these experiments typically have used only simple tasks with movement about a single joint. These investigations represent a good start toward the understanding of movement control changes with practice. The generally simple movements employed in this work, however, have avoided the difficult problems concerned with coordination involved in most common movement tasks: the difficulties posed by having to control a limb composed of multiple, connected, interacting segmental links in three-dimensional gravitational space.

In comparison to work in motor learning, research in motor control has focused somewhat more on the underlying mechanisms of movement control. These studies have examined the formation of arm and hand trajectories in humans (Abend et al., 1982; Atkeson and Hollerbach, 1983; Lacquaniti and Soechting, 1982) or robotic systems (Hollerbach, 1982), kinematic invariances (Gentner, 1987; Viviani and Cenzato, 1985) or electromyographic invariances (Gielen et al., 1985) or principles of optimization (Flash and Hogan, 1985; Hogan, 1984; Nelson, 1983) in a variety of movement tasks. Nevertheless, as noted by Atkeson and Hollerbach (1985), these studies usually involved simple, restricted movements, and the findings agreed with each other only in part. Furthermore, the experiments were mostly analyzed in terms of kinematics, and little information exists on dynamical aspects (Hollerbach and Flash, 1982).

Dynamical analyses, however, are necessary to quantify the mechanical causes of a movement, because kinematical analyses only quantify the resultant movement (the effect). Traditional kinematical measures such as joint displacements, correlated with the onset and termination of muscle activity, cannot reveal fully how limb movements are controlled. The reason is that, in addition to those forces arising from muscle contractions, limb trajectories can be influenced by gravitational forces and passive limb reactions to muscle actions. The passive reactions of limb segments to active muscle forces include inertial, Coriolis, and centripetal forces, as well as those from various connective tissues. Limbs are systems of linked bodies, in which motion of any one segment exerts forces on the remaining parts of the linkage. Consequently, passive-interactive forces can act on a limb segment, even if a given segment is not exposed to active muscle forces.

The way in which limb trajectories are influenced by this complex combination of forces is a difficult but
tractable problem in rigid-body dynamics (cf. Smith and Zernicke, 1987). In particular, recent dynamical analyses have focused on the little-studied moments arising from the passive interactions between limb segments, and, thus, have begun to explain how these intersegmental or movement-dependent moments can influence unrestrained limb trajectories during pointing and reaching tasks (Atkeson and Hollerbach, 1985; Lacquaniti and Soechting, 1982); the swing phase of human walking (Mena et al., 1981), running (Phillips et al., 1983), and kicking (Putnam, 1983); the swing phase of cat locomotion (Hoy and Zernicke, 1985) and the oscillatory hindlimb motions during the cat paw-shake response (Hoy et al., 1985; Hoy and Zernicke, 1986; Smith and Zernicke, 1987). This research, however, has focused mainly on motor control mechanisms in well-practiced or stereotypical movements and has not examined how motor control may change during the practice of a movement.

To the extent that we can consider the acquisition of skill as alterations in how the motor system controls movement, a promising approach would be to evaluate the changes in intersegmental dynamics over the course of practice. Although these concepts have not been used in detail, some intriguing general ideas were raised two decades earlier by the Russian physiologist Bernstein (1967). Among other things, Bernstein hypothesized with respect to the control of active and passive forces that ' . . . the secret of co-ordination lies not only in not wasting superfluous force in extinguishing reactive phenomena but, on the contrary, in employing the latter in such a way as to employ active muscle forces only in the capacity of complementary forces' (1967, p. 109). Although decades have passed since Bernstein formulated his concepts, until now his hypothesis had not been examined quantitatively. Thus, we conducted dynamical analyses of a human multisegmental movement during the practice of a task involving the upper extremity to examine Bernstein's idea that practice alterations in how the motor system controls movement, a promising approach would be to evaluate the changes in intersegmental dynamics over the course of practice. Although these concepts have not been used in detail, some intriguing general ideas were raised two decades earlier by the Russian physiologist Bernstein (1967). Among other things, Bernstein hypothesized with respect to the control of active and passive forces that ' . . . the secret of co-ordination lies not only in not wasting superfluous force in extinguishing reactive phenomena but, on the contrary, in employing the latter in such a way as to employ active muscle forces only in the capacity of complementary forces' (1967, p. 109). Although decades have passed since Bernstein formulated his concepts, until now his hypothesis had not been examined quantitatively. Thus, we conducted dynamical analyses of a human multisegmental movement during the practice of a task involving the upper extremity to examine Bernstein's idea that practice alters the co-ordination among the muscular and passive joint moments. Preliminary results of this study have been reported in abstract form (Schneider et al., 1986, 1987).

METHODS

Experimental procedures

Seven male human volunteers (26.5 ± 3.8 yr) performed unrestrained, maximal-speed movements with their nondominant left arm. During the upward and downward phases of the motion, the hand had to circumvent a T-shaped barrier located midway between upper and lower target areas (Fig. 1). Subjects held a circular black metal plate (see No. 1 in Fig. 1) connected by a stem (2 cm length) to a wooden-dowel handle (9 cm length, 1.8 cm diameter, 28 g combined plate and handle), and had to interrupt light beams with the plate at the targets (No. 2). The stem of the T-shaped barrier was 3.5 × 21.5 cm, and its cross-piece was 0.3 × 32 cm (No. 3). Thus, boundary constraints (targets and barrier) were placed on the hand path, but otherwise the movement was unrestrained.

Each subject faced a clear plexiglas sheet (No. 4) while sitting on a straight-backed chair (No. 5). The sheet contained the targets and a 7 × 80 cm center slit that restricted the right–left motion as subjects entered either the upper or lower target. Because subjects were required to break the light beams with the circular metal plate, the plate's diameter (7.4 cm) restricted the vertical width of upper and lower targets. The position of the plexiglas sheet was adjusted so that the upper light beam was level with each subject's shoulder joint, and each subject could reach the lower light beam with a comfortable shoulder angle (∼2.0 rad) and elbow angle (∼2.3 rad). The pelvis and torso of each subject were secured to the chair by lap and shoulder seat-belts (No. 6) to minimize trunk motion. Subjects tended to keep the shoulder joint and hand in vertical alignment, but varying degrees of humeral abduction occurred so that, across filmed trials, the maximum orthogonal deviation of the hand from the sagittal plane was 11.2 ± 3.6 cm.

