

## Inter-Joint Coupling Strategy During Adaptation to Novel Viscous Loads in Human Arm Movement

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**Debicki, D. B. and P. L. Gribble.** Inter-joint coupling strategy during adaptation to novel viscous loads in human arm movement. *J Neurophysiol* 92: 754–765, 2004; 10.1152/jn.00119.2004. When arm movements are perturbed by a load, how does the nervous system adjust control signals to reduce error? While it has been shown that the nervous system is capable of compensating for the effects of limb dynamics and external forces, the strategies used to adapt to novel loads are not well understood. We used a robotic exoskeleton [kinematic instrument for normal and altered reaching movements (KINARM)] to apply novel loads to the arm during single-joint elbow flexions in the horizontal plane (shoulder rotation was allowed). Loads varied in magnitude with the instantaneous velocity of elbow flexion, and were applied to the shoulder in *experiment 1* (interaction loads) and the elbow in *experiment 2* (direct loads). Initial exposure to both interaction and direct loads resulted in perturbations at both joints, even though the load was applied to only a single joint. Subjects tended to correct for the kinematics of the elbow joint while perturbations at the shoulder persisted. Electromyograms (EMGs) and computed muscle torque showed that subjects modified muscle activity at the elbow to reduce elbow positional deviations. Shoulder muscle activity was also modified; however, these changes were always in the same direction as those at the elbow. Current models of motor control based on inverse-dynamics calculations and force-control, as well as models based on positional control, predict an uncoupling of shoulder and elbow muscle torques for adaptation to these loads. In contrast, subjects in this study adopted a simple strategy of modulating the natural coupling that exists between elbow and shoulder muscle torque during single-joint elbow movements.

### INTRODUCTION

To achieve accurate limb movements, the CNS must generate appropriate time-varying control signals that account for both limb dynamics and external loads. Several studies have shown that the CNS compensates for limb dynamics (such as interaction torques) in an anticipatory manner (Almeida et al. 1995; Cooke and Virji-Babul 1995; Gribble and Ostry 1999; Koshland et al. 1991b, 2000; Sainburg et al. 1995, 1999). Other studies have shown that, with practice, the nervous system is capable of adapting control signals to account for various kinds of external forces (Conditt et al. 1997; Flanagan and Wing 1997; Hore et al. 1999, 2001; Lackner and Dizio 1994; Malfait et al. 2002; Shadmehr and Mussa-Ivaldi 1994; Tremblay et al. 2003). To reduce the perturbing effects of loads, the CNS must transform kinematic deviations into appropriate changes in descending motor commands. The mechanisms underlying these transformations are not well understood.

There are two broad classes of models that are currently used to predict how the nervous system controls movement: force control models and position control models. Force control models propose that motor commands explicitly specify the time-varying forces that must be generated by muscles to achieve a desired movement. These commands are derived from a desired trajectory in spatial coordinates by the explicit computation of inverse dynamics (Atkeson 1989; Katayama and Kawato 1993; Kawato and Gomi 1992; Kawato et al. 1987, 1990; Schweighofer et al. 1998; Shidara et al. 1993; Uno et al. 1989), forward dynamics (Jordan and Rumelhart 1992; Wolpert et al. 1995), or some combination of inverse and forward dynamics (Bhushan and Shadmehr 1999; Kawato 1999; Wolpert and Ghahramani 2000; Wolpert and Kawato 1998) by neural circuitry that contains a representation (sometimes referred to as an “internal model”) of limb dynamics and external loads.

In contrast, position control models avoid the explicit computation of muscle forces and joint torques. Instead, descending motor commands are positional in nature and specify thresholds for muscle activation (Feldman 1986; Feldman and Levin 1995; Feldman et al. 1990, 1998; Flanagan et al. 1993; Flash and Gurevich 1997; Gribble and Ostry 2000; Gribble et al. 1998; Ostry and Feldman 2003). Changes in thresholds are associated with changes in an equilibrium position of the limb. Muscle forces evolve as a consequence of the interaction of the moving equilibrium position with muscle mechanical properties, limb dynamics, reflexes, and passive tissue properties. Because the motor commands generated by this class of model are positional in nature, there is no requirement for an explicit inversion. Indeed, relatively simple iterative procedures may be used to modify control signals to adapt to limb dynamics and external loads (Flash and Gurevich 1997; Gribble and Ostry 2000).

These two classes of models postulate different mechanisms for adapting to novel loads. In the case of force control models, movement error is used to update the forward and/or inverse models (Jordan and Rumelhart 1992), since they are no longer adequate for the desired movement in the new context. On subsequent movements, the computed forces and torques necessary to control the limb are modified according to the new representation of dynamics. In a recent formulation of a positional control model, a different proposal is made: kinematic error is directly incorporated into the generation of an updated control signal (Gribble and Ostry 2000). Thus in an iterative

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process over a number of trials, changes in control signals for subsequent movements are made in a direction opposite to kinematic errors at each joint.

In this study, we applied a viscous interaction torque to the shoulder joint during single-joint elbow flexions, and in a second experiment, a viscous torque to the elbow joint during single-joint elbow flexions using the kinesiological instrument for normal and altered reaching movements (KINARM) robotic exoskeleton (Scott 1999). In both experiments, the load applied by the robot was to a single joint but generated deviations in movement (with respect to unloaded conditions) at both the elbow and shoulder joints. Force and position control models predict different strategies for adapting to loads applied to a single joint that result in kinematic error at more than one joint. Force control models based on inverse dynamics calculations predict changes in muscle torque only at the joint on which the load is acting (i.e., the shoulder joint in *experiment 1* and the elbow joint in *experiment 2*). If the motor system has available an accurate model of limb dynamics (in the absence of external forces) and the ability to invert this model to compute required torques, then based on the (unadapted) control signals and the resulting perturbed movement kinematics, an explicit model of the external load and hence the required changes in control signals would be computed. The modifications to control signals would then be equal in magnitude and opposite in the direction of the load and would be localized to the joint at which the load was applied.

In contrast, position control models predict that descending commands would initially be modified to correct for the positional deviations occurring at both joints. Thus for loads in this study that produce perturbations at both the shoulder and elbow, changes in commands would initially be made at both joints in the opposite direction of the kinematic deviations. Surprisingly, subjects in these studies adopted a strategy not predicted by either class of model.

## METHODS

### Subjects

Eight subjects participated in each of the two experiments (16 subjects total). All subjects were males, were 22–39 yr old (mean age, 26 yr), were right hand dominant for writing, and did not report any neurological or musculoskeletal impairment. The study was approved by the University of Western Ontario Ethics Review Board, and all subjects gave informed consent.

