Supplemental Data

Long-Latency Reflexes of the Human Arm Reflect an Internal Model of Limb Dynamics

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Supplemental Experimental Procedures

The following text and figures will further elaborate on the methods used and results presented in the main text. Figures S1–S3 support Figures 1–3 in the main text by showing the high degree of experimental control we achieved with joint-based perturbations and presenting the results of a different shoulder muscle (shoulder flexor, pectorlis major). Figures S4–S6 support Figure 4 in the main text. These figures explain how we estimated the limb's inertia at different configurations and chose the requisite torque to induce similar motion at the two configurations and show complementary results of a different shoulder muscle (shoulder flexor, pectorlis major).

Subjects

Eighteen subjects (11 males and 7 females, median age = 25 years) participated in one of several sessions that lasted 60–90 min each. One session comprised the first and second experiment; ten subjects participated in experiment 1, whereas eight subjects participated in experiment 2. Ten subjects participated in experiment 3. Lastly, ten subjects participated in an associated experiment on postural maintenance. The procedures were approved by the ethics committee of Queen's University, and subjects were paid for their time.

Apparatus and Task

As described in previous studies [S1, S2], we utilized a robotic exoskeleton (KINARM, BKIN Technology, Kingston, ON) that permits flexion and extension movements of the shoulder and elbow in the horizontal plane and can selectively apply torques to each joint. The device is also coupled to a virtual-reality system for displaying the target and hand-aligned cursor; a cloth bib and metal partition obscured any direct vision of the arm.

All trials for the reflex experiments proceeded in a similar order:

1. A background shoulder load was slowly ramped from 0 to ±2 Nm to elicit steady-state activity of the shoulder extensor muscle or shoulder flexor muscle.
2. Subjects stabilized their hand-aligned cursor (0.4 cm radius) within the center of a small target area (2 cm radius) for a random interval (500–3500 ms). Subjects were instructed not to anticipate the time or direction of the impending perturbation. During this period, the cursor was extinguished so that subsequent corrective responses were guided entirely by proprioception.
3. The perturbation load was then rapidly applied (sigmoid-interpolation over a 10 ms window to lessen the high-frequency ring). The direction of this perturbation was randomly varied between trials.
4. The new load level was maintained for a fixed interval (1000 ms) while subjects needed to return to the target within 500 ms and remain within it. The circle was filled green or red if their performance was accurate or inaccurate, respectively.
5. Finally, the load slowly ramped back to zero (500 ms) and remained at zero for a brief intertrial period (1000 ms).
6. Thirty repeats were collected for each perturbation condition, see below.

Experiment 1

This experiment applied a single-joint perturbation to induce induced similar amounts of shoulder motion but different amounts of elbow motion (see Figure S1). For the shoulder extensor muscle described in the main text, we alternately imposed 2 Nm shoulder-flexor torque and 2 Nm elbow-extensor torque to induce the same level of shoulder flexion and different amounts of elbow extension. Sign-reversed perturbations were used for studying the shoulder flexor muscle: 2 Nm shoulder extension torque and 2 Nm elbow flexor torque.

Experiment 2

This experiment applied a multijoint perturbation to create single-joint motion (2 Nm shoulder-flexor/2 Nm elbow-flexor torque or 2 Nm shoulder-extensor/2 Nm elbow-extensor torque). The two perturbations induced substantial elbow flexion or extension motion but negligible shoulder motion (see Figure S1).

Both experiments 1 and 2 utilized a target whose origin was shoulder angle = 45° and elbow angle = 75°; shoulder angle is relative to the frontal plane, whereas elbow angle is relative to the forearm and upper arm; 0° is full extension.

Experiment 3

This experiment applied multijoint perturbations to induce single-joint motion of the elbow while the limb was either near the body (shoulder angle = 45°, elbow angle = 120°) or far from the body (shoulder angle = 45°, elbow angle = 45°) (see Figure S4). Also note that this property explains why the limb configuration used in experiments 1 and 2 (shoulder angle = 45° and elbow angle = 75°) allowed equal levels of shoulder and elbow torque to induce similar amounts of shoulder motion or no shoulder motion.

