

1 Title: Fast feedback control involves two independent processes utilizing  
2 knowledge of limb dynamics  
3 Abbreviated Title: two feedback internal models

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17 Authors and addresses:

18 Isaac Kurtzer<sup>1</sup>, Frédéric Crevecoeur<sup>2</sup>, and Stephen H. Scott<sup>2-3</sup>

19 <sup>1</sup>Department of Biomedical Sciences

20 New York Institute of Technology - College of Osteopathic Medicine,  
21 Old Westbury, NY USA

22 <sup>2</sup>Centre for Neuroscience Studies and <sup>3</sup>Department of Medicine  
23 Queen's University, Kingston, ON Canada

24

25

26 Corresponding author:

27 Isaac Kurtzer, Ph.D.

28 Department of Biomedical Sciences NYIT - College of Osteopathic Medicine,  
29 Old Westbury, NY USA

30 Tel: 516 686 3913; Fax: 516 686 3750

31 Email: ikurtzer@nyit.edu

32

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43 **Abstract**

44         Corrective muscle responses occurring 50-100 ms after a mechanical  
45 perturbation are tailored to the mechanical features of the limb and its environment.  
46 For example, the evoked response by the shoulder's extensor muscle counters an  
47 imposed shoulder torque, rather than local shoulder motion, by integrating motion  
48 information from the shoulder and elbow appropriate for their dynamic interaction.  
49 Previous studies suggest that arm muscle activity within this epoch, alternately termed  
50 the R2/3 response or long-latency reflex, reflects the summed result of two distinct  
51 components, an activity-dependent component which scales with the background  
52 muscle activity and a task-dependent component which scales with the required vigour  
53 of the behavioural task. Here we examine how the knowledge of limb dynamics  
54 expressed during the shoulder muscle's R2/3 epoch is related to these two functional  
55 components. Subjects countered torque steps applied to their shoulder and/or elbow  
56 under different conditions of background torque and target size to recruit the activity-  
57 dependent and task-dependent component in varying degrees. Experiment 1 involved  
58 four torque perturbations, two levels of background torques and two target sizes; this  
59 design revealed that both background torque and target size impacted the shoulder's  
60 R2/3 activity indicative of knowledge of limb dynamics. Experiment 2 involved two  
61 perturbation torques, five levels of background torque and two target sizes; this design  
62 demonstrated that the two factors had an independent impact on the R2/3 activity  
63 indicative of knowledge of limb dynamics. We conclude that a sophisticated feature of  
64 upper limb feedback control reflects the summation of two processes having a common  
65 capability.

## 66 Introduction

67 Mechanical interactions across the different joints of the arm create a complex  
68 relation between the applied torques and resulting motion. For example, applying a  
69 flexor torque to the shoulder will flex the shoulder and extend the elbow whereas  
70 applying an extensor torque to the elbow will extend the elbow and flex the shoulder  
71 (Craig 2005; Graham et al. 2003; Hollerbach and Flash 1982). A wealth of evidence  
72 indicates that these interactions are properly anticipated during planned reaching  
73 movements (Gottlieb et al. 1996; Gribble et al. 1999; Gritsenko et al. 2011). The  
74 mechanical interactions also create a difficulty for feedback control based solely on local  
75 muscle stretch since the same local muscle stretch can be caused by different imposed  
76 torques. Consider a shoulder extensor muscle that only responded to its own stretch.  
77 The same response would be evoked by a given shoulder flexion caused by either  
78 shoulder flexor torque or elbow extensor torque when, in fact, the shoulder extensor  
79 muscle must only compensate shoulder flexor torque to create a balance of forces. A  
80 similar situation occurs for all the muscles of the upper limb – local stretch can be  
81 induced by torque applied at the opposite joint – indicating that local feedback is  
82 inadequate to account for the complexity of intersegmental dynamics<sup>1</sup>.

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<sup>1</sup> 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

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

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

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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 act in concert to respond to perturbations.

