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Fast feedback control involves two independent processes utilizing knowledge of limb dynamics

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Kurtzer I, Crevecoeur F, Scott SH. Fast feedback control involves two independent processes utilizing knowledge of limb dynamics. *J Neurophysiol* 111: 1631–1645, 2014. First published January 29, 2014; doi:10.1152/jn.00514.2013.—Corrective muscle responses occurring 50–100 ms after a mechanical perturbation are tailored to the mechanical features of the limb and its environment. For example, the evoked response by the shoulder's extensor muscle counters an imposed shoulder torque, rather than local shoulder motion, by integrating motion information from the shoulder and elbow appropriate for their dynamic interaction. Previous studies suggest that arm muscle activity within this epoch, alternately termed the R2/3 response, or long-latency reflex, reflects the summed result of two distinct components: an activity-dependent component which scales with the background muscle activity, and a task-dependent component which scales with the required vigor of the behavioral task. Here we examine how the knowledge of limb dynamics expressed during the shoulder muscle's R2/3 epoch is related to these two functional components. Subjects countered torque steps applied to their shoulder and/or elbow under different conditions of background torque and target size to recruit the activity-dependent and task-dependent component in varying degrees. *Experiment 1* involved four torque perturbations, two levels of background torques and two target sizes; this design revealed that both background torque and target size impacted the shoulder's R2/3 activity, indicative of knowledge of limb dynamics. *Experiment 2* involved two perturbation torques, five levels of background torque and two target sizes; this design demonstrated that the two factors had an independent impact on the R2/3 activity indicative of knowledge of limb dynamics. We conclude that a sophisticated feature of upper limb feedback control reflects the summation of two processes having a common capability.

long-latency reflex; multijoint dynamics; feedback

MECHANICAL INTERACTIONS ACROSS the different joints of the arm create a complex relation between the applied torques and resulting motion. For example, applying a flexor torque to the shoulder will flex the shoulder and extend the elbow, whereas applying an extensor torque to the elbow will extend the elbow and flex the shoulder (Craig 2005; Graham et al. 2003; Hollerbach and Flash 1982). A wealth of evidence indicates that these interactions are properly anticipated during planned reaching movements (Gottlieb et al. 1996; Gribble and Ostry 1999; Gritsenko et al. 2009). The mechanical interactions also create a difficulty for feedback control based solely on local muscle stretch since the same local muscle stretch can be caused by different imposed torques. Consider a shoulder extensor muscle that only responded to its own stretch. The same response would be evoked by a given shoulder flexion caused by either shoulder flexor torque or elbow extensor torque when, in fact, the shoulder extensor muscle must only compensate shoulder flexor torque to create a balance of forces. A similar situation occurs for all the muscles of the upper limb, local stretch can be induced by torque applied at the opposite joint, indicating that local feedback is inadequate to account for the complexity of intersegmental dynamics.[1]

Our most rapid arm response (R1 or short-latency reflex) occurs within 20 ms of the perturbation onset and is based solely on the muscle's local stretch (Gielen et al. 1988; Kurtzer et al. 2008; Soechting and Lacquaniti 1988). In contrast, corrective muscle responses, which occur 50–100 ms after an imposed displacement, termed the long-latency reflex or R2/3, do account for the limb's dynamics (Gielen et al. 1988; Kurtzer et al. 2008; Soechting and Lacquaniti 1988). Displacing the shoulder into flexion evokes a larger R2/3 response by a shoulder extensor when the motion results from applied shoulder flexor torque than elbow extensor torque (Kurtzer et al. 2008) due to the nervous system properly integrating motion from both shoulder and elbow muscles. The R2/3s of the shoulder muscles express this knowledge of limb dynamics over a wide range of contexts, postural and movement tasks (Crevecoeur et al. 2012; Kurtzer et al. 2009), small and large perturbations (Crevecoeur et al. 2012), and young and elderly subjects (Kurtzer et al. 2013), indicating that it is a core capability of upper limb feedback control.

Accumulating evidence suggests that the arm's R2/3 does not reflect a single process, but rather is the summed result of (at least) two distinct processes. The contribution of multiple processes is evident when contrasting two highly studied capabilities of the R2/3. First, the magnitude of R2/3 activity

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[1] Biarticular muscles deserve additional attention in whether they could utilize a simple control mechanism adequate for the arm's dynamics. The arm's biarticulars contribute shoulder and elbow torques of the same sign: flexion torques from biceps brachii; extension torques from triceps longus. Depending on the arm's configuration (and associated inertial Jacobian and position-dependent moment arms), then a simple feedback control strategy of these muscles would be suitable in countering particular perturbations. Specifically, if the moment arm of the biarticular is aligned with an eigenvector of the inertia matrix (where a torque perturbation induces a displacement only in the parallel direction), then local feedback and torque compensation are equivalent for perturbations in this direction. However, perturbations in all other directions would necessarily require contributions from other muscles to counter the underlying torque and involve complex integration of their partially overlapping actions. Hence, biarticular muscles do not provide a general solution to account for the arm's dynamics. A cohesive framework will need to address how all the muscles of the upper limb work to act in concert to respond to perturbations.

changes in parallel with the muscle's preperturbation activity, such that greater background muscle activity leads to a greater evoked response (Bedingham and Tatton 1984; Jaeger et al. 1982; Pruszynski et al. 2009). Second, the magnitude of R2/3 activity changes in parallel with the explicit goal of a behavioral task: greater R2/3 activity occurs when subjects are instructed to "resist" the imposed perturbation than "do not voluntarily intervene" (Calancie and Bawa 1985; Crago et al. 1976; Hammond 1956; Jaeger et al. 1982; Lewis et al. 2006; Pruszynski et al. 2008; Rothwell et al. 1980). By varying the background muscle activity and task goal, we recently tested for the independence of these changes. If the activity-dependent and task-dependent change in activity reflected a single process, then the changes should covary: low task-dependent activity with low background muscle activity and high task-dependent activity with high background muscle activity. Alternatively, the R2/3 could reflect the contribution of functionally distinct components so that the magnitude of task-dependent activity is not altered by the level of background activity. Our results were consistent with the second hypothesis, leading us to conclude that two distinct functional components contribute to the R2/3 epoch, an activity-dependent component and a task-dependent component (Pruszynski et al. 2011a). (Also see Lewis et al. 2006 for a complementary approach to this issue.)

Here we examine how the knowledge of limb dynamics expressed during the shoulder's R2/3 is related to these two functional components (Fig. 1). Almost all previous studies demonstrating R2/3's knowledge of limb dynamics utilized significant background muscle activity and a vigorous task goal which would strongly engage both functional components (Crevecoeur et al. 2012; Gielen et al. 1988; Kimura et al. 2006; Kurtzer et al. 2008, 2009; Latash 2000; Soechting and Lacquaniti 1988), and no study varied the muscle's preperturbation activity and task goal. Therefore, they could not distinguish whether knowledge of limb dynamics was only expressed by the task-dependent component (*model #1*, Fig. 1*A*), only expressed by the activity-dependent component (*model #2*, Fig. 1*B*), or expressed by components (*model #3*, Fig. 1*C*). We conducted two experiments utilizing a range of torque pertur-

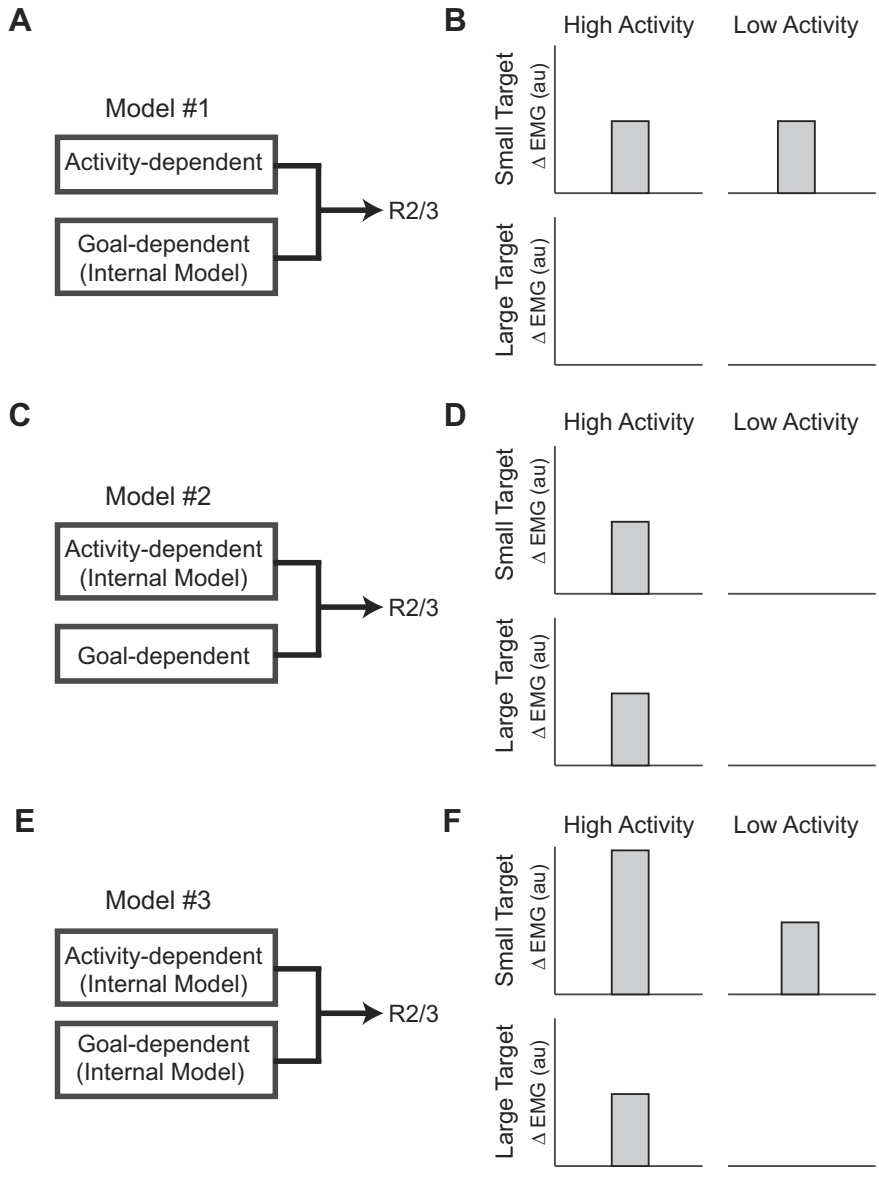

Fig. 1. Contrasting models of the knowledge of limb dynamics expressed in the R2/3 epoch. Note that these are didactic simplifications and do not show sensory inflow, descending commands, or feedback from action to sensory inflow. *A*: in *model #1*, the R2/3 is generated by an activity-dependent component and a task-dependent component, but only the task-dependent component has knowledge of limb dynamics. *B*: this model predicts that the knowledge of limb dynamics expressed by the R2/3 would exhibit a particular pattern with changes in target size and background muscle activity. Bar height reflects the differential amount of shoulder R2/3 activity to the paired perturbations which indicates the knowledge of limb dynamics (*experiment 1*: shoulder flexion vs. elbow extension torque; *experiment 2*: combined flexion vs. combined extension torque). Only the task-dependent component has knowledge of limb dynamics, so differential activity only occurs with the small target and does not change with background muscle activity. *C*: in *model #2*, only the activity-dependent component has knowledge of limb dynamics. *D*: predicted differential activity of *model #2* only occurs with conditions having high background muscle activity and does not change with the target size. *E*: in *model #3*, both components have knowledge of limb dynamics. *F*: predicted differential activity of *model #3* occurs with either high background muscle activity or the small target, and their combination causes the greatest differential. ΔEMG, change in EMG; au, arbitrary units.