Here is one form of the dynamic equations for the two-link arm [S3]:

τ = joint torque; Θ = joint angle; l = link length; m = mass; I = moment of inertia; and subscripts e and s = elbow & shoulder.

$$\tau_e = \ddot{\theta}_e\left(I_e + \frac{m_e l_e^2}{4}\right) + \ddot{\theta}_s\left(I_e + \frac{m_e l_e^2}{4} + \frac{m_e l_e l_s}{2}\cos(\theta_e)\right) + \left(\frac{m_e l_e l_s}{2}\dot{\theta}_s^2\sin(\theta_e)\right)$$

$$\begin{aligned}\tau_s = {} & \ddot{\theta}_s\left(I_s + I_e + \frac{m_s l_s^2 + m_e l_e^2}{4} + m_e l_s^2 + m_e l_e l_s\cos(\theta_e)\right) \\ & + \ddot{\theta}_e\left(I_e + \frac{m_e l_e^2}{4} + \frac{m_e l_e l_s}{2}\cos(\theta_e)\right) - \left(\frac{m_e l_e l_s}{2}\dot{\theta}_e^2\sin(\theta_e)\right) - \left(m_e l_e l_1\dot{\theta}_e\dot{\theta}_s\sin(\theta_e)\right)\end{aligned}$$

Below, we simplify the equations by removing the velocity-dependent terms (because of their low values immediately after the perturbation) and combining all constants except those involving joint angles.

$$\tau_e = \ddot{\theta}_e(A_1) + \ddot{\theta}_s(A_1 + A_2\cos(\theta_e))$$

$$\tau_s = \ddot{\theta}_s(A_3 + 2A_2\cos(\theta_e)) + \ddot{\theta}_e(A_1 + A_2\cos(\theta_e))$$

This helps to clarify that torque at one joint depends on motion at both joints. Furthermore, elbow angle (but not shoulder angle) has an influence on intersegmental dynamics that increased with elbow extension; 0° is defined as full elbow extension. For the two elbow angles we used (45° and 120°), the interaction torque is smaller for the flexed posture than the extended posture: $(A_1 - 0.5A_2)$ versus $(A_1 + 0.7A_2)$.

To induce similar motion at these two arm postures, we imposed two different joint-torque combinations that were tailored for each subject on the basis of an estimation of their limb's inertia: (1) We imposed eight torque pulses of equal magnitude (±2 Nm) and equally distributed in shoulder-elbow torque space; (2) we determined the covariance matrix between joint torque and joint motion at 50 ms; and (3) we used the inverse of this covariance matrix to select the joint torques needed to displace the elbow by 1° within 50 ms. This amount of induced elbow motion was generally smaller than in experiment 2 because the elbow was closer to its limit of motion and we wished to avoid the subject reaching this limit or changing their motor strategy. For inducing this amount of elbow motion, the mean shoulder torque across subjects was ± 1.7 Nm and ± 0.92 Nm in the extended and flexed elbow posture, respectively. The mean elbow torque was ± 1.29 Nm and ± 1.44 Nm in the extended and flexed elbow posture, respectively.

Note that the procedures in experiments 1–3 were used to study posterior deltoid/shoulder extensor (shown in the primary document) and pectoralis major/shoulder flexor.

Associated Experiment

The relatively short perturbation durations of experiment 1 and 2 precluded long periods of stabilization for examining steady-state postural responses. Instead, we used the information from a separate study on postural maintenance—similar to a previous study with nonhuman primates [S4]—in which subjects adopted a stable posture (shoulder angle = 45° and elbow angle = 75°) against eight combinations of shoulder-elbow loads: shoulder flexion, shoulder extension, elbow flexion, elbow extension, shoulder flexion-elbow flexion, shoulder extension-elbow extension, shoulder extension-elbow flexion, and shoulder flexion-elbow flexion. Three magnitudes (±1, 2, and 3 Nm) of each load combination were employed for a total of 24 conditions, plus a no-load condition. Three trials of 3 s each were collected for each condition.

