

Intersegmental Dynamics Are Controlled by Sequential Anticipatory, Error Correction, and Postural Mechanisms

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Sainburg, R. L., C. Ghez, and D. Kalakanis. Intersegmental dynamics are controlled by sequential anticipatory, error correction, and positional control mechanisms. *J. Neurophysiol.* 81: 1045–1056, 1999. The purpose of this study is to examine the mechanisms underlying control of intersegmental dynamics during reaching movements. Two experiments were conducted to determine the relative contributions of anticipatory and somatosensory feedback mechanisms in controlling intersegmental dynamics and whether adaptation to novel intersegmental dynamics generalizes across a range of movement directions. The mechanisms used to control interaction torques were examined by altering the inertial load of the forearm. Movements were restricted to the shoulder and elbow and supported on a horizontal plane by a frictionless air-jet system. Subjects made rapid out-and-back movements over a target line presented on a computer screen. The screen cursor disappeared at movement onset, and hand paths were displayed after each movement. After subjects adapted to a novel inertial configuration, the position of an attached mass was changed on pseudorandom trials. During these “surprise” trials, movements were initiated with the torque patterns appropriate to the previously learned inertial condition. As a result, characteristic errors in initial movement direction were predicted by an open-looped forward simulation. After these errors occurred, feedback mediated changes in torque emerged that, surprisingly, further decreased the accuracy of movement reversals. Nevertheless at the end of movement, the hand consistently returned to the starting position. It is plausible that the final position was determined completely by feedback-mediated changes in torque. In a second experiment, adaptation to a novel inertial load during movements made in a single direction showed limited transfer across a range of directions. These findings support and extend those of previous reports, which indicated combined anticipatory and postural mechanisms to coordinate rapid reaching movements. The current results indicate a three-stage control system that sequentially links anticipatory, error correction, and postural mechanisms to control intersegmental dynamics. Our results, showing limited generalization across directions, are consistent with previous reports examining adaptation to externally applied forces and extend those findings to indicate that the nervous system uses sensory information to recalibrate internal representations of the musculoskeletal apparatus itself.

INTRODUCTION

To produce a desired hand trajectory, the nervous system must coordinate muscle forces with both external forces imposed by the environment and internal forces that arise within the musculoskeletal system itself. Internal forces include those produced by stretch and compression of noncontractile tissues,

and “interaction forces” imposed on each limb segment by motion of the segments attached to it. Adaptation to perturbations arising from outside the musculoskeletal system has been postulated to occur through the learning and recalibration of neural representations or “internal models” of the perturbing forces (Gandolfo et al. 1996; Goodbody and Wolpert 1998; Imamizu et al. 1995; Jordan and Rumelhart 1992; Lackner and Dizio 1994; Shadmehr and Mussa-Ivaldi 1994). Recent reports have shown that, with practice, subjects adapt to coriolis forces (Lackner and Dizio 1994) and viscous forces applied to the hand by a manipulandum (Gandolfo et al. 1996; Goodbody and Wolpert 1998; Shadmehr and Mussa-Ivaldi 1994). The development of neural representations of applied forces was demonstrated by the persistence of hand-path curvatures that mirrored the directions and magnitudes of such forces after they had been removed (“after effects”). After effects even occurred for movements made in different regions of space (Shadmehr and Mussa-Ivaldi 1994), in different directions (Gandolfo et al. 1996), and at different speeds than that of practice (Goodbody and Wolpert 1998). These reports indicate that during practice of novel tasks, the nervous system gradually develops an internal representation of the associated environmental dynamics. This internal model is subsequently used to control movements made under identical or similar task conditions.

The externally applied forces described in the previous paragraph can be detected directly through muscle spindles and tactile receptors in the hand. However, because interaction forces vary with segment accelerations and are transferred across the segments through bony and ligamentous connections, they cannot be detected in this way. Although the nervous system can detect changes in muscle length and its first derivative through muscle spindles, the rotational effect of interaction forces at the joint (interaction torque), which varies most substantially with joint angular accelerations (Hollerbach and Flash 1982; Hoy and Zernicke 1986; Sainburg et al. 1995; Schneider et al. 1989; Winter 1990), is not directly encoded by muscle and tendon proprioceptors (Hasan 1983; Hasan and Houk 1975; Matthews 1981). Because of the differences in available sensory information, it is not known whether intersegmental forces and extrinsically applied forces are controlled through the same neural mechanisms.

Mechanisms for controlling limb movements without explicitly representing musculoskeletal dynamics have been proposed by equilibrium point theories of control (Bizzi 1987; Bizzi et al. 1976, 1984; Feldman 1986; Flash 1987; Polit and Bizzi 1979). According to these ideas, once a single endpoint

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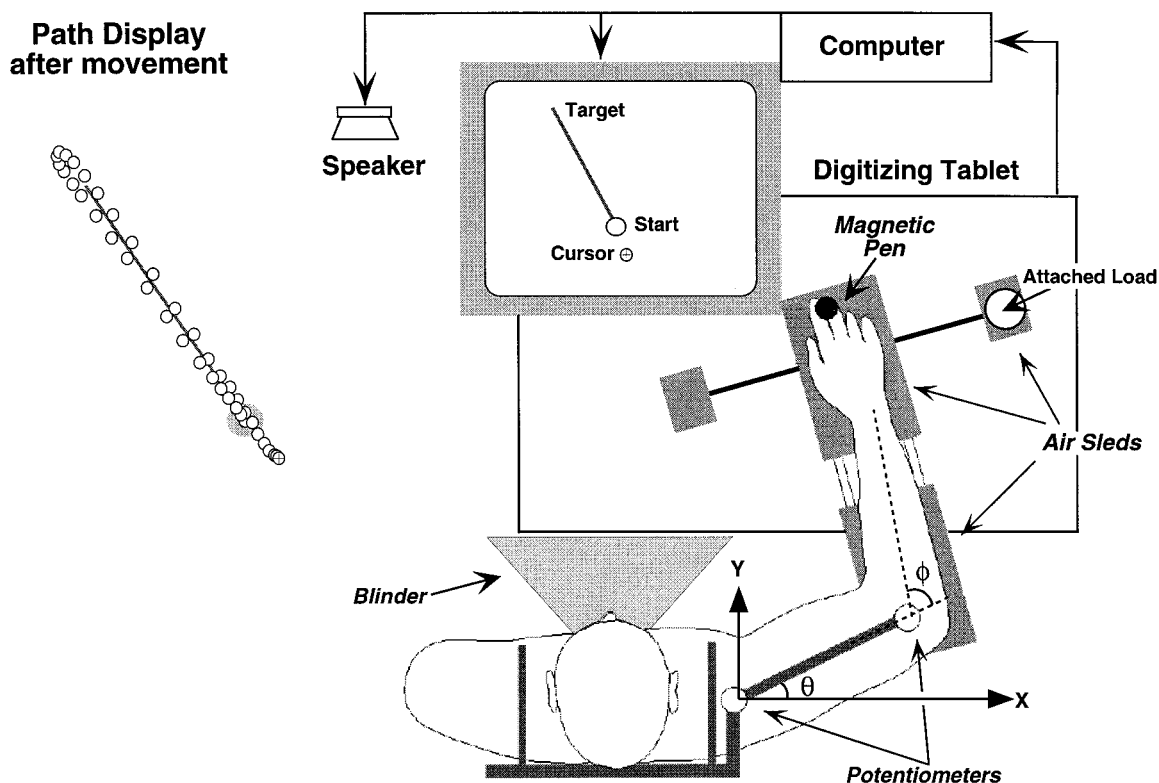


FIG. 1. Experimental set-up: X and Y represent axes of coordinate system originating at shoulder. Shoulder and elbow angles were measured as θ and ϕ , respectively. After each trial, the hand path was displayed on the computer screen, each circle representing the hand position every 25 ms.

or a sequence of desired positions is specified, the springlike properties of the muscles are exploited. Joint torque emerges as a function of the difference between the muscle lengths for the current and the desired limb positions. Equilibrium point mechanisms thus do not require that the controller explicitly represent or predict the effects of musculoskeletal dynamics. Other authors (Gottlieb et al. 1995; Hirayama et al. 1993) incorporated this type of controller into hybrid mechanisms that initiate movements through open-looped processes, subsequently employing equilibrium-type mechanisms to specify the end posture and compensate unexpected loads. In this way, equilibrium point mechanisms can compensate for inaccuracies in learned control strategies.

