Report

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

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Summary

A key feature of successful motor control is the ability to counter unexpected perturbations. This process is complicated in multijoint systems, like the human arm, by the fact that loads applied at one joint will create motion at other joints [1–3]. Here, we test whether our most rapid corrections, i.e., reflexes, address this complexity through an internal model of the limb's mechanical properties. By selectively applying torque perturbations to the subject's shoulder and/or elbow, we revealed a qualitative difference between the arm's short-latency/spinal reflexes and long-latency/cortical reflexes. Short-latency reflexes of shoulder muscles were linked exclusively to shoulder motion, whereas its long-latency reflexes were sensitive to both shoulder and elbow motion, i.e., matching the underlying shoulder torque. In fact, a long-latency reflex could be evoked without even stretching or lengthening the shoulder muscle but by displacing just the elbow joint. Further, the shoulder's long-latency reflexes were appropriately modified across the workspace to account for limb-geometry changes that affect the transformation between joint torque and joint motion. These results provide clear evidence that long-latency reflexes possess an internal model of limb dynamics, a degree of motor intelligence previously reserved for voluntary motor control [3–5]. The use of internal models for both voluntary and reflex control is consistent with substantial overlap in their neural substrates and current notions of intelligent feedback control [6–8].

Results

One of the most influential concepts in the field of motor control is that our nervous system possesses neural structures that mimic the properties of our limbs and interactions with the world [4–6]. Such internal models would allow us to achieve rapid and accurate voluntary behavior despite the difficulties presented by motor noise, delayed sensory feedback, and a complex musculoskeletal apparatus. Although the existence of internal models has been strongly established for voluntary limb control [3, 9–12], their involvement in reflex limb control is less clear. This issue is particularly compelling because countering unexpected and external perturbations is a ubiquitous occurrence of everyday life. Furthermore,

recent theories of motor control imply an intimate link between the strategies and mechanisms employed for feedforward and feedback control of movement [7].

To address this issue, we examined the rapid compensatory responses of a shoulder extensor muscle (posterior deltoid) to multijoint perturbations while subjects maintained a fixed arm posture. If the shoulder muscle's reflex action (20–100 ms postperturbation) includes an internal model of shoulder-elbow dynamics, then the compensatory response should mirror the mechanical interactions that naturally occur between the two joints. In contrast, the nervous system could base its reflex responses on sensory information that is local to each muscle and follow this with a more integrated (but delayed) voluntary response (>100 ms postperturbation).

Our first experiment imposed single-joint torque (Figures 1A and 1B) at either the shoulder or elbow joint that, in both cases, induced multijoint motion due to the limb's intersegmental dynamics. Critically, we chose two perturbation magnitudes that induced equal amounts of shoulder motion but different amounts of elbow flexion: The shoulder perturbation caused shoulder flexion and a small amount of elbow extension, whereas the elbow perturbation caused shoulder flexion and a large amount of elbow extension (Figure S1 available online). If shoulder reflexes only depend on the local muscle stretch then similar activity would be observed in the two conditions due to the same amount of shoulder motion. Instead, if the shoulder reflexes incorporate both shoulder and elbow motion into an internal model of limb dynamics, then greater activity would follow the shoulder torque perturbation than elbow torque perturbation.

This simple but direct approach revealed a qualitative difference between posterior deltoid's earliest and later reflex periods (Figures 1C and 1D). The earliest burst of activity (R1) occurred ~20–45 ms and was significantly above baseline (shoulder torque $t_{(9)} = 5.8$, $p < 0.001$; elbow torque $t_{(9)} = 6.7$, $p < 0.001$) but was similar between conditions ($t_{(9)} = -1.8$, $p = 0.11$). Hence, the earliest reflex activity did not utilize an internal model. In contrast, later reflex periods were influenced by elbow motion in a manner consistent with an internal model of limb dynamics. Greater sensitivity to the shoulder torque perturbation began ~55 ms and achieved significance within the R2 interval of 45–75 ms ($t_{(9)} = 4.2$, $p < 0.005$), R3 interval of 75–100 ms ($t_{(9)} = 4.5$, $p < 0.005$), and subsequent voluntary period ($t_{(9)} = 4.7$, $p < 0.005$). Note that this differential effect was not merely a consequence of greater limb motion because less elbow motion (and hence total joint motion) was induced by the shoulder torque than elbow torque perturbation (Figure 1B). Similar results were also observed for the opposing shoulder muscle (pectoralis major) in the complementary conditions (Figure S2).