### Apparatus

Subjects made planar arm movements with their right arm while interacting with the KINARM robotic exoskeleton (Gribble and Scott 2002; Scott 1999). Subjects sat in front of a glass table surface and placed their upper arm and forearm segments into troughs attached to the KINARM mechanical linkages (see Fig. 1A). The level of the chair was adjusted such that the shoulder was abducted 90° from the sagittal plane. The forearm was in a pronated position, and the forearm/hand trough prevented radial-ulnar deviation and wrist flexion. The linkages were adjusted for each subject until the vertical shoulder and elbow axes of the subject were aligned with the linkage joints of the robot. Thus the arm spanned a horizontal plane at the level of the shoulder and the robotic linkages allowed only flexion and extension around vertical axes at the shoulder and elbow joints. Compressed air was forced through pucks attached to the bottom of the linkages, which created a frictionless surface and supported the

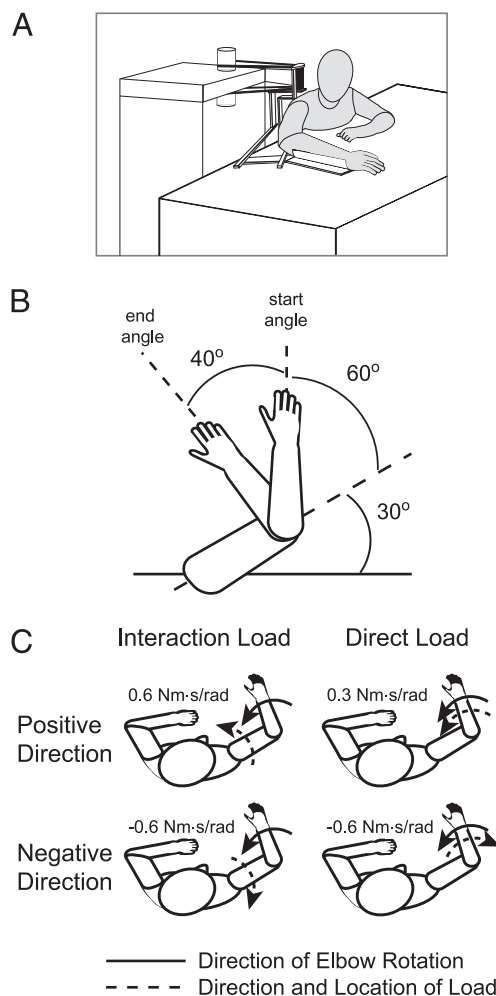


FIG. 1. Apparatus and experimental design. *A*: subjects made reaching movements (constrained to the horizontal plane) to targets placed on a glass surface in front of them while interacting with the kinesiological instrument for normal and altered reaching movements (KINARM) robotic exoskeleton. *B*: orientation of the arm at start and end targets. All movements consisted of a 40° elbow flexion from an initial elbow angle of 60° and shoulder angle of 30° (outside angles). *C*: 2 experiments were performed, each consisting of positive and negative load conditions: interaction load was dependent on elbow flexion but applied to the shoulder ( $\pm 0.6 \text{ Nm} \cdot \text{s/rad}$ ); direct load was also dependent on elbow flexion velocity but was applied to the elbow ( $+0.3/-0.6 \text{ Nm} \cdot \text{s/rad}$ ).

arm against gravity. Torque motors applied torques to the shoulder and elbow joints of the KINARM linkage.

### Movement tasks

Subjects were asked to produce single joint elbow flexions (40°) to targets located on the glass surface. For the start target, the elbow angle was 60°, and the shoulder angle was 30° (outside angles; Fig. 1B). The targets were placed such that the shoulder angle was the same at the beginning and end of the movement. Subjects were not specifically instructed to keep their shoulder joint stationary throughout the movement (i.e., they were free to move their shoulder if they wished). Subjects were required to maintain a target peak elbow angular velocity of 5 rad/s ( $\sim 287^\circ/\text{s}$ ). Subjects received verbal feedback about the velocity of their movement. When movement speed was too slow or too fast, subjects were asked to speed up or slow down accordingly.

The KINARM was used to apply two different types of loads. The magnitudes of both loads were proportional to the velocity of the

elbow joint and were applied in both positive (flexion) and negative (extension) directions (Fig. 1C). In *experiment 1*, the load was applied to the shoulder joint at a rate of  $\pm 0.6 \text{ Nm} \cdot \text{s/rad}$ . Since this load was dependent on the velocity of the elbow but applied to the shoulder, this load is referred to as a viscous interaction load. In *experiment 2*, the load was applied to the elbow and is thus referred to as a direct viscous load. To address the potential safety concern associated with a positive feedback load, we reduced the magnitude of the positive load in *experiment 2* to  $+0.3 \text{ Nm} \cdot \text{s/rad}$  but kept the negative load consistent with *experiment 1* at  $-0.6 \text{ Nm} \cdot \text{s/rad}$ .

In both experiments, subjects performed 225 movements. Subjects experienced five blocks of trials: 25 no-load trials, 75 trials with a positive load, 25 no-load trials, 75 negative-load trials, and finally 25 no-load trials. The order of the positive- and negative-load trials was reversed for three subjects in each experiment. On selected random trials during the load blocks (6 trials/block), single catch-trials (trials in which the load was unexpectedly removed) were given.

### Signal recording

Joint angular positions of the elbow and shoulder were obtained from KINARM motor encoders. All kinematic and electromyographic (EMG) data were sampled at 1,000 Hz and stored on a computer. Surface EMG electrodes (Delsys) were attached to the skin using hypoallergenic adhesive tape (Transpore, 3M). We recorded from eight flexor and extensor muscles spanning the elbow and shoulder joints: biceps brachii (long and short heads); brachioradialis; triceps brachii (lateral and long heads); pectoralis major (clavicular head); anterior deltoid; and posterior deltoid. Because the upper arm was supported against gravity, the anterior deltoid was predominantly quiescent both at rest and during the elbow flexions. For some subjects in *experiment 1* and for all subjects in *experiment 2*, the records of anterior deltoid were replaced with records of a second (sternocostal) head of pectoralis major. Thus we report the EMG activity of pectoralis major (clavicular head) for *experiment 1* and the activity of both clavicular and sternocostal heads of pectoralis major for *experiment 2*. To minimize the possibility of cross-talk, the placement of electrodes was determined using anatomical landmarks and was verified by observing muscle activity on a digital oscilloscope while subjects performed isometric and movement tests.

### Data analysis

Analyses made use of custom algorithms written in MATLAB (The Mathworks). Angular joint positions were low-pass filtered at 15 Hz and differentiated to obtain joint velocities and accelerations. Hand position was calculated using joint angles and segment lengths. Movement onset was defined as the time when tangential velocity of the hand exceeded a threshold of 0.05 m/s. Movement end was defined as the time when tangential velocity of the hand dropped below the velocity threshold of 0.05 m/s.

To quantify elbow and shoulder joint rotation during movement, we determined maximum excursion on a trial-by-trial basis. For the elbow, excursion was defined as the maximum angular displacement between movement onset and end. For the shoulder, excursion was defined as the maximum angular displacement between movement onset and peak tangential velocity. This criterion was established for the shoulder to confine the analysis to the initial portion of the movement.

EMG signals were digitally band-pass filtered (30–300 Hz), full-wave rectified, and low-pass filtered at 15 Hz. We quantified the amount of EMG activity recorded during a time window from 100 ms prior to movement onset to 50 ms post-movement onset. This window captured the initial bursts of elbow and shoulder flexor activity associated with movement before the possibility of voluntary corrections. For each trial we calculated the mean EMG amplitude over this window. For each subject and each muscle, mean EMG amplitude

was normalized to the maximum value observed for that muscle across the experiment. During the measurement window, joint extensors were reciprocally inhibited by the activity of flexors; thus, although we recorded EMG activity from both flexor and extensor muscles, here we report only the activity of the joint flexors. Shoulder and elbow muscle torques were computed using inverse-dynamics equations for a two joint planar link-segment model of the human arm (Gribble and Ostry 1999; Hollerbach and Flash 1982). Torques associated with the dynamics of the KINARM linkages were calculated using a similar model (Scott 1999) and physical constants associated with the KINARM. Statistical tests were carried out using single-factor repeated-measures ANOVA. Posthoc tests (Tukey) were used to test differences between individual means.

## RESULTS

Force control and position control models predict different strategies for adapting to novel external loads. One common feature of both strategies is the predicted uncoupling of the relationship that normally exists between shoulder and elbow muscle torque for unloaded single-joint elbow movements (e.g., Gribble and Ostry 1999; also see Fig. 7). Surprisingly, in this study, subjects adopted a different strategy whereby they maintained this coupling.