bations, background torques, and target sizes to examine R2/3 activity when the two components contributed in varying degrees. Our results indicate that knowledge of limb dynamics is expressed by both the activity-dependent and task-dependent component of the shoulder's R2/3 and highlight that a sophisticated feature of sensorimotor control is expressed by parallel mechanisms.

MATERIALS AND METHODS

Subjects. A total of 11 subjects participated in the experiments, following informed consent to procedures approved by the ethics committee at Queen's University (n = 9, *experiment 1*; *n* = 6, *experiment 2*). Eight subjects were men, and three subjects were women (mean age = 28.7 yr). Each experiment lasted ≈2.5 h, and subjects were paid for their time.

Apparatus. Similar to our previous studies (Scott 1999; Kurtzer et al. 2008; Pruszynski et al. 2008), subjects performed the motor tasks with a robotic exoskeleton (KINARM, BKIN Technologies, Kingston, ON, Canada). This device was adjusted to the size of the subject's right arm, supported its weight, enabled flexion/extension movements of the shoulder and elbow in the horizontal plane, and could 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 also presented in the horizontal plane via a virtual-reality system, while a cloth bib and metal partition obscured direct vision of the subject's arm.

Muscle recording. In *experiment 1*, we recorded surface EMG from each subject's posterior deltoid, a shoulder extensor muscle, whereas in *experiment 2* we recorded surface EMG from each subject's posterior deltoid and pectoralis major, a shoulder flexor muscle. We have previously demonstrated knowledge of limb dynamics in the R2/3s of these muscles. Since the current study did not utilize conditions which would reveal this property in other arm muscles, we restricted our recording to shoulder muscles. In all cases, 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 or knee following light abrasion of the overlying skin surfaces with alcohol. Our procedures are fully described in earlier papers (Pruszynski et al. 2008).

General task. Each trial began with the appearance of a target and application of a background torque ramped up over 500 ms. Subjects stabilized their hand-aligned cursor (0.5-cm radius) at the target's center, corresponding to a shoulder angle of 45° and elbow angle of 75°. During the hold period, subjects were told to avoid co-contracting their muscles. After a random time interval of 1–4 s, a step torque was applied to their arm (rise time = 10 ms; plateau = 900–1,300 ms; fall time = 500 ms). To achieve task success, subjects had to remain within the target for 900 ms of the subsequent 1,300 ms. Corrections were guided without visual feedback of their hand, although the target was colored green or red when their hand was inside or outside the target, respectively. The total applied torque then ramped down to zero, remained off during an intertrial period of 1 s, and the hand-aligned cursor reappeared. Trials differed in which targets, background torques, and perturbation torques were utilized. The same target was always used within a block of trials, whereas the background and perturbation torque were always randomly assigned. This minimized the impact of task-switching, while ensuring that subjects could not predict the upcoming perturbation.

Experiment 1: Testing if background load, voluntary task, or both factors contribute to knowledge of limb dynamics. Experiment 1 tested if the background load, or voluntary task, or both factors impacted the knowledge of limb dynamics expressed in the R2/3 of shoulder muscles. Two background torques, two targets, and four perturbation torques were utilized (see Table 1 and Fig. 2). We collected 30 repeats of all 16 combinations of background torque-target size-perturbation torque for a total of 480 trials.

Table 1. *Summary of conditions for experiments 1 and 2*

Target Size	Background Torque	Perturbation Torques
Experiment 1		
Small	SF (2 Nm)	SF, EE, SF/EF, SE/EE
Small	SE (−2 Nm)	SF, EE, SF/EF, SE/EE
Large	SF (2 Nm)	SF, EE, SF/EF, SE/EE
Large	SE (−2 Nm)	SF, EE, SF/EF, SE/EE
Experiment 2		
Small	SF (3 Nm)	SF/EF, SE/EE
Small	SF (1.5 Nm)	SF/EF, SE/EE
Small	No Sho (0 Nm)	SF/EF, SE/EE
Small	SE (−1.5 Nm)	SF/EF, SE/EE
Small	SF (−3 Nm)	SF/EF, SE/EE
Large	SF (3 Nm)	SF/EF, SE/EE
Large	SF (1.5 Nm)	SF/EF, SE/EE
Large	No Sho (0 Nm)	SF/EF, SE/EE
Large	SE (−1.5 Nm)	SF/EF, SE/EE
Large	SF (−3 Nm)	SF/EF, SE/EE

SF, shoulder flexor torque; EE, elbow extensor torque; No Sho, no shoulder.

The two magnitudes of background torque allowed us to examine how a change in background muscle activity altered the shoulder's evoked response to a perturbation (Fig. 2*A*). With a background shoulder flexor torque of 2 Nm, the shoulder extensor muscle needed a relatively high level of activity to oppose the load. With a background shoulder extensor torque of −2 Nm, the shoulder extensor muscle needed relatively low level of activity to not assist the load.

The two sizes of the visual target allowed us to examine how a change of voluntary task altered the shoulder's evoked response to a perturbation (Fig. 2*B*). The "small target" had a radius of 2 cm and required a vigorous response to return one's hand to the target within the time-accuracy requirement (i.e., remain within the target for 900 ms of the subsequent 1,300 ms). The large target had a radius of 30 cm and afforded a much less vigorous response; subjects were further instructed "do not voluntarily intervene" to facilitate the minimal voluntary response.

By employing four different pairs of the background torque and target size, we aimed to recruit the shoulder muscle R2/3's activity-dependent and task-dependent components in four different patterns (Fig. 2, *D* and *F*). The high activity/large target combination (*bottom left* panels of Fig. 2, *D* and *F*) should strongly recruit the activity-dependent component (given the high preperturbation muscle activity), but not the task-dependent component (given the weak vigor needed to remain within the large target). The low activity/small target combination (*top right* panels of Fig. 2, *D* and *F*) should strongly recruit the task-dependent component (given the greater vigor needed to remain within the small target), not the activity-dependent component (given the low preperturbation muscle activity). The high activity/small target combination should strongly recruit both components (*top left* panels of Fig. 2, *D* and *F*). Finally, the low activity/large target combination should strongly recruit neither component (*bottom right* panels of Fig. 2, *D* and *F*).

Four perturbation torques were selected to reveal knowledge of limb dynamics in the shoulder extensor muscle (Fig. 2, *C* and *E*) (Kurtzer et al. 2008). The linkage between the arm's segments results in mechanical interaction across its joints (Craig 2005; Graham et al. 2003; Hollerbach and Flash 1982) such that torque applied at one joint will induce motion at several joints. Likewise, motion of a particular joint could arise from torque applied to that joint or to another joint. We leveraged this property of limb dynamics with a pair of single-joint torques, shoulder flexion torque and elbow extension torque, whose relative magnitude resulted in a similar amount of shoulder flexion (Fig. 2*C*). If the shoulder extensor's R2/3 was based solely on shoulder motion, then this pair of perturbations would evoke the same amount of activity as they induced the same amount of shoulder motion. In contrast, a larger muscular response to shoulder flexion