To further examine whether the R2 and R3 reflex periods (termed long-latency reflexes) possess an internal model of limb dynamics, we conducted a second experiment in which a combined elbow and shoulder torque induced substantial elbow motion with almost no shoulder motion (Figures 2A and 2B). This perturbation neither stretched nor slackened the shoulder muscle, so its local sensors detecting muscle length, velocity, and tension [13] were unaffected. Nonetheless, the

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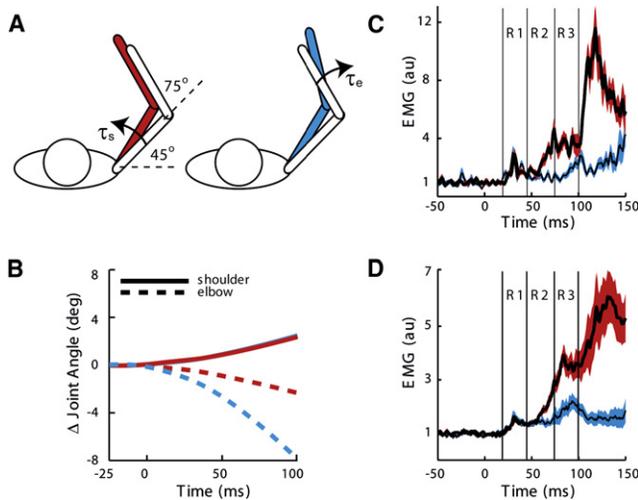
Figure 1. Reflex Activity after Single-Joint Torque Perturbations that Induced Equal Shoulder Motion but Different Elbow Motion

(A) From experiment 1: Depiction of a subject's limb configuration after the shoulder torque (red) or elbow torque perturbation (blue). Initial posture has a 45° shoulder angle and 75° elbow angle; full elbow extension is 0°. Data are taken from a representative subject at 50 ms postperturbation (scaled by 15× for clarity).

(B) Time course of joint displacement reveals that shoulder motion is highly similar across the two conditions, 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.
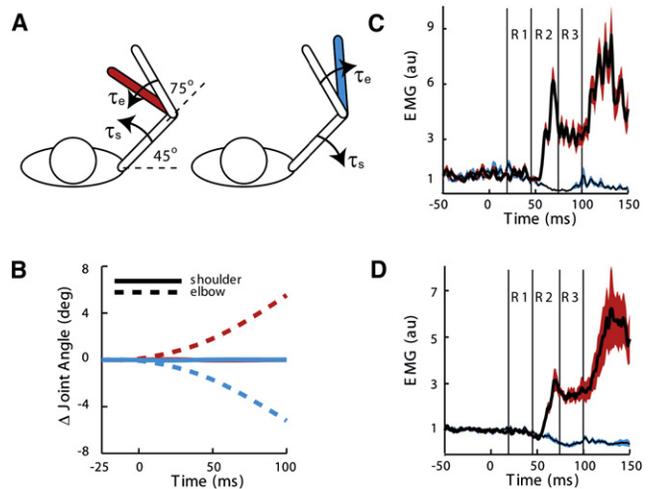
(C) Evoked muscle activity from the subject's posterior deltoid (a shoulder extensor muscle) normalized to the preperturbation baseline (mean ± SEM across trials). Vertical lines delineate the reflex periods (see "Data Analysis" in Experimental Procedures).