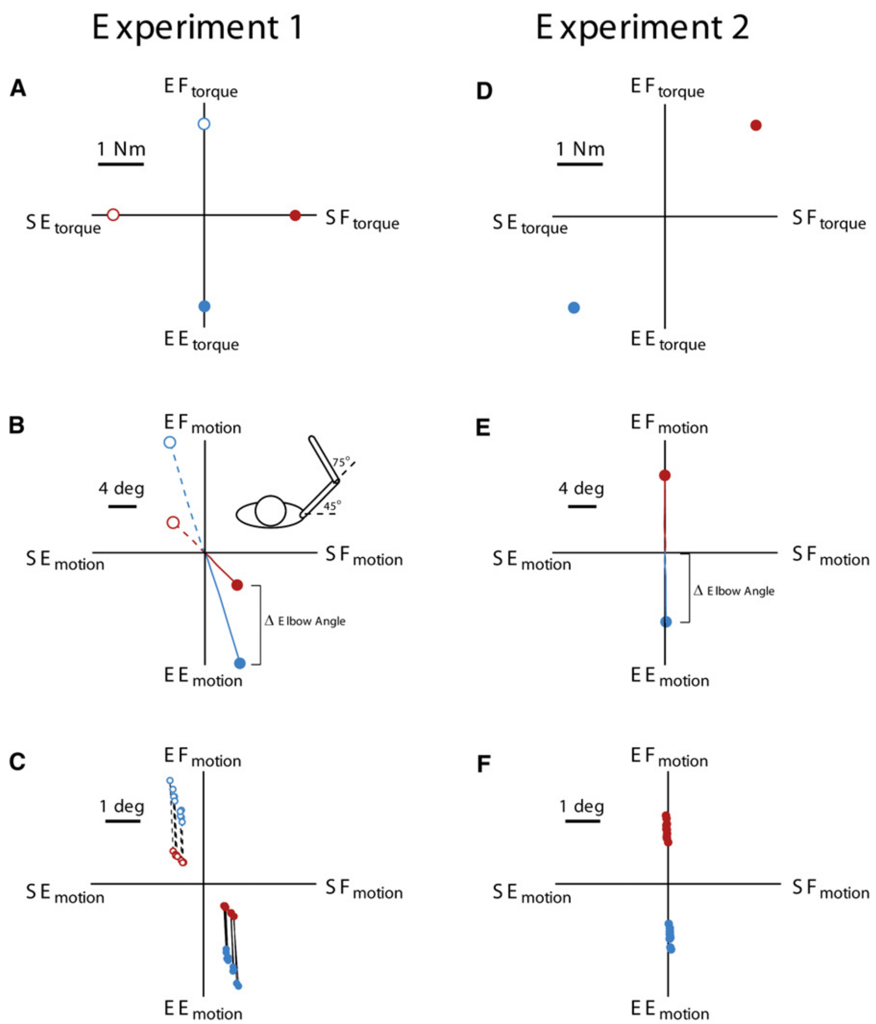

Figure S1. Joint Torques and Resulting Motion for Experiments 1 and 2

(A) Imposed joint torques during experiment 1. Four single-joint torques of equal magnitude were utilized: Shoulder flexion (SF) and elbow extension (EE) are filled red and blue circles; shoulder extension (SE) and elbow flexion (EF) are unfilled red and blue circles. This color scheme is also utilized in (B) and (C).

(B) Mean joint trajectories from the representative subject of experiment 1: "equal shoulder motion and different elbow motion." Shoulder-elbow trajectories are traced in joint space from 0–100 ms postperturbation with circles at 100 ms; note that the origin is at the starting limb configuration of 45° shoulder and 75° elbow angle (see inset). The solid joint trajectories in the bottom-right quadrant resulted from shoulder-flexor torque and elbow-extensor torque and have similar amounts of shoulder motion but different amounts of elbow motion (see Δ elbow angle); we used these conditions to study the shoulder extensor muscle as they stretched that muscle by an equal amount. The dashed joint trajectories in the upper-left quadrant resulted from shoulder-extensor torque and elbow-flexor torque and show similar amounts of shoulder extension but different amounts of elbow flexion; we used these conditions to study the shoulder flexor muscle as they stretched that muscle by an equal amount. Note the straightness of the shoulder-elbow trajectories over time such that similar kinematic inputs are available throughout the reflex period.

(C) Snapshot of each subject's joint motion at 50 ms postperturbation with thin lines connecting their data across conditions, same color format as above. Although there is a significant spread of data across subjects, each subject has nearly identical shoulder motion in the paired conditions as indicated by the nearly vertical lines. For the two paired trajectories (bottom-right pair and upper-left pair), the mean change in shoulder angle across conditions was ~4% of the mean change in elbow angle across conditions. (A)–(C) relate to experiment 1.

(D) Imposed joint torques during experiment 2. Two multijoint torques of equal magnitude were utilized: shoulder flexion-elbow flexion (SF-EF) is a filled red circle; shoulder extension-elbow extension (SE-EE) is a filled blue circle. This color scheme is also utilized in (E) and (F).

(E) Mean joint trajectories from the representative subject of experiment 2. Thin lines show joint motion from 0–100 ms postperturbation (open circles at 100 ms) has significant elbow flexion (red) or elbow extension (blue) (see Δ elbow angle). However, the minimal amount of shoulder motion would lead to little stretch or shortening of the shoulder muscles.

(F) Snapshot of joint motion at 50 ms postperturbation, same color format as above with circles denoting an individual subject's data. Despite the absolute spread of data across subjects, each subject has very small shoulder motion compared to their elbow motion, as indicated by the clustering about the vertical axis. The mean change in shoulder angle within a condition was ~3% of the mean change in elbow angle within a condition. (D)–(F) relate to experiment 2.