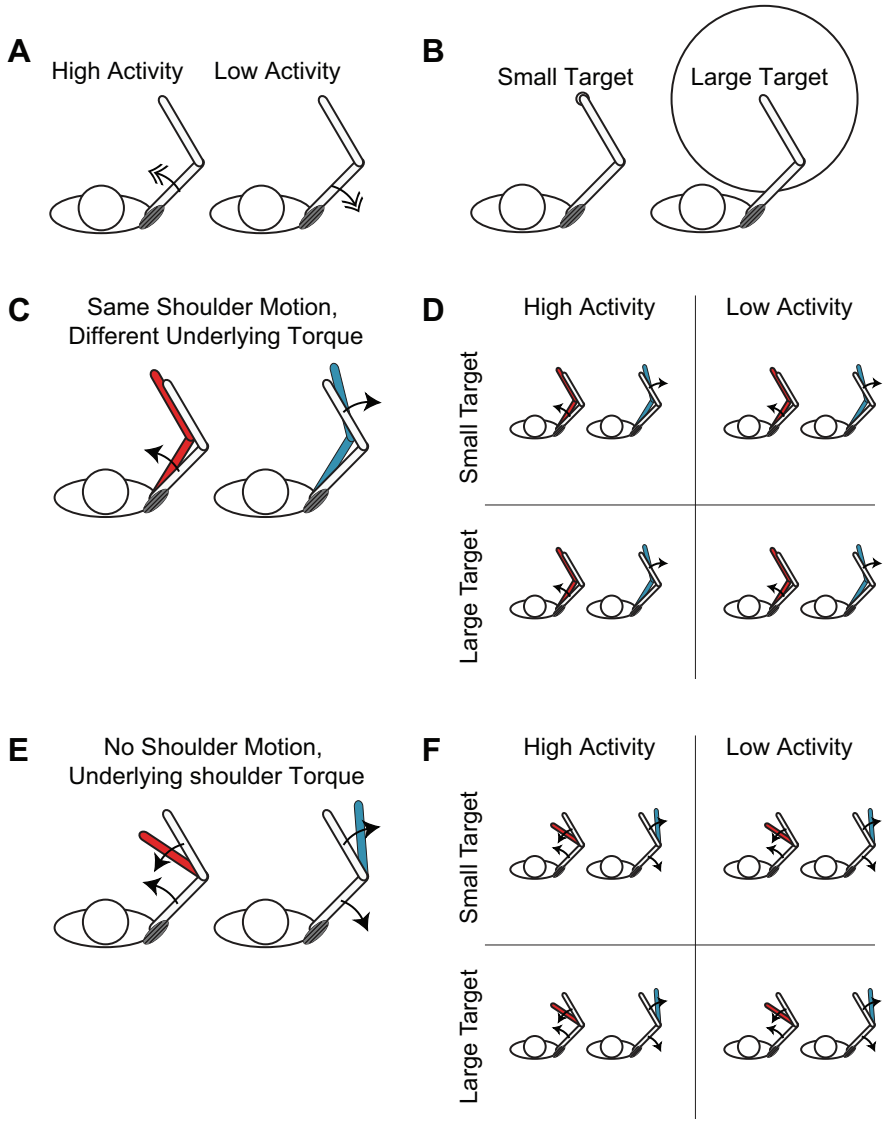

Fig. 2. Background torques, targets, and perturbation torques for *experiment 1*. *A*: a constant flexor (2 Nm) or extensor (−2 Nm) torque was applied to the subject's shoulder joint to create a relatively high or low amount of steady-state activity by the shoulder extensor muscle. *B*: the small target (2-cm radius) required relatively vigorous responses to achieve task success, whereas the large target (30-cm radius) required relatively weak responses. Four combinations of background muscle activity and target size were used with all four torque perturbations (16 conditions in total). *C*: the red-armed cartoon depicts arm motion following shoulder flexion torque, whereas the blue-armed cartoon depicts arm motion following elbow extension torque. *D*: the four target size/background activity combinations are shown with the pair of perturbation torques selected to induce similar amounts of shoulder motion (corresponding to *B* in *left* column). *E*: the red-armed cartoon depicts arm motion following combined flexion torque, whereas the blue-armed cartoon depicts arm motion following combined extension torque. *F*: the four target size/background activity combinations are shown with the pair of perturbation torques selected to induce motion of just the elbow joint (corresponding to *C* in left column).

torque than elbow extensor torque would be consistent with integrating information from both joints appropriate for the underlying perturbation. Data obtained with these torques is grouped as *experiment 1a*.

Mechanical interaction across the arm's joints also means that torque must be applied at both the shoulder and elbow to create motion at just one joint. We leveraged this fact of limb dynamics with a pair of multijoint torque, shoulder flexion-elbow flexion torque and shoulder extension-elbow extension torque, which caused flexion or extension of the elbow joint and minimal shoulder motion (Fig. 2*E*). If the shoulder extensor's R2/3 response was based solely on shoulder motion, then this pair of perturbations would fail to elicit a shoulder muscle response, as they induced no shoulder motion. In contrast, knowledge of limb dynamics would be apparent as an excitatory response to the flexor torque perturbation and an inhibitory response to the extensor torque perturbation. Data obtained with these torques are grouped as *experiment 1b*.

By applying the selected torque perturbations during different combinations of background torque and target size, we tested how knowledge of limb dynamics is expressed by the different components of the R2/3 epoch. A schematic of the three alternative organizations is presented in Fig. 1. Note that these are didactic simplifications and do not show sensory inflow, descending commands, or feedback from action to sensory inflow. Moreover, our approach is neutral on whether these components receive similar sensory information, the role of descending commands, and the internal architecture which provides knowledge of limbs dynamics, such as an inverse model, recurrent forward model, or direct controller (for review, see Tin and Poon 2005). Our approach aims to address whether knowledge of limb dynamics is expressed in the different conditions of target size and preperturbation activity, and the computational aspects of the control architecture are beyond the scope of the present paper.

We tested between three possible models by examining the differential response to the paired perturbations as this reveals the knowledge of limb dynamics (i.e., larger response to shoulder flexion than elbow extension torque; larger response to combined flexion torque than combined extension torque) (Fig. 2, *C* and *E*). In *model #1* (Fig. 1*A*), the knowledge of limb dynamics is expressed by just the task-dependent component; hence, a differential response is only present with the small target requiring a vigorous response and does not change with the background muscle activity (Fig. 1*B*). In *model #2* (Fig. 1*C*), knowledge of limb dynamics is expressed by just the activity-dependent component; hence, a differential response is only present when the muscle has relatively high activity and does not change with the target size (Fig. 1*D*). In *model #3* (Fig. 1*E*), knowledge of limb dynamics is expressed by both components. Hence, a differential response is present when the muscle either has relatively high activity or the small target is used, and the largest differential

occurs with the high activity/small target combination when both components can contribute (Fig. 1*F*). All models predict weak differential activity with the low activity/large target combination, as neither component is strongly engaged.

Experiment 2: Testing if background load and voluntary task have an independent contribution to knowledge of limb dynamics. Results consistent with *model #3* (both activity-dependent and task-dependent component) motivated this experiment. Here we tested if the background load and voluntary task had an independent impact on the knowledge of limb dynamics expressed in the R2/3 epoch. Five background torques, two targets, and two perturbation torques were utilized (see Table 1). We collected 25 repeats of all 20 combinations of background torque-target size-perturbation torque for a total of 500 trials.

Five different background torques were applied to the shoulder (−3, −1.5, 0, 1.5, and 3 Nm) to provide a more detailed examination of background muscle activity on the R2/3 magnitude. We utilized the same two targets from *experiment 1*: a "small target" with a radius of 2 cm and a "large target" with a radius of 30 cm. And the two perturbations were multijoint torques, shoulder flexion-elbow flexion torque and shoulder extension-elbow extension torque, to cause motion at just the elbow joint.

Independent expression of knowledge of limb dynamics would be evident as a constant contribution from the task-dependent component for each level of background torque. That is, if the contribution by the task-dependent component is independent of the contribution expressed by the task-dependent component, then the change in activity associated with a change in target size should not vary with the background load. Note that we only examined the evoked activity to combined flexor torque, as combined extensor torque leads to inhibitory responses and a floor effect with low background muscle activity.

Data analysis. Angular positions of the shoulder and elbow were low-pass filtered (25 Hz, 2-pass, sixth-order Butterworth). Surface electrical activity of posterior deltoid was amplified (gain = 1–10 K), digitally sampled at 1,000 Hz, band-pass filtered (10–350 Hz), and rectified. The EMG signals were finally normalized by the individual muscle's mean activity during the hold period with an activating torque. Each subject's activity in the posterior deltoid was normalized by his/her mean activity from all conditions having a shoulder flexion background torque −2 Nm during *experiment 1* and 1.5 Nm during *experiment 2*. Each subject's activity in the pectoralis major was normalized by the mean activity from all conditions having a shoulder extension background torque (−1.5 Nm during *experiment 2*).

We examined the change in the joint angle from its starting position.

$$\Delta\text{ShoAng} = \text{change in shoulder angle from starting position}$$

$$\Delta\text{ElbAng} = \text{change in elbow angle from starting position}$$

We defined position error as the net displacement from the starting angle.

$$\text{Position error} = \sqrt{\Delta\text{ShoAng}^2 + \Delta\text{ElbAng}^2}$$

Movement reversal was defined as the time of the maximum position error, and final position error is the position error 900 ms following the perturbation. Accordingly, joint kinematics were examined shortly after the perturbations (50 ms), at the movement's reversal, and near the end of the trial.

For the muscle activity, we focused on a postperturbation epoch, alternately called the long-latency reflex, long-latency response, M2/3, and R2/3 (Crago et al. 1976; Lee et al. 1982; Kurtzer et al., 2008; Pruszynski et al. 2008). We adopt the R2/3 designation to unambiguously abbreviate primary motor cortex as M1 and avoid the connotation of "reflex" as a simple and inflexible process (Prochazka et al. 2000). This epoch spans 50- to 100-ms postperturbation when the muscle countered any opposing background load. We shifted the time window by 5 ms (55–105 ms) whenever the muscle acted with an assisting background load. This small shift accounts for the slight delay observed in the onset of task-dependent responses, consistent with previous reports (Bedingham and Tatton 1982; Pruszynski et al. 2011a) and likely reflecting the impact of preinhibition of the motoneurons. In addition to the R2/3, we also examined an earlier and later epoch. The R1, also called the short-latency reflex, is the fastest stretch-evoked response by the nervous system (20–45 ms postperturbation) and is exclusively mediated by spinal circuitry. Early voluntary activity occurs 120–180 ms postperturbation. These epochs are consistent with previous studies, including our own (Calancie and Bawa 1985; Crago et al. 1976; Jaeger et al. 1982; Kurtzer et al., 2008; Lee et al. 1982; Lewis et al. 2006; Pruszynski et al. 2008).

Paired *t*-tests contrast the evoked response from baseline and between conditions. Repeated-measure ANOVAs also examined trends across different conditions. Significance for all tests was set at $P < 0.05$.

RESULTS

Experiment 1a: Behavior and muscle activity evoked by shoulder displacement. The different conditions led to distinct patterns of limb motion. Figure 3*A* shows the trajectory of the hand following the single-joint step torques (data only shown for high background torque), whereas Fig. 3*B* shows the corresponding joint displacements (corresponds to Fig. 2*C*). Note that the induced motion is grouped into four combinations of background muscle activity and target size. The shoulder flexion torque and elbow extension torque displaced the shoulder into flexion and the elbow into extension. Critically, the initial amount of shoulder motion caused by these two perturbations was quite similar. Across all four background activity-target size combinations, the shoulder displacement measured 50 ms postperturbation was 10 ± 3% greater following the elbow torque than shoulder torque; hence, feedback response based on local motion would be similar (or slightly smaller) following the shoulder torque than elbow torque perturbation.

The absolute amount of initial shoulder was similar but not identical across the background activity conditions. Shoulder displacement was 12 ± 4% less with low-shoulder extensor activity (extensor background torque) than high activity (flexor background torque). Lastly, target size had little impact on the initial joint displacement, but a powerful impact over the duration of the trial. With the small target, subjects reversed their outward movement 223 ± 32 ms following the perturbation and obtained a final positional error of 1 ± 1°, whereas the large target led to movement reversals at 630 ± 250 ms and a final positional error of 28 ± 11°.