(D) Group data for the same muscle, same format (mean ± SEM across subjects).

Figure 2. Reflex Activity after Multijoint Torque Perturbations that Induced Large Elbow Motion and Negligible Shoulder Motion

(A) From experiment 2: Depiction of a subject's limb configuration after flexion torque applied at both joints thereby resulting in elbow flexion (red) and almost no shoulder motion. Extension torque at both joints resulted in elbow extension (blue) and almost no shoulder motion.

(B) The time course of joint displacement reveals substantial elbow motion and negligible shoulder motion.

(C) Evoked muscle activity from the representative subject's posterior deltoid (mean ± SEM across trials).

(D) Group data for the same muscle (mean ± SEM across subjects). All panels are in the same format as Figure 1.

shoulder's long-latency reflex should be evoked if it possessed an internal model that decoded pure elbow motion into the underlying shoulder torque perturbation.

Elbow flexion and elbow extension failed to influence activity in the R1 period (elbow flexion $t_{(7)} = -1.8$, p = 0.12; elbow extension $t_{(7)} = 0.5$, p = 0.65) consistent with the negligible shoulder motion. In contrast, we found that elbow flexion motion evoked a significant increase in activity for the R2 ($t_{(7)} = 4.3$, p < 0.005), R3 ($t_{(7)} = 6.2$; p < 0.001), and voluntary periods ($t_{(7)} = 4.4$, p < 0.001). Such increases were appropriate to counter the underlying shoulder flexion (and elbow flexion) torque. Moreover, elbow-extension motion (induced by a combination of elbow-extension and shoulder-extension torque) resulted in significant inhibition in the R2 ($t_{(7)} = -3.8$, p < 0.01), R3 ($t_{(7)} = -8.4$, p < 0.01), and voluntary period ($t_{(7)} = -3.9$, p < 0.01). This reciprocal pattern of reflex activation rules out a nonspecific cocontraction and provides further evidence of a coordinated readout of multijoint motion via an internal model for the later reflex periods and beyond. Similar results were also observed for pectoralis major in the complementary conditions (Figure S3).

To determine the efficacy of this putative internal model, we analyzed the data from both experiments by using a multiple regression of observed reflex activity versus the imposed shoulder and/or elbow torques (four loads total, see Experimental Procedures). The orientation of the resulting planar fit expresses the sensitivity of muscle activity to the perturbing shoulder-elbow torque, i.e., preferred torque direction (PTD), and was compared to the predicted sensitivity of an ideal internal model (PTD aligned to shoulder torque only) and no internal model (PTD aligned to the torque combination that induces the greatest shoulder motion).

The measured PTDs were consistent with our earlier analyses (Figure 3A) and displayed a transition from no internal model in the earliest period toward the ideal internal model in the later periods. Short-latency PTDs were indistinguishable from the prediction of no internal model (R1 $t_{(9)} = -1.4$, p > 0.2), whereas long-latency PTDs were significantly different (R2/3 $t_{(19)} = 7.5$, p < 0.001). This shift in PTD in the long-latency period involved a substantial approach toward the ideal internal model (61% on average) rather than slight systematic bias. Although the PTDs undershot the ideal prediction (R2/3 $t_{(19)} = -4.8$, p < 0.001), similar undershoots were observed for voluntary reactions and even during postural maintenance (83% on average) when the nervous system expresses its steady-state response; in fact, the preference of single-joint muscles to moderately biased multijoint torque probably reflects the optimal pattern of coordination for redundant, multifunctional muscle systems [14–16]. Analysis of the shoulder flexors (Figure 3B) revealed the same pattern.