Muscle Recording

We recorded surface EMG from two single-joint shoulder muscles of each subject: posterior deltoid and pectoralis major. The skin surfaces were first lightly abrased with alcohol. A two-bar electrode (DE-2.1 Delsys, Boston, MA) was then coated with electrode gel and affixed to the muscle belly while the ground electrode was placed on the subject's ankle.

Data Analysis

Angular position of the shoulder and elbow was lowpass filtered (25 Hz, 2-pass, sixth order Butterworth). Processing of the EMG signals included an amplification (gain = 10 K), bandpass filter (20–450 Hz), digital sampling at 1000 Hz (PCI 6071E, National Instruments, Austin, TX), and normalization by each muscle's mean activity prior to perturbation (−100 to 0 ms).

We considered several periods of reflex activity on the basis of earlier reports [S5, S6] and our pilot studies: R1 = 20–45 ms; R2 = 45–75 ms; and R3 = 75–100 ms. The voluntary response was considered to occur at 120–180 ms postperturbation.

We utilized several analyses to examine the patterns of reflex action. Our t tests determined changes from baseline and changes between conditions after subtracting away baseline ($p < 0.05$). We also examined the coordinated activity across the first two experiments by using a planar regression. Accordingly, the activity in a particular reflex period is regressed against the shoulder-elbow torques that were imposed, two from each experiment; the shoulder and elbow slope coefficients from the resulting plane fit describe the relative sensitivity to shoulder and elbow joint torque [S4]. This so-called preferred torque direction (PTD) was measured counterclockwise such that preferred shoulder flexion, elbow flexion, shoulder extension, and elbow extension torques occur 0/360°, 90°, 180°, and 270°, respectively.

The measured PTDs of the reflex, voluntary, and postural periods were judged against two contrasting predictions: pure shoulder torque or pure shoulder motion. As described above, a PTD for pure shoulder torque would be at 0/360° or 180° for encoding shoulder flexion or extension torque, respectively. The prediction of pure shoulder motion is the combination of joint torques that result in the greatest amount of measured shoulder motion, i.e., a plane fit of the shoulder motion to the applied shoulder and elbow torques. The resulting PTDs of 313° and 133° are quite close to the ideal case (315° and 135°) in which single-joint perturbations (matched shoulder and elbow) induce the exact same shoulder motion and multijoint

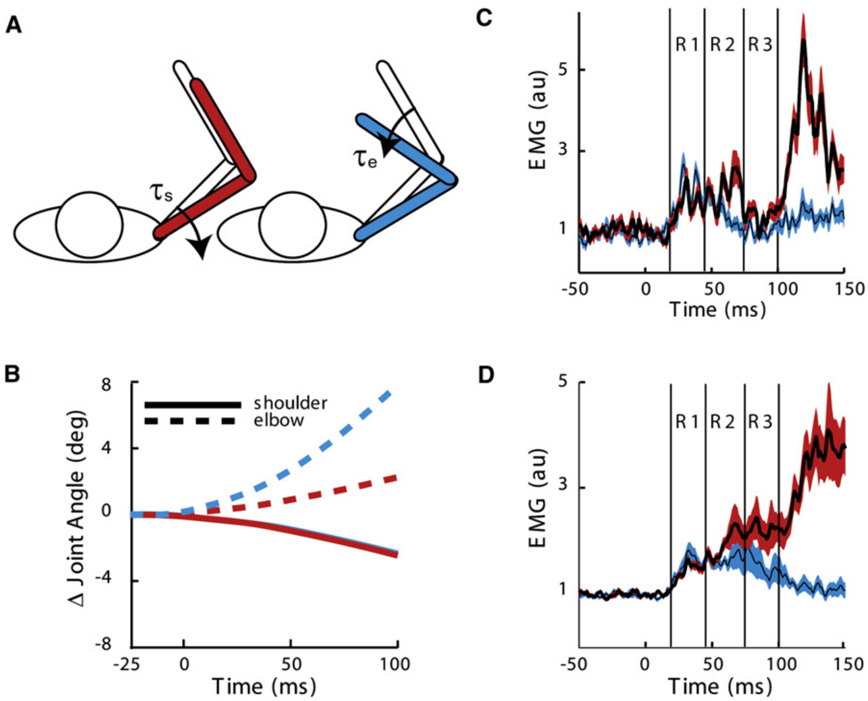

Figure S2. Reflex Activity of the Shoulder Flexor Muscle after Experiment 1: "Equal Shoulder Motion and Different Elbow Motion"

(A) Depiction of a subject's arm motion after the shoulder torque perturbation (red) or an elbow torque perturbation (blue). Data are taken from a representative subject at 50 ms postperturbation (scaled by 15× for clarity).