Subjects were naive about the task and apparatus. No detailed instructions were given to subjects about the hand path during the task, but they were told to start at the lower light beam, 'go as fast as possible,' circumnavigate the barrier, break the upper light beam, round the barrier and stop in the lower light beam. On a verbal 'get ready' signal, subjects placed the circular plate in the lower light beam and held (approx. 1–2 s) that position until an experimenter said 'go'. Subjects could begin the movement at any time after the 'go' signal, but movements were generally initiated after approximately 1 s; reaction times were neither stressed nor measured. A successful trial occurred when a subject interrupted the upper light beam, cleared the barrier during both upward and downward movements, and held steady for 2–3 s in the lower light beam at the end of the trial. If any of these criteria were not met, the trial was repeated (which occurred on fewer than 10% of the trials). After each trial, subjects rested for 10–15 s. All subjects practiced until 100 successful trials had been recorded.

Movement time of each trial was defined as elapsed time between when the circular plate left the lower light beam and again entered the lower light beam. An electronic timer (± 0.5 ms) was triggered as the circular plate left the lower light beam and was stopped when the plate entered the lower beam at the end of the movement. A counter was triggered to verify that subjects had successfully entered the top target. Verbal feedback of movement time in ms was provided to subjects after each trial.

During the practice trials for four of the seven subjects, arm movements were recorded by high-speed ciné film (Photosonics 1PL 16 mm camera, 150 frames s⁻¹ verified by camera-internal timing-light pulses) for 12 trials in six, two-trial blocks: trials 1–2, 9–10, 24–25, 44–45, 70–71, and 90–100. Prior to
Practice effects on intralimb coordination

Fig. 1. Subject position with frontal and lateral views of experimental set-up. Numbers denote the following: (1) circular black-metal plate (3.7 cm radius) connected by a stem (2 cm length) to a wooden-dowel handle (9 cm length, 1.8 cm diameter, 28 g weight for plate plus handle) which subjects grasped with the left hand; (2) light beams (photosensitive cells plus infrared LEDs) attached to the plexiglas sheet, with black arrows indicating the targets' positions; (3) T-shaped barrier that subjects had to circumnavigate (stem of the T-shaped barrier was 3.5 × 21.5 cm, and the perpendicular cross-piece was 0.3 × 32 cm); (4) suspended, clear plexiglas sheet (6.4 mm thick) with center slit (7 × 80 cm); (5) straight-backed chair; (6) seat belts and (7) markers (1 cm diameter) attached at the glenohumeral, elbow, wrist, and third metacarpophalangeal (MP) joints, and the center of the circular metal plate. Subjects started and ended the movement with the circular plate held steady in the lower light beam. The upper light beam only had to be interrupted by the metal plate as subjects reversed their upward motion to begin the downward phase of the task.

Filming, black markers (see No. 7 in Fig. 1) were placed on each filmed subject's left glenohumeral, elbow, wrist, and third metacarpophalangeal (MP) joints. The third MP was an indicator of a subject's hand motion. Room illumination and testing protocol remained constant throughout the entire testing session, and subjects were not told which trials would be filmed.

For three of the seven subjects, myopotentials from selected upper-extremity muscles were recorded using electromyography (EMG). Bipolar, surface electrodes (Ag/AgCl) were positioned on the mid-belly regions of the biceps brachii (caput longum) and triceps brachii (caput longum) and anterior and posterior deltoids. Myopotentials were amplified (× 100; GRASS Model 79D), filtered (high-pass filter = 15 Hz, low-pass filter = 100 Hz), and sampled (1 kHz) using an analog-to-digital converter (RC Computerscope, RC Electronics, Santa Barbara, CA). Each channel of EMG, along with an event indicator, was stored in digital format on an IBM/AT microcomputer disc. The event indicator produced discrete 1 V offsets as the metal plate left, entered, or passed through either of the light beams.

Data reduction

Because subjects' limb movements were not mechanically constrained to a sagittal plane, for each frame in each filmed trial, we used standard geometrical relationships between the segment lengths measured directly on the subjects and the segment lengths recorded on the film to calculate three-dimensional joint coordinates (see Appendix A). Inclination angles of the upper arm, forearm, and hand were determined from the three-dimensional joint coordinates. All linear and angular displacement-time data were smoothed, and first and second derivatives calculated, using cubic splines (Reinsch, 1967) as implemented by Zernicke et al. (1976). Because we sampled the ciné film data from 20 ms before the hand moved until 20 ms after the hand stopped at the lower target, movements revealed zero accelerations at the beginning and ending. Thus natural cubic splines were appropriate for these data.

Data analysis

In addition to the slowest trial (trial 1), the faster trial out of each pair of consecutive two-trial blocks (9–10, 24–25, 44–45, 70–71, and 99–100) was analyzed for a total of six trials per filmed subject. The task was partitioned into three phases for analysis: upward, reversal, and downward. To define these phases, a reversal point was determined when the hand changed direction (anterior–posterior) at the upper target. The reversal phase started as the hand entered the upper target and ended as the hand left the upper target. The
times of entering and leaving the upper target were determined when the value of the coordinate of the hand in the superior-inferior direction came within 5% of the value of the coordinate at the reversal point of the movement. The 5% range was equivalent to reaching or leaving a height approximately equal to the radius of the circular plate.

**Intersegmental dynamics.** Moments were calculated for shoulder, elbow, and wrist joints using the equations detailed mathematically in Appendix B. A comprehensive model of the entire shoulder complex is particularly difficult (e.g. Engin and Peindl, 1987), thus for the purposes of our study, we assumed only that the upper extremity was three interconnected rigid links (upperarm, forearm, and hand) with frictionless joints at shoulder, elbow, and wrist. The glenohumeral joint was allowed to move freely, and the resulting moments due to the linear accelerations of the glenohumeral joint were included in the equations of motion for each joint (see Appendix B, terms SLA).