Motivated by these positive results, we conducted a final experiment that tested whether the putative internal model for long-latency reflexes accounts for an additional mechanical complexity, the influence of limb configuration on limb dynamics [17]. The relationship between joint motion and joint torque depends on the limb's configuration and, in particular, the mechanical interaction across the shoulder and elbow joints increases with greater elbow extension (Figure S4). Accordingly, shoulder torque will induce greater elbow motion, and elbow torque will induce greater shoulder motion when the elbow is more extended. Conversely, the same pattern of induced joint motion will reflect different underlying torque perturbations when the elbow is more or less extended. If the long-latency reflexes
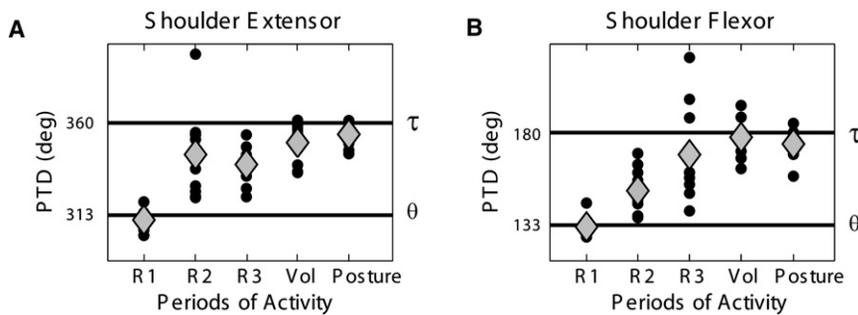
Figure 3. Preferred Torque Directions of the Different Reflex Epochs

(A) PTDs of the posterior deltoid. Small circles show PTDs of individual subjects for each activity period (see "Apparatus and Task" in Experimental Procedures); note that the postural data are from a separate group of subjects. Diamonds indicate the mean PTD averaged across subjects. The two horizontal lines are the predicted PTDs if reflexes only reflect shoulder motion (θ) or shoulder torque (τ). A PTD of 360° is directed to pure shoulder flexion torque; <360° involves a combination of shoulder flexion-elbow extension torque, and >360° involves a combination of shoulder flexion-elbow flexion torque; 313° is the predicted PTD for shoulder-extension motion.

(B) Same format for the pectoralis major (a shoulder flexor muscle). A PTD of 180° is directed toward pure shoulder-extension torque, whereas <180° and >180° involves shoulder-extension-elbow flexion torque and shoulder-extension-elbow-extension torque; 133° is the predicted PTD for shoulder flexion motion.

represent this level of mechanical complexity, then they should respond differently to the same pattern of joint motion when delivered at different limb configurations. To test this possibility, we examined how the shoulder's long-latency reflexes respond to a fixed level of elbow motion at a flexed and extended elbow posture at which greater activity was expected for the extended posture (Figures 4A and 4B); ~85% more shoulder torque was imposed at the extended posture to counterbalance the greater interaction torque from the elbow (Figure S5). Note that the small shoulder motion in the extended posture would shorten the shoulder muscle and tend to decrease its evoked response.

As before, induced elbow motion failed to evoke a short-latency reflex in the shoulder muscle but effectively recruited its long-latency reflexes and voluntary response. Furthermore, the compensatory reflex and voluntary responses varied with
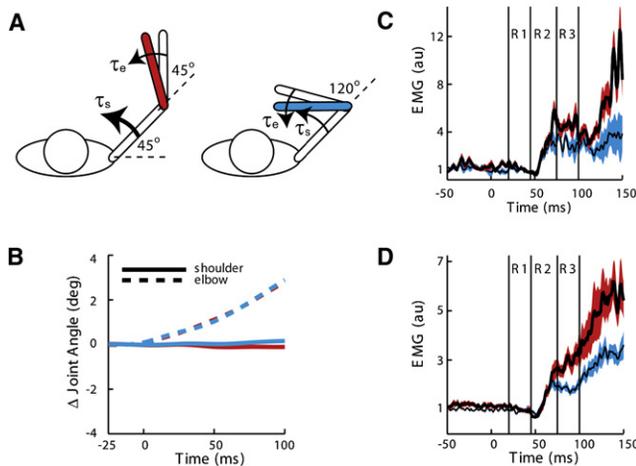