Imamizu and coworkers (1995) described methods for experimentally discriminating between alternative representations of learned control strategies based on patterns of generalization. They proposed that different patterns of generalization could differentiate between pure analytic representations and tabular representations. The former would predict complete transfer of learning anywhere in space because the precise dynamic or kinematic transformation would be represented in abstract terms. The latter implies a simple recording of input-output relationships, such as a memory of a muscle-activation/sensory-feedback pattern, and as such does not predict generalization. A third type of representation is characterized by neural network models, which do not directly represent physical parameters and can result in intermediate patterns of generalization.

The purpose of the current paper is to examine the mechanisms underlying control of intersegmental dynamics. Two

experiments were conducted to examine whether control of intersegmental forces normally occurs through anticipatory mechanisms based on internal representations of limb dynamics and whether adaptation to novel intersegmental dynamics transfers across a range of movement directions. The mechanisms used to control interaction torques were examined by altering the inertial load of the forearm. By comparing our experimental results to an ideal open-looped forward simulation, we could assess the contributions of somatosensory feedback to the control of intersegmental dynamics. Furthermore we examined whether control strategies learned during adaptation to one load remained evident when the load was unexpectedly changed.

Some of these results have previously been reported in abstract form (Sainburg and Ghez 1995).

METHODS

Subjects and apparatus

Subjects were 13 neurologically intact adults (8 females, 5 males), aged 28–46. Five subjects (3 females, 2 males) participated in *experiment 1*, whereas eight participated in *experiment 2* (5 females, 3 males). Figure 1 illustrates the experimental setup. All subjects provided informed consent before participation in this study, which was approved by the institutional review board of Columbia University. Subjects sat facing a computer screen with their dominant arm supported over a digitizing tablet by a frictionless air-jet system. A thermoplastic splint was fitted to the subject's forearm and hand, immobilizing all joints distal to the elbow. A magnetic pen (200 Hz), attached to the tip of the splint, allowed the hand position to be monitored and displayed as a screen cursor. Vision of the arm and

table was blocked using a horizontal screen. An outrigger was fixed to the splint for the attachment of a 1.2 kg mass placed 25 cm medial or lateral to the forearm. Two precision, single-turn, linear potentiometers (Beckman Instruments) were used to monitor the elbow and shoulder joint angles, and data were digitized using a Macintosh computer equipped with an A/D board (National Instruments PCI-MIO-16 × E-50). The experimental tasks and hand position feedback were presented to the subjects using a second computer connected to the digitizing tablet. Computer routines for data analysis were written in Igor (Wavemetrics).

Task

A single target line with the starting circle were presented on the computer screen (see Fig. 1). The hand position was displayed in real time as a screen cursor. Subjects were to hold the cursor within the starting circle for 1 s to initiate each trial. Then an auditory GO signal was given, and the cursor was blanked. Subjects were to trace the line using a rapid overlapping, out-and-back movement of the hand. The movement was to be completed within a 1.5-s sampling window. Subjects were instructed to focus on making their movements straight and to retrace forward and backward motions. Movement paths were displayed on the computer screen at the end of every trial (see Fig. 1).

The two experiments conducted in this study are described in the following text.

EXPERIMENT 1. Each experimental session consisted of three different blocks of trials. The first block consisted of 100 trials performed with the medial load. The second block consisted of 108 trials: 100 trials were made with the medial load, whereas 8 trials, interspersed among the others, were made with the lateral load. Because subjects were not aware of this change, we refer to these trials as “surprise” trials. We used eight surprise trials because pilot data indicated that after approximately nine trials, subjects began to report “expecting” a change in dynamics. Finally, the third block of 100 trials was made with the lateral load. Statistical comparisons were made between the last eight trials of the first block, the eight surprise trials, and the last eight trials of the final block. The surprise trials thereby could be compared with trials performed after the subject had adapted to each mass position.

Because our task was designed to study control of interaction torques, we used a target that required substantial motion at each joint. The target line was 20 cm long, and oriented 135° relative to the horizontal axis. Given the limb dimensions of all five subjects, this target required from 18 to 21° displacements at each joint. We tested reversals in hand motion because joint accelerations and thus inertial interactions are maximized during such movements (Sainburg et al. 1995). By beginning the movements with an elbow angle of 90° and a shoulder angle of 10°, the extremes in joint range were avoided to minimize the forces that result from deformation of noncontractile tissues.

EXPERIMENT 2. In the second experiment, we investigated whether practice toward one target direction and with a given load configuration influences the accuracy of movements made toward other directions. All eight subjects learned to control movements made toward a single direction and over a single target line. Generalization in this learning was tested for movements made to three different target lines. We chose 10-cm-long targets at directions that differed by 18° (90, 108, and 126°) because they required substantial displacements at both joints. To control for the effect of direction on movement accuracy, half the subjects trained with the 126° target, while the other half trained with the 90° target. Every subject completed two experimental sessions, training with the medial and lateral loads on separate days. On their first day, half the subjects comprising each target group trained with the lateral load, whereas the other half trained with the medial load.

Each daily experimental session consisted of two blocks of trials. In

the first block of 100 trials, subjects practiced movements with a single load configuration over a single target line (90 or 126°). In the second block, consisting of 500 trials, subjects continued to make movements over the trained target line. In 50 randomly presented trials, subjects were tested with a different load configuration and/or a different target line. For each of the three directions, 10 trials were performed with the mass in the same position as that of training, whereas for another 10 the position was switched.

The effects of training on the accuracy of test trials were assessed by comparing the movements between the two experimental sessions that were made with a given mass position and to a given target. For example, adapted lateral load trials from the lateral mass training session were compared with surprise lateral load trials from the medial mass training session.

Kinematic analysis

The primary data consisted of the shoulder and elbow potentiometer signals that were digitized at 1 kHz, low-pass filtered at 12 Hz (2nd order, no-lag, Butterworth), and double differentiated to yield angular velocity and acceleration values. Elbow (ϕ) and shoulder (θ) joint angles are defined in Fig. 1.

Hand paths were calculated from joint angle data by using the measured length of the upper arm and the distance from the elbow to the magnetic pen. The angular data were transformed to a Cartesian coordinate system with origin at the shoulder (see Fig. 1). Movement onset and termination were defined as 1% of the maximum tangential hand velocity, measured before the first peak in velocity (V_{max_1}) and after the second peak in velocity (V_{max_2}), respectively.