The use of different background torques and target sizes resulted in characteristic patterns of preperturbation and evoked activity in the shoulder extensor muscle. Figure 4*A* presents the time-varying muscle activity (group data) to the four combinations. Not surprisingly, the background torque resulted in large systematic difference in the muscle's preperturbation activity. On average, the background extensor torque led to low level of activity, 18% of that obtained with the background flexor torque. Note that this low level of muscle activity is likely near the physiological and measurement floor, since the signal from a no-torque condition was 22% of that obtained during background flexion torque ($n = 6$ subjects). Target size had a small, although systematic, impact on background muscle activity: high activity/small target = 1.03 ± .06

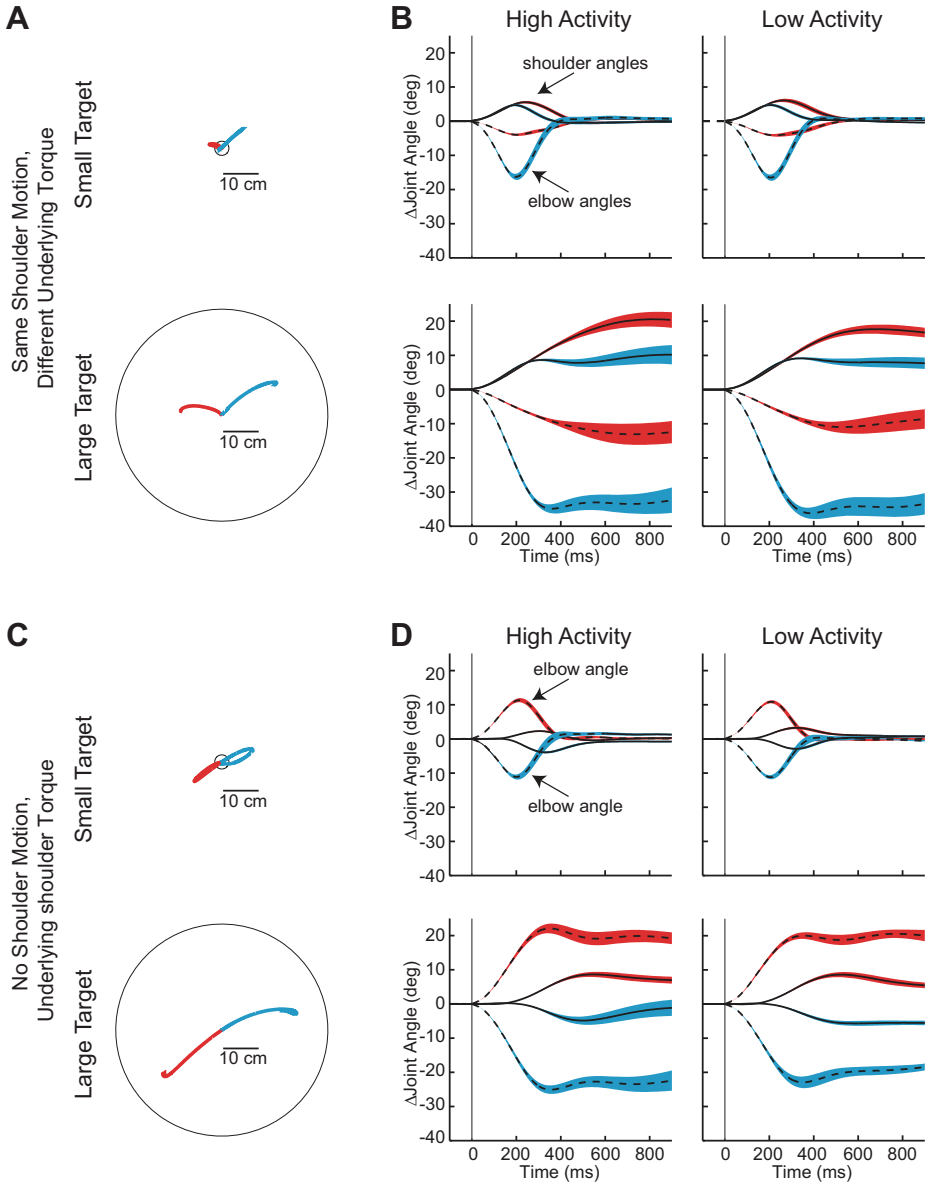

Fig. 3. Joint motion during *experiment 1*. *A*: group average of hand motion following the pair of single-joint torque perturbations [shoulder flexor torque (SF) indicated by red, elbow extensor torque (EE) indicated by blue]. Data are only shown for the high-activity condition. *B*: each panel displays the group's shoulder and elbow motion following the same torque perturbations; vertical lines indicate perturbation onset and 50 ms after perturbation onset. Solid and dashed lines show the average shoulder and elbow position, respectively. Red and blue outlines show the standard error for joint motion. Each panel is associated with a particular combination of target size and background muscle activity (same format as Fig 2*B*). *C*: group average of hand motion following the pair of multijoint torque perturbations (flexor torque indicated by red, extensor torque indicated by blue). Data are only shown for the high-activity condition. *D*: the four panels display the group's shoulder and elbow motion following the same torque perturbations. Red and blue outlines show the standard error for joint motion.

arbitrary units (au); high activity/large target = 0.97 ± .08 au; low activity/small target 0.21 ± 0.07 au; low activity/large target 0.16 ± .07 au.

Background muscle activity, target size, and perturbation direction all impacted the evoked muscle activity in the R2/3 epoch. During the high activity/small target combination (*top left* panel of Fig. 4*A*), evoked responses tended to increase across the R1, R2/3, and voluntary epochs. Moreover, the shoulder flexion torque evoked more muscle activity in the R2/3 [subject's mean *t*-value $>$ 4.6; group $t_{(8)}$ = 9.2, $P < 0.001$ one-sided] and voluntary epoch [subject's mean *t*-value $>$ 7.9; group $t_{(8)}$ = 5.4, $P < 0.001$ one-sided] than the elbow extension torque (*top left* panel of Fig. 4*B*), consistent with it expressing knowledge of limb dynamics.

The impact of target size was apparent in the high activity/large target combination. Significantly weaker R2/3 activity [$F_{(1,8)} = 56.8$, $P < 0.001$] and voluntary activity [$F_{(1,8)} = 38.3$, $P < 0.001$] occur here than during the high activity/small target condition described above (*bottom left* panel of Fig. 4*A*). Regardless, shoulder flexion torque evoked more activity than the elbow extension torque in the R2/3 epoch [subject's mean *t*-value $>$ 2.9; group $t_{(9)} > 3.0$, $P < 0.01$ one-sided] and the voluntary epoch [subject's mean *t*-value $>$ 2.9; group $t_{(9)} > 3.0$, $P < 0.01$ one-sided] (*bottom left* panel of Fig. 4*B*).

During the low activity/small target combination (*top right* panel of Fig. 4*A*), the shoulder muscle expressed a robust evoked response in the R2/3 epoch and voluntary epoch, despite the weak level of preperturbation activity. In particular, the shoulder flexion torque evoked more activity in the R2/3 epoch [subject's mean *t*-value = 3.8; group $t_{(8)} > 6.6$, $P < 0.001$ one-sided] and voluntary epoch [subject's mean *t*-value = 7.5; group $t_{(8)}$ = 3.9, $P < 0.005$ one-sided] than the elbow extension torque (*top right* panel of Fig. 4*B*).

The final combination involved low preperturbation activity and the large target. The shoulder extensor's subsequent evoked activity was quite weak, consistent with the low preperturbation activity and low amount of required vigor (*bottom right* panel of Fig. 4*A*). For example, the mean evoked activity

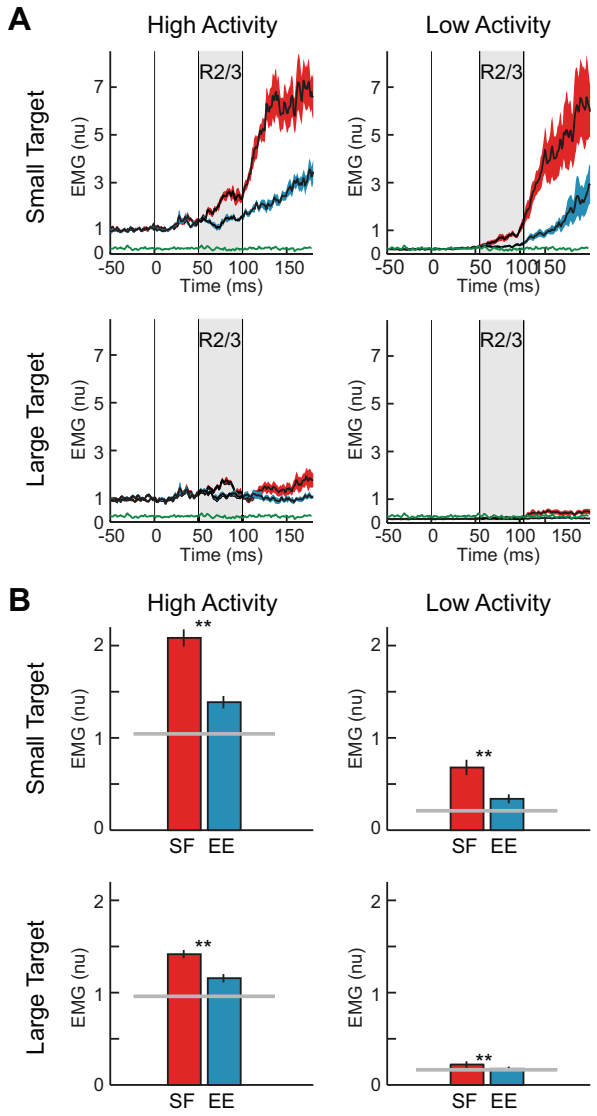

Fig. 4. Evoked muscle activity in *experiment 1a* (torque perturbations which induce similar amounts of shoulder motion). *A*: the four panels display the shoulder extensor activity during the four combinations of target size and background muscle activity (same format as Fig 2, *B* and *C*). The black line with red outline depicts the group mean and standard error with the SF. The black line with blue outline depicts the group's mean and standard error with the EE. Green line depicts the group's mean activity with no background torque. Vertical black lines in each panel indicate the onset of the step torque, whereas the gray rectangles bracket the R2/3 epoch. *B*: bar plots showing group mean and standard error of muscle activity with SF (red) and EE (blue). Gray horizontal line indicates baseline muscle activity before perturbation; evoked activity is the bar height relative to the gray horizontal line. Bars are grouped according to the target size and background torque. Significant contrasts: $^{**}P < 0.01$.

in the R1, R2/3 and voluntary epochs to the shoulder flexion torque was 3%, 6% and 5%, respectively, of the mean response with flexor background torque/small target combination. Activity in the R2/3 epoch [$F_{(1,8)} = 38.9$, $P < 0.001$] and voluntary epoch [$F_{(1,8)} = 16.9$, $P < 0.001$] was also significantly lower than that present with low activity/small target combination. Despite the low level of evoked activity, the R2/3 epoch showed small differences between the two torque conditions [subject's mean t-value = 1.7; group $t_{(8)} = 2.9$, $P = 0.01$ one-sided] as did the voluntary epoch [subject's mean t-value > 2.6; group $t_{(8)} = 3.4$, $P < 0.01$ one-sided] (*bottom right* panel of Fig. 4*B*).