(B) The joint motion is shown over time revealing that shoulder motion is highly similar, whereas the elbow motion is substantially different. Both the shoulder (solid lines) and elbow (dashed lines) angles are relative to the initial limb configuration with flexion and extension motion being positive and negative, respectively.

(C) Evoked muscle activity from the subject's pectoralis major (±SEM) normalized to the preperturbation baseline. Vertical lines delineate the reflex periods (see "Data Analysis" in Experimental Procedures).

(D) Group data for the same muscle, same format. Note the similar evoked response to the two perturbations during the R1 period and the subsequent greater response to the shoulder torque in the R2, R3, and voluntary periods. This figure parallels Figure 1 in the main text.

perturbations induce exactly no shoulder motion. Comparisons of the measured and predicted PTDs were conducted with t tests.

A final analysis for experiment 3 examined the degree to which reflex activity expressed a perfect compensation for changes in limb configuration or no compensation. We utilized the ratio of activity from baseline across the two conditions in which the simplest pattern (with no postural dependence) is unity and the ideal response (compensating the underlying torque) is that observed during postural maintenance (last 300 ms of each trial); note that this approach accounts for different EMG-force relations across muscles and subjects. Because the ratio measure is nonlinear, we employed nonparametric statistics (ranksum and sign test) to compare the group medians against the contrasting predictions.

Supplemental References

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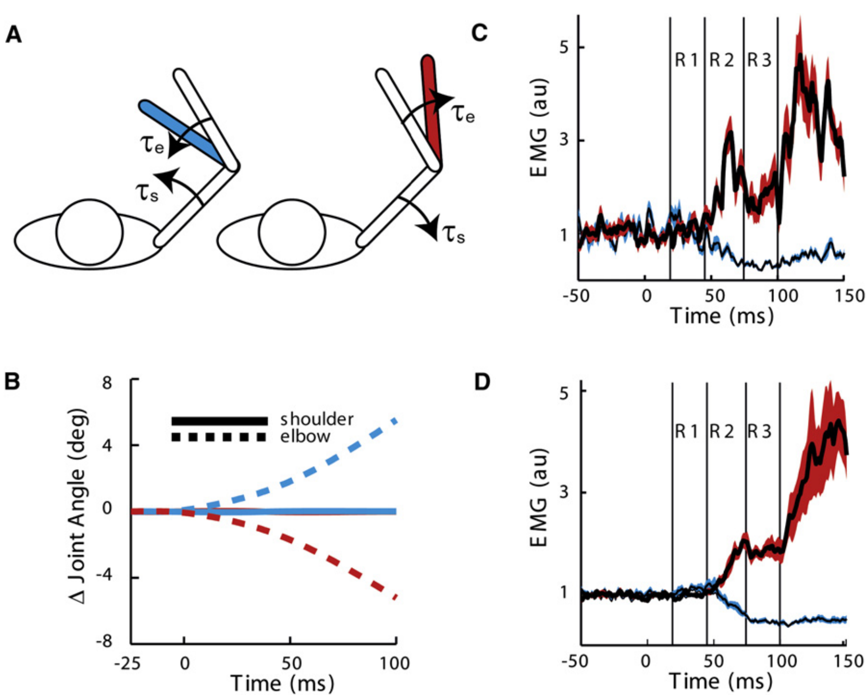

Figure S3. Reflex Activity of the Shoulder Flexor Muscle after Experiment 2

(A) Depiction of a subject's arm motion after the simultaneous application of torque at both joints thereby resulting in elbow flexion motion (blue) or elbow extension motion (red).

(B) The subject's joint motion is shown over time revealing that shoulder motion is negligible, whereas the elbow motion is substantial.

(C) Evoked muscle activity from the representative subject's pectoralis major.

(D) Group data for the same muscle. Note the absence of evoked activity during the R1 period and the subsequent increase and decrease in activity during the R2, R3, and voluntary periods. The increase in activity for elbow flexion motion was appropriate to counter the shoulder flexion/elbow flexion load, whereas the decrease in activity for elbow extension motion was appropriate to counter the shoulder extension/elbow extension load. This figure parallels Figure 2 in the main text.