For each filmed trial, the three-dimensional coordinates of the upper extremity were used to determine the two-dimensional dynamics of the limb in a moving-local plane which passed through the coordinates of the wrist, elbow, and shoulder joints; thus at each joint, moments were calculated about axes that were normal to the moving-local plane. Rigid-body equations of motion can be formulated in several ways, but the form of the equations that we used allowed us to quantify not only how gravity and muscles influenced limb motion, but also how the motion of one segment affected other segments. At each of the three joints, we partitioned the moments into four categories that can be generally defined as follows (Hoy et al., 1985; Hoy and Zernicke, 1985, 1986; Smith and Zernicke, 1987).

1. **Net joint moment.** The sum of all the positive and negative moment components (gravitational, interactive, and muscle) that act at a joint.

2. **Gravitational moment.** A passive moment resulting from gravity acting at the center of mass of each segment.

3. **Interactive moments.** Passive moments arising from mechanical interactions between segments, such as inertial forces proportional to segmental accelerations or centripetal forces proportional to the square of segmental velocities. These moments are consistent with the notion of 'reactive phenomena' as described by Bernstein (1967).

4. **Generalized muscle moment.** A 'generalized' moment that includes forces arising from active muscle contractions and from passive deformations of muscles, tendons, ligaments, and other periaxial tissues. Because the effects of active muscular forces are embedded within this component, the generalized muscle moment comprises the actively-controlled elements of limb-trajectory motor programs.

While the net, gravitational and interactive moments were calculated directly from the limb kinematics, the generalized muscle moment was calculated as a 'residual' term, because the sum of the generalized muscle moment and the other moments equaled the net moment. There is no universally agreed upon term for this moment component, and our term generalized muscle moment (Hoy and Zernicke, 1985, 1986; Smith and Zernicke, 1987) or residual moment has also been called 'joint torque' (e.g. Atkeson and Hollerbach, 1985). For each of the filmed subjects, all moments were time-normalized with respect to the slowest trial. For each of the movement phases (upward, reversal, and downward), positive and negative peak values of the moment components were determined.

**Anthropomorphic data.** Computational techniques were used to determine segmental masses, center of mass locations, and segmental moments of inertia for each of the filmed subjects. Prior to filming, anthropometric measurements of each subject's left upper extremity were taken with precision calipers and metal tape measure. The computer program ANSEP, which was designed for a 17-segment model of the human body (Hatze, 1980), was modified by one of the authors (K.S.) to make it applicable for the limbs only. The average segmental parameters for the subjects were: upper arm (mass = 2.7 ± 0.2 kg, center of mass from proximal joint = 11.7 ± 0.4 cm, moment of inertia = 2.3 ± 0.2 x 10^-2 kg m^2); forearm (mass = 1.3 ± 0.1 kg, center of mass = 11.1 ± 0.2 cm, moment of inertia = 0.8 ± 0.1 x 10^-2 kg m^2); hand (mass = 0.5 ± 0.0 kg, center of mass = 6.3 ± 0.4 cm, moment of inertia = 0.1 ± 0.0 x 10^-2 kg m^2).

**Electromyography.** From the full-wave rectified EMGs (ANAPAC, RUN Technologies, Los Angeles, CA), the following parameters were determined for each muscle: duration of EMG bursts; duration of EMG bursts with respect to total movement time; absolute time of EMG onset relative to movement initiation and relative times of EMG burst onset with respect to upper target entry and exit.

**Statistics.** Multivariate analyses of variance in conjunction with general linear-model ANOVAs (Statistical Analysis System, SAS Institute, Cary, NC) were used to detect significant differences among dependent variables. Changes in movement time were analyzed across the six filmed trials. Kinematical (hand displacements, velocities, and accelerations) and dynamical (peak moment) variables were analyzed for slowest vs fastest trials. All post hoc comparisons were made using Tukey's Studentized range (HSD) tests (Tukey, 1953). All significant differences in kinematical and dynamical variables reported in Results were statistically significant, with p < 0.01.

EMG data were averaged for descriptive statistics. A repeated measures analysis of variance (Statistical Analysis System, SAS Institute, Cary, NC) was used to detect significant differences among burst characteristics (absolute values of onset and of duration of EMG bursts, duration of EMG bursts in relation to total movement time, and EMG burst onset with respect to upper target entry and exit) of the sampled muscles during practice trials. Post hoc comparisons were accomplished with the Ryan–Einot–Gabriel–
Welsch multiple range test (SAS), and a significance level of $p \leq 0.05$ was used for all tests related to EMG variables.

**RESULTS**

**Movement times**

During practice, movement times decreased significantly for all subjects (Fig. 2(b); from the slowest to the fastest trial, a decrease of $36 \pm 7\%$ in movement time was achieved. That relative difference in time translated into an absolute decrease in movement time of $0.39 \pm 0.13 \text{s}$, with the slowest trial equaling $1.04 \pm 0.20 \text{s}$ and the fastest trial equaling $0.66 \pm 0.10 \text{s}$. The reduction in movement time during practice was most evident in the reversal phase ($56\%$).

**Coordination of intralimb dynamics**

In Fig. 3, the changes that occurred during practice in intersegmental dynamics between slowest (solid line) and fastest (dashed line) trials are illustrated for the shoulder and elbow joint for a representative subject (subject 4); all other subjects displayed similar trends. With practice, at each joint the moment–time series of the net moments (Fig. 3A) and the generalized muscle moments (hereafter referred to as ‘muscle moment’; Fig. 3B) showed similar profiles in the upward and downward phase. Moment minima and maxima increased in magnitudes between slowest and fastest trials and displayed shifts in relative timing. In the upward phase the flexor-muscle moments of the shoulder and the extensor moments of the elbow peaked proportionally later for the fastest trials than for the slowest trials. Throughout practice in both the upward and downward phases all joints had in-phase net and muscle moments.