For ease of presentation, data were segmented into three different acceleration phases, separated by the two main peaks in tangential velocity of the hand (V_{max_1} , V_{max_2}): outward acceleration, reversal (outward deceleration and inward acceleration), and inward deceleration (see Fig. 2). The transitions among three phases corresponded well to angular acceleration and torque zero crossings at each joint. These phases will be referred to as outward, reversal, and inward, respectively.

Two measures of movement accuracy were calculated from the hand path, initial direction error, and reversal error. The initial direction error was calculated as the angle between the target line and the line originating at the starting location of the hand (at *time 0*) and terminating at the point at which the first peak in tangential hand velocity (V_{max_1}) occurred. The reversal error of the hand path was measured as the area circumscribed by the hand path during the reversal phase of motion (see Fig. 4).

Averages of time series data were obtained, first by synchronizing each trial (single time series) to V_{max_1} , and second by clipping the data so that each trial had an equal number of frames. Corresponding frames from each trial then were averaged and standard errors calculated.

Kinetic analysis

We partitioned the terms of the equations of motion at each joint into three main components, interaction torque, muscle torque, and net torque (Sainburg et al. 1995). At each segment, interaction torque represents the rotational effect of the forces resulting from motion of the other linked segment. The muscle torque primarily represents the rotational effect of muscle forces. Finally, net torque represents the inertial resistance of the segments to joint acceleration. This component varies directly with joint acceleration and limb inertia and is equal to the combined muscle and interaction terms.

It is important to note that the computed muscle torque cannot be considered a simple proxy for the neural activation of the muscles acting at that joint, as it includes also the passive effects of soft tissue deformation. The muscle torque does not distinguish muscle forces that counter one another, such as during contraction. Additionally, the force generated

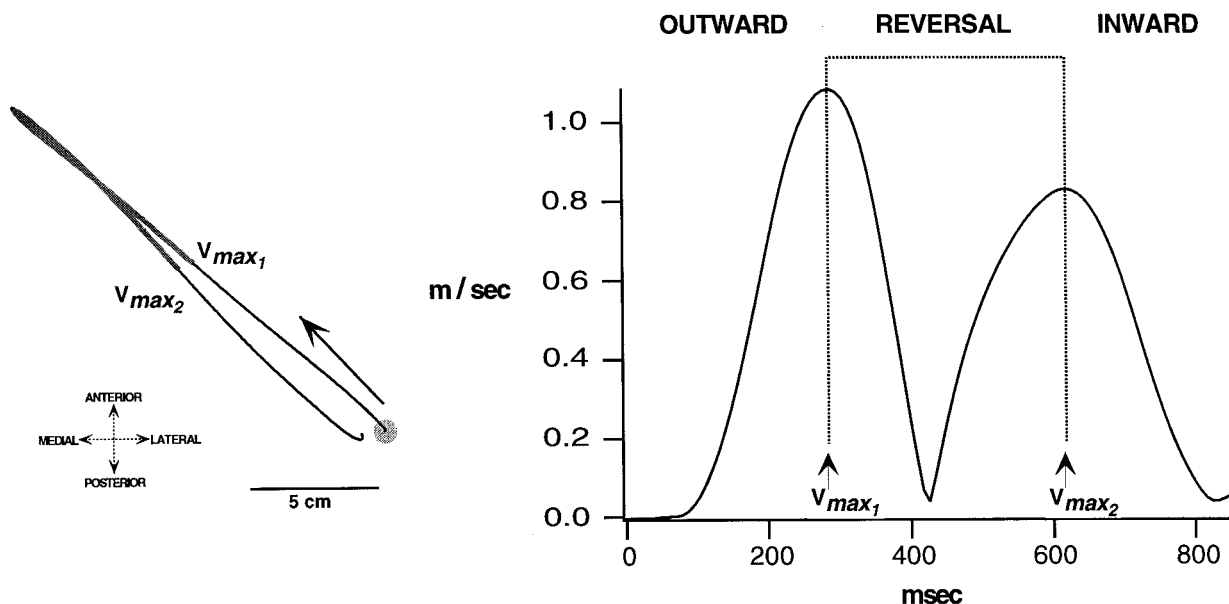


FIG. 2. Hand path (left) and tangential velocity (right) profile for a typical trial. Trials were segmented into 3 temporal phases: outward, inward, and reversal. The portion of the hand path occurring within the reversal phase is shown in bold.

by muscle to a given neural input signal is dependent on muscle length, speed of muscle length change, and recent activation history (Abbott and Wilkie 1953; Wilkie 1956; Zajac 1989).

Torques were computed and analyzed for the shoulder and elbow joints as detailed in the following equations.

ELBOW JOINT TORQUES.

$$\begin{aligned} \text{Interaction} &= -\ddot{\theta}[A \cos(\phi) + B \cos(\phi + \delta) + C] \\ &\quad - \dot{\theta}^2[A \sin(\phi) + B \sin(\phi + \delta)] \\ \text{Net} &= \ddot{\phi}C \end{aligned}$$

$$\text{Muscle}_{\text{elbow}} = \text{Net} - \text{Interaction}$$

SHOULDER JOINT TORQUES.

$$\begin{aligned} \text{Interaction} &= -\ddot{\phi}[A \cos(\phi) + B \cos(\phi + \delta)] \\ &\quad + (\dot{\phi} + \dot{\theta})^2[A \sin(\phi) + B \sin(\phi + \delta)] \\ \text{Net} &= \ddot{\theta}[D + A \cos(\phi) + B \cos(\phi + \delta)] \end{aligned}$$

$$\text{Muscle}_{\text{shoulder}} = \text{Net} - \text{Interaction} - \text{Muscle}_{\text{elbow}}$$

SYMBOLS

$$A = m_2 L_1 r_2 + m_d L_d r_d$$

$$B = m_m L_1 r_m$$

$$C = I_2 + m_2 r_2^2 + I_d + m_d r_d^2 + m_m r_m^2$$

$$D = I_1 + m_1 r_1^2 + [m_2 + m_d + m_m] L_1^2$$

m = mass

r = distance to center of mass from proximal joint

L = length

I = inertia

θ = shoulder angle

ϕ = elbow angle

δ = angle between forearm and line connecting attached mass with elbow joint

SUBSCRIPTS

1 = upper arm segment

2 = forearm/hand segment

d = air sled device

m = attached mass

For these calculations, the attached mass (1.2 kg), consisting of a small block of lead, was modeled as a point mass. In addition, the aluminum rod attaching the shoulder potentiometer to the elbow potentiometer was not considered because its mass was only 0.052 kg. The inertia and mass of the forearm support were 0.0069 kg/m² and 1.6 kg, respectively. Limb segment inertia, center of mass, and mass were computed from regression equations (Winter 1990) using subjects' body weight and measured limb segment lengths.

Simulations

We solved the equations of motion (shown above) for $\ddot{\theta}$ and $\ddot{\phi}$, then forward integrated using a fixed 1-ms time step. Inputs to each simulation were initial θ and ϕ values, subjects' limb dimensions and inertial values, the configuration of the attached mass, and the joint torque histories calculated from each recorded movement trial. Thus we could predict the effects of an ideal open-looped controller by using the muscle torques computed from a movement made with a given mass position to drive the simulation with an "altered" mass position. We calculated the forward integration error by comparing a simulated hand path to that of the actual trial. The maximum error was 0.61 mm.

Statistical analysis

The individual measures used in this paper were analyzed in separate ANOVAs with experimental blocks (adapted medial, surprise lateral, adapted lateral) as a within subject variable. Post hoc comparison of cell means was done using the Bonferoni/Dunn method.