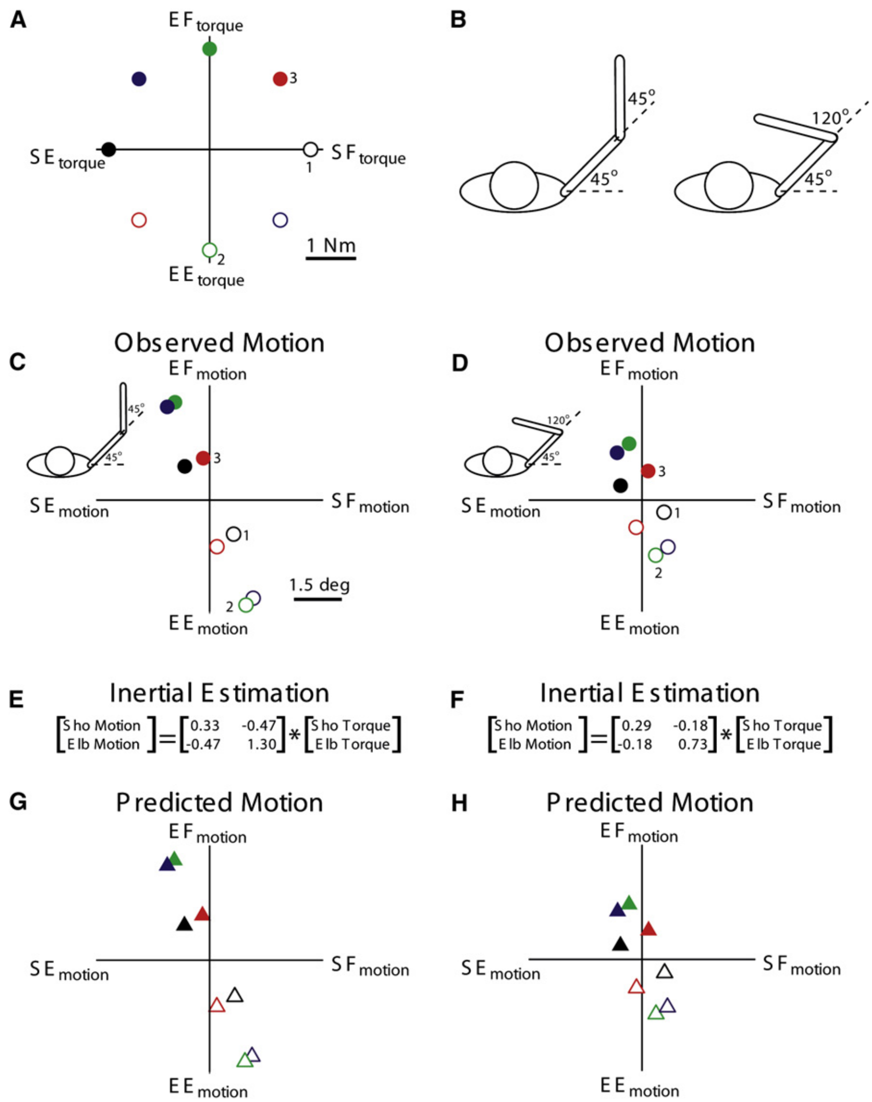

Figure S4. Limb Configuration Influences the Relation between Imposed Torque and Induced Motion

(A) The following procedures were separately completed for each subject. We used eight torque pulses (75 ms duration) to estimate limb inertia: equal magnitude (2 Nm) and equally distributed in joint space. The code of color and fill for matching torque and motion are retained throughout the panels. Also note the italicized numbers *1–3* that mark the conditions of shoulder flexion torque, elbow extension torque, and shoulder flexion/elbow flexion torque.

(B) The two limb configurations that were employed involve the same shoulder angle (45°) with either an extended elbow angle (45°) or flexed elbow angle (120°).

(C) Resulting shoulder-elbow displacement at 50 ms postperturbation for the extended elbow condition (see inset).

(D) Resulting shoulder-elbow displacement at 50 ms postperturbation for the flexed elbow condition (see inset). Clearly the two configurations lead to significant differences in joint motion. The extended configuration results in a noticeably more tall and narrow distribution than the flexed configuration. This behavior can be attributed to several differences in the underlying dynamics including greater interaction torques between the two joints with greater elbow extension. With less interaction torque, there is less influence of torque at one joint on motion at the other joint. Conditions *1–3* are prime examples of this behavior. In (C), shoulder flexion torque (1) leads to less shoulder motion than elbow extension torque (*2*), whereas this pattern is reversed in (D). (This explains why a limb configuration between these extremes was needed for equal magnitude torques to induce matched levels of elbow motion in experiment 1.) Moreover, shoulder flexion/elbow flexion (*3*) induced a small shoulder extension versus a small shoulder flexion in the extended and flexed posture, respectively. (This explains why a limb configuration between these extremes was need for equal magnitude torques to induce negligible shoulder motion in experiment 2.)

(E) We found the 2 × 2 matrix that was the best linear mapping from the known torque to the known motion (lscov, MATLAB [The Mathworks, Natick, MA]). This is the inertial estimation for the joint motion in (C).

(F) This is the inertial estimation for the joint motion in (D).