Moment magnitudes significantly increased with practice during the reversal. At the three joints, the increases in moment peak values were between 188 and 641\% during the reversal for slowest vs fastest trials. The greatest relative increase in net joint moments was found at the elbow (336\% in flexion), whereas in muscle moments the greatest relative increase was noted at the shoulder joint (641\% in extension). The absolute magnitudes of the net and muscle moments seen for the wrist joint were significantly less than at the shoulder and elbow joint. The average ratio of the peak absolute magnitudes in the fastest trials of the shoulder, elbow, and wrist net moments was $21:7:1$, and the ratio of the peak shoulder, elbow, and wrist muscle moments was $15:7:1$.

Because the most pronounced changes in the movement time occurred during the reversal region at the upper target, this region was likely to be the place where most changes in intersegmental dynamics would be seen. Therefore, we restricted our discussion of the dynamical results to the reversal region. This was done with no loss in generality, however; comprehensive quantitative analyses were conducted for all joints and all moment components, and the changes in the component moments during the limb reversal at the top of the movement were consistent with, although somewhat greater than, the corresponding changes in moments throughout each phase of the movement. Therefore, an exhaustive presentation of all data would have been repetitious, and the dynamical results from the reversal phase provided a representative basis for testing Bernstein’s hypothesis.

Examples of the intersegmental dynamics during the reversal region at the top of the motion are illustrated for the shoulder (Fig. 4), elbow (Fig. 5), and wrist (Fig. 6) for the same representative subject as in Fig. 3 (subject 4); all other subjects displayed similar trends. In each of these figures, the moment–time series for the same slowest (solid line) and fastest (dashed line) trials are shown. The time base in each of the three moment figures was normalized with respect to the movement time of the slowest trial. Only the most dominant moment components are displayed in each of these examples, although all moment components were analyzed for each trial and subject. Transitions in shoulder joint and elbow joint motions (e.g. flexion–extension) are marked with arrowheads in the corresponding moment profiles.

**Shoulder joint moments during reversal phase**

Shoulder moments during the reversal phase are illustrated in Fig. 4, with the signs of the values such that positive moments tended to cause shoulder flexion, and negative moments tended to cause shoulder extension. The moments for the slowest trial are shown with solid lines, and those for the fastest trial are shown with dotted lines. The two arrowheads indicate the end of shoulder flexion and the start of extension for the slowest (black arrowhead) and fastest (white arrowhead) trials.
Fig. 3. Exemplar time series of the shoulder and elbow net (A) and generalized (B) muscle moments for the slowest (solid line) and fastest (dashed line) trials for a representative subject (subject 4). Time is normalized with respect to the movement time of the slowest trial. The stick-figure orientations of the arm are shown at: start, barrier, reversal, barrier and end. Moment minima and maxima increased significantly in magnitudes between slowest and fastest trials and displayed shifts in relative timing.

As subjects approached the upper target, the shoulder joint was flexing, and shoulder extension started as the hand left the upper target (at about 0.54 s in Fig. 4, black and white arrowheads). With respect to Bernstein's hypothesis, the key feature of the shoulder moments occurred between 0.50 and 0.55 s in Fig. 4. Consider first the solid traces which show the slowest trials in early practice. Here, the moment due to upper arm angular acceleration (UAA; see also Appendix B), a passive tendency to flex the shoulder joint, was small in the direction of flexion. This small flexion moment was sufficient to counterbalance a small extension moment at the shoulder caused by gravity (GRA), together with a relatively small muscle moment at the shoulder (MUS), and a small interactive extension moment caused by the forearm-angular acceleration (FAA). This was essentially a 'static' equilibrium developed at the shoulder. Notice that the muscle moment (MUS) and the passive moment associated with forearm-angular acceleration (FAA) were very small in early practice.

In the dotted traces, representing the fastest trial seen in the last block of practice, there was a considerable increase in the upper-arm-angular acceleration moment (UAA), the tendency for shoulder flexion caused by the passive-interactive properties of the upper arm. In addition, the effect of the forearm's angular motion exerted a small passive extension
Fig. 4. Exemplar time series of the shoulder moments during the reversal phase for the slowest (solid line) and fastest (dashed line) trials for the same representative subject (subject 4): generalized muscle moment (MUS); upper-arm-angular acceleration (UAA) and forearm-angular acceleration (FAA). The changes in shoulder-joint moments that occurred with practice during the reversal were consistent with Bernstein's hypothesis. As subjects decreased their movement times, shoulder-extensor muscle moments (MUS) counterbalanced a passive-interactive moment (UAA) that caused the shoulder to flex.

Fig. 5. Exemplar time series of the elbow moments during the reversal phase for the slowest (solid line) and fastest (dashed line) trials for the same representative subject (subject 4): generalized muscle moment (MUS); upper-arm-angular acceleration (UAA) and forearm-angular acceleration (FAA). The peak flexor-muscle moment (MUS) significantly increased. This increase in elbow-flexor muscle moment was required to counterbalance heightened forearm angular acceleration moments (FAA) generated by the altered movement pattern, and the changes were consistent with Bernstein’s hypothesis.

Elbow joint moments during reversal phase

Elbow moments for the same representative subject (subject 4) in the slowest trial (solid lines) and fastest trial (dotted lines) during the reversal phase are illustrated in Fig. 5. At the elbow, positive moments tended to cause elbow flexion, and negative moments tended to cause extension. During the reversal phase shown in the figure, the motion of the elbow was extension followed by flexion as the hand was pulled from the target in preparation for the downward phase. The transition from elbow extension to flexion is denoted in Fig. 5 by a black arrowhead for the slowest trial and a white arrowhead for the fastest trial.

For the slowest trials (solid lines), all subjects tended to use a small muscle-flexor moment (MUS) to slow and stop the extension of the elbow, and this same elbow-flexor moment continued to flex the elbow as subjects left the upper-target region. During the reversal of slowest trial (from 0.45 to 0.55 s in Fig. 5), the muscle-flexor moment was relatively small in magnitude and oscillatory in nature. The moments caused by forearm-angular acceleration (FAA) and upper-arm-angular acceleration (UAA) were also very small, and relatively constant, in early practice.