100 capabilities of the R2/3. First, the magnitude of R2/3 activity changes in parallel with  
101 the muscle's pre-perturbation activity such that greater background muscle activity  
102 leads to a greater evoked response (Bedingham and Tatton 1984; Jaeger et al. 1982;  
103 Pruzynski et al. 2009). Second, the magnitude of R2/3 activity changes in parallel with  
104 the explicit goal of a behavioural task – greater R2/3 activity occurs when subjects are  
105 instructed to “resist” the imposed perturbation than “do not voluntarily intervene”  
106 (Calancie and Bawa 1984; Crago et al. 1976; Hammond 1956; Jaeger et al. 1982; Lewis et  
107 al. 2006; Pruzynski et al. 2008; Rothwell et al. 1980). By varying the background muscle  
108 activity and task goal we recently tested for the independence of these changes. If the  
109 activity-dependent and task-dependent change in activity reflected a single process,  
110 then the changes should co-vary: low task-dependent activity with low background  
111 muscle activity and high task-dependent activity with high background muscle activity.  
112 Alternatively, the R2/3 could reflect the contribution of functionally distinct components  
113 so that the magnitude of task-dependent activity is not altered by the level of  
114 background activity. Our results were consistent with the second hypothesis leading us  
115 to conclude that two distinct functional components contribute to the R2/3 epoch, an  
116 activity-dependent component and a task-dependent component (Pruzynski et al.  
117 2011a) (Also see Lewis et al 2006 for a complementary approach to this issue).

118 Here we examine how the knowledge of limb dynamics expressed during the  
119 shoulder's R2/3 is related to these two functional components (Fig. 1). Almost all  
120 previous studies demonstrating R2/3's knowledge of limb dynamics utilized significant  
121 background muscle activity and a vigorous task goal which would strongly engage both

122 functional components (Crevecouer et al. 2012; Gielen et al. 1988; Kimura et al. 2006;  
123 Kurtzer et al 2008; Kurtzer et al 2009; Latash 2000; Soechting and Lacquaniti 1988). And  
124 no study varied the muscle's pre-perturbation activity and task goal. Therefore, they  
125 could not distinguish whether knowledge of limb dynamics was only expressed by the  
126 task-dependent component (model #1, Fig. 1A), only expressed by the activity-  
127 dependent component (model #2, Fig. 1B), or expressed by components (model #3, Fig.  
128 1C). We conducted two experiments utilizing a range of torque perturbations,  
129 background torques, and target sizes to examine R2/3 activity when the two  
130 components contributed in varying degrees. Our results indicate that knowledge of  
131 limb dynamics is expressed by both the activity-dependent and task-dependent  
132 component of the shoulder's R2/3 and highlight that a sophisticated feature of sensori-  
133 motor control is expressed by parallel mechanisms.

## 134 Materials and Methods

### 135 *Subjects*

136 A total of 11 subjects participated in the experiments following informed  
137 consent to procedures approved by the ethics committee at Queen's University (n = 9,  
138 Experiment 1; n = 6, Experiment 2). 8 subjects were male and 3 subjects were female  
139 (mean age = 28.7 yrs). Each experiment lasted ≈2.5 hrs and subjects were paid for their  
140 time.

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142 *Apparatus*

143           Similar to our previous studies (Scott 1999; Kurtzer et al. 2008; Pruszyński et al.  
144 2008) subjects performed the motor tasks with a robotic exoskeleton (KINARM, BKIN  
145 Technologies Ltd, Kingston, ON). This device was adjusted to the size of the subject's  
146 right arm, supported its weight, enabled flexion/extension movements of the shoulder  
147 and elbow in the horizontal plane, and could selectively apply torques to each joint.  
148 Shoulder angle is measured relative to the frontal plane and elbow angle is measured  
149 between the forearm and upper arm, 0° is full extension. Visual targets and a hand-  
150 aligned cursor were also presented in the horizontal plane via a virtual-reality system  
151 while a cloth bib and metal partition obscured direct vision of the subject's arm.