In summary, a differential response to the shoulder flexor and elbow extensor torque was expressed in the R2/3 and voluntary epoch for all combinations of target and background torque. R1 activity never differentiated between the two torque perturbations [mean $|t\text{-value}| < 0.5$; group $|t_{(8)}| < 0.6$, $P > 0.5$ two-sided].

Experiment 1b: Behavior and muscle activity evoked by elbow displacement. Figure 3*C* shows the trajectory of the hand following the multijoint step torques (data only shown for high background torque), whereas Fig. 3*D* shows the corresponding joint displacements (corresponds to Fig. 2*E*). The combined flexor torque and combined extension torque displaced the elbow into flexion and extension, respectively. Moreover, almost no shoulder displacement initially resulted from the perturbation. Across all four background-target combinations, the shoulder displacement measured 50 ms postperturbation was 2 ± 1% the size of the initial elbow displacement. The absolute amount of initial joint displacement was similar, but not identical, across the different combinations; elbow displacement was 3 ± 3% less with low shoulder extensor activity (extensor background torque) than high activity (flexor background torque). Target size also had a negligible impact on the initial joint displacement, but a powerful impact over the duration of the trial. Subjects reversed their outward movement around 211 ± 17 ms and obtained a final positional error of 1 ± 1° with the small target vs. 585 ± 254 ms and 21 ± 6° with the larger target.

The different levels of background muscle activity and target size powerfully impacted the responses to multijoint torques which caused motion almost entirely at the elbow joint. Figure 5*A* presents the time-varying shoulder muscle activity (group data) to these conditions. During the high activity/small target combination (*top left* panel of Fig. 5*A*), excitatory and inhibitory bursts resulted from the combined flexion torque and combined extension torque, respectively. Differential activity to these perturbations, consistent with knowledge of limb dynamics, achieved statistical significant in the R2/3 epoch [subject's mean t-value = 10.5; group $t_{(8)} > 15.7$, $P < 0.001$ one-sided] and voluntary epoch [subject's mean t-value = 15; group $t_{(8)} = 7.2$, $P < 0.001$ one-sided] (*top left* panel of Fig. 5*B*).

With the background flexor torque and large target combination (*bottom left* panel of Fig. 5*A*), the evoked responses in the R2/3 epoch [$F_{(1,8)} = 160.1$, $P < 0.001$] and the voluntary epoch [$F_{(1,8)} = 57.8$, $P < 0.001$] were significantly weaker, indicating an impact of target size. The combined flexion torque continued to evoke more activity than the combined extension torque in the R2/3 epoch [subject's mean t-value = 6.6; group $t_{(8)} = 4.7$, $P < 0.005$ one-sided] and the voluntary epoch [subject's mean t-value = 8.4; group $t_{(8)} = 6.4$, $P < 0.001$ one-sided] (*bottom left* panel of Fig. 5*B*).

The background extensor torque and small target combination (*top right* panel of Fig. 5*A*) resulted in weak preperturbation activity but robust R2/3 and voluntary responses. The weak level of muscle activity precluded inhibitory response. Nonetheless, the two step torques evoked different levels of R2/3 activity [subject's mean t-value = 3.8; group $t_{(8)} > 6.6$, $P < 0.001$ one-sided] and voluntary activity [subject's mean t-value = 3.8; group $t_{(8)} > 6.6$, $P < 0.001$ one-sided] (*top right* panel of Fig. 5*B*).

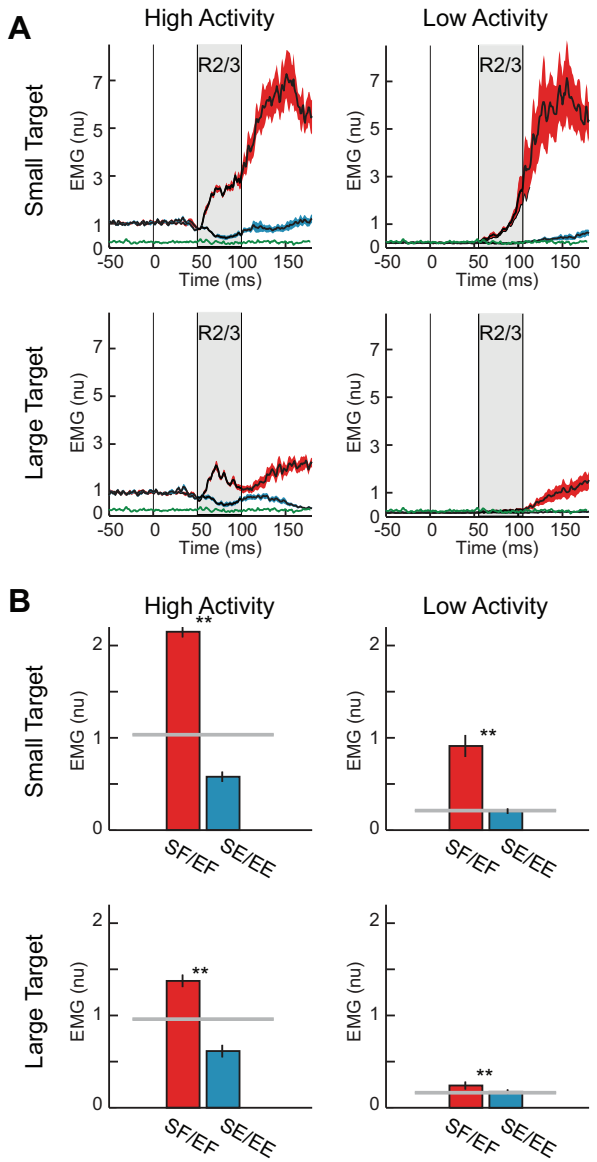

Fig. 5. Evoked muscle activity with torque perturbations induced no elbow motion. *A*: the four panels display the shoulder extensor activity during the four combinations of target size and background muscle activity (same format as Fig 2, *B* and *C*). The black line with red outline depicts the group mean and standard error with the combined flexor torque. The black line with blue outline depicts the group's mean and standard error with the combined extensor torque. Green line depicts the group's mean activity with no background torque. Vertical black lines in each panel indicate the onset of the step torque, whereas the gray rectangles bracket the R2/3 epoch. *B*: bar plot showing group mean and standard error of muscle activity with the combined flexor torque (red) and combined extensor torque (blue). Gray horizontal line indicates baseline muscle activity before perturbation; evoked activity is the bar height relative to the gray horizontal line. Bars are grouped according to the target size and background torque. Significant contrasts: $^{**}P < 0.01$.

The final combination involved a background extensor torque and large target (*bottom right* panel of Fig. 5*A*). Shoulder muscle activity was significantly lower than during the extensor torque and small target combination, R2/3 epoch [$F_{(1,8)} = 39.4$, $P < 0.001$]; voluntary epoch [$F_{(1,8)} = 29.2$, $P < 0.001$], indicating the impact of target size. The two multijoint torques also evoked weak but significant differences of muscle activity in the R2/3 epoch [subject's mean t-value = 2.1; group $t_{(8)} = 2.1$, $P = 0.033$ one-sided] and voluntary epoch [subject's mean t-value = 7.6; group $t_{(8)} = 3.3$, $P < 0.01$ one-sided] (*bottom right* panel of Fig. 5*B*).

In summary, a differential response to the multijoint torques was expressed in the R2/3 and voluntary epoch in all conditions. R1 activity was never found to differentiate between the two torque perturbations [mean t-value $< |0.5|$; group $t_{(8)} < |1.1|$, $P > 0.2$ two-sided].

Experiment 1: Relating R2/3's knowledge of limb dynamics to the activity-dependent and task-dependent components. To determine how the task-dependent and activity-dependent components contribute to R2/3's knowledge of limb dynamics (compare to Fig. 1, *B*, *D*, and *F*), we examined how the differential response to paired torque perturbations changes with background torque and target size (Fig. 6, *A* and *B*). The magnitude of differential activity was lowest during the low activity/large target combination (*bottom right* panels), which would weakly engage either component [single-joint torques: group $t_{(8)} = 7.6$, $P < 0.001$ two-sided; multijoint torques: group $t_{(8)} = 13.7$, $P < 0.001$ two-sided]. Differential activity was greater than this combination during either the high activity/large target combination (*bottom left* panels) [single-joint torques: group $t_{(8)} = 4.0$, $P < 0.005$ two-sided; multijoint torques: group $t_{(8)} = 8.1$, $P < 0.001$ two-sided] or low activity/small target combination (*top right* panels) [single-joint torques: group $t_{(8)} = 4.4$, $P < 0.005$ two-sided; multijoint

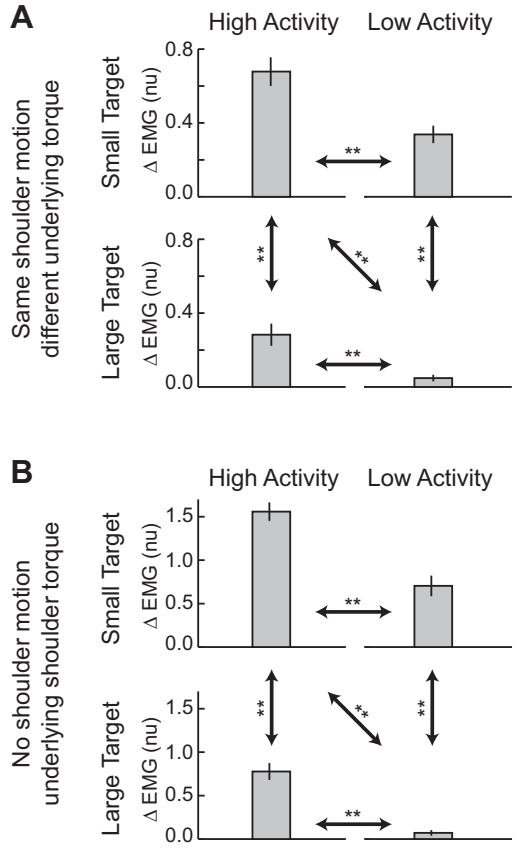

Fig. 6. R2/3 activity for all conditions of *experiment 1*. *A*: group mean and standard error of the differential muscle activity between the SF and EE conditions. *B*: group mean and standard error of differential muscle activity between the combined flexor torque and combined extensor torque conditions. Significant contrasts: $^{**}P < 0.01$.

torques: group $t_{(8)} = 5.2$, $P < 0.001$ two-sided]. Greater differential activity with an increase in background muscle activity or the small target suggests that a greater engagement of either the activity-dependent or the task-dependent component allows a stronger expression of R2/3's knowledge of limb dynamics.

