Long-Latency Responses During Reaching Account for the Mechanical Interaction Between the Shoulder and Elbow Joints

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Kurtzer I, Pruszynski JA, Scott SH. Long-latency responses during reaching account for the mechanical interaction between the shoulder and elbow joints. *J Neurophysiol* 102: 3004–3015, 2009. First published August 26, 2009; doi:10.1152/jn.00453.2009. Although considerable research indicates that reaching movements rely on knowledge of the arm's mechanical properties and environment to anticipate and counter predictable loads, far less research has examined whether this degree of sophistication is present for on-line corrections during reaching. Here we examine the R2/3 response to mechanical perturbations (45–100 ms, also called the long-latency reflex), which is highly flexible and includes the fastest possible contribution from primary motor cortex, a key neural substrate for self-initiated action. Torque perturbations were occasionally and unexpectedly applied to the subject's shoulder and/or elbow in the course of performing reaching movements. Critically, these perturbations would evoke different patterns of feedback corrections from a shoulder extensor muscle if it countered only the local shoulder displacement relative to unperturbed motion or accounted for the mechanical interactions between the shoulder and elbow joints and countered the underlying shoulder torque. Our results show that the earliest response (R1: 20–45 ms) reflected local shoulder displacement, whereas the R2/3 response (45–100 ms) reflected knowledge of multijoint dynamics. Moreover, the same pattern of feedback occurred whether the shoulder muscle helped initiate the movement (during its agonist phase) or helped terminate the movement (during its antagonist phase). These results contribute to the accumulating evidence that highly sophisticated feedback control underlies motor behavior and are consistent with a shared neural substrate, such as primary motor cortex, for feedforward and feedback control.

INTRODUCTION

Increasing theoretical and empirical work suggests that skilled motor behavior is achieved by sophisticated feedback control (Scott 2004; Todorov 2004; Todorov and Jordan 2002). For example, we have recently shown that feedback control of arm posture accounts for the mechanical interactions between the shoulder and elbow joints (Kurtzer et al. 2008), reminiscent of the anticipatory capabilities of self-initiated actions (Gottlieb et al. 1996; Gribble and Ostry 1999; Hollerbach and Flash 1982; Lackner and DiZio 1994; Shadmehr and Mussa-Ivaldi 1994). Long-latency responses (45–100 ms postperturbation, also termed R2/3 responses) of a shoulder muscle appropriately expressed greater activity when shoulder motion (and shoulder muscle stretch) was caused by torque applied to the shoulder than when the same shoulder motion (and shoulder muscle stretch) was caused

by torque applied to the elbow. Long-latency responses of a shoulder muscle could also be evoked by displacing just the elbow joint (without stretching or lengthening the shoulder muscle), which was an appropriate response to counter the underlying shoulder–elbow torque causing pure elbow motion. Notably, this capability was not exhibited by the short-latency response (20–45 ms postperturbation, also termed R1), which was sensitive only to shoulder motion (and shoulder muscle stretch). It is likely that the functional differences between the short-latency and long-latency responses reflect differing neural substrates because the former depends entirely on spinal cord processing and the latter includes contributions from the primary motor cortex (Lee et al. 1983; Marsden et al. 1983; Matthews 1991), a key neural substrate for self-initiated action (Porter and Lemon 1993; Scott 2003, 2004).

Although our earlier study provided clear evidence that feedback during postural maintenance accounts for the mechanical interaction between the shoulder and elbow it would be premature to conclude that such knowledge of limb dynamics is a general feature of skilled arm control. In fact, a number of studies have suggested a fundamental difference between the control of posture and movement. Studies on motor behavior have found differences in how proprioceptive information is used during posture and movement tasks (Brown et al. 2003; Scheidt and Ghez 2007), complementing neurophysiological studies showing significant changes in cortical processing between the tasks (Kurtzer et al. 2005). Several authors have also reported a general suppression of sensory processing (Brooke 1997; Chapman and Beauchamp 2006; Collins et al. 1998) and reflexes (Bawa and Sinkjaer 1999; Seki et al. 2003) during movement compared with posture that would mitigate the contribution of fast feedback control during movement, irrespective of the degree of sophistication; however, other authors have found that sensory information is usefully integrated even in the earliest phase of initiating a movement (Adamovich et al. 1997; Brown and Cooke 1986). Finally, there is evidence of functional differences even within different periods of a single movement such as complex time-varying changes in reflex gain throughout a movement (Bennett 1994; Dufrense et al. 1980; Shapiro et al. 2002) and the agonist and antagonist bursts of muscle activity (which accelerate and decelerate the limb) relying on partially distinct neural pathways (MacKinnon and Rothwell 2000).

Given the evidence of functional differences between posture and movement we extended our previous paradigm to determine whether feedback control of reaching movements also accounts for the mechanical interaction between the shoul-

der and elbow. We applied perturbations to the moving limb such that *1*) a shoulder torque and an elbow torque would induce the same amount of shoulder displacement (and shoulder muscle stretch) relative to the unperturbed reaching movement and *2*) two different shoulder–elbow torques would selectively displace the elbow (without stretching or lengthening the shoulder muscle) relative to the unperturbed reaching movement. These conditions were used while the shoulder muscle acted as either an agonist or antagonist to the reaching movement to see whether the feedback responses possessed the same capability throughout the movement. In all cases, the shoulder's long-latency responses incorporated information from both the elbow and shoulder appropriate for the underlying torque perturbation. Future studies will need to test whether this knowledge of limb dynamics reflects an internal model or a direct mapping of sensory inputs.

METHODS

Subjects

In all, 10 subjects participated in four experiments (6 males and 4 females; mean age = 24.9 yr). Eight subjects participated in a session that comprised *experiments* 1 and 3 and 8 subjects participated in a separate session for *experiments* 2 and 4. All subjects were paid for their time following procedures approved by the ethics committee at Queen's University.

Apparatus

As described in previous studies (Kurtzer et al. 2008; Prusyznski et al. 2008; Scott 1999; Singh and Scott 2002) we used a robotic exoskeleton (KINARM, BKIN Technologies, Kingston, Ontario), which permits flexion/extension movements of the shoulder and elbow in the horizontal plane and can selectively apply torques to each joint; shoulder angle is measured relative to the frontal plane and elbow angle is measured between the forearm and upper arm; 0° is full extension. Visual targets and a hand-aligned cursor were presented in the same plane as the limb movement via a virtual-reality system while a cloth bib and metal partition obscured direct vision of the subject's arm.

Muscle recording

We recorded surface electromyograms (EMGs) from each subject's posterior deltoid, a shoulder extensor muscle, according to procedures fully described in our earlier studies (Kurtzer et al. 2008; Pruszynski et al. 2008, 2009). A two-bar electrode (DE-2.1, Delsys, Boston, MA) was affixed to the muscle belly and a ground electrode was placed on the subject's ankle following light abrasion of the overlying skin surfaces with alcohol.

Tasks

Experiments 1–4 examined feedback control of reaching movements against step-torque perturbations. Note that four types of perturbation trials/conditions were employed with each reaching direction/session. A particular session and pair of conditions defined one experiment: 2 pairs of conditions × 2 sessions = 4 experiments (see Table 1). Perturbation trials were randomly interspersed among the unperturbed trials (4 perturbation trials per 16 unperturbed trials). Therefore to obtain 30 repeats with each type of perturbation we collected 600 trials in each session (120 perturbed trials and 480 unperturbed trials). Visual feedback was removed on half of the unperturbed trials and all the perturbed trials so that subsequent movement corrections were guided entirely by proprioception. Subjects were instructed not to anticipate the presence or direction of the torque perturbations but attempt endpoint accuracy should they occur.

The trial flow always followed the same order (for specific examples of reaching direction/session and perturbation type/condition, see *Experiments 1–4*).

1 The start and final targets (0.5- and 1.5-cm radius, respectively) were displayed at the same time a background load of shoulder flexion torque (1 Nm) was applied to elicit steady-state activity in the shoulder extensor muscle.

2 Subjects stabilized their hand-aligned cursor (0.4-cm radius) within the center of the start target and awaited the cue to reach to the final target (random interval of 1,000–3,500 ms). Reaching was cued by the final target changing color from red to green.