152 *Muscle recording*

153           In Experiment 1, we recorded surface EMG from each subject's posterior deltoid,  
154 a shoulder extensor muscle, whereas in Experiment 2 we recorded surface EMG from  
155 each subject's posterior deltoid and pectoralis major, a shoulder flexor muscle. We  
156 have previously demonstrated knowledge of limb dynamics in the R2/3s of these  
157 muscles. Since the current study did not utilize conditions which would reveal this  
158 property in other arm muscles, we restricted our recording to shoulder muscles. In all  
159 cases, a two-bar electrode (DE-2.1 Delsys Inc., Boston, MA) was affixed to the muscle  
160 belly and a ground electrode was placed on the subject's ankle or knee following light  
161 abrasion of the overlying skin surfaces with alcohol. Our procedures are fully described  
162 in earlier papers (Pruszyński et al. 2008).

163 *General Task*

164           Each trial began with the appearance of a target and application of a background  
165 torque ramped up over 500 ms. Subjects stabilized their hand-aligned cursor (0.5 cm  
166 radius) at the target's center corresponding to a shoulder angle of 45° and elbow angle  
167 of 75°. During the hold period subjects were told to avoid co-contracting their muscles.  
168 After a random time interval of 1-4 seconds, a step torque was applied to their arm (rise  
169 time = 10 ms; plateau = 900-1300 ms; fall time = 500ms). To achieve task success  
170 subjects had to remain within the target for 900 ms of the subsequent 1300 ms.  
171 Corrections were guided without visual feedback of their hand although the target was  
172 coloured green or red when their hand was inside or outside the target, respectively.  
173 The total applied torque then ramped down to zero, remained off during an inter-trial  
174 period of 1 second, and the hand-aligned cursor reappeared. Trials differed in which  
175 targets, background torques, and perturbation torques were utilized. The same target  
176 was always used within a block of trials whereas the background and perturbation  
177 torque were always randomly assigned. This minimized the impact of task-switching  
178 while ensuring that subjects could not predict the upcoming perturbation.

179 *Experiment 1 – Testing if background load, voluntary task, or both factors contribute to*  
180 *knowledge of limb dynamics*

181           Experiment 1 tested if the background load, or voluntary task, or both factors  
182 impacted the knowledge of limb dynamics expressed in the R2/3 of shoulder muscles. 2  
183 background torques, 2 targets, and 4 perturbation torques were utilized (see Table 1



184 and Fig. 2). We collected 30 repeats of all 16 combinations of background torque-target  
185 size-perturbation torque for a total of 480 trials.

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

192         The two sizes of the visual target allowed us to examine how a change of  
193 voluntary task altered the shoulder's evoked response to a perturbation (Fig. 2B). The  
194 "small target" had a radius of 2 cm and required a vigorous response to return one's  
195 hand to the target within the time-accuracy requirement (i.e. remain within the target  
196 for 900 ms of the subsequent 1300 ms). The large target had a radius of 30 cm and  
197 afforded a much less vigorous response; subjects were further instructed "do-not-  
198 voluntarily-intervene" to facilitate the minimal voluntary response.

199         By employing four different pairs of the background torque and target size we  
200 aimed to recruit the shoulder muscle's R2/3's activity-dependent and task-dependent  
201 components in four different patterns (Fig. 2D,F). The high activity/large target  
202 combination (lower-left panels of Fig. 2D,F) should strongly recruit the activity-  
203 dependent component (given the high pre-perturbation muscle activity), but not the  
204 task-dependent component (given the weak vigour needed to remain within the large

205 target). The low activity/small target combination (upper-right panels of Fig. 2D,F)  
206 should strongly recruit the task-dependent component (given the greater vigour needed  
207 to remain within the small target), not the activity-dependent component (given the low  
208 pre-perturbation muscle activity). The high activity/small target combination should  
209 strongly recruit both components (upper-left panels of Fig. 2D,F). Finally, the low  
210 activity/large target combination should strongly recruit neither component (lower-right  
211 panels of Fig. 2D,F).