RESULTS

Experiment 1: Control of interaction torques with different loads

KINEMATIC ANALYSIS. When first presented with the medial mass, subjects made consistent deviations in initial move-

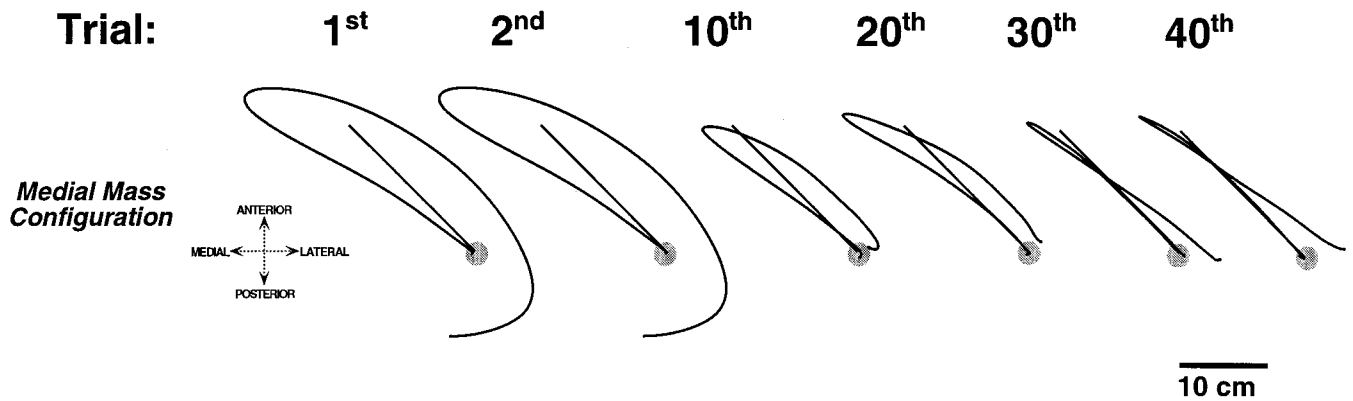


FIG. 3. Typical hand paths during adaptation to the medial load. Gray circles indicate the “start” location.

ment direction and in reversing the direction of hand motion (see Fig. 3). The initiation of hand movement was deviated counterclockwise and the direction reversed through a wide clockwise curve. Initial direction errors were reduced and direction reversals became sharp, as required by the task, during the first 40 trials of practice. This indicates that accurate control over the medial load requires learning of a unique control strategy.

Figure 4 shows typical hand paths and joint trajectories for a trial after adaptation to the medial load (*left*), a surprise trial

in which the mass was switched lateral (*center*), and a trial after adaptation to the lateral load (*right*). After adaptation to the medial load, the hand movements were straight, directed over the target line, and reversed direction sharply. In surprise trials, the initial movement direction deviated clockwise, and the direction reversal followed a broad counterclockwise curve. After adaptation to the lateral load, subjects again made straight sharply reversing movements.

Across all subjects, initial direction errors were 10 times greater for surprise trials than for trials after adaptation to the

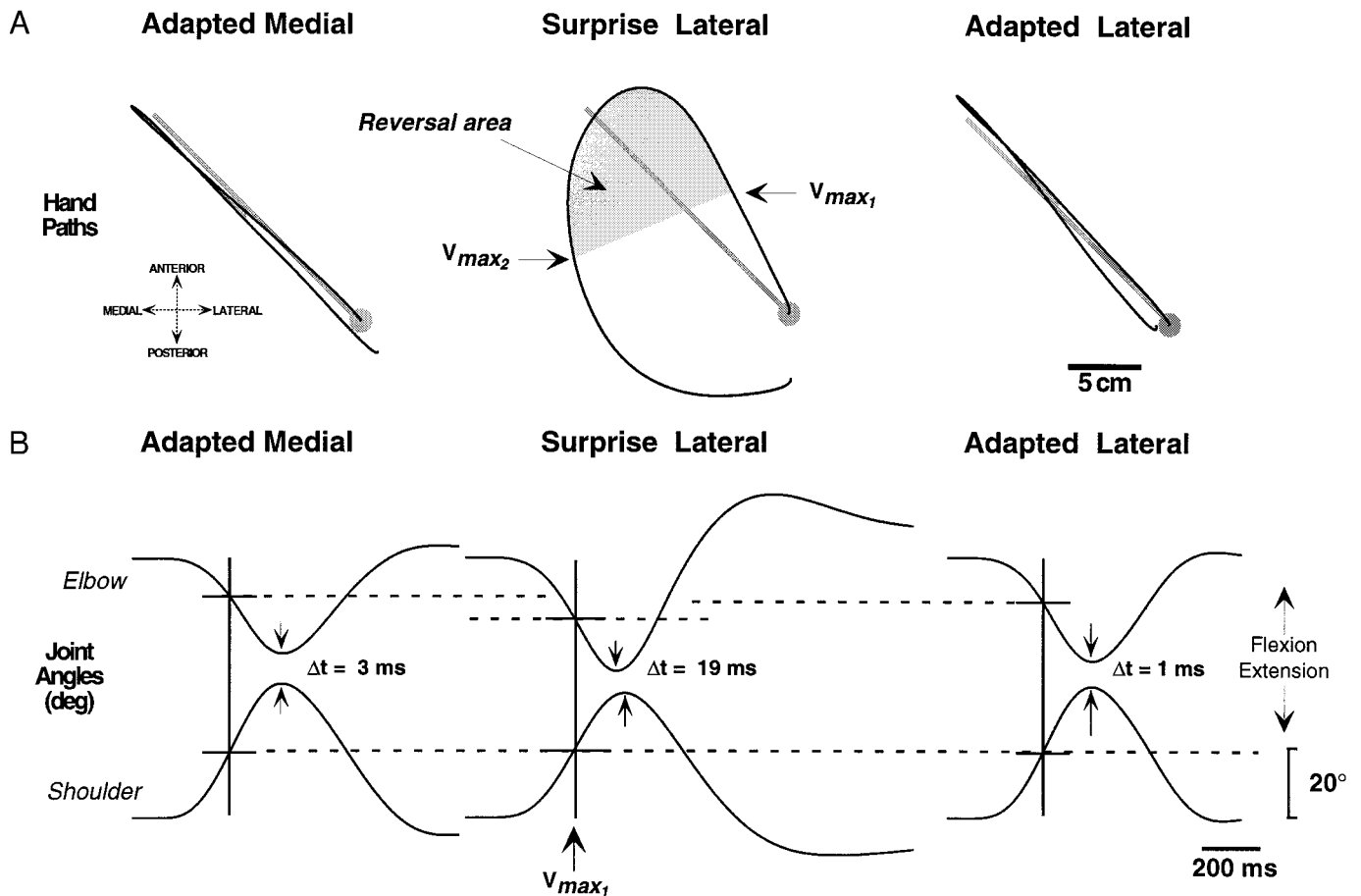


FIG. 4. A: typical hand paths after adaptation to the medial load (*left*), for a surprise trial (*center*), and after adaptation to the lateral load (*right*). B: elbow and shoulder joint angles corresponding to the hand paths in A. Time of direction reversal at each joint is marked by arrows. Interjoint coupling time, between these reversals, is denoted by Δt . Cross hairs represent the joint angle measured at V_{max_1} . Dashed lines allow comparison of these angles across the trials.

medial or lateral mass positions (mean \pm SE: 31.6 ± 1.8 , 0.9 ± 1.0 , and $3.4 \pm 1.8^\circ$, respectively). Similarly, the area circumscribed by the path in the reversal phase was consistently larger for surprise than for medial or lateral adapted trials (71.63 ± 6.28 , 3.68 ± 0.75 , 3.73 ± 0.84 cm², respectively).