In the fastest trials (dotted traces, Fig. 5), elbow extension during the approach to the upper target was aided by the interactive moment related to forearm-angular acceleration (FAA), whereas this moment was generally absent in the slowest trial. The FAA moment significantly increased (322% on the average) between early and late practice. There was a small moment caused by upper-arm-angular acceleration (UAA), but this was nearly unchanged relative to early practice. The most obvious change was that the peak flexor-muscle moment (MUS) significantly increased.
(188% on the average), and its oscillatory behavior was not present in the fastest trial. This increase in elbow-flexor muscle moment was apparently required to counterbalance heightened forearm-angular acceleration moments (FAA) generated by the altered movement patterning. In contrast to the shoulder joint, at the elbow joint the interactive moment associated with upper-arm-angular acceleration (UAA) remained relatively unimportant throughout all trials.

**Wrist joint moments during reversal phase**

Various moment components at the wrist are shown in Fig. 6 for the same representative subject (subject 4) as shown previously. At the wrist, positive moments tended to cause radial deviation (i.e. upward movements of the hand relative to the forearm), and negative moments tended to cause ulnar deviation (downward movements of the hand). The change from radial to ulnar deviation is not indicated by arrowheads in Fig. 6, because during the reversal phase of the slowest trials, the motion of the wrist consisted of several small-amplitude oscillations about the neutral position, and during the fastest trials the wrist was basically stable in the neutral position.

The magnitudes of the moments at the wrist were typically ten times smaller than at the shoulder and elbow joints, but the patterns of muscular and interactive moments at the wrist were similar to the patterns at the elbow joint shown in Fig. 5. For the slowest trial (solid traces in Fig. 6), the muscle moment (MUS) was small in magnitude, somewhat oscillatory in nature, with an action that was prolonged across almost 150 ms. The upper-arm-angular acceleration moment (UAA) contributed almost nothing to wrist action in early practice. The major interactive moment was associated with forearm-angular acceleration (FAA), although this effect was relatively small.

Next, consider the moments at the wrist taken from the fastest trial in later practice (dotted traces in Fig. 6). As for the elbow (Fig. 5), in the fastest trials an interactive moment related to forearm-angular acceleration (FAA) became considerably larger during the reversal phase as the movement changed in speed, with this effect tending to cause increased ulnar-deviation moment at the wrist. This increase was, on the average, 316%. This was the major interactive moment operating at the wrist joint, as the effect of the upper-arm-angular acceleration moment (UAA) remained negligible here. These interactive moments now balanced the heightened muscle moment at the wrist (MUS), which significantly increased (231% on the average) with practice. This muscular moment was also changed in form, with the moment–time function being considerably greater in magnitude, less oscillatory, and shorter in duration, than it was in early practice.

Thus, the interactive moment's tendency to ulnar-deviate the wrist was counterbalanced with a muscle moment whose tendency was to radially-deviate the wrist. Again, these findings are consistent with Bernstein's notion that subjects must acquire the capability to balance the passive-interactive moments provided by the movement with appropriate muscular action. In a way similar to that shown at the elbow joint, the subjects timed the wrist muscle moments to compensate for the motion-dependent moments generated by other limb segments, here primarily by the interactive moments related to the angular acceleration of the forearm (FAA).

**Electromyography**

Figure 7 contrasts the EMG burst patterns for the biceps brachii (caput longum) and triceps brachii (caput longum) (Fig. 7A) and the anterior and posterior deltoids (Fig. 7B) during exemplary slowest (900 ms) and fastest (519 ms) trials (subject 5). The dotted vertical lines successively indicate when the circular metal plate left the bottom target, entered the upper target, left the top target, and returned to the bottom target at the end of the movement.

For the slowest trial, subjects used shortening contractions of the biceps to flex the elbow while leaving the lower target and approaching the barrier. The biceps again was used for elbow flexion as the hand left the upper target and rounded the barrier during the downward motion. Triceps activity in early practice (slowest trials) showed low-level activity throughout the entire motion with more pronounced activity as the elbow extended and the hand entered the lower target. Throughout practice, the initial elbow flexion

![Fig. 6. Exemplar time series of the wrist moments during the reversal phase for the slowest (solid line) and fastest (dashed line) trials for the same representative subject (subject 4): generalized muscle moment (MUS); upper-arm-angular acceleration (UAA) and forearm angular acceleration (FAA).](image)
Fig. 7. Exemplar EMG burst patterns for the biceps brachii (caput longum) and triceps brachii (caput longum) (A) and the anterior and posterior deltoids (B) during slowest and fastest trials (subject 5). The dotted vertical lines indicate successively when the circular metal plate left the bottom target, entered the upper target, left the top target, and re-entered the bottom target at the end of the movement. The recruitment of the posterior deltoid as the hand approached the upper target occurred significantly sooner in the movement as subjects became faster. Further, cocontraction occurred in anterior and posterior deltoids in early practice, but with practice, the EMG showed only the phasic recruitment of posterior deltoid. During practice, the absolute and relative durations of all anterior and posterior deltoid bursts decreased significantly.

as the hand left the lower target was caused by a shortening contraction of the biceps. At the upper target, however, with practice subjects were able to use a lengthening contraction of the biceps as the elbow extended. The lengthening contraction of the biceps served to slow the rate of elbow extension as the hand entered the upper target. The biceps then actively shortened as the hand left the upper target. In the fastest trials, the triceps no longer was active tonically, but instead triceps' bursts alternated with biceps' bursts. Triceps became active during elbow flexion as the hand rounded the barrier during the upward motion; this potential stretch of the triceps may have facilitated a more rapid elbow extension as the hand moved toward the upper target. The triceps contracted with the biceps to stabilize the elbow as the hand entered the lower target.