### *Experiment 1—viscous interaction loads: kinematics*

Figure 2 shows, for a single subject, kinematic parameters associated with the mean of 10 trials recorded at the end of the no-load condition (thick solid gray traces), the positive load condition (thick solid traces), and the negative load condition (thick dashed traces). Records are aligned on the onset of movement (vertical line). The first trials associated with the positive and negative loads are shown using thin solid and thin dashed traces, respectively. The mean hand path recorded at the end of the positive-load condition deviated away from the subject (compared with the no-load condition), and the hand path for the negative-load condition deviated toward the subject.

At the end of each load condition, deviations in hand paths were not caused by large differences in the rotation of the elbow—angular positions and velocities (Fig. 2, *B* and *D*, respectively) were similar at the end of the two load conditions. Instead, the deviations in hand path were associated with relatively large and persistent perturbations at the shoulder (with respect to no-load trials). Shoulder angular positions (Fig. 2C) and velocities (Fig. 2E) show that during the no-load conditions the shoulder extended briefly during the movement before returning to its original starting position. For the positive load, which acted to reduce the viscous component of the naturally occurring interaction torque, shoulder extension was reduced and turned to flexion part way through the movement before returning to its original orientation. For the negative load, which acted to amplify the magnitude of interaction torque, the shoulder extended more than during the no-load condition.

Initially in each of the load conditions, movements were associated with perturbations at both the shoulder (on which the torque was directly applied) and elbow. The magnitude of these deviations gradually decreased over trials. Figure 3 shows the joint excursion of the shoulder (Fig. 3A) and elbow (Fig. 3B), and peak elbow angular velocity (Fig. 3C) as a



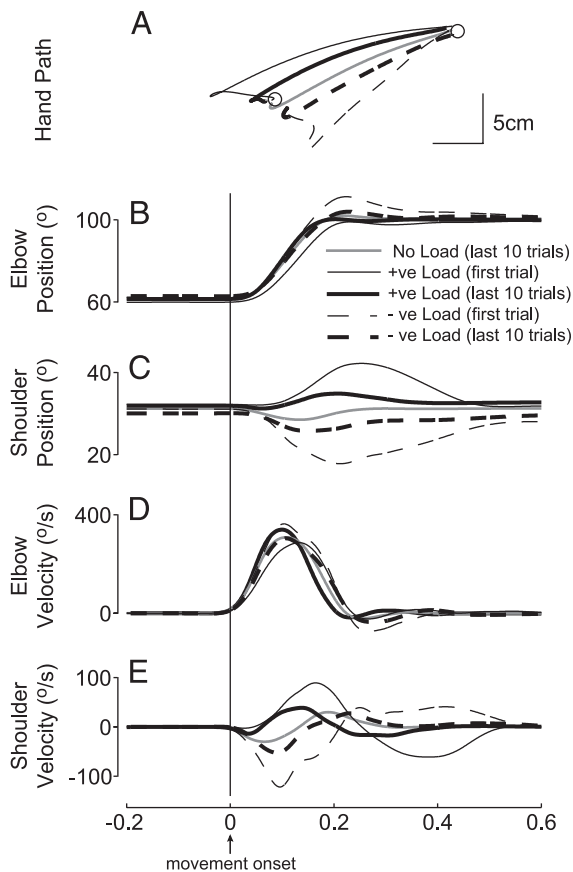


FIG. 2. Kinematics for a representative subject during the interaction torque experiment. Thick gray traces represent mean of the last 10 trials in the 1st no-load condition. Thick solid traces and thick dashed traces represent mean of the last 10 trials in the positive and negative load conditions, respectively. The 1st trial in positive and negative load conditions are also shown (thin solid and dashed lines, respectively). A: hand path (in Cartesian coordinates). B–E: angular positions and velocities of elbow and shoulder joints temporally aligned to movement onset (thin solid vertical line).

function of trials. The initial trials in both negative and positive loads were significantly different from the no-load condition and from each other ( $P < 0.05$ ) for each measure (except for elbow excursion with the positive load;  $P > 0.05$ ). The reference no-load condition value for each measure was calculated as the overall mean of the last 10 trials recorded at the end of each of the three no-load conditions, averaged across subjects. These values are indicated in Fig. 3 by the dashed horizontal lines. Over the course of trials in each load condition, the perturbations observed at both the elbow and shoulder joints decreased such that joint excursions and velocities began to return in the direction of baseline (no-load) values. The majority of changes in joint kinematics appeared to occur within the first 20 trials.

Figure 3 shows catch-trials (the sudden unexpected removal of the load for a single trial) averaged across subjects and plotted as asterisks. The sudden removal of the positive load resulted in greater flexion and velocity of the elbow, as well as extension of the shoulder. The final catch-trial was significantly different from the no-load condition for each of the three kinematic measures ( $P < 0.05$ ). Similarly, shoulder excursion and elbow velocity associated with the final catch-trial in the negative-load condition was significantly different from the

no-load condition ( $P < 0.05$ ). In this case, elbow velocity decreased and the shoulder excursion was near zero.

While there was evidence of kinematic changes at both joints, subjects did not fully counteract the effects of the interaction loads. Statistical tests (repeated-measures ANOVA and posthoc Tukey tests) were performed to assess differences in the mean excursion of the shoulder and elbow, and the peak velocity of the elbow at the end of the load conditions. Figure 4 shows the mean of 10 trials representing the end of the no-load condition (lightly-filled bar), the end of the positive-load condition (solid bar), and the end of the negative-load condition (open bar) across subjects for shoulder excursion, elbow excursion, and peak elbow velocity. There were significant differences in shoulder excursion between all three conditions ( $P < 0.05$ ). Thus, although initial perturbations at the shoulder during elbow movements decreased (as shown in Fig. 3A), the magnitudes of the deviations at the end of the load conditions were still significantly different (in the direction of flexion and extension for positive and negative loads, respectively) from the no-load conditions. At the elbow, there were significant differences in elbow excursion between the negative-load and no-load conditions ( $P < 0.05$ ) and no difference between the positive- and no-load conditions ( $P > 0.05$ ). It should be noted that the difference in elbow excursion between the no-load and negative-load conditions was relatively small ( $3^\circ$  during  $\sim 40^\circ$  flexions). At the end of the loads, there were no significant differences in peak elbow velocity ( $P > 0.05$ ).

In summary, initial exposure to a positive or negative viscous interaction load applied to the shoulder by the KINARM resulted in perturbations at both the shoulder and elbow. Subjects did not fully correct for the effect of the loads. At the end of each of the load conditions, significant deviations remained at the shoulder. In contrast, elbow excursion and peak velocity generally returned to no-load values and any remaining statistically reliable differences were small.

#### Viscous interaction loads: EMG patterns and joint dynamics

The kinematic changes observed during the positive and negative load conditions were associated with changes in recorded muscle activity and computed joint torque. These are shown for a representative subject in Fig. 5. Elbow (Fig. 5A) and shoulder (Fig. 5B) movement in the positive load (thick lines) was associated with an increase in EMG activity of the elbow flexor muscle biceps brachii long head (Fig. 5E), relative to the no-load condition (thin solid trace). This was despite the fact that the load was applied only to the shoulder joint (cf. Fig. 5C). This pattern is not consistent with force control formulations that predict changes only at the shoulder. However, changes in elbow activity are in a direction opposite to the kinematic deviation at the elbow; this is consistent with position control models.