3 Although no reaction time constraints were imposed, subjects needed to execute the movement (move their hand from the start target into the final target and remain inside) within 400–600 ms. During perturbation trials the movement time criteria was wider (400–1,000 ms) so that subjects could remain successful.

4 On perturbation trials a step torque was applied when the subject's elbow passed a position threshold of 75°.

5 At the end of the trial the final target was filled green or red to indicate accurate or inaccurate performance, respectively. The load then slowly ramped back down (500 ms) and remained off for a brief intertrial period (1,000 ms).

Start and final target positions were selected so that the unperturbed reaching movements mostly involved elbow extension or elbow flexion. Due to the limb's intersegmental dynamics, single-joint elbow extension requires anticipatory activation of the shoulder extensor muscle to counter flexor interaction torque from the elbow during movement initiation (Craig 2005; Graham et al. 2003; Hollerbach and Flash 1982). Likewise, single-joint elbow flexion requires anticipatory activation of the shoulder extensor muscle to counter flexor interaction torque from the elbow during movement termination. Thus the shoulder extensor muscle acted as an agonist during the elbow extension movement and an antagonist during the elbow flexion movement.

The step torque perturbations described in the following sections displaced the elbow and shoulder in particular patterns *relative to the unperturbed reaching movement*. The same torque perturbations were used for each subject because our earlier study showed that they

TABLE 1. *Summary of experimental design*

Experiment	Reaching Direction	Muscle Activity	Perturbation Type, Nm	Induced Motion
1	Elbow extension	Agonist	(2 Sho, 0 Elb) (0 Sho, −2 Elb)	Same shoulder and different elbow
2	Elbow flexion	Antagonist	(2 Sho, 0 Elb) (0 Sho, −2 Elb)	Same shoulder and different elbow
3	Elbow extension	Agonist	(2 Sho, 2 Elb) (−2 Sho, −2 Elb)	No shoulder and large elbow
4	Elbow flexion	Antagonist	(2 Sho, 2 Elb) (−2 Sho, −2 Elb)	No shoulder and large elbow

reliably induce the targeted patterns of joint motion (Kurtzer et al. 2008), although some subjects experienced more overall motion than others.

Experiment 1: agonist feedback to same shoulder motion, different underlying torques. This experiment examined how a shoulder extensor muscle (posterior deltoid) rapidly responded to torque perturbations while the muscle acted as an agonist. The start and final target positions required mostly elbow extension (~35°) from an initial elbow angle of 74° to a final elbow angle between 32 and 47° across subjects (Fig. 1*A*). The initial and final shoulder angles were 60 and 53–63° across subjects. Perturbations were applied early during movement initiation when the hand moved outside the start target by 1°. Thus perturbation onset coincided with the agonist phase of shoulder muscle activity.

We applied two different torque perturbations—a shoulder flexor torque (2 Nm) and elbow extensor torque (−2 Nm) (Fig. 1*C*, Table 1)—that induced motion at both the shoulder and elbow due to the limb's intersegmental dynamics (Craig 2005; Graham et al. 2003; Hollerbach and Flash 1982). Critically, the two loads were scaled to ideally induce an identical amount of shoulder flexion and stretch of the shoulder extensor muscle relative to the unperturbed reaching movement (Fig. 1*D*). This allowed us to test whether feedback control during the shoulder's agonist phase is sensitive only to local muscle stretch, thus responding identically to the two perturbations. Alternatively, if feedback control of the shoulder combines information from both the elbow and shoulder in a manner that accounts for the mechanical interactions between the shoulder and elbow joints then a larger response will be elicited by the shoulder torque, given that the shoulder extensor muscle is ultimately needed to counter that load.

Experiment 2: antagonist feedback to same shoulder motion, different underlying torques. The principal difference between *experiment* 1 and *experiment* 2 is whether the perturbations were applied during the shoulder muscle's agonist or antagonist phase of activity. Thus the two torques, induced joint motion, and contrasting predictions are the same as those in *experiment* 1 (Fig. 1, *C* and *D*, Table 1). Here subjects made mostly elbow flexion movements (~40°) with minimal shoulder motion. Across subjects, ranges of initial and final elbow angles were 50–53 and 90–93°, respectively, whereas initial and final shoulder angles were 57–59 and 56–62°, respectively. We examined the feedback corrections of the shoulder extensor muscle by applying torque loads near the middle of the movement (when the elbow passed 75°) when that muscle acted as an antagonist.

Experiment 3: agonist feedback to pure elbow motion, underlying shoulder torque. This experiment examined how the posterior deltoid rapidly responded to torque perturbations that displaced only the elbow and did not stretch the shoulder muscle relative to the unperturbed movement. As described in *experiment* 1, subjects performed elbow-extension movements that required concomitant agonist activity in the shoulder extensor muscle. The loads used in this experiment were flexor torques at both joints (2 Nm, 2 Nm) or extensor torques at both joints (−2 Nm, −2 Nm) (Fig. 1*C*, Table 1). These multijoint loads were selected to counter the interaction torques from the elbow to the shoulder joint so that pure elbow motion resulted—elbow-flexion motion induced by the flexion loads and elbow-extension motion induced by the extension loads (Fig. 1*D*). If feedback is sensitive only to local muscle stretch then the shoulder muscle should exhibit no response—i.e., no shoulder muscle stretch and no shoulder muscle response. Alternatively, if feedback accounts for the mechanical interactions between the shoulder and elbow joints then a reciprocal pattern of shoulder muscle activity would be expected to counter the underlying torque loads, an increase in shoulder extensor activity following flexion loads, and a decrease following extension loads.
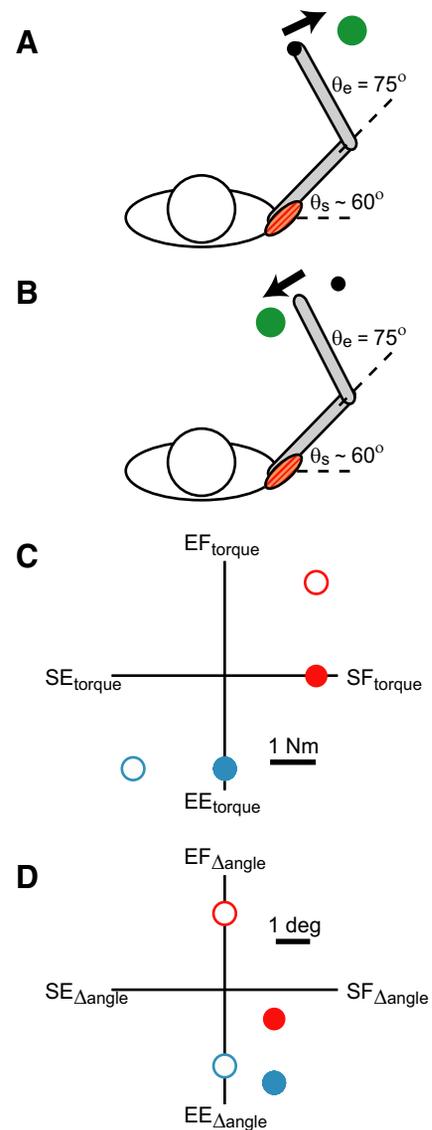

FIG. 1. Reaching task and load conditions. *A*: cartoon of subject and the posterior deltoid muscle during an elbow extension movement of *experiments* 1 and 3. The small black and large green circles indicate the start target and final target, respectively. The arrow indicates the direction of hand movement. Torque perturbations occurred immediately past the start target at the limb configuration depicted; θ_e and θ_s denote the elbow and shoulder angles. *B*: subject performing an elbow-flexion movement for *experiments* 2 and 4, where torque perturbations occur near the middle of the movement (same format as above). *C*: depiction of the 4 load conditions used within shoulder–elbow torque coordinates: *x*-axis is shoulder torque, *y*-axis is elbow torque, flexion torque is positive, and extension torque is negative. *Experiments* 1 and 3 used single-joint torques (red and blue filled circles for shoulder flexion torque and elbow extension torque, respectively), whereas *experiments* 2 and 4 used multijoint torques (red and blue open circles for shoulder-flexion/elbow-flexion torque and shoulder-extension/elbow-extension torque). *D*: idealized pattern of shoulder and elbow joint displacement ($\Delta\theta_e$ and $\Delta\theta_s$) from the unperturbed reaching movement shortly following the 4 imposed loads (50 ms postperturbation). Same color code as above with filled and open circles for single-joint and multijoint torques, respectively. Ideally, the load conditions of *experiments* 1 and 3 induce the same amount of shoulder flexion with different amount of elbow extension, whereas the load conditions of *experiments* 2 and 4 should induce motion at just the elbow joint.