212 Four perturbation torques were selected to reveal knowledge of limb dynamics  
213 in the shoulder extensor muscle (Fig. 2C,E) (Kurtzer et al. 2008). The linkage between  
214 the arm's segments results in mechanical interaction across its joints (Hollerbach and  
215 Flash 1982; Graham et al. 2003; Craig 2005) such that torque applied at one joint will  
216 induce motion at several joints. Likewise, motion of a particular joint could arise from  
217 torque applied to that joint or to another joint. We leveraged this property of limb  
218 dynamics with a pair of single-joint torques – shoulder flexion torque and elbow  
219 extension torque – whose relative magnitude resulted in a similar amount of shoulder  
220 flexion (Fig. 2C). If the shoulder extensor's R2/3 was based solely on shoulder motion  
221 then this pair of perturbations would evoke the same amount of activity as they induced  
222 the same amount of shoulder motion. In contrast, a larger muscular response to  
223 shoulder flexion torque than elbow extensor torque would be consistent with  
224 integrating information from both joints appropriate for the underlying perturbation.  
225 Data obtained with these torques is grouped as Experiment 1a.

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

237 By applying the selected torque perturbations during different combinations of  
238 background torque and target size we tested how knowledge of limb dynamics is  
239 expressed by the different components of the R2/3 epoch. A schematic of the three  
240 alternative organizations is presented in Figure 1. Note that these are didactic  
241 simplifications and do not show sensory inflow, descending commands, or feedback  
242 from action to sensory inflow. Moreover, our approach is neutral on whether these  
243 components receive similar sensory information, the role of descending commands, and  
244 the internal architecture which provides knowledge of limbs dynamics such as an  
245 inverse model, recurrent forward model, or direct controller ( for review see Tin and  
246 Poon 2005). Our approach aims to address whether knowledge of limb dynamics is  
247 expressed in the different conditions of target size and pre-perturbation activity, and

248 the computational aspects of the control architecture are beyond the scope of the  
249 present paper.

250 We tested between three possible models by examining the differential  
251 response to the paired perturbations as this reveals the knowledge of limb dynamics  
252 (i.e. larger response to shoulder flexion than elbow extension torque; larger response to  
253 combined flexion torque than combined extension torque) (Fig. 2C,E). In model #1 (Fig.  
254 1A) the knowledge of limb dynamics is expressed by just the task-dependent  
255 component; hence, a differential response is only present with the small target  
256 requiring a vigorous response and does not change with the background muscle activity  
257 (Fig. 1B). In model #2 (Fig. 1C) knowledge of limb dynamics is expressed by just the  
258 activity-dependent component; hence, a differential response is only present when the  
259 muscle has relatively high activity and does not change with the target size (Fig. 1D). In  
260 model #3 (Fig. 1E) knowledge of limb dynamics is expressed by both components.  
261 Hence, a differential response is present when the muscle either has relatively high  
262 activity or the small target is used, and the largest differential occurs with the high  
263 activity/small target combination when both components can contribute (Fig. 1F). All  
264 models predict weak differential activity with the low activity/large target combination  
265 as neither component is strongly engaged.

266 *Experiment 2 –Testing if background load and voluntary task have an independent*  
267 *contribution to knowledge of limb dynamics*

268 Results consistent with model #3 (both activity-dependent and task-dependent  
269 component) motivated this experiment. Here we tested if the background load and

270 voluntary task had an independent impact on the knowledge of limb dynamics  
271 expressed in the R2/3 epoch. 5 background torques, 2 targets, and 2 perturbation  
272 torques were utilized (see Table 1). We collected 25 repeats of all 20 combinations of  
273 background torque-target size-perturbation torque for a total of 500 trials.

274           5 different background torques were applied to the shoulder (-3, -1.5, 0, 1.5 and  
275 3 Nm) to provide a more detailed examination of background muscle activity on the  
276 R2/3 magnitude. We utilized the same two targets from Experiment 1, a “small target”  
277 with a radius of 2 cm and a “large target” with a radius of 30 cm. And the two  
278 perturbations were multi-joint torques – shoulder flexion-elbow flexion torque and  
279 shoulder extension-elbow extension torque – to cause motion at just the elbow joint.