An increase in EMG activity was also observed for shoulder flexor muscle pectoralis major (clavicular head) in the positive load (Fig. 5F). Force control models predict that shoulder flexor activity would decrease in response to the positive load. Position control models also predict that shoulder activity would decrease (in response to the excess flexion associated with the positive load, see Fig. 3A). Instead, the change in muscle activity at the shoulder was in the same direction as the

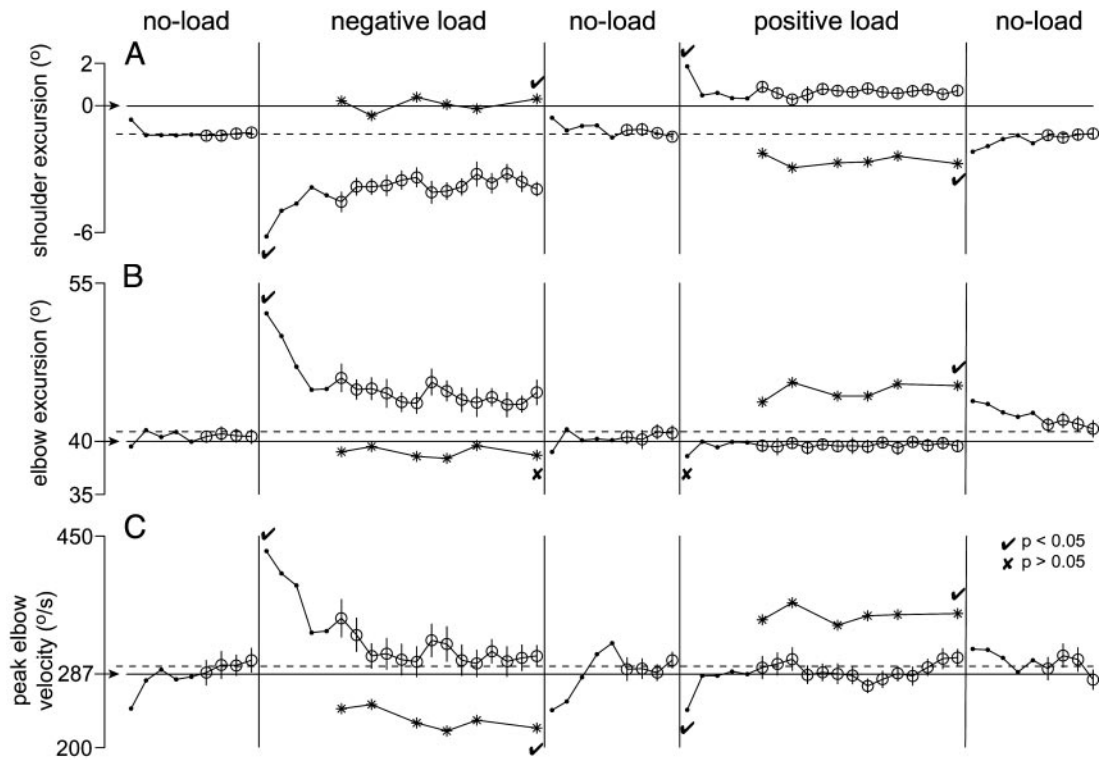


FIG. 3. Joint excursion and velocity averaged across subjects as a function of trials. ●, single trial; ○, mean of 5 trials  $\pm$  SE; \*, single catch-trial. A: shoulder excursion. B: elbow excursion. C: peak elbow joint velocity (see METHODS). Solid horizontal lines, parameter goals (value indicated by rightward pointing arrows); dashed horizontal lines, overall mean of the last 10 trials in each of the 3 no-load conditions for each respective parameter. For each measure, the initial trial and last catch trial in each load condition was compared against the no-load mean (single-factor repeated-measures ANOVA). Significant ( $P < 0.05$ ; ✓) and nonsignificant ( $P > 0.05$ ; X) differences determined by posthoc analysis (Tukey).

observed change in elbow EMG even though this resulted in persistent perturbations at the shoulder joint.

Similarly, for the negative load, a decrease in muscle activity was observed both at the elbow and shoulder. This pattern was also evident in the computed muscle torques, which increased in the positive load and decreased with the negative load, at both the elbow and shoulder (Fig. 5, *G* and *H*).

To quantify the activity of elbow and shoulder muscles, mean EMG amplitude was computed during a time window beginning 100 ms before and ending 50 ms after movement onset (indicated in Fig. 5 using lightly shaded vertical bars). This particular window was used because it captures agonist activity associated with elbow movement and muscle activity associated with the anticipatory compensation of interaction torques at the shoulder (Gribble and Ostry 1999), presumably prior to voluntary corrections. Three elbow flexors (biceps brachii long head, biceps brachii short head, and brachioradialis) and one shoulder flexor (pectoralis major clavicular head) were examined here. In addition, peak muscle torque between movement onset and peak tangential velocity were computed for both the elbow and shoulder.

Statistical tests (repeated-measures ANOVA and posthoc Tukey tests) were conducted to assess differences in mean EMG and muscle torque. Data from one subject was excluded from analysis due to a poor quality EMG recording. Figure 6 shows mean normalized EMG across subjects for elbow and shoulder flexors (where 1.0 was the maximum recorded mean amplitude) and mean peak shoulder and elbow muscle torque in the no-load condition (lightly filled bars), positive-load

condition (filled bars), and negative-load condition (open bars). Two of the three elbow agonists, biceps brachii long head and brachioradialis, showed significant differences between conditions ( $P < 0.05$ ). EMG activity decreased during the negative load in comparison to both the no-load and positive-load conditions. In addition, brachioradialis activity during the positive load was significantly greater than in the no-load condition ( $P < 0.05$ ). EMG activity for pectoralis major clavicular head during the positive load was significantly greater than during the negative load ( $P < 0.05$ ). The overall pattern of changes in both elbow and shoulder muscles was similar to the pattern of computed muscle torques, which were significantly greater during the positive load and less during the negative load when compared with the no-load condition ( $P < 0.05$  for both shoulder and elbow torque).

The similar changes in muscle activity and muscle torque in the different load conditions suggest that the relationship between elbow and shoulder torque remained the same over the course of all movements irrespective of the direction of the interaction load. Indeed, it has been shown that during single joint movements such as these, muscle torque at the nonfocal (stationary) joint varies directly with muscle torque generated at the focal (moving) joint (Almeida et al. 1995; Gribble and Ostry 1999). This same pattern can be seen in this study by examining the trial-to-trial variation in shoulder and elbow muscle torque in the no-load condition. Figure 7 shows peak shoulder muscle torque as a function of peak elbow muscle torque for 45 no-load trials. A clear positive relationship can be seen between shoulder and elbow muscle torque ( $r = 0.98$ ). As

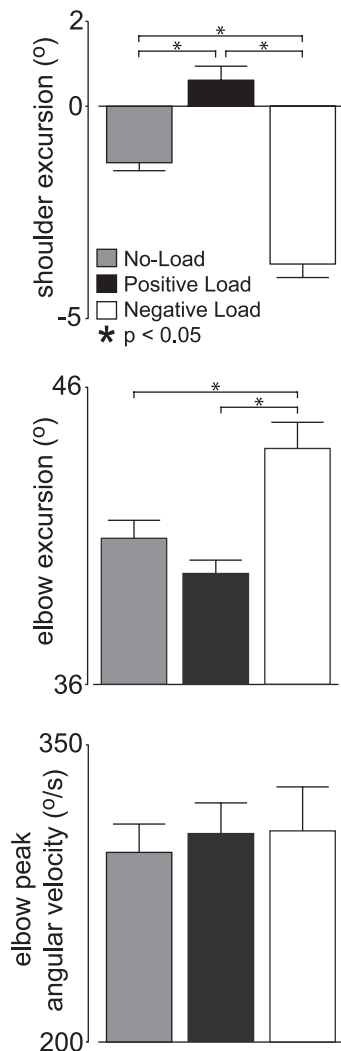


FIG. 4. Means of kinematic parameters for interaction torque experiment averaged across subjects. Means of the last 10 trials in each of the 3 no-load conditions (lightly filled bars), means of the last 10 trials in the positive load condition (solid bars), and negative load condition (empty bars) for shoulder excursion, elbow excursion, and elbow peak angular velocity.

elbow muscle torque varied in magnitude (due to trial-to-trial variation in the velocity of the elbow movement), shoulder muscle torque varied in the same direction. This strong natural coupling between the shoulder and elbow was consistent across all subjects ( $r > 0.97$  for each subject).