Experiment 4: antagonist feedback to pure elbow motion, underlying shoulder torque. The principal differences between *experiment* 3 and *experiment* 4 are that perturbations occurred during the shoulder muscle's agonist or antagonist phase, respectively.

Therefore the two torque conditions, induced joint motion, and contrasting predictions are the same as those in *experiment* 3 (Fig. 1, *C* and *D*, Table 1) and perturbations were applied near the middle of the elbow-flexion movement as described in *experiment* 2.

Data analysis

We processed the kinematic and electromyographic data following procedures described in our earlier studies (Kurtzer et al. 2008; Pruszynski et al. 2008). Angular positions of the shoulder and elbow were low-pass filtered (25 Hz, two-pass, sixth-order Butterworth). Processing of the EMG signals included an amplification (gain = 1–10K), band-pass filter (20–450 Hz), digital sampling at 1,000 Hz (PCI 6071E; National Instruments, Austin, TX), rectification, and normalization by each muscle's mean activity during the prereach hold period against the 1-Nm shoulder flexion load.

We considered several periods of evoked activity based on earlier reports (Crago et al. 1976; Kurtzer et al. 2008; Lee et al. 1983; Marsden et al. 1983; Nakazawa et al. 1997; Prusyznski et al. 2008): R1 = 20–45 ms; R2 = 45–75 ms; R3 = 75–100 ms; and Voluntary (Vol) = 120–180 ms. This temporal categorization is similar to the earlier M1–M3 convention (Lee et al. 1983), but avoids the confusion between the earliest response (R1, previously M1) and primary motor cortex (M1), which is thought to contribute to R2/R3 (previously M2/M3).

Our experimental design allowed us to make straightforward comparisons between conditions to determine whether feedback responses of the shoulder muscle reflect the local muscle stretch or underlying torque perturbation; *t*-tests determined changes from baseline and/or changes between conditions ($P < 0.05$). We also used a planar regression to examine the coordinated activity across the single- and multijoint loads of *experiments* 1 and 3 (or *experiments* 2 and 4). Accordingly, the change in activity from the unperturbed reaching movement is regressed against the four combinations of imposed shoulder–elbow torque used in each session: Evoked activity = [a × (shoulder torque)] + [b × (elbow torque)] + constant.

The orientation of the best-fitting plane (muscle activity vs. shoulder and elbow torques) describes the relative sensitivity to shoulder and elbow joint torques during a particular epoch (Herter et al. 2007; Kurtzer et al. 2006a,b, 2008), which we term the "preferred torque direction" (PTD). PTDs are measured counterclockwise, such that maximal excitation to shoulder-flexion, elbow-flexion, shoulder-extension, and elbow-extension torques would result in PTDs at 0, 90, 180, and 270°, respectively.

If the imposed loads resulted in identical shoulder motion for *experiments* 1 and 3 (single-joint torques), no shoulder motion for *experiments* 2 and 4 (multijoint torques), and feedback reflected only shoulder motion then the PTD would be midway between the shoulder-flexion torque and elbow-extension torque at 315°. We call this angle θ_i the ideal angular prediction (Fig. 6A). Alternatively, if feedback involved a perfect mapping from shoulder–elbow motion into shoulder torque then the PTD would be at 360°, which we call τ_i for the ideal torque prediction (Fig. 6B). In contrast to these idealized predictions we opted for empirically measured shoulder motion and steady-state postural activity to provide contrasting predictions for the feedback response. The PTD of pure shoulder motion was the plane-fit of the measured shoulder displacement versus the shoulder and elbow torques, which we call θ_a for the actual angular prediction and was about 312° (Fig. 6A). The PTD of the postural response, which we call τ_a for the actual torque prediction (Fig. 6B), was taken from our previously published data and is slightly biased away from pure shoulder-flexion torque toward elbow-extension torque at 354° (Kurtzer et al. 2008; see also Kurtzer et al. 2006a,b). Comparisons of the measured and predicted PTDs were conducted by calculating the circular mean and variance (Baschelet 1981). Statistical significance was met when the 95% confidence interval (CI) of the measured PTD did not overlap with the predicted PTD.

RESULTS

Experiment 1: agonist feedback to same shoulder motion, different underlying torques

In this experiment we examined how posterior deltoid, a shoulder-extensor muscle, responded to the same amount of muscle stretch induced by either a shoulder or elbow torque perturbation. Subjects performed a series of reaching movements from a start target near the body and midline, to a final target placed away from the body and rightward (Fig. 2A). The mean hand displacement for these movements was 27 cm (SD 3) across subjects and primarily reflected elbow motion with a mean change of −35° extension at the elbow versus −2° extension at the shoulder (Fig. 2B). These unperturbed movements were performed at moderate speeds with a mean movement time of 578 ms (SD 11).

We occasionally perturbed the limb with a shoulder-flexion torque or elbow-extension torque as the hand exited the start target (elbow angle = 75°). The two perturbations created significant outward and leftward deviations from the hand's baseline trajectory (range of peak deviation = 3–11 cm), although subjects largely achieved terminal accuracy (range of endpoint deviation ≅ 0–4 cm) (Fig. 2A). The displacement pattern may be better appreciated by examining how the shoulder and elbow move in opposite directions from their baseline trajectories followed by an eventual convergence (Fig. 2B). Subtracting the unperturbed joint pattern from the perturbed joint patterns reveals that similar amounts of shoulder-flexion motion were induced by the two loads, but with larger elbow-extension motion following elbow torque than shoulder torque (Fig. 2C). In fact, at 50 ms postperturbation the shoulder displacement from the unperturbed reaching movement was similar across conditions, whereas the elbow displacement was quite different (Fig. 2D). On average there was 11% more shoulder motion and 190% more elbow motion following the elbow torque than the shoulder torque; the small difference in shoulder motion was opposite the appropriate pattern of muscle activity for countering the underlying torques that made the test for knowledge of multijoint dynamics more difficult to pass. In sum, the shoulder extensor muscle experienced a similar amount of (relative) muscle stretch following two different torque perturbations.

During unperturbed movements the shoulder muscle extensor exhibited a burst of activity that preceded the elbow extension motion (Fig. 3, A and B) and countered the flexor interaction torque acting at the shoulder. When perturbations were applied, a stereotyped sequence of activity was superimposed on this burst (Fig. 3, A and B): the earliest evoked response (20–45 ms) was similar between conditions, whereas later responses (>45 ms) were larger for shoulder torque than those for thr elbow torque condition. Notably, later responses were an appreciable fraction of the unperturbed pattern of muscle activity.