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

#### 288 *Data analysis*

289           Angular positions of the shoulder and elbow were low-pass filtered (25 Hz, 2-  
290 pass, 6<sup>th</sup> order Butterworth). Surface electrical activity of posterior deltoid was

291 amplified (gain = 1-10 K), digitally sampled at 1000 Hz, band-pass filtered (10-350 Hz),  
292 and rectified. The EMG signals were finally normalized by the individual muscle's mean  
293 activity during the hold period with an activating torque. Each subject's activity in the  
294 posterior deltoid was normalized by his/her mean activity from all conditions having a  
295 shoulder flexion background torque -2 Nm during Experiment 1 and 1.5 Nm during  
296 Experiment 2. Each subject's activity in the pectoralis major was normalized by the  
297 mean activity from all conditions having a shoulder extension background torque (-1.5  
298 Nm during Experiment 2).

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

*$\Delta S\ho Ang$  = change in shoulder angle from starting position*

*$\Delta Elb Ang$  = change in elbow angle from starting position*

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

301  *$Position\ error = \sqrt{\Delta S\ho Ang^2 + \Delta Elb Ang^2}$*

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

306 For the muscle activity, we focused on a post-perturbation epoch alternately  
307 called the long-latency reflex, long-latency response, M2/3, and R2/3 (Crago et al. 1976;  
308 Lee et al. 1983; Kurtzer et al., 2008; Pruszyński et al. 2008). We adopt the R2/3  
309 designation in order to unambiguously abbreviate primary motor cortex as M1 and

310 avoid the connotation of “reflex” as a simple and inflexible process (Prochazka et al  
311 2000). This epoch spans 50-100ms post-perturbation when the muscle countered any  
312 opposing background load. We shifted the time window by 5ms (55-105ms) whenever  
313 the muscle acted with an assisting background load. This small shift accounts for the  
314 slight delay observed in the onset of task-dependent responses consistent with previous  
315 reports (Bedingham and Tatton 1982; Pruszyński et al. 2011a) and likely reflecting the  
316 impact of pre-inhibition of the motor neurons. In addition to the R2/3 we also  
317 examined an earlier and later epoch. The R1, also called the short-latency reflex, is the  
318 fastest stretch-evoked response by the nervous system (20-45 ms post-perturbation)  
319 and is exclusively mediated by spinal circuitry. Early voluntary activity occurs 120-180  
320 ms post-perturbation. These epochs are consistent with previous studies including our  
321 own (Calancie and Bawa 1984; Crago et al. 1976; Jaeger et al. 1982; Lee et al. 1983;  
322 Lewis et al. 2006; Kurtzer et al., 2008; Pruszyński et al. 2008).

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

## 326 Results

### 327 *Experiment 1a: Behaviour and muscle activity evoked by shoulder displacement*

328 The different conditions led to distinct patterns of limb motion. Figure 3A shows  
329 the trajectory the hand following the single-joint step torques (data only shown for high  
330 background torque) whereas Figure 3B shows the corresponding joint displacements

331 (corresponds to Fig. 2C). Note that the induced motion is grouped into four  
332 combinations of background muscle activity and target size. The shoulder flexion  
333 torque and elbow extension torque displaced the shoulder into flexion and the elbow  
334 into extension. Critically, the initial amount of shoulder motion caused by these two  
335 perturbations was quite similar. Across all four background activity-target size  
336 combinations, the shoulder displacement measured 50ms post-perturbation was  $10 \pm$   
337  $3\%$  greater following the elbow torque than shoulder torque; hence, feedback response  
338 based on local motion would be similar (or slightly smaller) following the shoulder  
339 torque than elbow torque perturbation.

340 The absolute amount of initial shoulder was similar but not identical across the  
341 background activity conditions. Shoulder displacement was  $12 \pm 4\%$  less with low  
342 shoulder extensor activity (extensor background torque) than high activity (flexor  
343 background torque). Lastly, target size had little impact on the initial joint  
344 displacement, but a powerful impact over the duration of the trial. With the small  
345 target subjects reversed their outward movement  $223 \pm 32\text{ms}$  following the  
346 perturbation and obtained a final positional error of  $1 \pm 1^\circ$  whereas the large target led  
347 to movement reversals at  $630 \pm 250\text{ms}$  and a final positional error of  $28 \pm 11^\circ$ .