Figure 4. Reflex Activity for the Same Joint Motion at Two Different Limb CONFIGURATIONS

(A) From experiment 3: Depiction of the limb configuration for the far target (45° shoulder angle, 45° elbow angle) and near target (45° shoulder angle, 120° elbow angle). Different combinations of flexion torques were applied at both joints to induce a similar amount of elbow flexion motion at the far target (red) and near target (blue); the shoulder torque perturbation was ~85% larger for the far target than the near target. 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 a subject's posterior deltoid (mean ± SEM across trials).
(D) Group data for the same muscle, same format (mean ± SEM across subjects). Panels are in the same format as Figure 1.

the limb's starting position. Larger evoked activity was observed for the more extended posture in the R3 ($t_{(9)} = 4.47$; $p < 0.001$, one-tailed) and voluntary periods ($t_{(9)} = 5.2$, $p < 0.001$, one-tailed) although not for the R2 period ($t_{(9)} = -1.1$, $p = 0.85$, one-tailed). Hence, the long-latency reflex possesses an evolving degree of motor intelligence in which both R2 and R3 periods express multijoint responses appropriate for an internal model, but only the R3 period appears to be tuned to the limb configuration. Similar patterns were observed in the shoulder flexor muscle (Figure S6). A model-based comparison further confirmed the efficacy of these reflex modulations (see Supplemental Experimental Procedures).

Discussion

The motivation for using internal models in voluntary control has long been recognized and extensively explored [4–6]. Less appreciated is that the same difficulties are present when countering an external perturbation: How can we quickly and accurately stabilize our limb with motor noise, delayed sensory feedback, and a complex musculoskeletal apparatus? Although insightful, the few previous studies on this topic [18–21] possessed several experimental and technological limitations including highly variable joint motions, inferring joint torques from the resultant unconstrained kinematics, and a nonspecific sampling of test conditions. In contrast, we applied known loads directly to the shoulder and elbow joints while the limb was constrained to a single plane. This led to better control of the imposed motion, background motion, and muscle activity, all factors known to affect reflex processing [22–24]. Moreover, our carefully matched comparisons ensured that only a single experimental variable was altered across conditions and thereby provide an unambiguous and model-free test of multijoint processing. Accordingly, our findings clearly indicate that long-latency reflexes of the human upper limb include an internal model of limb dynamics.

Importantly, we found that not all reflexes were equal. Short-latency reflexes (R1) of the shoulder muscles reflected the local shoulder motion, whereas its long-latency reflexes (R2/3) were sensitive to both shoulder and elbow motion in a manner that reflected the underlying torque perturbation. Short-latency reflexes are known to depend on processing confined to the spinal cord [25]. In contrast, the broad window of 45–100 ms postperturbation is termed a long-latency reflex because it is too early to result from voluntary commands but occurs after the short-latency reflex [26–28]. Moreover, long-latency reflexes possess a greater degree of task dependency [26, 29–31] and

intermuscular coordination [32, 33] than the short-latency reflex.

Previous authors have suggested that long-latency reflexes are coordinated approximations of voluntary responses [32, 34]. We believe that functional similarities of long-latency reflexes and voluntary responses are a direct consequence of a shared neural substrate. In particular, over 30 years of evidence suggests long-latency reflexes are predominately supported by primary motor cortex (MI) [35–37], a cortical region known to support voluntary control [38]. MI includes substantive somatosensory inputs, diverse effects at the spinal cord, context-dependent responses, and a rich intrinsic connectivity that is highly modifiable [8]. Accordingly, it becomes understandable, even predictable, that long-latency reflexes share many of the functional properties of voluntary control. Such overlapping substrates and strategies for reflexive and voluntary motor control are also consistent with modern concepts of feedback control in which flexible feedback gains and internal models work together to balance the multiple competing requirements defined by each task [7]. This view motivates leveraging the vast literature on the properties of internal models for voluntary control to unravel the organization of long-latency reflexes including their function in motor learning [39] and dysfunction in motor pathology [40].