These characteristics can be emphasized by subtracting away the temporally evolving baseline pattern during unperturbed reaching (Fig. 3C) and averaging within each temporal epoch (Fig. 3D). The visible pattern was consistent with our statistical tests on each epoch of muscle activity: activity in the
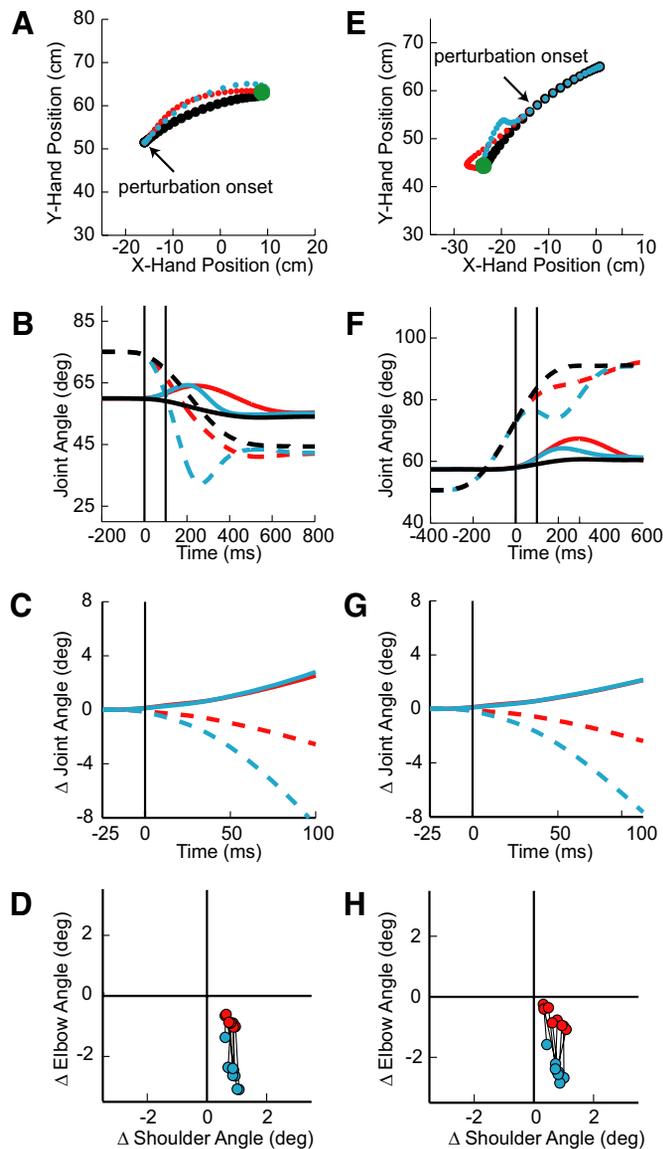
FIG. 2. Limb kinematics during unperturbed reaching and with single-joint torque perturbations. *A* and *E*: hand motion from an exemplar subject during elbow extension (*left column, experiment* 1) and elbow flexion (*right column, experiment* 2). The center of the subject's right shoulder is the *x–y* origin and the mean hand path of each condition is shown at 50-ms intervals with colored dots. Black, red, and blue dots correspond to the unperturbed, shoulder-flexor torque and elbow-extensor torque conditions, whereas arrows indicate perturbation onset. *B* and *F*: shoulder angle (solid lines) and elbow angle (dashed lines) vs. time for the same reaching movements. Data were temporally aligned to perturbation onset with the 1st and 2nd vertical lines marking 0 and 100 ms postperturbation, respectively. *C* and *G*: the change in joint trajectory from the unperturbed reaching movement obtained by subtracting the unperturbed joint motion from the perturbed joint motion: flexion is positive, extension is negative. *D* and *H*: the shoulder–elbow displacement at 50 ms postperturbation is shown for each subject. Lines connect their data from the 2 conditions.

R1 epoch was greater than baseline for the shoulder torque condition [$t_{(7)} = 2.9$, $P = 0.023$] and elbow torque condition [$t_{(7)} = 2.9$, $P = 0.022$], but not different between the two conditions [$t_{(7)} = 0.1$, $P > 0.5$]. In contrast, shoulder muscle activity was consistently larger following shoulder-flexion torque than elbow-extension torque for the R2 epoch [$t_{(7)} = 3.1$, $P = 0.017$], R3 epoch [$t_{(7)} = 4.2$, $P = 0.004$], and Voluntary (Vol) epoch [$t_{(7)} = 6.5$, $P < 0.001$]. Corrective

reactions also tended to increase in successive epochs (Fig. 3*D*). Following the shoulder torque perturbation the evoked activities in the R1, R2, R3, and Vol epochs were 8, 33, 71, and 143%, respectively, the peak activity during unperturbed reaching.
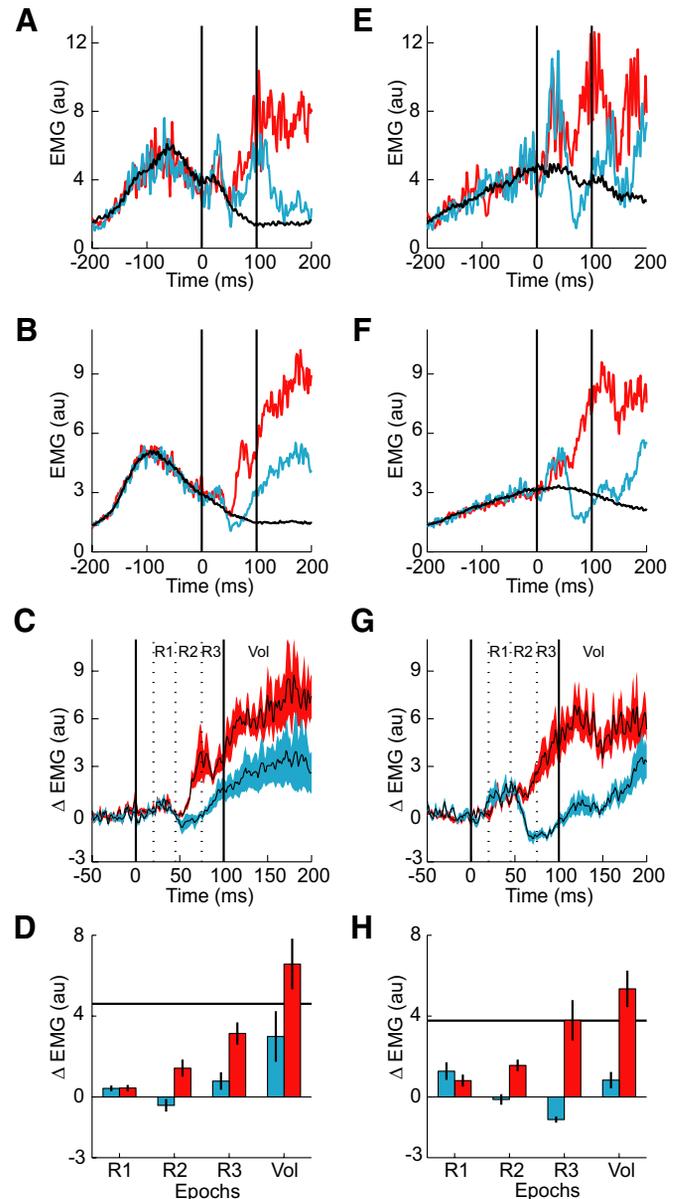
FIG. 3. Muscle activity during elbow-extension movements (*left column, experiment* 1) and elbow-flexion movements (*right column, experiment* 2). *A* and *E*: shoulder muscle activity from the exemplar subject aligned to perturbation onset; black, red, and blue traces indicate the mean muscle activity in the unperturbed, shoulder-flexor torque and elbow-extensor torque conditions, whereas the 1st and 2nd vertical lines mark 0 and 100 ms postperturbation, respectively. *B* and *F*: muscle activity patterns averaged across subjects (same format as above). *C* and *G*: perturbation-evoked muscle activity of the group obtained by subtracting each subject's unperturbed muscle activity from the perturbed muscle activity and then averaging across subjects; black lines and colored surround indicate the group mean and SE. Dashed vertical lines demarcate the response epochs. *D* and *H*: bar plots of evoked muscle activity within the different epochs; vertical height and error bars indicate the group mean and SE. Horizontal line at 0 is the unperturbed muscle activity for each epoch and the horizontal line at about 4 a.u. (arbitrary units) is the average peak muscle activity during unperturbed reaching.

Experiment 2: antagonist feedback to same shoulder motion, different underlying torques

Here we examined the evoked muscle response during its antagonist phase of activity. Accordingly, subjects performed reaching movements with the start target and final target nearly reversed from those of *experiment* 1. Subjects reached from a start target placed away from the body and rightward, to a final target placed near the body and midline (Fig. 2*E*). The required movement was mostly elbow flexion with a mean change of 40 versus 2° at the shoulder (Fig. 2*F*, black line). The associated mean hand displacement and movement time were 32 cm (SD 3) and 598 ms (SD 26), respectively.