The quantitative analysis of relationships between the biceps and the triceps EMG activities was inhibited by the near-tonic activity of the triceps during the early-practice trials; however, the phasic patterns of the anterior and posterior deltoids produced distinct records of the quantitative EMG changes during practice. In early practice, the posterior deltoid initiated shoulder extension to help pull the hand out of the lower target. Prior to entering the upper target, the posterior deltoid slowed the shoulder flexion by a lengthening contraction. During the slowest trials, the anterior deltoid was active (lengthening contraction) as the hand left the lower target, and after rounding the barrier, a shortening contraction flexed the shoulder to move the hand toward the upper target. In the downward phase of the movement, the anterior deltoid displayed a lengthening contraction as the hand rounded the barrier, and a final burst flexed the shoulder as the hand began to move toward the lower target.

Like the slowest trials, during the fastest trials a shortening contraction of the posterior deltoid initiated shoulder extension. In the reversal region, however, marked differences occurred in the recruitment of the posterior deltoid. The posterior deltoid, in the fastest trials, became active before the hand entered the upper target; this lengthening contraction served to slow the rate of shoulder flexion and to put the posterior deltoid on an increased stretch to augment the speed of shoulder extension as the hand left the upper target. The recruitment of the posterior deltoid
as the hand approached the upper target occurred significantly sooner in the movement as subjects became faster. Further, in the reversal region of slower trials, cocontraction occurred typically in anterior and posterior deltoids, but with practice, the EMG showed only the phasic recruitment of the posterior deltoid during the reversal at the upper target. During practice, the absolute and relative durations of all anterior and posterior deltoid bursts decreased significantly.

**DISCUSSION**

Given the goal of moving as fast as possible during a rather complex unrestrained arm movement, with practice, subjects achieved significantly shorter movement times. The exponential decrease in total movement time was congruent with traditional motor learning studies that have described motor performance via an outcome score (e.g. movement time). Our study, however, extended that traditional approach by revealing how movement dynamics were modulated throughout practice, although total movement time did not change significantly after approximately the 25th trial.

At all three joints of the arm, moment components (except gravity) significantly increased in peak values within each of the movement phases (upward, reversal, downward). Even though the between-subject differences in moment magnitudes were rather large, these differences did not mask the significant changes that occurred in moment magnitudes as a result of practice. The moment-time series showed similar profiles during the upward phase, but were significantly changed during the reversal and the downward phases of the movement. For example in the slowest trials, the interactive moments were nearly zero in the reversal region. With practice, however, the moment profiles were significantly changed, displaying large muscle and interactive moment components. The results of the dynamics analysis were consistent with the changes in the recruitment patterns of elbow and shoulder flexors and extensors during practice.

Our results substantiate that intersegmental dynamics are important for the control of arm trajectories, and these findings are consistent with the results of Hollerbach and Flash (1987) and Soechting and Lacquaniti (1981) for human limb trajectories and also with results for mechanical manipulator trajectories (e.g. Benati et al., 1980a, b; Hollerbach, 1984). In addition, our results emphasize that the analysis of intersegmental limb dynamics is vital for understanding the causes of movement, rather than relying solely on kinematic data to make inferences about the control of limb dynamics. Our findings go further, by documenting in some detail how such complex dynamical interactions can be changed with practice.

Our results corroborate Bernstein’s concepts of coordination in several ways. Bernstein defined motor coordination as the organizational control between central impulse (or program) and peripheral requirements of a movement, and motor coordination is acquired and altered through practice. He hypothesized that practice consists of solving a problem ‘... again and again by techniques which are changed and perfected from repetition to repetition’ (1967, p. 134). The result is a ‘... restructuring of the (motor) program’ (which) ‘may range from minor purely technical alterations in the trajectories of the movement to other adjacent paths, to qualitative reorganizations’ (1967, p. 135). With respect to control of active and passive forces Bernstein concluded that ‘... the secret of co-ordination lies not only in not wasting superfluous force in extinguishing reactive phenomena but, on the contrary, in employing the latter in such a way as to employ active muscle forces only in the capacity of complementary forces’ (1967, p. 109).

Firstly, our results show that, with practice, subjects were able to use muscle moments as ‘complementary forces’ to the passive-interactive moments of the moving limb. Already in the slowest trials, intersegmental moments played an important role in the control of this multisegmented arm movement. Practice, nevertheless, was necessary for the subjects to coordinate the active and passive intersegmental dynamics of the moving arm. This is a particularly important feature of skilled-movement control, in that the person not only avoids ‘wasting superfluous force in extinguishing reactive phenomena’ (Bernstein, 1967), but, on the contrary, employs the latter forces so that they are exploited for movement control.

Significant changes in moment relationships were observed at all three phases of the task (upward, reversal, and downward), but the most dramatic examples were found as subjects reversed their motion at the upper target. In their first trials, subjects showed a near static equilibrium at the reversal point, displaying moment components close to zero. Subjects initially maintained the hand at the upper target with small muscular activities at the shoulder and elbow joints to counterbalance gravity. With practice, however, the moment profiles changed to a state of dynamic equilibrium between increased muscle moments counterbalancing similarly increased interactive moment components. These effects were most prominent at the shoulder. The interactive moments resulted from muscular activities produced earlier in the action (e.g. as the subjects rounded the barrier), which produced higher velocities and accelerations and systematically-larger passive effects from the various limb segments as the movement approached the upper target area. Although the changes in intersegmental limb dynamics were particularly striking at the shoulder joint during the reversal, with practice, subjects similarly used interactive moments to complement muscle moments at all joints, especially as they rounded the barrier and approached the upper and lower targets. With practice, elbow and wrist joints displayed similar moment relationships between muscle and interactive components.
The results of the dynamics analysis were consistent with the changes in the recruitment patterns of elbow and shoulder flexors and extensors during the practice trials. For example, as the hand approached the barrier during the upward phase of the motion, the shoulder was extending, the anterior deltoid was actively lengthening, while the shoulder muscle moment was flexor. As the hand approached the upper target, the shoulder was flexing; the posterior deltoid, however, was active to slow and reverse the shoulder joint action, and the muscle moment at the shoulder was extensor. Further, as the hand rounded the barrier in the downward portion of the movement, the shoulder was extending; the anterior deltoid was active, and the muscle moment at the shoulder tended to flex the shoulder. With practice, the timing and organization of muscle recruitment patterns were changed considerably. As seen in the intersegmental dynamics results, subjects used muscle moments to counterbalance motion-dependent moments and consequently produced a faster movement.