To test the idea that shoulder and elbow torque remained coupled during the load conditions, we examined the relationship between shoulder and elbow peak muscle torque. In Fig. 8A, a positive linear relationship can be seen between muscle torques generated at the elbow and shoulder across conditions ( $r = 0.99$ ). The strong positive linear relationship ( $P < 0.01$ ) reveals that this subject maintained the relationship between the generation of muscle torque at the two joints (i.e., when elbow muscle torque decreased, shoulder muscle torque decreased as well). This result was strikingly consistent across subjects, because the correlation coefficients between elbow and shoulder muscle torque were not  $< 0.98$  for any subject ( $P < 0.01$  in all cases). Examining the means across subjects (Fig. 8B) also revealed a strong positive relationship ( $r = 0.98$ ;

$P < 0.01$ ). A similar coupling was observed for shoulder and elbow EMG activity.

Overall, the results of *experiment 1* suggest that, although subjects did change control signals in response to the interaction loads applied by the KINARM, they did not fully counteract their effects. Subjects reduced kinematic deviations at the elbow by adjusting elbow muscle activity. Surprisingly, muscle torque at the shoulder varied with that of the elbow such that the positive relationship that existed during normal no-load movements persisted. These changes are not predicted by force control or position control models.

#### Experiment 2—direct viscous loads: kinematics

To test the generality of the strategy used in *experiment 1*, we tested a second elbow velocity-dependent load (this time applied to the elbow), which we refer to as a “direct load.” As in *experiment 1*, the direct loads initially perturbed both the elbow and shoulder joints. The direction of the perturbations associated with the direct loads was opposite to those associated with the interaction loads. The initial perturbations were generally followed by some return toward no-load values by the end of the load condition. This is shown for trials associated with positive loads (Fig. 9A) and negative loads (Fig. 9B). Lightly filled bars represent the mean of the last 10 trials in the no-load conditions, solid bars represent the mean of the first 10 trials in the load condition, and open bars represent the mean of the last 10 trials in the load conditions.

Statistical tests (repeated-measures ANOVA and posthoc Tukey tests) indicated significant initial deviations of joint excursions at both the elbow and shoulder ( $P < 0.05$ ), in addition to significant changes in peak velocity of the elbow ( $P < 0.05$ ), for both the positive and negative loads. For example, the positive load was associated with significantly greater shoulder extension, greater elbow flexion, and greater elbow flexion velocity (Fig. 9A). At the shoulder, subjects generally reduced the magnitude of joint excursion over the course of the load trials. However, it should be noted that in both load conditions, the reduction in shoulder excursion was quite small (no greater than one-third of the initial deviation of the shoulder). In the positive load condition, the difference in shoulder excursion between the first and last 10 trials was not statistically reliable ( $P > 0.05$ ), and in the negative load, this difference, although small, was statistically significant ( $P < 0.05$ ). Elbow excursion was also significantly different at the end of the load conditions than that recorded during the no-load conditions ( $P < 0.05$ ). However, for both loads, elbow velocity was corrected after the initial perturbation to a point where it was no longer significantly different from the no-load condition ( $P > 0.05$ ).

In summary, the direct loads initially perturbed both shoulder and elbow joint kinematics. As in *experiment 1*, differences in joint excursion at the elbow were relatively small (no more than  $5^\circ$  for  $40^\circ$  movements) by the end of the load conditions, but deviations persisted at the shoulder. Thus, although some changes occurred, subjects again did not fully counteract the effects of the loads.

#### Direct viscous loads: EMG patterns and joint dynamics

Changes in both EMG activity and muscle torque were observed at both joints in response to the direct load at the

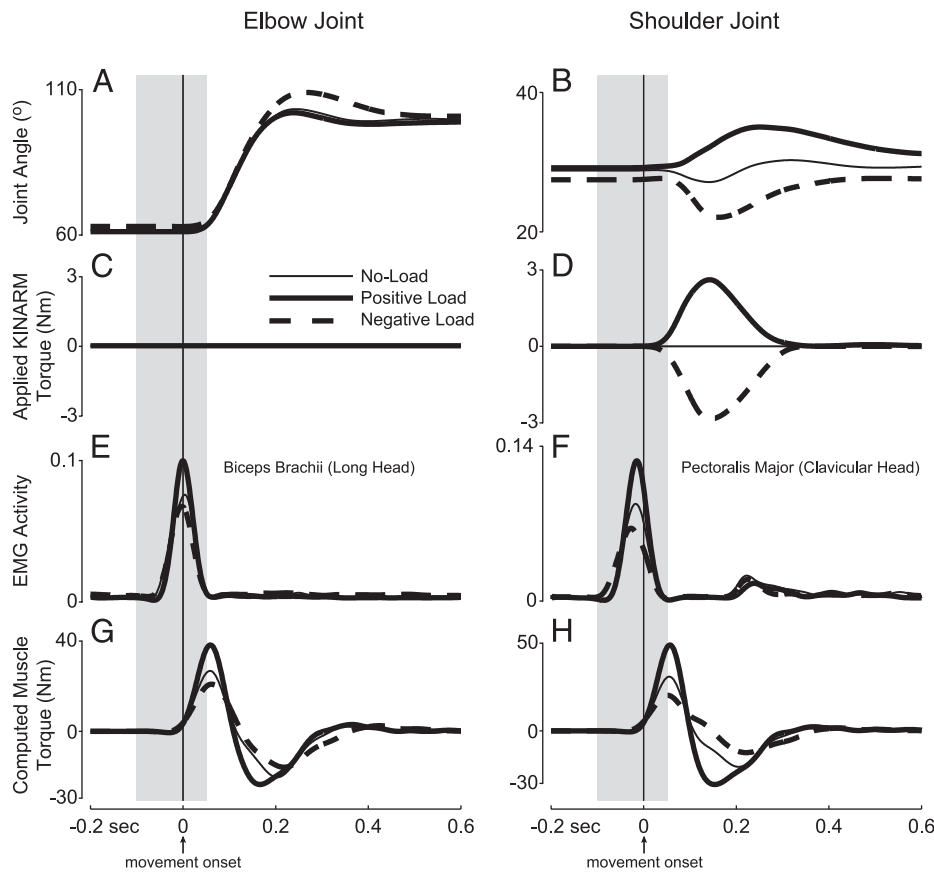


FIG. 5. Mean time-varying kinematic, dynamic, and EMG traces of a representative subject during the interaction torque experiment. *A* and *B*: joint angles. *C* and *D*: torque applied by KINARM. *E* and *F*: EMG activity of biceps brachii long head (elbow flexor muscle) and pectoralis major clavicular head (shoulder flexor muscle). *G* and *H*: computed muscle torque. Traces aligned to movement onset (vertical bars) and averaged over the last 10 trials in each condition. Shaded area indicates time epoch for quantifying EMG amplitude (–100 to 50 ms; see METHODS).

elbow. This is shown for the end of the no-load and load conditions for a single subject in Fig. 10. In comparison to the no-load condition (thin solid trace), the positive load (thick solid trace), which was applied only to the elbow (Fig. 10C), was associated with a decrease in muscle activity in biceps brachii long head (Fig. 10E), brachioradialis (data not shown), and pectoralis major clavicular head (Fig. 10F), as well as a decrease in peak joint torque at both the elbow (Fig. 10G) and shoulder (Fig. 10H). When the negative load was applied to the elbow (thick dashed trace), muscle activity and joint torque at both the elbow and shoulder increased.