We also found that differential activity was greatest during the high activity/small target combination (*top left* panels). Its differential was larger than during the low activity/small target combination [single-joint torques: group $t_{(8)} = 4.4$, $P < 0.005$ two-sided; multijoint torques: group $t_{(8)} = 7.7$, $P < 0.001$ two-sided], but this comparison is inadequate since low baseline muscle activity eliminates the possibility of a large inhibitory response. The critical comparison is between the high activity/small target and high activity/large target combinations, since both involve substantial background activity of the muscle. In fact, greater differential activity was observed for the high activity/small target combination (strongly engaging the task-dependent and activity-dependent components) than the high activity/large target combination (strongly engaging the activity-dependent component) [single-joint torques: group $t_{(8)} = 7.2$, $P < 0.001$ two-sided; multijoint torques: group $t_{(8)} = 9.2$, $P < 0.001$ two-sided].

As we previously mentioned, there was a small systematic difference in background shoulder extensor activity with the two different targets. If this difference significantly altered the excitability of feedback circuitry, then it would contaminate the alteration's R2/3 activity with target size and our attempt to dissociate the R2/3 response into a task-dependent component and activity-dependent component. To test for this possibility, we examined the R1 evoked during shoulder displacement, since the R1 is entirely generated by a spinal pathway. A two-way ANOVA revealed a significant effect of background load [shoulder flexion torque: $F_{(1,8)} = 12$, $P < 0.01$; elbow extension torque: $F_{(1,8)} = 6.7$, $P < 0.05$], but not target size [shoulder flexion torque: $F_{(1,8)} = 1.4$, $P = 0.27$; elbow extension torque: $F_{(1,8)} = 3.3$, $P = 0.11$] nor an interaction of background load and target size [shoulder flexion torque: $F_{(1,8)} = 0.42$, $P = 0.53$; elbow extension torque: $F_{(1,8)} = 2.1$, $P = 0.18$]. Hence, the small differences in background muscle activity with target size do not account for the robust change in R2/3 activity.

Further note that the relatively long experiment (480 trials over ≈2.5 h) did not lead to appreciable changes in the magnitude of the R2/3 over time. We tested this possibility with three-way ANOVA, which considered the four combinations of background activity and target size, four perturbations, and split the trials into the first half and second half of the experiment. This analysis indicated a significant main effect of the background muscle activity-target size combination [$F_{(3,24)} = 38.2$; $P = 0.0001$] and the torque perturbation [$F_{(3,24)} = 96$; $P = 0.0001$], as well as a significant interaction of the two [$F_{(9,72)} = 54.7$; $P = 0.0001$]. However, time did not have a significant main effect [$F_{(1,8)} = 2.0$; $P = 0.2$], nor a significant interaction with either the background muscle activity-target size combination [$F_{(3,24)} = 1.0$; $P = 0.42$] or the torque perturbation [$F_{(3,24)} = 0.9$; $P = 0.43$]. The interaction of all three categories (background activity-target size, perturbation, and time) was also not significant [$F_{(9,72)} = 1.1$; $P = 0.40$]. Hence, the R2/3 was stable over the course of the experiment (see Table 2).

Table 2. *Summary of evoked activity for experiment 1*

Muscle Activity	Target Size	Perturbation Torque	Early R2/3	Late R2/3
High	Small	SF	1.03 (0.10)	1.05 (0.09)
High	Small	EE	0.37 (0.08)	0.35 (0.06)
High	Small	SF/EF	1.18 (0.07)	1.03 (0.10)
High	Small	SE/EE	−0.43 (0.05)	−0.45 (0.05)
Low	Small	SF	0.37 (0.08)	0.37 (0.09)
Low	Small	EE	0.12 (0.04)	0.11 (0.04)
Low	Small	SF/EF	0.48 (0.08)	0.51 (0.11)
Low	Small	SE/EE	−0.01 (0.02)	−0.01 (0.02)
High	Large	SF	0.46 (0.03)	0.45 (0.05)
High	Large	EE	0.21 (0.07)	0.15 (0.05)
High	Large	SF/EF	0.49 (0.06)	0.33 (0.06)
High	Large	SE/EE	−0.37 (0.08)	−0.36 (0.08)
Low	Large	SF	0.06 (0.03)	0.04 (0.01)
Low	Large	EE	0.01 (0.01)	0.01 (0.01)
Low	Large	SF/EF	0.07 (0.02)	0.06 (0.03)
Low	Large	SE/EE	0.01 (0.00)	0.01 (0.00)

Values are means (SD).

Our results are consistent with both the task-dependent and activity-dependent components contributing to R2/3's knowledge of limb dynamics (*model #3*). If the two components are independent, then their joint contribution should be predicted from their separate effects. Accordingly, we summed the evoked R2/3 during the high activity/large target combination (strong contribution from the activity-dependent component) and the low activity/small target combination (strong contribution from the load-dependent component). This summed activity was compared with the evoked R2/3 activity during the high activity/small target combination (strong contribution from both components) (Fig. 7*A*). Figure 7*B* shows the predicted and observed activity for the shoulder flexion torque, elbow extension torque, and combined flexion torque perturbations; the combined extension torque was not tested due to a floor effect with low background activity. No statistical difference between the predicted and observed activity was obtained for any of the perturbations [group $t_{(8)} < 1.5$, $P > 0.15$ two-sided].

We also examined whether linear summation was present at the level of individual subjects by regressing each subject's predicted R2/3 activity against their observed R2/3 activity (Fig. 7*C*). We found a high correlation [$r = 0.88$, $P < 0.01$, degrees of freedom (df) = 25] and a linear regression that did not differ from unity (95% confidence interval). Note that this same pattern continued when we examined the predicted and observed R2/3 within each torque perturbation [$r > 0.62$, $P < 0.05$, df = 7].

Experiment 2: Behavior and muscle activity evoked by elbow displacement. We conducted a second experiment to provide a further test whether knowledge of limb dynamics was independently utilized by both the task-dependent and activity-dependent components. Independence would be evident as a constant contribution from the task-dependent component across a large range of background torque conditions, in contrast to the two levels of background torque used in *experiment 1*. Accordingly, *experiment 2* employed two target sizes, five background torques, and two torques randomly displacing the elbow into flexion or extension (see Table 1).

The induced motion is grouped into 10 combinations of background torque and target size (Fig. 8). Multijoint torque

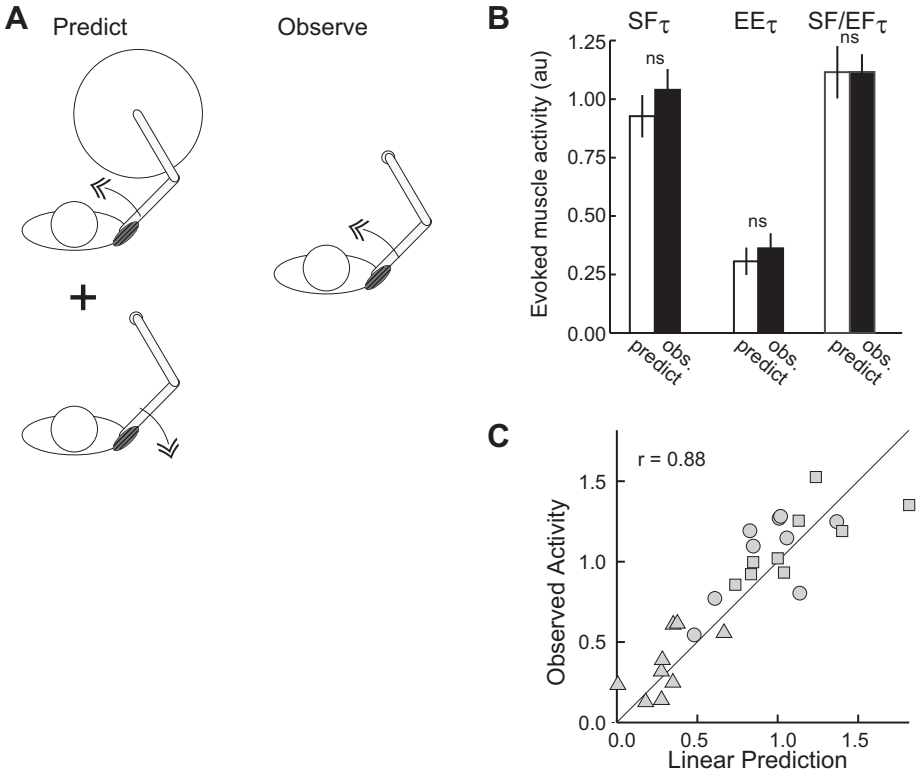

Fig. 7. Comparison of R2/3 responses across different conditions of *experiment 1*. *A*: the high activity/large target combination should primarily engage the activity-dependent component, whereas the low activity/small target combination should primarily engage the task-dependent component. If the activity-dependent component and task-dependent component of the R2/3 are independent, then a linear summation of evoked activity from the two conditions should accurately predict the evoked activity with the small target and extensor background torque. *B*: bar plot showing group mean and standard error for the linear prediction (open) and observed response (solid). Contrasts are shown for the SF, EE and combined flexor torque perturbations. *C*: each subject's predicted and observed activity for the SF (gray circles), EE (gray triangles) and combined flexor torque perturbations (gray squares). $r = 0.88$ is the linear correlation. ns, Nonsignificant.

perturbations and targets led to a similar pattern described in *experiment 1*. The combined flexor torque initially displaced the elbow into flexion, whereas the combined extension torque initially displaced the elbow into extension. Neither perturbation caused much shoulder displacement; across all targets and background loads, the initial shoulder displacement was 2 ± 1% the size of the initial elbow displacement. The different background torques led to minimal changes in the movement trajectories. In contrast, the two targets led to dramatically different movement trajectories. With the small target, subjects reversed their outward movement at 209 ± 17 ms and obtained a final positional error of 1 ± 1°, whereas the large target often led to movement reversal and a final positional error of 27 ± 6°.