(G and H) These panels showed that our simple estimations were relatively accurate in reproducing the observed motion.

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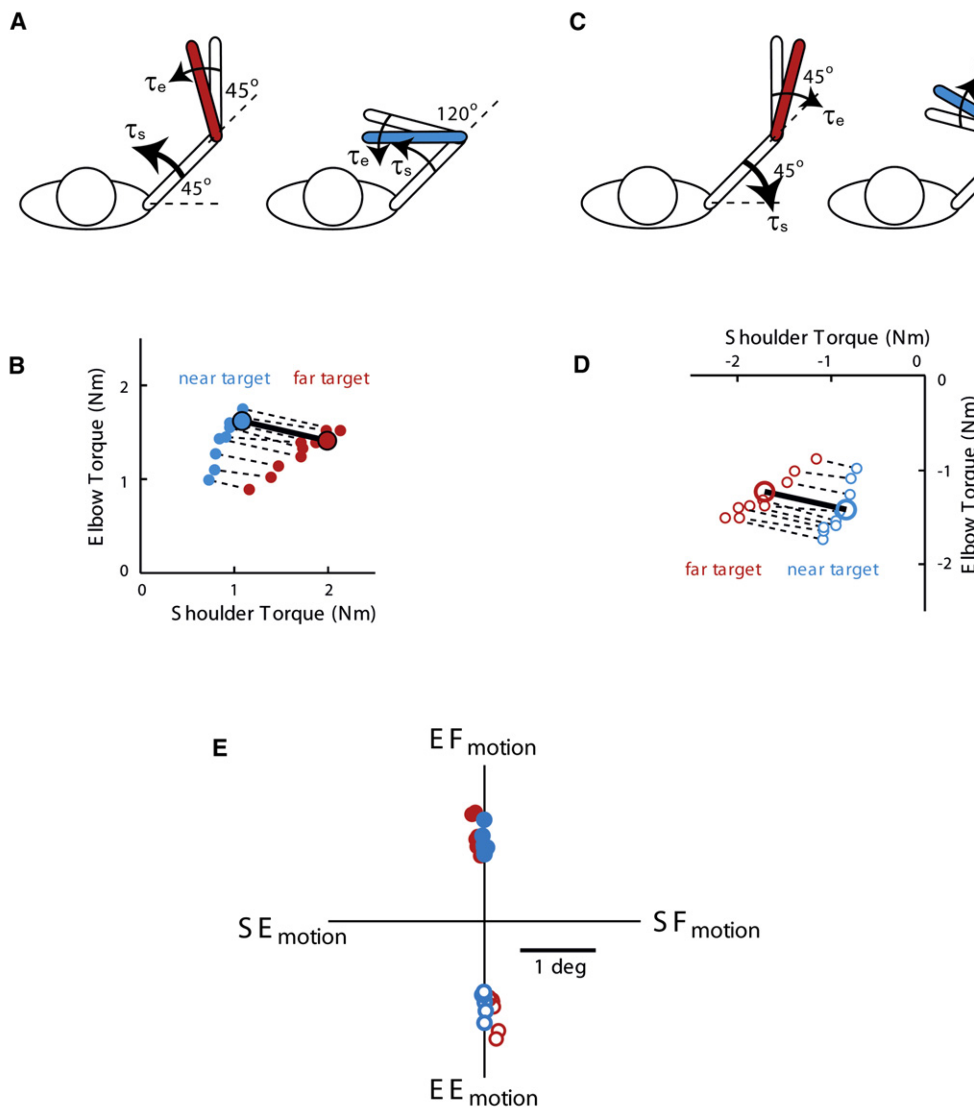

Figure S5. Joint Torques and Resulting Joint Motion for Experiment 3

(A) Depiction of a subject's arm motion after the simultaneous application of torque at both joints thereby resulting in elbow flexion motion when the elbow is extended (red) or flexed (blue).

(B) Torques utilized to achieve similar elbow flexion in the two postures. Determined from inverse of the estimated inertial matrix to achieve elbow-only motion of 1° within 50 ms, see Figure S4E. All subjects show a similar pattern of larger shoulder torque (85% on average) and smaller elbow torque (10% on average) between the extended and flexed postures. The thick line and large fills were the torques employed for the representative subject shown in Figure 4.

(C) Same format as (A) when elbow extension motion is induced.

(D) Same format as (B) when elbow extension motion is induced. Thick lines and large fills were the torques employed for the representative subject shown in Figure S6.

(E) Similar induced motion for the extended (red) and flexed (blue) postures for induced elbow flexion (solid) and elbow extension (open). Note the substantial overlap of the two distributions.