As in *experiment 1*, statistical tests (repeated-measures ANOVA and posthoc Tukey tests) were performed to compare the average normalized EMG amplitude during the anticipatory period of movement (–100 to 50 ms with respect to movement onset). This time period is indicated in Fig. 10 by the lightly

shaded vertical bars spanning movement onset. Significant differences were observed between each load condition ( $P < 0.05$ ) for each of the three elbow flexors and two shoulder flexors tested (Fig. 11). Similarly, there were significant differences in the average peak muscle torque at the elbow and shoulder across loads ( $P < 0.05$ ). In each case, muscle activity and muscle torque decreased at both joints during the positive-load condition and increased at both joints during the negative-load condition, relative to the no-load condition.

Once again, the changes in muscle activity and muscle torque associated with the different direct loads suggest that subjects modified elbow and shoulder muscle torque together. We tested the relationship between elbow and shoulder muscle torque to determine whether subjects maintained the coupling across all load conditions as they did in *experiment 1* with the interaction load. Again, it can be clearly seen for a single

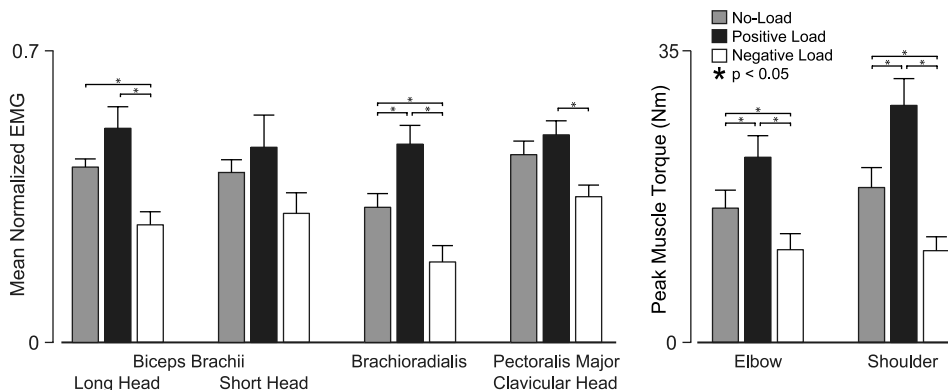


FIG. 6. Mean values of EMG and computed muscle torques averaged across subjects for the interaction torque experiment. Overall mean of the last 10 trials in each of the no-load conditions (lightly shaded bars), means of the last 10 trials in the positive load condition (solid bars), and negative load condition (empty bars).



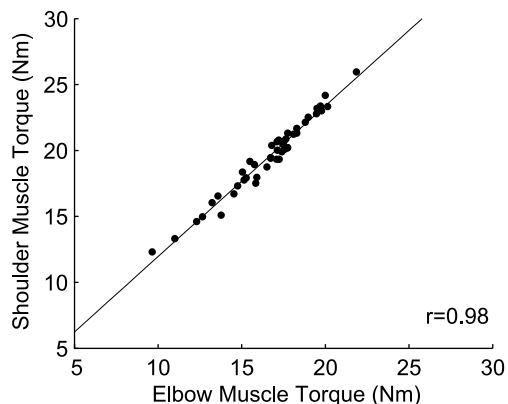


FIG. 7. Correlation between shoulder muscle torque and elbow muscle torque for 45 unloaded trials (the last 15 trials in each of no-load conditions) for a single subject.

representative subject in Fig. 12A that there was a strong positive linear relationship ( $r = 0.995$ ;  $P < 0.01$ ) across loads. For each subject, the correlation coefficient was not  $< 0.95$  ( $P < 0.01$ ), and in the majority of cases, it was  $> 0.98$ . Across subjects (Fig. 12B), elbow and shoulder muscle torque decreased with the positive load and increased with the negative load together, showing a strong linear relationship ( $r = 0.97$ ;  $P < 0.01$ ).

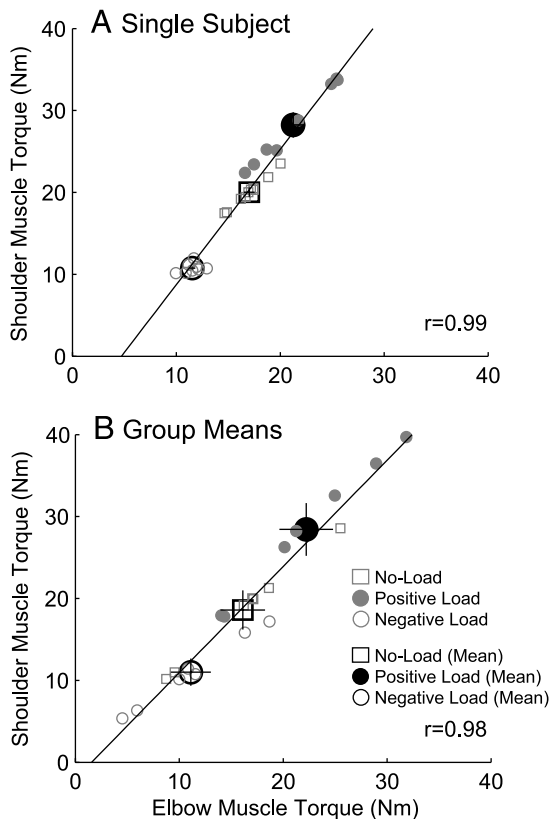


FIG. 8. Correlation between shoulder and elbow muscle torque during the different load conditions in the interaction torque experiment. Light markers represent single trials and larger dark markers represent means  $\pm$  SE. No-load ( $\square$ ), positive load ( $\bullet$ ), and negative load ( $\circ$ ) conditions. Linear regression line fit to single trial values. A: single representative subject. B: means across subjects.

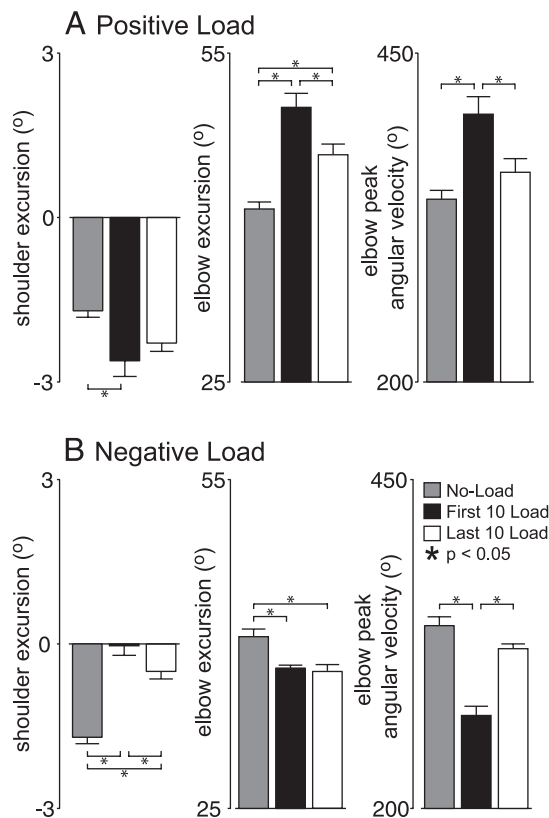


FIG. 9. Mean kinematic parameters across subjects for the direct load experiment. Overall mean of last 10 trials across the no-load conditions (lightly shaded bars); mean of 1st 10 trials (solid bars), and mean of last 10 trials (empty bars) for the positive load (A) and negative load (B) conditions.