The elbow and shoulder joint motions that produced the hand-path deviations seen in surprise trials are illustrated in Fig. 4B. The origin of the direction errors, measured at the first peak in tangential velocity (V_{max_1}) of the hand, is illustrated by examining joint displacements at V_{max_1} (cross hairs in Fig. 4B). Shoulder-joint excursions were the same across all three conditions (across subjects, Bonferoni/Dunn: $P = 0.72$). However, elbow extension was increased substantially during the surprise trial (across subjects, Bonferoni/Dunn: $P < 0.001$), leading to the initial clockwise direction errors. When hand reversals were sharp, the elbow and shoulder joint motions reverse direction synchronously (Fig. 4B) (see also Sainburg et al. 1993, 1995). The reversal errors of surprise trials occurred because the elbow reversed movement direction (from extension to flexion) before the shoulder reversed movement direction (from flexion to extension). Across subjects, the average interval between these joint-movement direction reversals (interjoint-coupling-interval) was 31 ± 4 (SE) ms. This brief simultaneous flexion at the two joints caused the hand to follow a broad counterclockwise path. In short, the clockwise direction errors of surprise trials resulted from failure to control the magnitude of elbow motion, whereas the reversal errors resulted from failure to coordinate the timing of elbow motion with shoulder motion. Average values for individual subjects are shown in Fig. 5.

INVERSE DYNAMIC ANALYSIS. Adapted trials. Figure 6 shows the torque profiles from the trials shown in Fig. 4. With both medial and lateral loads, the interaction torque at the elbow acts in the same direction as the net torque, indicating its action in accelerating joint flexion and extension. Muscle torque, however, acts in the opposite direction and thus counters the effects of interaction torque. Note that at the beginning of the reversal phase, initiation of extensor muscle torque coincides with the initiation of flexor interaction torque (Mean time difference across subjects = 5 ± 14 ms). Because the interaction torque for the lateral load trials is substantially larger, muscle torque amplitude increased to maintain similar elbow kinematics between the medial and lateral load conditions.

Although shoulder muscle torque affects elbow-joint acceleration through interaction torques, elbow muscle torque directly effects the acceleration of both segments (see METHODS). In the two adapted conditions, increases in interaction torque at both joints are countered predominantly by elbow muscle torque. While net torque at the elbow remains the same, load-dependent increases in shoulder net torque are countered by muscle torque.

Surprise trials. When subjects were presented with the unexpected lateral load, muscle torque at the elbow was initially the same as that in adapted medial trials (see Fig. 6, center). Across subjects, the mean muscle torque impulse, measured from movement initiation to peak hand acceleration, was the same for both conditions (Bonferoni/Dunn: $P = 0.9771$). Thus increases in extensor interaction torque at the elbow were not countered, resulting in excessive joint extension and thus

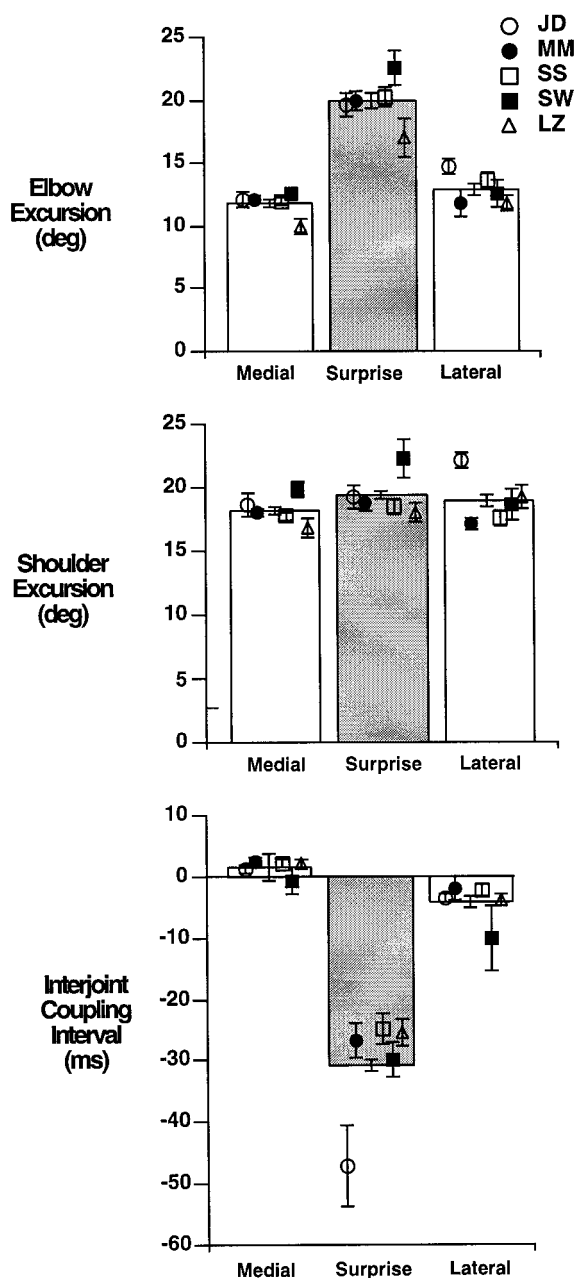


FIG. 5. Mean and SE of elbow (*top*) and shoulder (*center*) excursions measured at V_{max_1} (*left*) and of the interjoint coupling interval (*bottom*), measured as the time between the direction reversals at each joint (Δt in Fig. 4B). Individual mean and SEs for each subject are shown separately and marked with the subjects' initials in the legend. Grouped mean and SE of these average values is indicated by the bars.

clockwise direction errors. Furthermore in the early part of the reversal phase, the onset of extensor muscle torque occurred an average of 51 ± 16 ms (across subjects) after the initiation of flexor interaction torque. As a consequence, the increased interaction torque accelerated the elbow into flexion prior to the initiation of shoulder extensions. This accounts for the desynchronization of elbow and shoulder that produced the rounded movement reversals shown in Fig. 4. The resulting medial deflection of the hand finally was countered by elbow extensor muscle torque and extensor interaction torque to re-