During unperturbed movements the shoulder extensor had a burst of activity near the movement midpoint (Fig. 3*E*), which countered the flexor interaction torque from decelerating the elbow motion. We studied the feedback processes occurring during this antagonist phase of muscle activity by occasionally perturbing the limb when the elbow passed a threshold angle of 75°. The kinematic results of the single-joint perturbations are similar to those described earlier for *experiment* 1. The step torques deviated the hand outward and leftward from its nominal trajectory, although subjects achieved largely accurate final hand positions (Fig. 2*E*): range of peak deviation = 3–10 cm; range of endpoint deviation $\cong$ 0–2 cm. As before, subtracting the unperturbed joint pattern from the perturbed joint patterns shows that the loads induced similar amounts of shoulder motion but different amounts of elbow extension motion relative to the unperturbed reaching movement (Fig. 2, *F* and *G*). At 50 ms postperturbation, there was an average of 11% more shoulder motion for the elbow torque condition than for the shoulder torque condition and 240% more elbow motion (Fig. 2*H*); as in *experiment* 1, the small difference in shoulder motion was opposite the appropriate pattern of muscle activity to counter the underlying torque. Thus the shoulder-extensor muscle experienced a similar amount of (relative) muscle stretch via different torque loads.

These single-joint torque loads evoked a stereotyped sequence of muscle activity as shown for the exemplar subject (Fig. 3*E*) and the group average (Fig. 3*F*). The earliest burst of activity appeared similar for the two conditions, whereas the later bursts were visibly greater following the shoulder torque than elbow torque as well as large compared with the unperturbed antagonist baseline. Subtracting away the temporally evolving baseline pattern during unperturbed reaching (Fig. 3*G*) and averaging within each temporal epoch (Fig. 3*H*) confirms this impression: R1 > baseline for the shoulder torque [$t_{(7)} = 2.7$, $P = 0.029$] and elbow torque condition [$t_{(7)} = 3.0$, $P = 0.021$]. The two torque conditions led to a weak difference in R1 activity [$t_{(7)} = -2.32$, $P = 0.053$], although this difference was inappropriate for the underlying torque and may reflect the small amount (11%) of increased shoulder motion following the elbow torque than shoulder torque perturbations. In contrast, shoulder muscle activity was consistently larger following shoulder-flexion torque than elbow-extension torque for the R2 epoch [$t_{(7)} = 6.9$, $P < 0.001$], R3 epoch [$t_{(7)} = 4.8$, $P = 0.002$], and Vol epoch [$t_{(7)} = 5.9$, $P < 0.001$]. Later corrective responses also tended to be larger (Fig. 3*D*). As before, the responses also tended to grow over time. Following the shoulder torque perturbation the evoked activities

in the R1, R2, R3, and Vol epochs were 20, 45, 107, and 144%, respectively, the peak activity during unperturbed reaching.

Experiment 3: agonist feedback to pure elbow motion, underlying shoulder torque

The baseline movement and muscle patterns involved elbow extension and agonist muscle activity as previously described for *experiment* 1. Here we describe the kinematic and muscular results of perturbing the limb with torque loads simultaneously applied to the shoulder and elbow joints. These perturbations primarily slowed (flexion–flexion torques) or sped up (extension–extension torques) the limb movement along the path it normally traveled (Fig. 4*A*): range of peak deviation = 9–14 cm; range of endpoint deviation $\cong$ 0–2 cm. Subtracting the unperturbed angular pattern from the perturbed angular patterns (Fig. 4*B*) reveals that flexion (extension) torques at both joints induced substantial elbow flexion (extension) from the baseline motion but a negligible amount of shoulder motion (Fig. 4*C*). Data from all subjects confirm this general pattern because the shoulder displacement was 7% the size of the elbow displacement on average (Fig. 4*D*). Accordingly, the shoulder-extensor muscle experienced no significant (relative) muscle stretch in either condition via perturbations composed of shoulder and elbow torques.

The perturbations did not appear to evoke any activity until about 50 ms later when the activity increased from baseline for pure elbow flexion and decreased from baseline for pure elbow extension appropriately to counter the underlying shoulder flexion and extension torques, respectively. This pattern was evident in both single-subject (Fig. 5*A*) and group data (Fig. 5, *B* and *C*) and confirmed by our statistical tests on the defined epochs (Fig. 5*D*). The R1 epoch did not differ from baseline following either multijoint flexor torque [$t_{(7)} = -0.4$, $P > 0.5$] or multijoint extensor torque [$t_{(7)} = 0.2$, $P > 0.5$]. In contrast, shoulder muscle activity was significantly larger following multijoint flexor torque than multijoint extensor torque for the R2 [$t_{(7)} = 3.5$, $P = 0.01$], R3 [$t_{(7)} = 4.8$, $P = 0.002$], and Voluntary epochs [$t_{(7)} = 6.3$, $P < 0.001$]. The size of the responses also tended to increase over time. Relative to the peak activity during unperturbed reaching the response magnitudes to the flexor–flexor torque perturbation were −2, 74, 81, and 145% in the R1, R2, R3, and Vol epochs, respectively (Fig. 5*D*).

Experiment 4: antagonist feedback to pure elbow motion, underlying shoulder torque

The final reaching experiment involved the same baseline pattern of movement and muscle activity as that in *experiment* 2: elbow flexion and antagonist muscle activation. Similar to *experiment* 3, the multijoint loads primarily slowed (extension–extension torques) or sped (flexion–flexion torques) the limb movement along the path it normally traveled followed by substantial corrections by the endpoint (Fig. 4*E*): range of peak deviation = 8–13 cm; range of endpoint deviation $\cong$ 0–5 cm. Subtracting the unperturbed angular pattern from the perturbed angular patterns (Fig. 4*F*) reveals that flexion (extension) torques at both joints induced substantial elbow flexion (extension) from baseline and negligible shoulder motion (Fig. 4*G*) for the exemplar subject. Moreover, the mean change in shoulder angle was 3% of the mean change in elbow angle
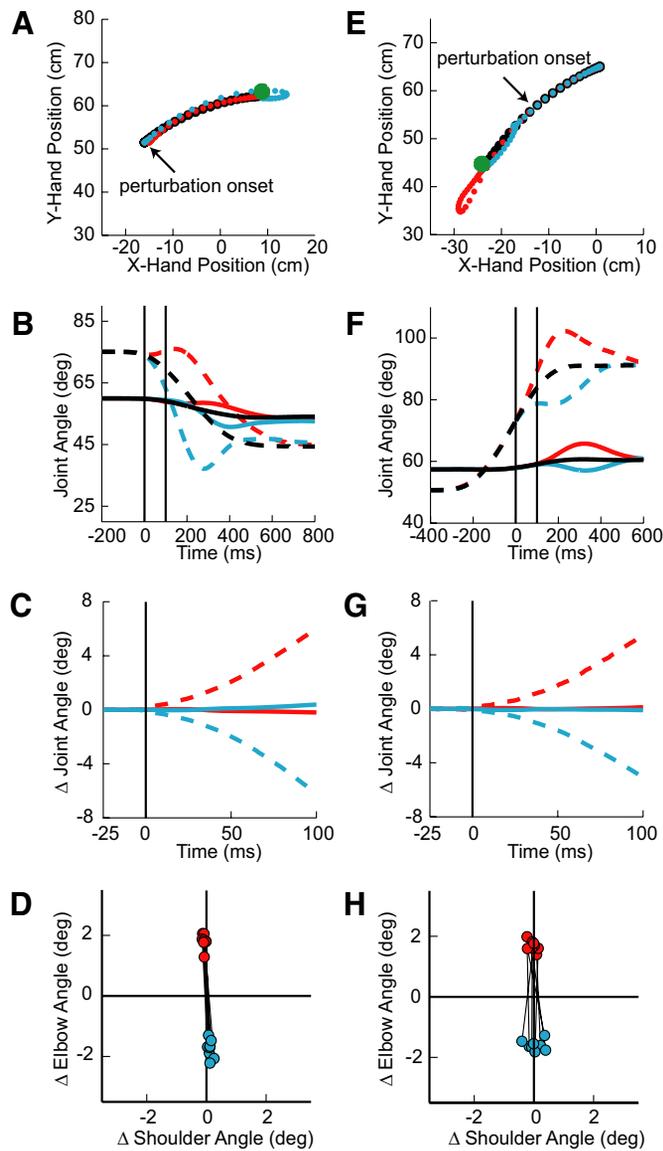
FIG. 4. Limb kinematics during elbow-extension movements (*left column*, *experiment* 3) and elbow-flexion movements (*right column*, *experiment* 4). Same format as Fig. 2. *A* and *E*: hand movement data from the same exemplar subject. Black, red, and blue dots correspond to the unperturbed, elbow-flexor/shoulder-flexor torque, and elbow-extensor/shoulder-extensor torque conditions. *B* and *F*: shoulder angle (solid lines) and elbow angle (dashed lines) vs. time for the same reaching movements as above. *C* and *G*: change in joint trajectory from unperturbed reaching resulting from the perturbations. *D* and *H*: shoulder and elbow displacement (50 ms postperturbation) from unperturbed reaching (data are shown for all subjects).