DISCUSSION

The goal of this study was to test two current models of how the nervous system adapts to novel external loads. Force control models postulate that the nervous system explicitly computes the forces required to execute a desired movement based on a representation of dynamics. According to these formulations, it would be predicted that, to compensate for a novel external load, a representation of the load would be established, and the necessary change in control signals would be computed to match and counter it. In contrast, position control models postulate that the nervous system does not explicitly compute dynamics. Instead, control signals are positional in nature and specify a time-varying series of equilibrium positions (or muscle activation thresholds) that result in the desired movement trajectory. This class of models predicts that adaptation to novel loads occurs by incorporating kinematic error (positional deviations) directly into the updated control signal (Gribble and Ostry 2000). Although both classes of models predict that the nervous system can fully compensate for loads (i.e., they both predict a convergence back to no-load kinematic patterns), each formulation makes a unique prediction as to how this solution is reached.

We tested the strategies predicted by these two proposals by applying two different viscous loads to the arm as subjects performed single-joint elbow flexions. In *experiment 1*, an interaction load was applied to the shoulder (that was dependent on elbow flexion velocity), and in *experiment 2*, a direct viscous load was applied to the elbow (also dependent on



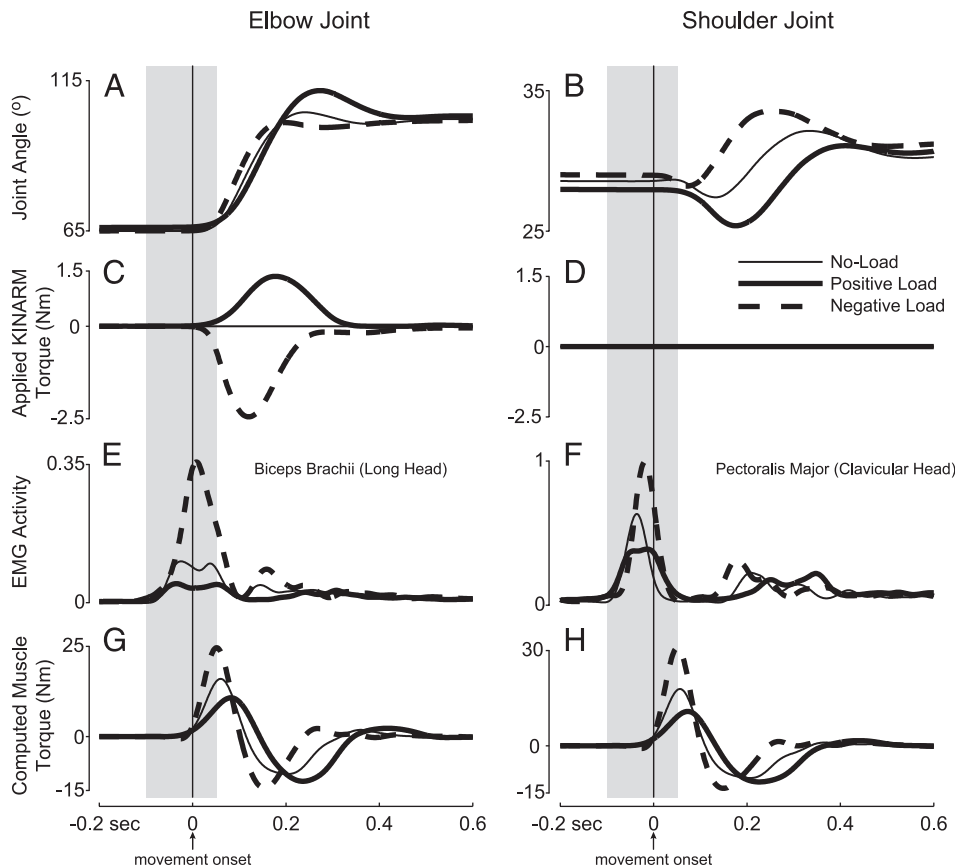


FIG. 10. Mean time-varying kinematic, dynamic, and EMG traces from a representative subject during the direct torque experiment. Same format as Fig. 5.

elbow flexion velocity). Surprisingly, subjects did not fully correct for the effects of the loads. Instead, for both the interaction and direct loads, subjects tended to correct for errors in kinematics at the elbow joint by changing the magnitude of flexor muscle torque at the elbow. In both experiments, subjects also changed muscle torque at the shoulder. However the change in shoulder muscle torque was always in the same direction and proportional to the change in elbow muscle torque. Subjects adopted a strategy whereby they maintained the relationship between the shoulder and elbow that normally exists during unloaded conditions (e.g., Fig. 7; also see Gribble and Ostry 1999). Both force control and position control models predict an uncoupling of this relationship. In contrast, every subject exhibited a strong adherence to the natural coupling between the two joints. Therefore subjects did

not converge to the solution predicted by either of the models. Subjects adopted a simple strategy of modulating the pre-existing (no-load) relationship between the elbow and shoulder such that elbow kinematics were corrected even if this resulted in persistent perturbations at the shoulder.

Why did subjects adopt this simple strategy? One possibility is that they attributed the load as being dependent on the motion of the wrong joint. Singh and Scott (2003) proposed that, in cases where a load is highly correlated with the kinematics of more than one joint, the nervous system employs a default strategy in which it attributes the load as being dependent on the joint on which it is applied (i.e., a mapping of motor action to sensory feedback). The interaction load is directly dependent on the velocity of the elbow; however, perhaps the nervous system misattributed the load as being

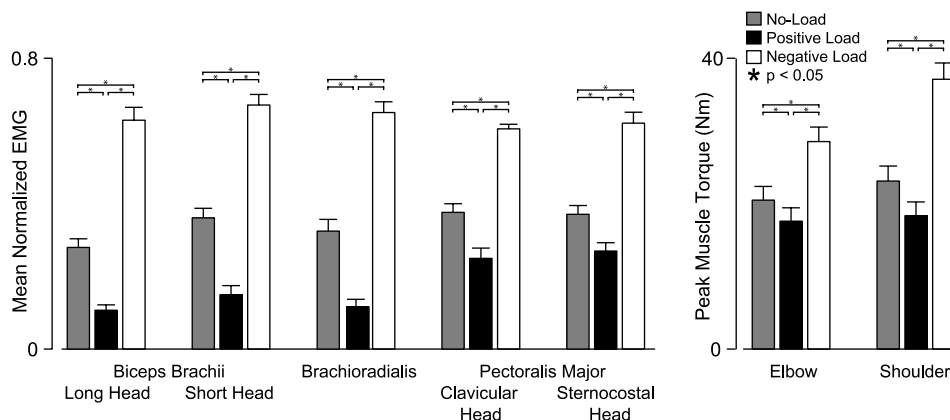


FIG. 11. Mean values of EMG and computed muscle torques across subjects for the direct torque experiment. Same format as Fig. 6.