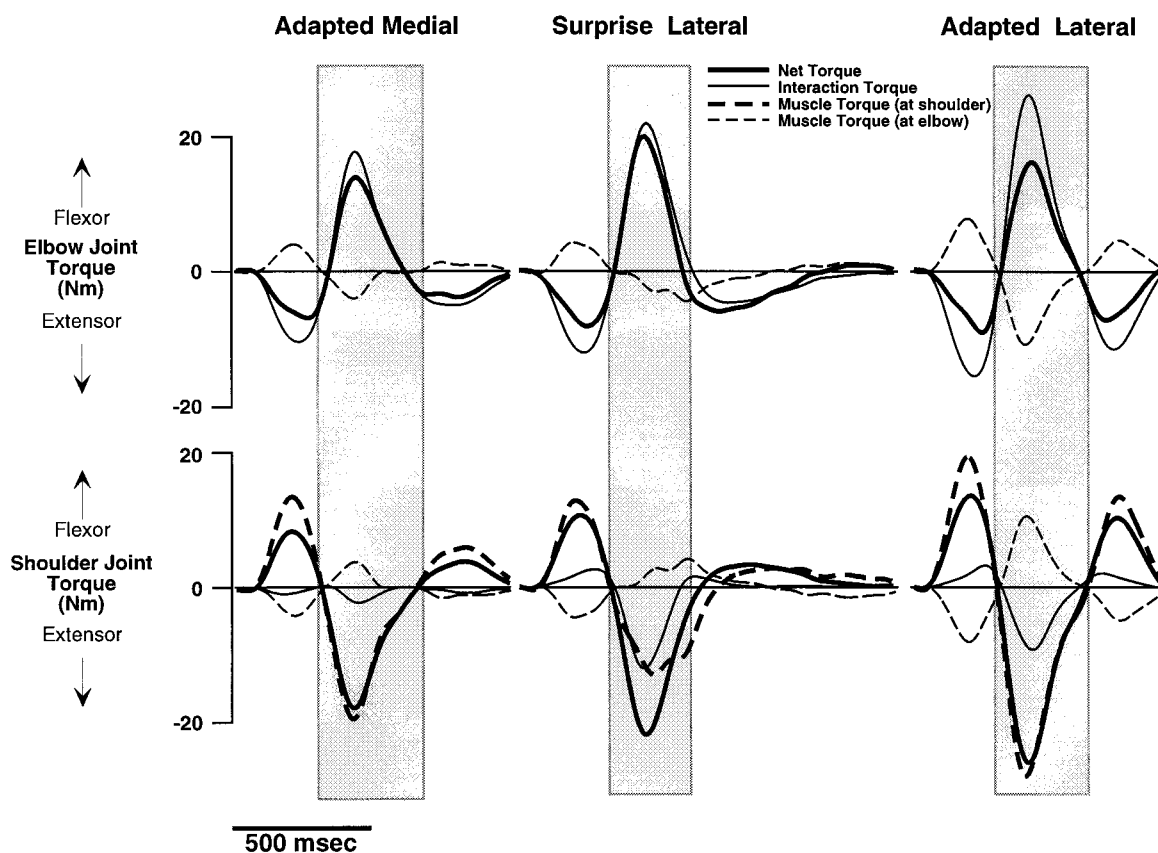


FIG. 6. Elbow (*top*) and shoulder (*bottom*) joint torques from the trials shown in Figs. 4 and 5. Interaction, net, and muscle torques are shown separately at each joint. Reversal phase is indicated by the gray rectangle drawn across each set of torque profiles.

turn the hand to near its initial position. Similar to the adapted conditions, a load-dependent increase in net torque at the shoulder was countered by shoulder muscle and interaction torques.

FORWARD SIMULATIONS. We implemented a simple open-looped controller to better understand the origin of the changes in torque that resulted in hand path deviations of surprise trials. The muscle torques calculated from the adapted medial load trials were used as inputs to the dynamic equations of motion. The forward simulation was performed with the inertial values of the distal segment altered to mimic the lateral mass condition. In effect, this predicted what would have happened if the subject had used the torques needed to accurately control the medial load throughout a surprise trial. A forward simulation was obtained for all trials. Figure 7A shows the results for a typical trial, whereas simulated direction and reversal errors are averaged for each subject in Fig. 7B.

These simulations accurately predicted the initial portion of the trajectory (see Fig. 7). Across all subjects, initial direction errors for actual surprise trials were not significantly different from those from the simulated paths (Bonferoni/Dunn: $P = 0.884$; Fig. 7B, *left*). However, the simulated paths reversed more sharply than those of actual surprise trials. As a result, measured reversal areas were substantially smaller for simulated trials (mean across subjects: $50 \pm 4.9 \text{ cm}^2$) than for actual trials (mean across subjects: $70 \pm 10 \text{ cm}^2$). The simulated trajectory diverges from the actual trajectory after the onset of

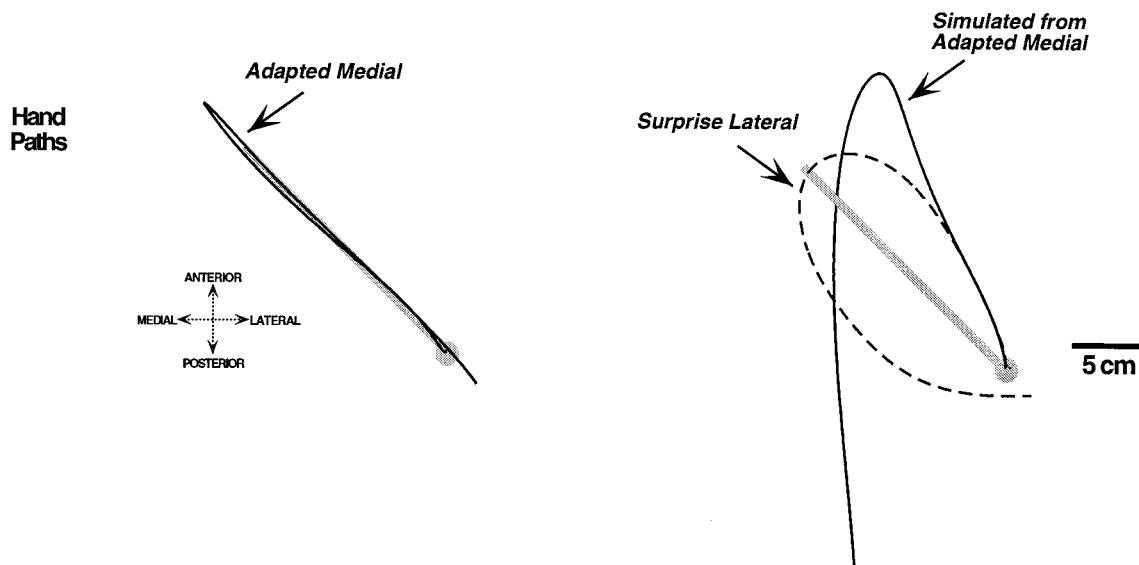
the reversal phase ($V_{\max 1}$). Although actual trials always curved back toward the start of the target line, simulated trials did not. These findings indicate that the early part of the trajectory and the associated direction error resulted exclusively from anticipatory processes.

Experiment 2: Generalization of learning across directions

While it is possible that adaptation to altered intersegmental dynamics occurs through memorization of a single stereotyped muscle activation pattern, it is also possible that subjects develop a more general representation of the altered inertial dynamics. To discriminate between these alternatives, we examined whether learning to control a novel inertial load for movements to a single direction generalizes to movements made in different directions. After adaptation in a single direction (90 or 126°) and with a single mass configuration (medial or lateral), subjects were pseudorandomly tested, every five to eight trials, on movements made to each of the three targets (90 , 108 , and 126°) with the same or a surprise mass configuration. Subjects completed a training session with each mass configuration on separate days to either the 90 or 126° target. Learning was assessed as the difference in accuracy between trials that were matched for inertial load and target but followed different training sessions.