Secondly, our results agree with Bernstein’s notion that practice is the process of solving a motor problem using techniques which are perfected from repetition to repetition, resulting in a reorganization of the motor program within this process. Bernstein’s view was that the subject’s motor problem involved ‘supplementing’ the passive-interactive properties of the moving limb system, in effect making up the difference between the dynamics produced initially, and the dynamics that produced the time-minimized movement that was desired. In this sense, the central control structure was modified over the course of practice. Evidence was presented that the timing of muscle moments and muscular activities were altered substantially. In a few subjects, the actions of the muscle moments at a particular time and place in the movement were changed completely, shifting, for example, from the actions of the shoulder flexors at the reversal point to the shoulder extensors. Potentially, in late practice the subjects appeared to use the stretch–shorten cycle of the shoulder and elbow extensors. Here, a given muscle (e.g. a flexor) is activated when the muscle is lengthening under stretch, so that the actions of the muscle brake the action, reverse it, and bring about flexion into the subsequent movement phase. This activation while lengthening exploits the passive-mechanical (i.e. viscoelastic) properties of the muscle and tendon. In addition, though, the activated but lengthening muscle is able to generate considerably more force than in static contractions, further speeding the reversal in direction at the upper target area. Our EMG results showed that muscles were activated during stretch so that their action was use of slowing and reversing the joint motion to enhance the subsequent speed of movement. Thus, as Bernstein (1967) argued, the system exploits the passive-interactive properties of the moving system, together with the mechanical properties of the muscle, to make the movement faster.

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**Appendix A. Determination of Spatial Coordinates**

The anthropometrically measured real lengths for the segments of the upper arm, forearm, and hand were defined as: $A_i =$ upper arm, $F_i =$ forearm and $H_i =$ hand. In the film image these lengths were shorter and were seen with maximum values of: $A_i =$ upper arm, $F_i =$ forearm and $H_i =$ hand; for the segments each time being parallel and closest to the film plane during motion. By comparing the real and film lengths an average conversion factor ($\Omega$) for each trial was calculated

$$\Omega = (A_i/A_i + F_i/F_i + H_i/H_i)/3$$

to convert film coordinates to real Cartesian coordinates. From the converted coordinates for the joints of the shoulder, elbow, and wrist, and the third metacarpophalangeal actual segment lengths were calculated in real Cartesian space for each frame: $A_i =$ upper arm; $F_i =$ forearm and $H_i =$ hand; from

$$A_i = [(x_i - x_{i-1})^2 + (y_i - y_{i-1})^2]^{0.5}$$

$$F_i = [(x_i - x_{i-1})^2 + (y_i - y_{i-1})^2]^{0.5}$$

$$H_i = [(x_i - x_{i-1})^2 + (y_i - y_{i-1})^2]^{0.5}$$

in real Cartesian space, where $(x_i, y_i)$ are coordinates of the shoulder joint, $(x_i, y_i)$ are coordinates of the elbow joint, $(x_i, y_i)$ are coordinates of the wrist joint, and $(x_i, y_i)$ are coordinates of the third metacarpophalangeal joint. By comparing those actual lengths with the directly-measured segment lengths, the angle for each joint's rotation out of the plane parallel to the film plane was determined as:

$$\psi_A = \cos(A_i/A_i)$$

$$\psi_F = \cos(F_i/F_i)$$

$$\psi_H = \cos(H_i/H_i)$$

with the assumptions that: (1) the shoulder joint remained fixed; (2) the upper arm (humerus) performed abduction and (3) the forearm and hand each performed a rotation toward the reference movement plane. The reference movement plane was defined as parallel to the film plane and normal to the plane containing the target light beams, intersecting both the upper and lower beams at mid-beam.

The linear-out-of-plane deviations of the upper-extremity joints were given by

$$A_i = (A_i^2 - A_i^2)^{0.5}$$

for the elbow,

$$F_i = (F_i^2 - F_i^2)^{0.5}$$

for the wrist, and

$$H_i = (H_i^2 - H_i^2)^{0.5}$$

for the third metacarpophalangeal joint.

The z-coordinate for the shoulder joint was zero, and the z-coordinates for the other joints were defined as: $A_i = z_i$ for the elbow; $F_i = z_i$ for the wrist and $H_i = z_i$ for the third metacarpophalangeal joint. Using these calculated $x_i$, $y_i$, and $z$-coordinates, the outwardly rotated plane through the shoulder, elbow, and wrist joints was rotated into the plane parallel to the film plane containing the shoulder joint. This was analogous to maintaining the camera's optical axis orthogonal to the plane in which the segments were moving during each instant in time.

The distance from shoulder to wrist joint seen in the film was obtained

$$d_i = [(x_i - x_{i-1})^2 + (y_i - y_{i-1})^2]^{0.5}$$

by knowing the amount of lateral excursion of the wrist from the reference plane

$$d_i = [(x_i - x_{i-1})^2 + (y_i - y_{i-1})^2 + (z_i - z_{i-1})^2]^{0.5}$$

The coordinates for the wrist within the reference plane were determined so that the distance from the shoulder to wrist joint equaled $d_i$. Geometrically, that was interpreted as rotation of the shoulder–wrist connection about an axis through the shoulder joint, perpendicular to the upper arm–forearm plane. Subsequently, the elbow joint was rotated back to the reference plane by determining the cross point of two circles about the shoulder joint with radius equal to the anthropometrically-measured length of the upper arm and the wrist joint with radius equal to the anthropometrically-measured length of the forearm. The elbow joint coordinates were then given by

$$x_e = x_i - (F_i^2 - (y_i - y_{i-1})^2)^{0.5}$$
and
\[ y = y_a + F_t \sin \phi, \]
with \( x_a \) and \( y_a \) the calculated \( x \)- and \( y \)-coordinates for the wrist after rotation. The sine function had two possible solutions
\[ \sin^{-1} \phi = \left( \frac{d_4 \pm d_4 \sqrt{D}}{a} \right), \]
with
\[ d_4 = x_c - x, \]
\[ d_2 = y_c - y, \]
\[ a = d_4^2 + d_2^2, \]
\[ b = (A_c^2 - F_a^2 - a)/(2F_a), \]
and
\[ D = a - b^2. \]

From these two solutions, the elbow angle was selected which was anatomically possible.