decrease following multijoint extensor torque [$t_{(7)} = -2.6$, $P = 0.035$] opposite the appropriate pattern. In contrast, later epochs expressed changes in activity that were larger and appropriate for the underlying torque perturbation: R2 epoch [$t_{(7)} = 6.7$, $P < 0.001$], R3 epoch [$t_{(7)} = 7.4$, $P < 0.001$], and the Voluntary epoch [$t_{(7)} = 7.3$, $P < 0.001$]. Relative to the peak activity during unperturbed reaching the response magnitudes increased over time with -8, 43, 94, and 169% in the R1, R2, R3, and Vol epochs, respectively, following the flexor–flexor torque perturbation (Fig. 5*H*).
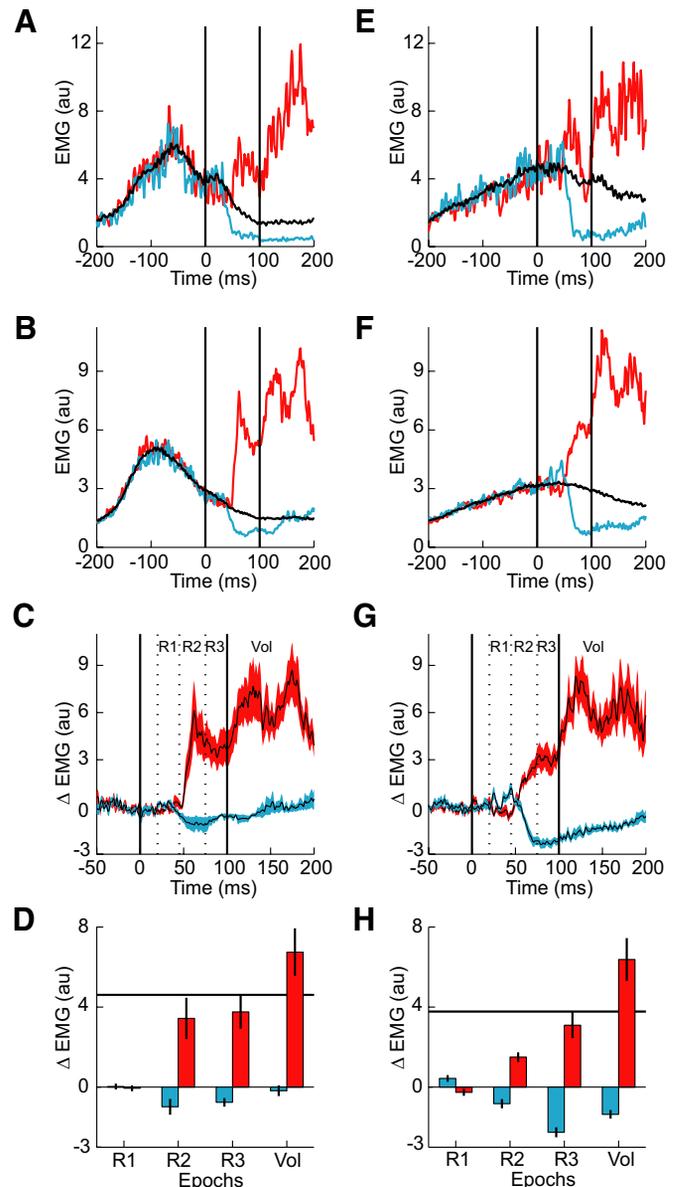

FIG. 5. Muscle activity during elbow-extension movements (*left column*, *experiment* 3) and elbow-flexion movements (*right column*, *experiment* 4). Same format as Fig. 3. *A* and *E*: data from the same exemplar subject aligned to perturbation onset; black, red, and blue traces indicate the mean shoulder muscle activity in the unperturbed, shoulder-flexor torque and elbow-extensor torque conditions. *B* and *F*: the mean pattern of muscle activity across subjects. *C* and *G*: group average after the baseline pattern of unperturbed movements. *D* and *H*: bar plots of evoked muscle activity (mean ± SE) within the different response epochs.

(Fig. 4*H*), such that the shoulder extensor muscle experienced little (relative) muscle stretch in either condition.

The evoked muscle activity from these perturbations involved either weak or no evoked change at short latency followed by a robust and reciprocal pattern of increase and decrease from baseline for the flexion–flexion and extension–extension torque conditions, respectively, that began around 50 ms postperturbation. This pattern was visible for the exemplar subject (Fig. 5*E*) and group data (Fig. 5, *F* and *G*) and statistically confirmed on the defined epochs (Fig. 5*D*). The R1 epoch was not different from baseline following multijoint flexor torque [$t_{(7)} = 1.5$, $P > 0.15$] but did show a small

Pattern of feedback responses across experiments compared with the contrasting predictions of single-joint motion and steady-state postural activity

All four experiments point to a clear functional difference between the earliest (R1) and later epochs (R2, R3, Vol) of the rapid feedback corrections during reaching movements. Here we combine the results within each session (Agonist session: *experiments* 1 and 3; Antagonist session: *experiments* 2 and 4) to determine the overall pattern of feedback within each epoch. We used a linear regression of evoked muscle activity versus the imposed shoulder and elbow torques to determine the preferred torque direction (PTD) within each epoch and then compared the measured PTDs to the contrasting predictions of single-joint motion and the steady-state postural activity (see *Data analysis* in METHODS).

The PTDs for single-joint motion reflect the combination of joint torques that induced the greatest amount of measured shoulder flexion (and stretch of the shoulder extensor muscle). Ideally, the shoulder-flexion and elbow-extension torques would create the exact same amount of shoulder motion (*experiments* 1 and 3), whereas multijoint torques would result in no shoulder motion (*experiments* 2 and 4) (Fig. 6A, gray arrow). This ideal pattern of shoulder motion would lead to a PTD of 315°, which the actual pattern of joint motion nearly achieved, with average PTDs of 311 and 313° for the agonist

and antagonist sessions, respectively (Fig. 6, *A*, black arrow and *C* and *D*, bottom lines). The second predicted PTD was the steady-state postural response of the shoulder extensor muscle. As described in our earlier study (Kurtzer et al. 2008), its postural PTD is slightly biased away from shoulder-flexion torque (360°, Fig. 6B, gray arrow) toward elbow-extension torque (354°, Fig. 6, *A*, black arrow, and *C* and *D*, top lines). Multijoint activity of a single-joint muscle has been reported for muscles of the arm, wrist, and leg and likely reflect how biarticular muscles influence the pattern of muscle recruitment (Kurtzer et al. 2006a,b; Nozaki et al. 2005; van Zuylen et al. 1988).