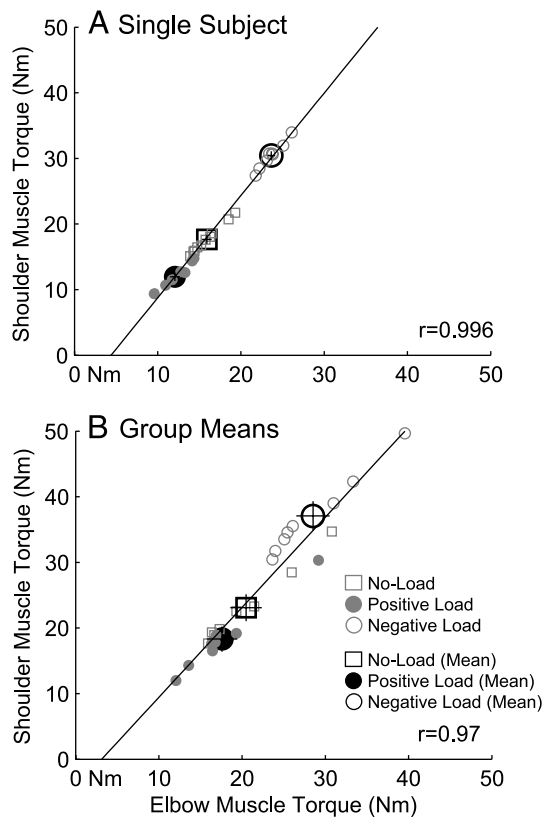


FIG. 12. Correlation between shoulder and elbow muscle torque during the different load conditions in the direct torque experiment. Same format as Fig. 8.

dependent on the velocity of the shoulder (since the load was applied to the shoulder). This appears to be unlikely. Even though there was some rotation of the shoulder during unloaded conditions, this rotation was minimal (see Figs. 2, 3A, and 4). Singh and Scott (2003) found that the misattribution of applied torque was maximal when the desired movement required equal rotation of both joints, whereas the nervous system appropriately associated the load when the kinematic relationship between the two joints became less correlated. For the movements performed in this study, the elbow and shoulder were uncorrelated, thus the nervous system should be able to correctly attribute the load. Furthermore, even if subjects did misattribute the load, we would again predict a different strategy than the one observed. If the nervous system misattributed the negative interaction load as being dependent on shoulder extension, it would be expected that shoulder flexor muscles would increase their activity to oppose the load. However, this was not the case because for negative loads, shoulder flexor muscles decreased their activity. Finally, the nervous system would not misattribute the direct load since it was both applied to, and dependent on, elbow velocity.

Another possibility is that subjects were trying to avoid contact with the arm troughs of the KINARM. This may explain why in the interaction torque experiment changes in shoulder torque were in the same direction as the load direction. However, subjects consistently increased muscle torque at the elbow joint during the direct load experiment to resist the negative viscous load, which would have increased the contact force between the forearm and the forearm trough. This sug-

gests that subjects were not actively trying to avoid surface contact with the structure of the exoskeleton.

These results share some similarities with the “linear synergy” proposal of Gottlieb et al. (1996a, 1997). Their proposal is that, for reaching movements where there is no constraint on the path that the hand must follow, the nervous system uses a natural organizing principle for reducing degrees of freedom, which takes the form of a linear correlation between time-varying muscle torques at the shoulder and elbow (Gottlieb et al. 1996a,b, 1997; Zaal et al. 1999). For the single movement studied here, the data appear consistent with this idea (see Figs. 5 and 10). A strong relationship between shoulder and elbow muscle torque has been observed in a variety of other single-joint and multi-joint reaching movements in unloaded conditions (Almeida et al. 1995; Gribble and Ostry 1999; Koshland et al. 1991b), as well as in studies of reflex responses to external perturbations (Koshland and Hasan 2000; Koshland et al. 1991a).

In the absence of specific instruction to actively keep the shoulder stationary throughout the movement, it is possible that under load conditions, subjects were not interested in generating movements similar to those in unloaded conditions. Rather, it is possible that the nervous system was interested in maintaining the proportionality between shoulder and elbow muscle torque by scaling together muscle activity of shoulder and elbow flexor muscles in response to the applied loads. This maintenance of inter-joint coupling was sufficient for accomplishing the task. Even though subjects did not eliminate movement error at both joints, subjects did reduce overall error during the course of adaptation and were generally successful in reaching the target. In particular, subjects were able to maintain the target elbow velocity within the required range.

The majority of changes in kinematics occurred within the first 20 trials after the initial exposure to the load (see Fig. 3). Even when subjects were given more trials to adapt to the loads, it appears they did not change this strategy. Additional data were collected in *experiment 1*, in which the number of trials in the “load” block was doubled. Extending the number of these load trials did not affect the results.

The coupling of muscle torque between the shoulder and elbow is not a by-product of anatomical constraints (e.g., due to biceps brachii, which may produce flexor torque at both elbow and shoulder joints since it is a biarticular muscle). Behavioral evidence suggests that subjects use inter-joint coupling when making unloaded and unconstrained arm movements, but when required to do so, subjects are capable of reproducing prescribed kinematic trajectories by generating uncoupled patterns of muscle torque (Gottlieb et al. 1996a). Thus the principle of linearity between muscle torques at the shoulder and elbow is a constraint chosen by the nervous system and not one necessarily imposed by biomechanical considerations. In addition, for movements of the arm in the horizontal plane, it has been shown that biceps brachii activity tends to be related more to elbow motion than shoulder motion (Gribble and Ostry 1998, 1999; Osu and Gomi 1999). Osu and Gomi (1999) reported a higher co-variation between biarticular muscles and monoarticular muscles of the elbow than monoarticular muscles of the shoulder. The authors postulated that this relationship with elbow motion could have been due to different muscle moment arms associated with each joint. This is consistent with the morphometric analysis of the moment

arms of shoulder and elbow muscles in *Macaca mulatta* by Graham and Scott (2003), who found that vectors representing moment arms of biceps brachii (long and short heads) tended to be oriented toward the elbow rather than toward the shoulder. Osu and Gomi (1999) also discussed the possibility that a synergy exists between biarticular and monoarticular muscles of the elbow. Indeed, in the current study, we found that the activity of brachioradialis consistently changed in the same direction as that of biceps brachii (Figs. 6 and 11). This suggests that the correlation between elbow and shoulder muscle torque is not solely a consequence of the action of biarticular muscles. The consistent involvement of a monoarticular elbow flexor (brachioradialis) and shoulder flexor (pectoralis major) indicates an added active contribution to the total joint muscle torque beyond that generated by biceps brachii alone.

Data from neurophysiological studies suggest a possible neural basis for the inter-joint coupling strategy reported here. In experiments with awake, behaving monkeys McKiernan et al. (1998) studied the projections of corticomotoneuronal cells to proximal and distal limb muscles using spike-triggered averaging. Nearly one-half of the cells examined produced postspike effects in both proximal and distal muscles (similar results also were reported for cells in the red nucleus, see Belhaj-Saif et al. 1998; also see Gibson et al. 1985; van Kan et al. 1993). In one case, individual cells were found that produced postspike facilitation in both single-joint shoulder (pectoralis) and elbow (brachialis) muscles. This pattern of projection from motor cortex to arm muscles, if at all general, may provide a mechanism by which a coupling between shoulder and elbow muscles may be achieved. Similarly, in electrophysiological recordings in primary motor cortex, both in postural tasks (Cabel et al. 2001) and studies of arm movements in the presence of novel loads (Gribble and Scott 2002), it was found that in a large proportion of motor cortex neurons examined, neural discharge was related to joint torques at both shoulder and elbow joints. Moreover, a small population of neurons was sensitive only to torque at both joints and not to torques at either joint individually. It should be emphasized, however, that the corticomotoneuronal system only accounts for a relatively small proportion of overall descending neural drive. Other systems (both cortical and spinal) presumably play a major role in the coordination of muscles at multiple joints.

It should be noted that we are not proposing that the inter-joint coupling strategy observed here is the only way in which the nervous system adapts to novel loads. There are many examples of the ability of the nervous system to adapt to loads that could not have been accomplished without uncoupling the relationship between elbow and shoulder torque. In these experiments, subjects only experienced the interaction and direct loads in a limited context (one single-joint motion). The possibility exists that with the opportunity to gain additional information about the loads (e.g., by moving in multiple directions) other adaptation strategies may be employed.

In summary, when faced with the task of adapting to novel velocity-dependent loads, subjects adopted a simple strategy whereby they scaled the normally occurring coupling between shoulder and elbow muscle activity.

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