Figure 8A shows averaged hand paths for trials made with the lateral load from both 126° training sessions. The move-

A Actual and Simulated Hand Paths



B Actual Versus Simulated Errors

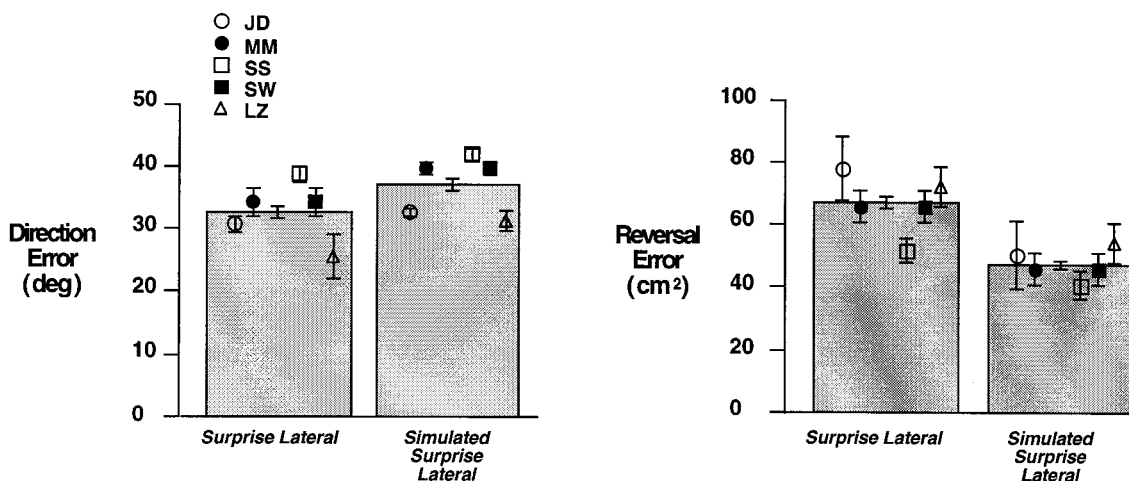


FIG. 7. A: actual compared with simulated hand paths. Simulated surprise trial (right) was calculated using the muscle torques from the adapted medial load trial (left). An actual surprise trial is overlaid on the simulated trial (right). B: measured initial direction and reversal errors for actual and simulated trials. Individual mean and SEs are shown separately and marked with the subjects' initials in the legend, while grouped means and SEs are represented by the bars.

ments made with the lateral load and to the trained direction, during the lateral load training session, are straight and the direction reversals are sharp. However, in the same direction, surprise lateral load movements made during the medial load training session showed large direction and reversal errors. As the movement direction diverged from that of training, movements performed during the lateral training session became less accurate and more similar to the surprise trials made during the medial training session. Similarly, as movement direction diverged from that of training, the errors in surprise movements made during the medial training sessions were reduced. This decay in the effects of training on movement

accuracy was not dependent on movement direction as indicated in Fig. 8B.

Figure 8B shows the effects of training, measured as the differences in movement errors between surprise and adapted trials performed with the same load. Whether subjects trained to 126 or to 90°, the effects of training decayed as the movement direction deviated from that of training. On average, differences in direction errors dropped by 29% when movements were made 36° to either side of the trained direction. Similarly, the differences in average reversal areas decreased an average of 26%. Thus regardless of the direction to which subjects trained, the effects of training decayed as movement direction diverged from that of training.

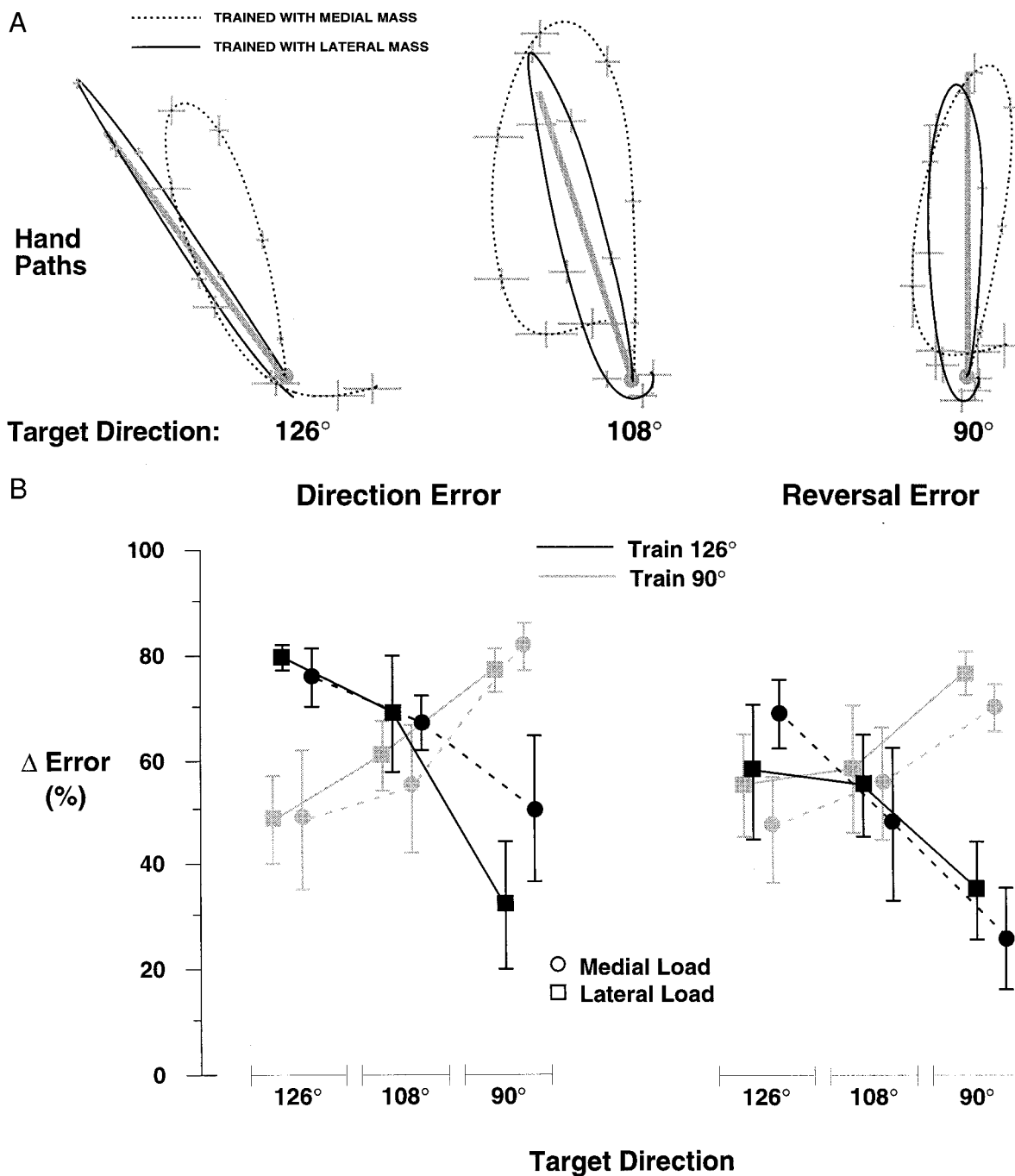


FIG. 8. *A*: averaged hand paths from a single subject who trained with the 126° target. All 10 trials from each condition shown were synchronized to peak tangential hand velocity (V_{max1}). Solid lines, averaged lateral mass trials from the lateral mass training session; dotted lines, averaged lateral mass trials from the medial mass training session. SE bars for the x and y dimensions are shown every 100 ms. *B*: difference in mean error between medial and lateral training sessions averaged across all subjects. Black, data from subjects who trained with the 126° target; gray, data from subjects who trained to the 90° target. Data from trials performed with the medial load are indicated with circles, whereas data from lateral load trials are indicated with squares.