As in *experiment 1*, the different target sizes, background torques, and perturbation directions dramatically impacted the pattern of shoulder extensor activity. Figure 9 presents the time-varying activity of the shoulder extensor (group data) to these conditions. Prior to the perturbation, the shoulder extensor exhibited low levels of activity with either no applied torque or applied extension torque, along with increasing levels of activity with increasing flexion torque. As seen in *experiment 1*, the two randomly intermingled perturbations evoked differential muscle responses by the R2/3 epoch, with greater activity to combined flexion torque than combined extension torque. The largest excitatory and inhibitory responses in this muscle occurred when the subject countered the largest flexion background torque (3 Nm) and the small target was presented (Fig. 9, *top left* panel). Likewise, the smallest responses occurred in this muscle when the subject countered the largest extension background torque (−3 Nm) and the large target was presented (*bottom right* panel). Between these two combinations was a continuum of R2/3 activity as confirmed by a main effect of perturbation direction [$F_{(1,5)} = 100.8$, $P < 0.001$] and its interaction with background torque [$F_{(4,20)} = 22.3$, $P < 0.001$] and target size [$F_{(1,5)} = 35.4$, $P < 0.005$].

To ascertain whether the task-dependent component had a constant contribution of knowledge of limb dynamics across different background torques, we focused on the combined flexion torque perturbation since it evokes an excitatory response; otherwise, the inhibitory response to combined extensor torque would have a floor effect with low preperturbation activity. Background extension torque resulted in weak shoulder extensor activity, whereas increased flexion torque resulted in increased shoulder extensor activity (Fig. 10*A*), a trend confirmed by a main effect of background torque [$F_{(4,20)} = 158$, $P < 0.001$]. Evoked activity in the R2/3 epoch largely paralleled this pattern, increasing activity with increasing flexion torque, and exhibited a main effect of background torque [$F_{(4,20)} = 11.2$, $P < 0.001$]. Importantly, the small target led to consistently larger responses than the large target [$F_{(1,20)} = 33.6$, $P < 0.005$], yet the interaction of target size and background torque failed to reach significance [$F_{(4,20)} = 0.83$, $P > 0.5$], indicating that the two variables had independent effects. As a final analysis, we conducted a regression of task-dependent activity against background torque to test for a systematic relation not flagged by the ANOVA. A linear regression failed to achieve significance ($P > 0.5$, df = 28), consistent with a constant contribution from the task-dependent component and independent use of knowledge of limb dynamics.

Similar findings were obtained with the shoulder flexor, pectoralis major, collected in the same session (Fig. 10*B*). Its excitatory R2/3 was evoked by combined extension torque and showed a main effect of background torque [$F_{(4,20)} = 9.4$, $P < 0.001$], greater activity when the subject countered greater background extension torque. The small target resulted in larger R2/3 to this perturbation than the large target [$F_{(1,20)} = 22.5$, $P < 0.01$];

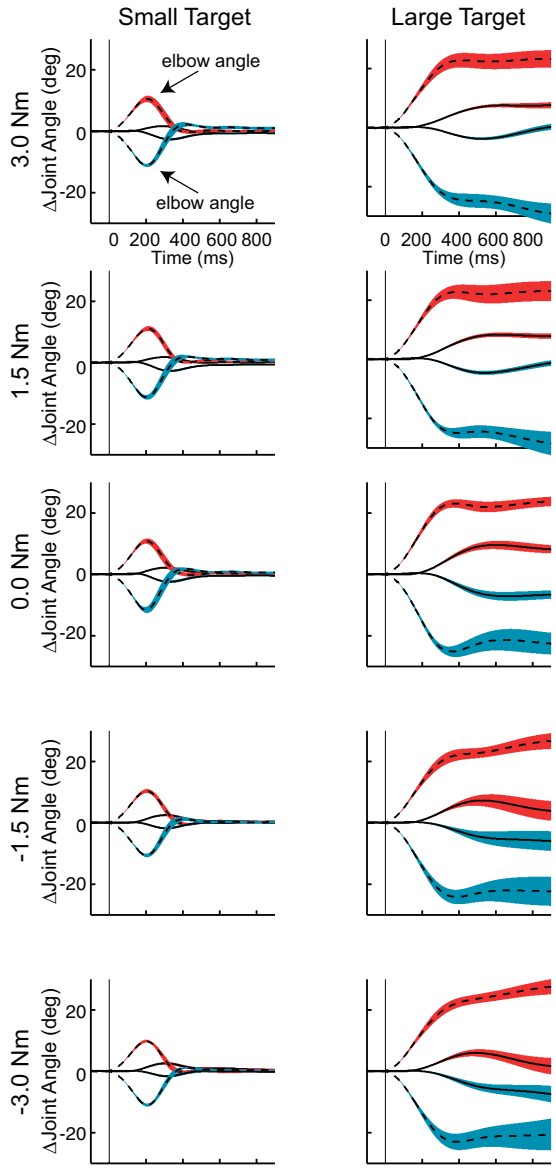

Fig. 8. Joint motion during *experiment 2*. Each panel displays the group's shoulder and elbow motion following the pair of multijoint torque perturbations; vertical lines indicate perturbation onset and 50 ms after perturbation onset. Solid and dashed lines show the average shoulder and elbow position, respectively. Red and blue outlines show the standard error for joint motion with SF and EE, respectively. Each panel is associated with a particular combination of target size and background torque.

however, target size did not show a significant interaction with background torque [$F_{(4,20)} = 1.7$, $P > 0.19$], indicating independent effects of the two variables. As a final analysis, we examined whether the task-dependent difference in activity had a systematic change with the level of background torque. The linear regression failed to achieve significance ($P > 0.13$, df = 28), consistent with a constant contribution from the task-dependent component and independent use of knowledge of limb dynamics.

DISCUSSION

The present study dissected a key capability of the arm's stretch-evoked R2/3 response: knowledge of limb dynamics. Our paradigm involved three experimental manipulations: *1*) background torque to modify the level of preperturbation muscle activity; *2*) target size to modify the level of voluntary reaction; and *3*) two pairs of perturbations to probe if the shoulder response utilized elbow motion appropriate for the arm's dynamics. In *experiment 1*, we observed that background torque and target size scaled the evoked shoulder muscle activity, indicative of knowledge of limb dynamics, and these two factors had a combined impact akin to linear summation. In *experiment 2* we found that background torque and target size had an independent impact on the evoked shoulder muscle activity, indicative of knowledge of limb dynamics. This pattern of results is consistent with a separate "activity-depen-

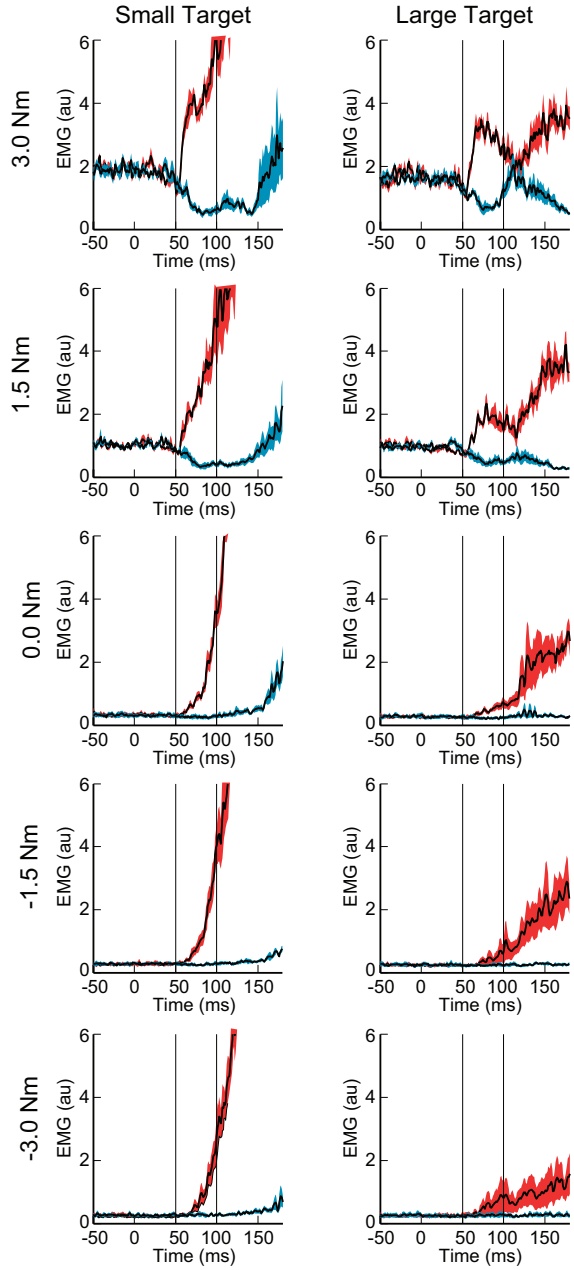

Fig. 9. Evoked muscle activity with combined flexor torque and combined extensor torque perturbations: *experiment 2*. *Left* column shows the shoulder muscle activity (group mean and SEM) during the combined flexor torque (red) and combined extensor torque (blue) and small target. *Right* column shows the shoulder muscle activity in the same format given the large target. The rows correspond to the background torque employed.