348 The use of different background torques and target sizes resulted in  
349 characteristic patterns of pre-perturbation and evoked activity in the shoulder extensor  
350 muscle. Figure 4A presents the time-varying muscle activity (group data) to the four  
351 combinations. Not surprisingly, the background torque resulted in large systematic  
352 difference in the muscle's pre-perturbation activity. On average, the background



353 extensor torque led to low level of activity, 18% of that obtained with the background  
354 flexor torque. Note that this low level of muscle activity is likely near the physiological  
355 and measurement floor since the signal from a no-torque condition was 22% of that  
356 obtained during background flexion torque (n = 6 subjects). Target size had a small,  
357 though systematic impact, on background muscle activity: high activity/small target =  
358  $1.03 \pm .06$  au; high activity/large target =  $0.97 \pm .08$  au; low activity/small target  $0.21 \pm$   
359  $0.07$  au; low activity /large target  $0.16 \pm .07$  au.

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

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

374 epoch (subject's mean t-value > 2.9; group  $t_{(9)} > 3.0$ ,  $P < 0.01$  one-sided) (lower-left  
375 panel of Figure 4B).

376 During the low activity/small target combination (upper-right panel of Fig. 4A),  
377 the shoulder muscle expressed a robust evoked response in the R2/3 epoch and  
378 Voluntary epoch despite the weak level of pre-perturbation activity. In particular, the  
379 shoulder flexion torque evoked more activity in the R2/3 epoch (subject's mean t-value  
380 = 3.8; group  $t_{(8)} > 6.6$ ,  $P < 0.001$  one-sided) and Voluntary epoch (subject's mean t-value  
381 = 7.5; group  $t_{(8)} = 3.9$ ,  $P < 0.005$  one-sided) than the elbow extension torque (upper-right  
382 panel of Fig. 4B).

383 The final combination involved low pre-perturbation activity and the large  
384 target. The shoulder extensor's subsequent evoked activity was quite weak consistent  
385 with the low pre-perturbation activity and low amount of required vigour (lower-right  
386 panel of Fig. 4A). For example, the mean evoked activity in the R1, R2/3 and voluntary  
387 epochs to the shoulder flexion torque was 3%, 6% and 5% of the mean response with  
388 flexor background torque/small target combination. Activity in the R2/3 epoch ( $F_{(1,8)} =$   
389  $38.9$ ,  $P < 0.001$ ) and voluntary epoch ( $F_{(1,8)} = 16.9$ ,  $P < 0.001$ ) was also significantly lower  
390 than that present with low activity/small target combination. Despite the low level of  
391 evoked activity, the R2/3 epoch showed small differences between the two torque  
392 conditions (subject's mean t-value = 1.7; group  $t_{(8)} = 2.9$ ,  $P = 0.01$  one-sided) as did the  
393 Voluntary epoch (subject's mean t-value > 2.6; group  $t_{(8)} = 3.4$ ,  $P < 0.01$  one-sided)  
394 (lower-right panel of Fig. 4B).

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

399 *Experiment 1b: Behaviour and muscle activity evoked by elbow displacement*

400 Figure 3C shows the trajectory the hand following the multi-joint step torques  
401 (data only shown for high background torque) whereas Figure 3D shows the  
402 corresponding joint displacements (corresponds to Fig. 2E). The combined flexor torque  
403 and combined extension torque displaced the elbow into flexion and extension,  
404 respectively. Moreover, almost no shoulder displacement initially resulted from the  
405 perturbation. Across all four background-target combinations, the shoulder  
406 displacement measured 50ms post-perturbation was  $2 \pm 1\%$  the size of the initial elbow  
407 displacement. The absolute amount of initial joint displacement was similar but not  
408 identical across the different combinations; elbow displacement was  $3 \pm 3\%$  less with  
409 low shoulder extensor activity (extensor background torque) than high activity (flexor  
410 background torque). Target size also had a negligible impact on the initial joint  
411 displacement, but a powerful impact over the duration of the trial. Subjects reversed  
412 their outward movement around  $211 \pm 17\text{ms}$  and obtained a final positional error of  $1 \pm$   
413  $1^\circ$  with the small target versus  $585 \pm 254\text{ms}$  and  $21 \pm 6^\circ$  with the larger target.