The measured PTDs of the evolving feedback response were consistent with our earlier analyses (Fig. 6, *C* and *D*). Activity in the R1 epoch was either indistinguishable from the prediction of single-joint motion (agonist session: $P > 0.1$, circular CI) or showed a weak bias from single-joint motion in the direction opposite to postural maintenance (antagonist session: $P = 0.03$, circular CI). In contrast, all later epochs in both the agonist and antagonist sessions displayed a significant deviation from single-joint motion ($P < 0.001$, circular CI) toward postural maintenance. The PTDs of both sessions also showed an unexpected pattern of overshooting before stabilizing near the postural response. Thus muscle activity in several periods did not statistically overlap the postural PTD (Agonist R2, Agonist Vol, and Antagonist R3, $P < 0.05$, circular CI), whereas other periods were
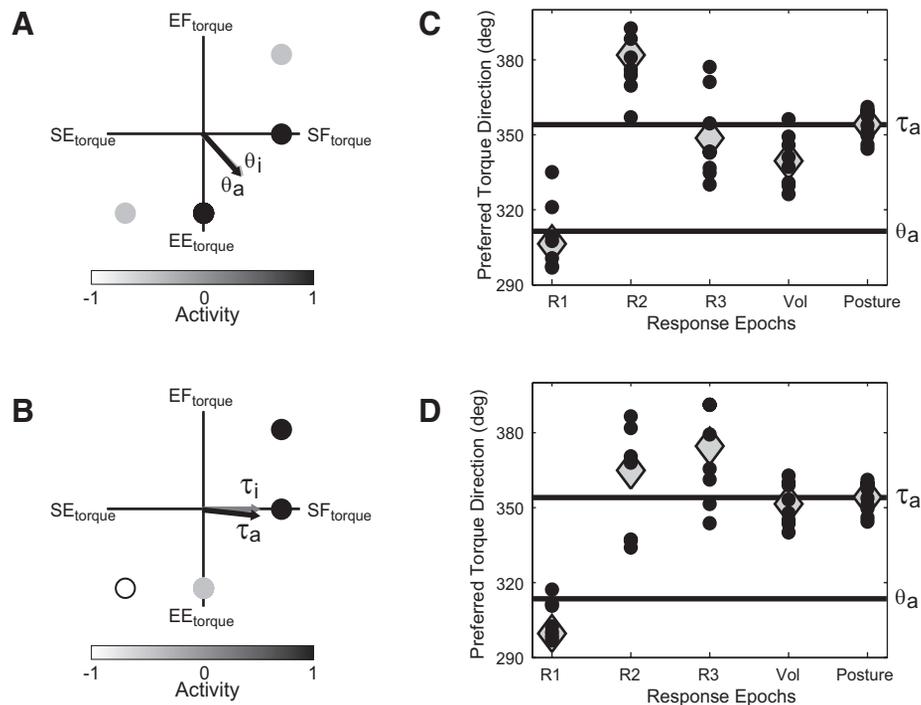

FIG. 6. Tuning to the applied shoulder–elbow torque. *A*: cartoon of muscle activity if the feedback reflected just shoulder motion. Black, gray, and open circles respectively indicate increases, no change, and decreases in muscle activity. The 2 black circles indicate activity in the torque conditions that induced similar amounts of shoulder stretch (*experiments* 1 and 3) and the gray circles indicate no activity for torque conditions that induced no shoulder stretch (*experiments* 2 and 4); see also Fig. 1D. The gray arrow (θ_i) indicates the preferred torque direction if the ideal motion results and feedback reflected just shoulder motion; the preferred torque direction (PTD) is midway between the two black circles at 315°. The prediction based on the actual shoulder motion (θ_a) is quite similar and is shown as a black arrow. *B*: cartoon of muscle activity if feedback reflects shoulder torque. The gray arrow shows a PTD at 360° as if the shoulder muscle reflected only shoulder torque (τ_i), whereas the black arrow shows the actual PTD of the shoulder muscle during postural maintenance (τ_i). *C*: PTDs of the shoulder muscle during the antagonist period of the elbow-extension movement. Small circles show PTDs of individual subjects as determined by planar regression for each response epoch and during voluntary reaction and postural maintenance. Diamonds indicate the mean PTD averaged across subjects. The two horizontal lines are the predicted PTDs if responses reflect single-joint shoulder-joint motion using the measured shoulder motion (θ) or empirically determined postural tuning (τ) (see *Data analysis* in METHODS). *D*: PTDs of the shoulder muscle during the antagonist period of the elbow flexion movement (same format for above).

indistinguishable from the postural PTD (Agonist R3 and Antagonist R2 and Vol, $P > 0.05$, circular CI).

DISCUSSION

Increasing theoretical and empirical work suggests that flexible and sophisticated motor behavior is engendered by flexible and sophisticated feedback control (Scott 2004; Shadmehr and Krakauer 2008; Todorov and Jordan 2002). For example, on-line feedback control can achieve global goals while allowing variability in the individual components of the task (Cole et al. 1984; Diedrichsen 2007; Franklin and Wolpert 2008; Liu and Todorov 2007; Robertson and Miall 1997; Scholz et al. 2002) as well as develop statistically optimal corrections that incorporate estimates of the body's sensorimotor noise and prior expectations (Fischbach et al. 2007; Izawa and Shadmehr 2008; Kording and Wolpert 2002). Far less research has examined whether feedback control possesses knowledge of the mechanical properties of the limb and body dynamics—a hallmark of motor sophistication in self-initiated actions (Kawato 1999; Lackner and DiZio 2005; Wolpert and Flanagan 2001). In particular, it is unknown whether feedback control of reaching movements accounts for the mechanical interaction between the shoulder and elbow joints in its R2/R3 response to mechanical perturbations since previous positive evidence during postural control (Kurtzer et al. 2008; see also Soechting and Lacquaniti 1988 for earlier evidence) may not generalize to reaching. In principle, activity in the R2/R3 epoch could support fast, smart, and powerful feedback control because it occurs prior to standard reaction time measures, exhibits considerable flexibility, and includes the fastest contribution from primary motor cortex (M1) (Lee et al. 1983; Marsden et al. 1983; Matthews 1991), a key neural substrate for self-initiated action (Porter et al. 1993; Scott 2003, 2004).

To address this issue we extended our earlier paradigm for postural maintenance (Kurtzer et al. 2008) to examine feedback control of reaching movements. Our results revealed that the earliest and smallest response (R1, 20–45 ms) was linked exclusively to motion of the shoulder. In contrast, the relatively large R2/3 response (45–100 ms) and voluntary reaction (120–180 ms) combined multijoint information in a manner appropriate to compensate the underlying torque. Both R2/3 and voluntary reactions exhibited greater activity when shoulder motion was caused by shoulder torque rather than by elbow torque (*experiments* 1 and 2) and could be evoked by displacements of just the elbow joint so that the shoulder muscle was not stretched (*experiments* 3 and 4). When the evoked muscle activity was examined across experiments a complementary result occurred: the PTDs during the R2/3 and Voluntary epochs were substantially deviated away from pure shoulder motion and similar to the PTD during postural maintenance. It should also be noted the R2/3 response was no mere "blip" riding on the unperturbed activity pattern, but rather a substantial increase or decrease from baseline that could nearly double or silence the muscle activity. Moreover, these patterns were apparent when the shoulder muscle acted both as an agonist during movement initiation and as an antagonist during movement termination.

These relatively clear-cut findings were enabled by several strengths in our paradigm. First, we directly imposed torques at the shoulder and/or elbow that allowed us to avoid the additional complexity of calculating the appropriate hand-based load to create the desired torques. Second, we selected combinations of loads that affected just one variable across conditions (amount of elbow motion) so that simple model-free comparisons were possible; the small inaccuracies of our approach would tend to obscure positive evidence of knowledge of multijoint dynamics. Third, the baseline movements involved mostly elbow motion so that length changes in the shoulder muscle were relatively small and did not complicate the issue. Finally, infrequent and unpredictable step-torque perturbations were chosen to minimize conscious anticipation and require maintained compensation to stabilize the limb.

As always, there are a number of earlier and insightful studies that examined the feedback responses of the multijoint arm during reaching. Two studies in particular showed that R2/3 response of a single-joint arm muscle could be evoked by motion of a remote joint, but their results do not address our main interest. Soechting (1988) used too few perturbations to determine whether the elbow muscle's response was related to elbow torque per se or a more general cocontraction response (Lacquaniti and Maioli 1987), whereas Latash (2000) showed that wrist reflexes were enslaved to the corrective action of the elbow rather than countering underlying wrist torque. Wang et al. (2001) and Wagner and Smith (2008) also explored whether forward models were used in feedback control of reaching but did not observe any evidence earlier than 100 ms after the mechanical perturbation; in fact, Wagner and Smith's elegant study was specifically designed so that force corrections via a forward model would occur about 180 ms postperturbation. This timescale is notably similar to manual corrections that account for the limb's dynamics following a target displacement (Gritsenko et al. 2009).