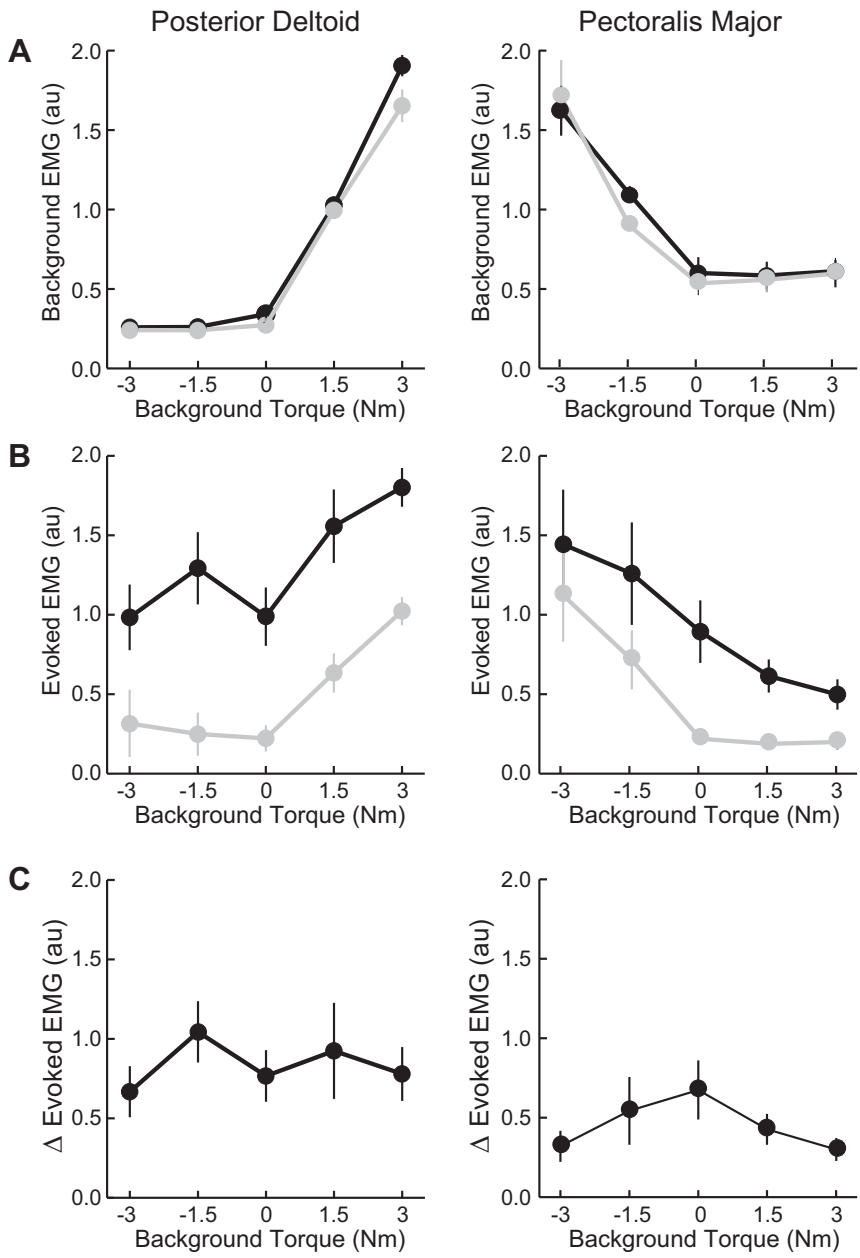

Fig. 10. R2/3 activity for all conditions of *experiment 2*. *A*: background muscle activity (group mean and standard error) across different background torques. Activity with the small and large targets is depicted by the black and gray lines, respectively. *B*: evoked activity (ground mean and standard error) in the R2/3 epoch to perturbation torque causing pure elbow flexion (for posterior deltoid) or pure elbow extension (for pectoralis major). *C*: difference in evoked activity for the two different target sizes.

dent" and "task-dependent" component contributing knowledge of limb dynamics to the R2/3 response.

A number of previous studies have argued that activity within the R2/3 epoch reflected the overlap of two components, one automatic and the other linked to the voluntary goal (Capaday et al. 1994; Lewis et al. 2006; Manning et al. 2012; Pruszynski et al. 2011a; Rothwell et al. 1980; Shemmell et al. 2009). This hypothesis is supported by the shared features of voluntary reactions and task-dependent changes in R2/3 activity. Both are impacted by stimulus predictability, where greater uncertainty in perturbation onset or perturbation direction leads to weaker task-dependent changes (Pruszynski et al. 2008; Rothwell et al. 1980). An even stronger association of the R2/3 and voluntary reaction is the trial-by-trial correlation in their magnitude of activity (Pruszynski et al. 2011a). The highest correlation occurs when the subject generates a vigorous response from a low-activity background which primarily recruits the task-dependent component; a significant but lower correlation occurs when the subject generates a vigorous response from a high-activity background which recruits both the task-dependent and activity dependent components.

Given this chain of associations, it is tempting to consider the task-dependent component as a hastened voluntary reaction (Rothwell et al. 1980; Capaday et al. 1994; Manning et al. 2012). However, the two are not equivalent. We observed knowledge of limb dynamics in the activity-dependent component, so this capability is not unique to the task-dependent component. In addition, perturbations that engage clear voluntary responses, such as a tendon tap (~100 ms) or a nonpainful shock of the finger (~90 ms), fail to evoke the task-dependent response which begins 55–70 ms after limb displacement (Jaeger et al. 1982; Lee and Tatton 1982; Rothwell et al. 1980).

Several previous studies have identified that the activity-dependent and task-dependent components have different

properties. During a "do not intervene" instruction, Lewis et al. (2006) abolished R2/3 activity when the perturbing displacement lasted less than 35 ms, whereas Shemmell et al. (2009) attenuated the R2/3 by increasing the stiffness of the robotic interface. In both cases, the manipulation had a powerful effect on the automatic aspect of the R2/3 activity and little impact on the additional evoked activity occurring with a "resist" instruction. Here we demonstrated that the activity-dependent and task-dependent components share a similar and notably sophisticated capability.

Our conclusions are based on the capability of the arm's shoulder flexor and extensor muscles. We focused on the shoulder muscles to extend our earlier studies, which demonstrated multijoint integration appropriate for the arm's mechanical properties (Kurtzer et al. 2008, 2010, 2013) and task-dependency (Pruszynski et al. 2008) in their R2/3. Accordingly, our conclusions only strictly apply to feedback control of the arm's shoulder muscles. It should be noted that the R2/3 of wrist muscles and elbow muscle also express knowledge of limb dynamics and task-dependency (Gielen et al. 1988; Jaeger et al. 1982; Koshland et al. 1991; Latash 2000; Lee and Tatton 1982; Lewis et al. 2006; Pruszynski et al. 2008; Soechting and Lacquaniti 1988), indicating that they are generally expressed by muscles of the upper arm. Testing whether their activity-dependent and task-dependent components both express multijoint integration could be readily tested with our paradigm: different levels of background muscle activity, different levels of required vigor, and torque perturbations evoke multijoint responses. We predict that a similar pattern will occur with the wrist and elbow muscles that we observed for the shoulder muscles.

Another important question is the neural substrates which underlie these functionally distinct components. Primary motor cortex (M1) certainly plays a key role in creating R2/3 activity (see Scott 2004 for review). Its physiological involvement in the arm's R2/3 is established by depressed hand and elbow muscular responses following sensorimotor stroke (Marsden et al. 1977; Trumbower et al. 2013), cortical responses preceding muscular responses of the wrist, elbow, and shoulder (Cheney and Fetz 1984; Evarts and Tanji 1976; Herter et al. 2009; MacKinnon et al. 2000), and altered hand, wrist, elbow, and shoulder muscle responses by transcranial magnetic stimulation (Day et al. 1991; Lewis et al. 2005; Tsuji and Rothwell 2002). By pairing our perturbation paradigm with transcranial magnetic stimulation in humans and single-unit recording in monkeys, we also demonstrated that M1 contributes to the shoulder R2/3's knowledge of limb dynamics (Pruszynski et al. 2011b). Accordingly, primary motor cortex appears to contribute to the R2/3 of all muscles of the upper limb. It is an open question whether primary motor cortex contributes a similar amount to the R2/3 of different upper limb muscles, since some neural disorders impact the R2/3s of distal more than proximal arm muscles (Fellows et al. 1996; Thilmann et al. 1991), and the relative size of the R2/3 can vary across different arm muscles (Lenz et al. 1983).

In addition to primary motor cortex, several studies provide evidence that spinal and brain stem circuits contribute to some of the arm's R2/3 activity. R2/3s in elbow muscles continue to be expressed when primary motor cortex is temporarily blocked via cooling probes (Miller and Brooks 1981) or even following spinalization (Ghez and Shinoda 1978; Tracey et al. 1980). Depressed R2/3s of wrist muscles are reported to occur in the presence of anti-spastics which inhibit spinal processing (Lourenco et al. 2006; Meskers et al. 2010). However, direct recording of spinal and brain stem circuits during limb perturbations are currently lacking.

One might reasonably expect that primary motor cortex underlies the task-dependent component, and that spinal cord circuits underlie the activity-dependent component. Primary motor cortex does express task-dependent responses which are appropriately timed to the task-dependent activity of R2/3 (Evarts and Tanji 1976). However, perturbation evoked activity is also observed under conditions requiring minimal voluntary reaction (Evarts and Tanji 1976), suggesting that M1 also supports the automatic activity-dependent component. Moreover, there is evidence that brain stem circuitry may contribute to the task-dependent component: *1*) a large pulse of transcranial magnetic stimulation will suppress activity within M1, but not R2/3 activity expressed during a "resist" instruction (Shemmell et al. 2009); *2*) neck muscle activity which is evoked by startling auditory stimuli (via a brain stem circuit) is associated with the task-dependent activity evoked by a limb perturbation (Ravichandran et al. 2013). The complex relation between function and neural substrate motivates further experimentation and may determine that the activity-dependent and task-dependent components do not engage completely distinct brain regions, but rather particular links among the regions.

The particular capabilities expressed by activity-dependent and task-dependent components are not entirely distinct, since we provide evidence that a notably sophisticated ability, knowledge of limb dynamics, is present in both. This fact is novel and suggests that the highly parallel organization of descending neural control does not provide unique functions for each pathway, but rather partially overlapping capabilities. The past 50 yr have uncovered a wide range of capabilities in the R2/3 epoch (see Pruszynski and Scott 2012 for review). Some examples include scaling with environmental instability (Doemges and Rack 1992; Kimura et al. 2006; Perreault et al. 2008), habituating with repeated exposures (Rothwell et al. 1986), adapting to different perturbation durations (Christakos et al. 1983; Hore and Vilis 1984), and coordinating actions across the two limbs (Dimitriou et al. 2012; Marsden et al. 1981; Omrani et al. 2013). At the moment, these capabilities are a loose collection. Relating these diverse capabilities to the activity-dependent and task-dependent components will reveal which capabilities are shared, which are unique, and possibly a general logic which lumps capabilities together. In sum, an approach which examines partially overlapping sets of capabilities could help identify the parallel structures that underlie fast feedback control.

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DISCLOSURES

S. H. Scott is associated with BKIN Technologies, which commercializes the KINARM robot used in this study.

AUTHOR CONTRIBUTIONS

Author contributions: I.L.K. and S.H.S. conception and design of research; I.L.K. and F.C. performed experiments; I.L.K. analyzed data; I.L.K., F.C., and S.H.S. interpreted results of experiments; I.L.K. prepared figures; I.L.K. drafted manuscript; I.L.K., F.C., and S.H.S. edited and revised manuscript; I.L.K., F.C., and S.H.S. approved final version of manuscript.

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