414 The different levels of background muscle activity and target size powerfully  
415 impacted the responses to multi-joint torques which caused motion almost entirely at

416 the elbow joint. Figure 5A presents the time-varying shoulder muscle activity (group  
417 data) to these conditions. During the high activity/small target combination (upper-left  
418 panel of Fig. 5A) excitatory and inhibitory bursts resulted from the combined flexion  
419 torque and combined extension torque, respectively. Differential activity to these  
420 perturbations – consistent with knowledge of limb dynamics – achieved statistical  
421 significant in the R2/3 epoch (subject's mean t-value = 10.5; group  $t_{(8)} > 15.7$ ,  $P < 0.001$   
422 one-sided) and Voluntary epoch (subject's mean t-value = 15; group  $t_{(8)} = 7.2$ ,  $P < 0.001$   
423 one-sided) (upper-left panel of Fig. 5B).

424 With the background flexor torque and large target combination (lower-left  
425 panel of Fig. 5A) the evoked responses in the R2/3 epoch ( $F_{(1,8)} = 160.1$ ,  $P < 0.001$ ) and  
426 the Voluntary epoch ( $F_{(1,8)} = 57.8$ ,  $P < 0.001$ ) were significantly weaker indicating an  
427 impact of target size. The combined flexion torque continued to evoke more activity  
428 than the combined extension torque in the R2/3 epoch (subject's mean t-value = 6.6;  
429 group  $t_{(8)} = 4.7$ ,  $P < 0.005$  one-sided) and the voluntary epoch (subject's mean t-value =  
430 8.4; group  $t_{(8)} = 6.4$ ,  $P < 0.001$  one-sided) (lower-left panel of Fig. 5B).

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

437           The final combination involved a background extensor torque and large target  
438 (lower-right panel of Fig. 5A). Shoulder muscle activity was significantly lower than  
439 during the extensor torque and small target combination – R2/3 epoch ( $F_{(1,8)} = 39.4$ ,  $P <$   
440  $0.001$ ); voluntary epoch ( $F_{(1,8)} = 29.2$ ,  $P < 0.001$ ) – indicating the impact of target size.  
441 The two multi-joint torques also evoked weak but significant differences of muscle  
442 activity in the R2/3 epoch (subject's mean t-value = 2.1; group  $t_{(8)} = 2.1$ ,  $P = 0.033$  one-  
443 sided) and voluntary epoch (subject's mean t-value = 7.6; group  $t_{(8)} = 3.3$ ,  $P < 0.01$  one-  
444 sided) (lower-right panel of Fig. 5B).

445           In summary, a differential response to the multi-joint torques was expressed in  
446 the R2/3 and Voluntary epoch in all conditions. R1 activity was never found to  
447 differentiate between the two torque perturbations (mean t-value  $< |0.5|$ ; group  $t_{(8)} <$   
448  $|1.1|$ ,  $P > 0.2$  two-sided).

449 *Experiment 1: Relating R2/3's knowledge of limb dynamics to the activity-dependent and*  
450 *task-dependent components*

451           To determine how the task-dependent and activity-dependent components  
452 contribute to R2/3's knowledge of limb dynamics (compare to Fig. 1B,D,F) we examined  
453 how the differential response to paired torque perturbations changes with background  
454 torque and target size (Fig. 6A,B). The magnitude of differential activity was lowest  
455 during the low activity/large target combination (bottom-right panels) which would  
456 weakly engage either component (single-joint torques: group  $t_{(8)} = 7.6$ ,  $P < 0.001$  two-  
457 sided; multi-joint torques: group  $t_{(8)} = 13.7$ ,  $P < 0.001$  two-sided). Differential activity

458 was greater than this combination during either the high activity/large target  
459 combination (bottom-left panels) [single-joint torques: group  $t_{(8)} = 4.0$ ,  $P < 0.005$  two-  
460 sided; multi-joint torques: group  $t_{(8)} = 8.1$ ,  $P < 0.001$  two-sided]) or low activity/small  
461 target combination (upper-right panels [single-joint torques: group  $t_{(8)} = 4.4$ ,  $P < 0.005$   
462 two-sided; multi-joint torques: group  $t_{(8)} = 5.2$ ,  $P < 0.001$  two-sided]). Greater  
463 differential activity with an increase in background muscle activity or the small target  
464 suggests that a greater engagement of either the activity-dependent or the task-  
465 dependent component allows a stronger expression of R2/3's knowledge of limb  
466 dynamics.