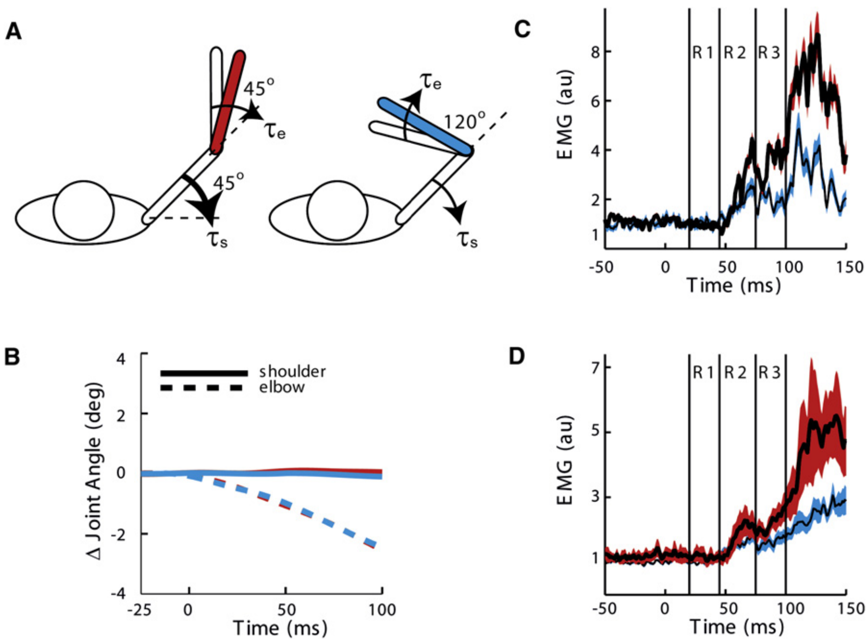

Figure S6. Reflex Activity of the Shoulder Flexor Muscle after Experiment 3

(A) Depiction of a subject's arm motion after the simultaneous application of torque at both joints thereby resulting in elbow extension motion when the elbow is extended (red) or flexed (blue). We applied different combinations of flexion torques at both joints to induce a similar amount of elbow flexion motion at the far target (red) and near target (blue). Data are taken from a representative subject at 50 ms postperturbation (scaled by 15× for clarity).

(B) The joint displacement of the representative subject reveals that elbow motion is similar across conditions and shoulder motion is minimal.

(C) Evoked muscle activity from the representative subject's pectoralis major.

(D) Group data for the same muscle. Note the absence of evoked activity during the R1 period and then an increase during the R2, R3, and voluntary periods. Moreover, the increase is larger for the extended condition that involved a larger shoulder torque perturbation. This figure parallels Figure 4 in the main text.

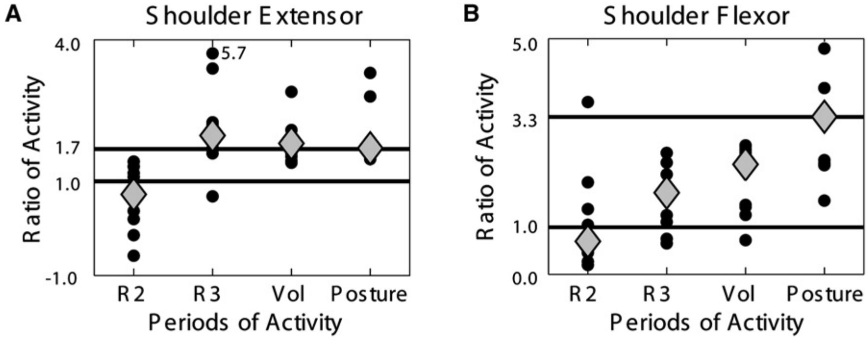

Figure S7. Tuning of Reflex Magnitude to Limb Configuration

(A) Ratio of activity during elbow extension versus elbow flexion (see "Apparatus and Task" in Experimental Procedures). Small circles show the measured configuration-dependent ratio of activity from individual subjects for each activity period; short-latency reflexes were not evoked. Diamonds indicate the median ratio across subjects. The two horizontal lines are the predicted ratio if reflexes only reflect elbow motion (1) or the underlying torque (postural period). One outlier is depicted that did not fit within the scale. This analysis further shows that the R2 period did not differ from the simplest response ($p > 0.5$, sign test), whereas the later periods expressed significant postural-dependence (R3, $p < 0.05$; voluntary, $p < 0.01$; posture, $p < 0.01$). In addition, the R3 and voluntary periods did not significantly differ from the idealized ratio observed during postural maintenance ($p > 0.3$, ranksum).

(B) Same format for the pectoralis major (a shoulder flexor muscle). An analysis of the shoulder flexors shows a similar pattern.