The coordinates of the third metacarpophalangeal joint were calculated under the assumption that only radio-ulnar deviations, but no flexion-extension occurred at the wrist joint. The result was a parallel transformation of the connection between wrist joint and third metacarpophalangeal joint from the old to the new wrist coordinates.

**APPENDIX B. THREE-SEGMENT EQUATIONS OF MOTION**

**Shoulder joint**

The net joint moment at the shoulder \([I_a + \Omega_a]\phi_a\) was equal to the sum of the moment components including: generalized muscle moment \([\text{MUS}]\), upper-arm-angular acceleration \([\text{UAA}]\); upper-arm-angular velocity \([\text{UAV}]\), forearm-angular acceleration \([\text{FAA}]\), forearm-angular velocity \([\text{FAV}]\), hand-angular acceleration \([\text{HAA}]\), hand-angular velocity \([\text{HAV}]\); shoulder-linear acceleration \([\text{SLA}]\); and gravity \([\text{GRA}]\). The moment equation for the shoulder was
\[ (I_a + \Omega_a)\phi_a = M_a. \quad \text{(MUS)} \]
\[ -[\beta_6 \cos(\phi_h - \phi_a) + \beta_7 \cos(\phi_t - \phi_a)] \phi_a \quad \text{(UAA)} \]
\[ + (\beta_4 + \beta_5) \cos(\phi_t - \phi_a)] \phi_t \quad \text{(UAV)} \]
\[ - [\beta_6 \sin(\phi_h - \phi_a)] \phi_h \quad \text{(HAA)} \]
\[ + [I_a + \Omega_a - \beta_2 \cos(\phi_h - \phi_t)] \phi_h \quad \text{(FAA)} \]
\[ - [\beta_2 \sin(\phi_h - \phi_t)] \phi_t \quad \text{(FAV)} \]
\[ + [I_a + \Omega_a - \beta_2 \cos(\phi_h - \phi_t)] \phi_t \quad \text{(HAV)} \]
\[ - [\beta_6 \sin(\phi_h - \phi_a) + \beta_7 \sin(\phi_t - \phi_a)] \phi_a \quad \text{(SLA)} \]
\[ + [\beta_6 \sin(\phi_h - \phi_a) + \beta_7 \sin(\phi_t - \phi_a)] \phi_a \quad \text{(GRA)} \]

where
\[ m_u, m_f, m_h = \text{masses of upper arm, forearm, and hand}, \]
\[ r_u, r_f, r_h = \text{distances from the proximal joint to center of mass of upper arm, forearm, and hand}, \]
\[ l_u, l_f, l_h = \text{lengths of upper arm, forearm, and hand}, \]
\[ l_u, l_f, l_h = \text{moments of inertia at center-of-mass of upper arm, forearm, and hand}, \]
\[ \phi_u, \phi_f, \phi_h = \text{orientation angles (at proximal end of segment from the right horizontal) for upper arm, forearm, and hand}, \]
\[ g = \text{gravitational constant (-9.81 m s}^{-2} \text{).} \]

**Elbow joint**

The net joint moment at the elbow \([I_e + \Omega_e]\phi_e\) was equal to the sum of the moment components including: generalized muscle moment; upper-arm-angular acceleration; upper-arm-angular velocity; forearm-angular acceleration; forearm-angular velocity; hand-angular acceleration; hand-angular velocity; shoulder-linear acceleration and gravity. The moment equation for the elbow was
\[ (I_e + \Omega_e)\phi_e = M_t. \quad \text{(MUS)} \]
\[ - [\beta_6 \cos(\phi_h - \phi_e) + \beta_7 \cos(\phi_t - \phi_e)] \phi_e \quad \text{(UAA)} \]
\[ + [\beta_6 \sin(\phi_h - \phi_e) + \beta_7 \sin(\phi_t - \phi_e)] \phi_t \quad \text{(UAV)} \]
\[ - [\beta_6 \sin(\phi_h - \phi_e)] \phi_h \quad \text{(HAA)} \]
\[ + [\beta_6 \sin(\phi_h - \phi_e)] \phi_e \quad \text{(FAA)} \]
\[ + [(\beta_5 \sin(\phi_h - \phi_e)] \phi_h \quad \text{(FAV)} \]
\[ - [(\beta_5 \sin(\phi_h - \phi_e)] \phi_e \quad \text{(SLA)} \]
\[ - [(\beta_5 \sin(\phi_h - \phi_e)] \phi_h \quad \text{(GRA)} \]

**Wrist joint**

The net joint moment at the wrist \([I_w + \Omega_w]\phi_w\) was equal to the sum of the moment components including: generalized muscle moment, upper-arm-angular acceleration; upper-arm-angular velocity; forearm-angular acceleration; forearm-angular velocity; shoulder-linear acceleration and gravity. The moment equation for the wrist was
\[ (I_w + \Omega_w)\phi_w = M_w. \quad \text{(MUS)} \]
\[ - [\beta_6 \cos(\phi_h - \phi_w) + \beta_7 \cos(\phi_t - \phi_w)] \phi_w \quad \text{(UAA)} \]
\[ - [\beta_6 \sin(\phi_h - \phi_w)] \phi_h \quad \text{(UAV)} \]
\[ - [\beta_6 \cos(\phi_h - \phi_w)] \phi_t \quad \text{(FAA)} \]
\[ + [(\beta_5 \sin(\phi_h - \phi_w)] \phi_e \quad \text{(FAV)} \]
\[ + [(\beta_5 \sin(\phi_h - \phi_w)] \phi_e \quad \text{(SLA)} \]
\[ - [(\beta_5 \sin(\phi_h - \phi_w)] \phi_w \quad \text{(GRA)} \]