Experimental Procedures

Subjects
Eighteen subjects participated in one of several sessions lasting 60–90 min. The Queen's University ethics committee approved the procedures. Complete methodological details are provided in the Supplemental Experimental Procedures.

Apparatus and Task
As previously described [12, 41], we utilized a robotic exoskeleton (KINARM, BKIN Technology, Kingston, ON) that permits flexion and extension movement of the shoulder and elbow within the horizontal plane. This device can apply torque only to one joint or simultaneously to both joints. The device is also coupled to a virtual-reality system for displaying the target and hand-aligned cursor while direct vision of the arm was obscured. The following procedures tested the reflex action of posterior deltoid and pectoralis major, a shoulder extensor and flexor muscle, respectively.

1. A background load elicited steady-state activity of the shoulder muscle while subjects stabilized their hand within the center of a small target (0.4 cm radius),
2. A step perturbation was applied after a random interval (500–3500 ms); perturbation direction was also randomly varied across trials.
3. Accurate performance required returning the hand to a larger target area (2 cm radius) within 500 ms.
4. Thirty repeats were collected for each perturbation condition.

Experiment 1 (n = 10): We applied different single-joint perturbations (2 Nm shoulder flexor torque or 2 Nm elbow extensor torque) to create multijoint motion. Importantly, the two perturbations induced similar amounts of shoulder flexion but different amounts of elbow extension (see Figures 1A and 1B and Figure S1).

Experiment 2 (n = 8): We applied different multijoint perturbations (2 Nm shoulder flexor/2 Nm elbow flexor torque or 2 Nm shoulder extensor/2 Nm elbow extensor torque) to create single-joint motion. The two perturbations induced substantial elbow motion but negligible shoulder motion (see Figures 2A and 2B and Figure S1).

Both experiments 1 and 2 utilized a target whose origin corresponded to a 45° shoulder angle and 75° elbow angle; 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 (n = 10): We induced similar amount of elbow motion while the elbow was in a flexed (shoulder angle = 45° elbow angle = 120°) or extended posture (shoulder angle = 45° elbow angle = 45°) (Figure 4A).

Because elbow angle impacts the relation between joint torque and motion, we needed to impose different multijoint perturbations: The average shoulder and elbow torque was ± 1.7 Nm and ± 1.29 Nm at the extended posture versus ± 0.92 Nm and ± 1.44 Nm at the flexed posture.

Associated experiment (n = 10): To examine steady-state muscle activity, we used a separate study on postural maintenance, similar to a previous study with nonhuman primates [10] in which subjects countered a wide range of shoulder and/or elbow loads.

Data Analysis
Surface EMG was obtained from the two shoulder muscles—posterior deltoid and pectoralis major—of each subject with standard preparation and filtering techniques. We selected the reflex periods on the basis of earlier reports [26, 42] and our pilot studies: R1 = 20–45 ms; R2 = 45–75 ms; and R3 = 75–100 ms. Voluntary responses were considered to occur at 120–180 ms postperturbation.

Several analyses examined the patterns of reflex action. Our t tests determined changes from baseline and/or changes between conditions ($p < 0.05$). We also examined the coordinated pattern across the first two experiments by regressing the evoked muscle activity against the imposed shoulder-elbow torques. Shoulder and elbow slope coefficients from this plane fit describe the relative sensitivity to shoulder and elbow joint torque [15] or "preferred torque direction (PTD)." Measured PTDs were then judged against two contrasting predictions: pure shoulder torque or pure shoulder motion. The plane fit of shoulder motion against the applied shoulder and elbow torques gives the prediction for pure shoulder motion.

Supplemental Data

Additional Experimental Procedures and seven figures are available at http://www.current-biology.com/cgi/content/full/18/6/449/DC1/.

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