DISCUSSION

Anticipatory control

This study examined the mechanisms underlying control of interaction torques during reaching movements. Subjects first adapted to a novel inertial load, the position of which altered the magnitude of interaction torques at the shoulder and elbow. After adaptation to the medial load, the mass was moved lateral

on pseudorandom surprise trials. In these trials, the initial portion of the muscle torque profiles at the shoulder and elbow remained remarkably similar to that of adapted medial load trials. As a result, subjects made errors in initial movement direction that resulted from uncompensated increases in interaction torque imposed by the new mass configuration. These deviations in the initial direction of hand motion could be attributed to open-looped control mechanisms calibrated to the

intersegmental dynamics of the adapted condition. This was demonstrated using a simple forward simulation that predicted what would have happened had subjects used the torques needed to accurately control the medial mass throughout the surprise trials. The simulation predicted initial direction errors, indicating that the early part of subjects' trajectories resulted from anticipatory processes. These findings support those of previous studies examining adaptation to external coriolis (Lackner and Dizio 1994) and viscous (Gandolfo et al. 1996; Goodbody and Wolpert 1998; Shadmehr and Mussa-Ivaldi 1994) forces applied to the limb during reaching movements. Those studies indicated that during adaptation, the nervous system develops internal models of the applied forces that subsequently are used to specify new movement commands. The current results extend previous findings, indicating that the intrinsic dynamics of the musculoskeletal system itself are controlled through similar anticipatory mechanisms.

Our results support and extend previous findings, indicating that proprioceptive information is needed to control the intrinsic mechanics of the musculoskeletal system. In previous studies of unconstrained reaching (Sainburg et al. 1993) and supported horizontal plane reaching movements (Sainburg et al. 1995), deafferented patients showed large errors in movement direction and curvature that varied with the magnitude of interaction torques. Visual feedback only partially improved movement accuracy, indicating that proprioceptive information is essential for controlling intersegmental dynamics (Ghez and Sainburg 1995; Sainburg et al. 1995). In light of these findings, the results presented here indicate that control of intersegmental dynamics is normally dependent on proprioceptive information to update and maintain neural representations of the musculoskeletal system.

Feedback control

In the surprise trials studied here, differences from the torque patterns of adapted medial load trials emerged as subjects decelerated the hand to reverse movement direction. The occurrence of feedback-mediated responses during movement deceleration is consistent with reports on single-joint movements (Cooke et al. 1985; Forget and Lamarre 1987; Gordon and Ghez 1984). Although elbow joint muscle torque countered interaction torque throughout adapted trials, in surprise trials shoulder flexion deceleration caused elbow flexor interaction torque that was not countered by extensor muscle torque. As a result, the elbow flexed in the early part of the reversal phase, desynchronizing the reversals at the two joints and causing reversal errors. We propose that this prolonged flexor torque was an attempt to compensate for the excessive elbow extension that contributed to initial direction errors. However, because of neural transmission and muscle activation delays, flexor muscle torque was actuated after interaction torque had become flexor. As a result, the sharpness of actual direction reversals was substantially less than that predicted by our forward simulation.

In the final deceleration phase of "return" motion, our forward simulation no longer predicted the trajectory. Instead, muscle torque appeared to be determined by feedback-mediated responses that invariably returned the hand to its starting position. This ability of subjects to return to the starting position despite large trajectory errors suggests that movement

endpoints are achieved by a mechanism that is distinct from trajectory control. For example, Feldman and Bizzi (Bizzi and Abend 1983; Bizzi et al. 1976, 1982; Feldman 1974, 1986) described an endpoint control model in which desired positions are achieved by instantaneously activating antagonistic muscles to specified levels at the beginning of movement. Because of the springlike properties of muscles, the final posture is attained independently of the trajectory, which can vary depending on musculoskeletal and environmental dynamics. Hirayama and coworkers (1993) incorporated a similar postural control mechanism into a two-phase control model in which initial trajectory features result from open-looped control while final position is achieved by coactivation of antagonist muscles. The postural controller used "visual" information about target location to specify levels of stationary motor commands to groups of muscles. Our findings support this type of combined anticipatory and postural controller; however, we expand these ideas to include three distinct mechanisms that operate successively to control rapid reaching movements: first, movements are controlled through anticipatory mechanisms that are adapted to expected mechanical conditions. Second, as sensory feedback becomes available, corrective modifications are made to the predetermined torque profile. If these corrective mechanisms are not calibrated to the current mechanical conditions, they may result in maladaptive responses. Third, the final position of the hand is controlled through postural mechanisms that are less subject to the dynamic conditions of the task.

Learned representations of musculoskeletal dynamics

In the second experiment, we examined whether adaptation to a novel inertial load during movements made in a single direction transfers to affect the accuracy of movements made in a range of directions. We found significant effects of learning over a 36° range either clockwise or counterclockwise from the trained direction. However, as the movement direction diverged from that of training, the effects of training on movement accuracy decreased substantially. This limitation in generalization agrees with previous reports examining generalization of learning rotated visual feedback (Ghahramani et al. 1996; Imamizu et al. 1995) as well as novel viscous force fields applied to the hand (Gandolfo et al. 1996; Goodbody and Wolpert 1998; Shadmehr and Mussa-Ivaldi 1994). The current results extend these findings by showing that the nervous system uses sensory information to develop and recalibrate internal models of the musculoskeletal system itself.

This does not necessitate that the nervous system explicitly models physical parameters such as segment geometries and inertias. In fact, the limitation in generalization suggests that a complete analytic model of the altered inertial system was not developed. Instead, the results presented here are consistent with the computational models of Jordan (Jordan and Rumelhart 1992) and Kawato (Kawato and Gomi 1992a,b) for transforming intended joint kinematics to joint torques. Those authors demonstrated the plausibility of using sensory feedback about movement errors to train the parameters of inverse dynamic models (Jordan and Rumelhart 1992; Kawato and Gomi 1992a,b) that employ neural network algorithms rather than analytic solutions to dynamic transformations. In these schemes, the inverse model allows a desired trajectory to be

transformed to appropriate muscle commands only when the parameters (synaptic weights) of the inverse model are correct. Both authors have employed forward dynamic models through which errors in the trajectory can be backpropagated to yield a motor command error. This command error then is used to train the parameters of the inverse model. The forward model, which transforms intended movement commands into a trajectory, has the advantage of allowing the system to estimate the results of a set of movement commands without actually performing the movement. Discrepancies between predicted and actual trajectories allow training of the parameters in the forward model. These neural network models provide plausible alternatives to exact analytic models and are thus consistent with our findings indicating limited generalization of learning across a range of movement directions.

It is also possible that instead of network or analytic models of the musculoskeletal system, the nervous system may use sophisticated tabular models to control intersegmental dynamics. For example, rules may be used for scaling a template muscle activation pattern developed through trial and error. This is similar to the ideas developed by Gottlieb (1996) suggesting scaling of preselected torque profiles to make movements in different directions under varied speed, load, and distance requirements. Because of the nonlinear and variable relationship between muscle activation and joint torque, it is likely that such rules would govern the relative timing and amplitude of muscle activations across joints. For example, Hasan and colleagues (Hasan and Karst 1989; Karst and Hasan 1987, 1991a,b; Koshland and Hasan 1994) explained agonist and antagonist muscle activations at the initiation of planar arm movements in terms of task and limb geometry. The current results indicate that intersegmental dynamics are controlled by three sequential processes acting in series: movements are initiated through anticipatory mechanisms based on learned representations of musculoskeletal and task-specific dynamics. Later, error corrections based on on-line sensory feedback are followed by positional control mechanisms that determine the final posture for the limb. Further studies are required to determine precisely how anticipatory control is represented and implemented by the nervous system.

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