Several researchers have also examined how the limb resists transient displacements during multijoint movements. The measured limb stiffness shows a complex time-varying pattern (Gomi and Kawato 1996) that is broadly consistent with the time-varying sensitivity of evoked responses during movement (Bennett et al. 1992; Dufresne et al. 1980), although some authors argue that the complex patterns of stiffness are largely artifactual (Gribble et al. 1998). Other studies have reported a reorienting of limb stiffness to compensate for directional instabilities (Burdet et al. 2001; Franklin et al. 2007; Frolov et al. 2006). Such effects could be caused by a sophisticated R2/3 response or by modulation of passive muscle stiffness through patterned cocontraction, but the authors did not test between these two contrasting possibilities.

In the present study we found a categorical pattern of evoked responses that was consistent with the R2/3 response possessing knowledge of multijoint dynamics. The overall pattern of R2/3 responses across experiments was also largely appropriate to counter the underlying torque perturbation, as judged by the similarity between the preferred torque direction of the long-latency response and postural maintenance; a more fully developed model (possibly including muscle dynamics and weighing effort and accuracy) would be needed to account for the more complex changes in PTD and deviations from the basic prediction. Accordingly, we consider the present work to be the clearest evidence to date that R2/3 responses use knowledge of limb dynamics for the feedback control of reaching movements. Given previous reports of substantial changes in feedback processing during reaching (including the suppres-

sion of short-latency responses around movement onset) it is also significant that long-latency responses would use knowledge of multijoint dynamics, whether the muscle acted as an agonist or an antagonist. Together, the present work and our earlier study on postural control (Kurtzer et al. 2008) suggest that such knowledge is a general feature of skilled motor behavior.

An essential property of multijoint systems (like the human arm) is that single-joint torque will induce multijoint motion and single-joint motion reflects multijoint torque. If a controller failed to recognize these facts it would be useless to say it possessed knowledge of multijoint dynamics, although it is debatable whether this knowledge can be designated an "internal model." Within the field of formal control theory an "internal model"—a subsystem that mimics the input–output relationship of the external plant—is just one of many sophisticated control schemes (Tin and Poon 2005). The present study cannot determine whether our findings reflect an internal model or a direct mapping between sensory inputs and motor outputs where a fixed proportion of elbow muscle afferents project to motor neurons controlling the shoulder muscles. This ambiguity is particularly relevant in that some researchers have argued that direct mappings underlie the predictive capacity of voluntary action rather than internal models (Debicki and Gribble 2004; Gottlieb et al. 1996; Quaney et al. 2003). Our previous study on postural control (Kurtzer et al. 2008) showed that the R2/3 responses were more sophisticated than expected from a fixed direct mapping since they accounted for the influence of limb configuration on limb dynamics. Accordingly, feedback control of posture possesses either multiple direct mappings or an internal model, a distinction that becomes more blurred as the maps become increasingly modifiable. Future experiments will need to test whether R2/3 responses during reaching also account for changes in limb configuration and whether they can be rapidly modified with novel dynamics, another key feature of internal models.

In either case—internal models versus direct mappings—our findings reflect the integration of sensory information from both shoulder muscles and muscles that cross the elbow, elbow muscles, and/or biarticulars. This is an essential point that can be missed. Our findings cannot be explained from a simple local mapping from force sensors within a shoulder muscle (or its antagonist) since there are no sensors within the shoulder muscle (muscle spindles or Golgi tendon organs), which could transmit unambiguous information about the underlying torque perturbations. Information from a muscle crossing the elbow is needed to resolve the ambiguity.

Torque applied to just the elbow will induce motion at both the elbow and shoulder if both are free to move. In *experiments* 2 and 4, we applied torque at both joints together, such that the applied shoulder torque was equal and opposite the "interaction torque" from the elbow to the shoulder. Since no shoulder motion occurred there was no change in the internal force of a muscle crossing just the shoulder and no change in its muscle spindles or Golgi tendon organs. From the viewpoint of the shoulder muscle, no event had occurred; the shoulder muscle could not detect the applied shoulder torque. In *experiments* 1 and 3 the torque applied to the shoulder or elbow alone resulted in similar amounts of shoulder motion. Muscle spindles and Golgi tendon organs in a shoulder muscle were certainly affected but would give similar responses to the two perturba-

tions due to similar local changes within the muscle. From the viewpoint of the shoulder muscle the same event had occurred; the shoulder muscle could not distinguish an applied shoulder torque from an applied elbow torque. Accordingly, in all experiments the qualitative difference in activity between the short-latency and long-latency responses of the shoulder muscle cannot be due to changes in the weighting of various sensors within that muscle, from muscle spindles conveying motion information in the R1 epoch to Golgi tendon organs conveying force information in the R2/3 epoch. Rather, sensitivity of long-latency activity to the underlying shoulder torque must incorporate sensory information from muscles spanning the elbow (either monarticulars or biarticulars) since only these muscle sensors experienced changes with conditions (*experiments* 2 and 4) or across conditions (*experiments* 1 and 3) that could be decoded into the underlying torque.

Our findings complement and extend the known capabilities of feedback corrections occurring within the R2/3 epoch to mechanical perturbations of the upper limb. Activity in this epoch is able to regulate limb stiffness in parallel with environmental instability (Doemges and Rack 1992; Kimura et al. 2006; Perrault et al. 2008), account for muscle actions across different joints (Gielen et al. 1988), habituate with repeated exposures (Rothwell et al. 1986), adapt to different perturbation durations (Christakos et al. 1983; Hore and Vilis 1984), tune its output to task goals (Crago et al. 1976; Hammond 1956; Mutha et al. 2008; Prusyznski et al. 2008; Rothwell et al. 1980; Soetching et al. 1981), express a consistent output across background loads conditions (Prusyznski et al. 2009), and coordinate actions across the two limbs (Marsden et al. 1981; Ohki and Johansson 1999). Accordingly, R2/3 responses exhibit a comparable degree of sophistication to self-initiated voluntary actions. This functional parallelism obviates strong distinctions between "voluntary" and "reflex" and mitigates the usefulness of this nomenclature, a point that has been elucidated by previous researchers (Prochazka et al. 2001) and that motivated our adoption of the R2/3 designation rather than the more traditional long-latency reflex (Pruszynski et al. 2008).

We suspect that similarities between the R2/3 response and voluntary actions are due to the common contribution of primary motor cortex (M1). Accumulating evidence for the M1 contribution to R2/3 is provided by monkey studies (Cheney and Fetz 1984; Evarts and Tanj 1976; Flament and Hore 1988; Herter et al. 2009) and human studies (Day et al. 1992; Kimura et al. 2006; MacKinnon et al. 2000; Matthews 1991; Suminski et al. 2007; Tsuji and Rothwell 2002), which variously recorded and interfered with M1 processing when it would influence the R2/3 response. Primary motor cortex is well situated to be a key node for flexible and sophisticated feedback control. In addition to its intrinsic plasticity (Sanes and Donoghue 2000) and large contribution to the corticospinal tract (Dum and Strick 1991), M1 receives rich somatosensory information from the limb as well as inputs from several nonprimary motor areas and subcortical regions (basal ganglia and cerebellum) (Porter et al. 1993; Scott 2004). Although accumulating evidence suggests that M1 makes an important contribution to the R2/3 response, future work will need to determine whether the knowledge of limb dynamics in the R2/3 response is due to a transcortical pathway or circuits within the spinal cord and/or brain stem because these areas also possess adaptive capacities (for review see Pierrot-Deseil-

ligny and Burke 2005). Regardless, we expect the R2/3 response will continue to provide an important window into the evolving feedback response and its coordination across a distributed neural network with distinctive timescales and capacities.

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