467 We also found that differential activity was greatest during the high  
468 activity/small target combination (upper-left panels). Its differential was larger than  
469 during the low activity/small target combination (single-joint torques: group  $t_{(8)} = 4.4$ ,  $P$   
470  $< 0.005$  two-sided; multi-joint torques: group  $t_{(8)} = 7.7$ ,  $P < 0.001$  two-sided) but this  
471 comparison is inadequate since low baseline muscle activity eliminates the possibility of  
472 a large inhibitory response. The critical comparison is between the high activity/small  
473 target and high activity/large target combinations since both involve substantial  
474 background activity of the muscle. In fact, greater differential activity was observed for  
475 the high activity/small target combination (strongly engaging the task-dependent and  
476 activity-dependent components) than the high activity/large target combination  
477 (strongly engaging the activity-dependent component) (single-joint torques: group  $t_{(8)} =$   
478  $7.2$ ,  $P < 0.001$  two-sided; multi-joint torques: group  $t_{(8)} = 9.2$ ,  $P < 0.001$  two-sided).

479 As we previously mentioned, there was a small systematic difference in  
480 background shoulder extensor activity with the two different targets. If this difference  
481 significantly altered the excitability of feedback circuitry then it would contaminate the  
482 alterations R2/3 activity with target size and our attempt to dissociate the R2/3  
483 response into a task-dependent component and activity-dependent component. To test  
484 for this possibility we examined the R1 evoked during shoulder displacement since the  
485 R1 is entirely generated by a spinal pathway. A 2-way ANOVA revealed a significant  
486 effect of background load (shoulder flexion torque:  $F_{(1,8)} = 12$ ,  $P < 0.01$ ; elbow extension  
487 torque:  $F_{(1,8)} = 6.7$ ,  $P < 0.05$ ) but not target size (shoulder flexion torque:  $F_{(1,8)} = 1.4$ ,  $P =$   
488  $0.27$ ; elbow extension torque:  $F_{(1,8)} = 3.3$ ,  $P = 0.11$ ) nor an interaction of background load  
489 and target size (shoulder flexion torque:  $F_{(1,8)} = 0.42$ ,  $P = 0.53$ ; elbow extension torque:  
490  $F_{(1,8)} = 2.1$ ,  $P = 0.18$ ). Hence, the small differences in background muscle activity with  
491 target size do not account for the robust change in R2/3 activity.

492 Further note that the relatively long experiment (480 trials over  $\approx 2.5$  hours) did  
493 not lead to appreciable changes in the magnitude of the R2/3 over time. We tested this  
494 possibility with 3-way ANOVA which considered the 4 combinations of background  
495 activity and target size, 4 perturbations, and split the trials into the first half and second  
496 half of the experiment. This analysis indicated a significant main effect of the  
497 background muscle activity-target size combination ( $F_{(3,24)} = 38.2$ ;  $P = .0001$ ) and the  
498 torque perturbation ( $F_{(3,24)} = 96$ ;  $P = .0001$ ) as well as a significant interaction of the two  
499 ( $F_{(9,72)} = 54.7$ ;  $P = .0001$ ). However, time did not have a significant main effect ( $F_{(1,8)} =$   
500  $2.0$ ;  $P = .2$ ) nor a significant interaction with either the background muscle activity-

501 target size combination ( $F_{(3,24)} = 1.0$ ;  $P = .42$ ) or the torque perturbation ( $F_{(3,24)} = 0.9$ ;  $P =$   
502  $.43$ ). The interaction of all three categories (background activity-target size,  
503 perturbation, and time) was also not significant ( $F_{(9,72)} = 1.1$ ;  $P = .40$ ). Hence, the R2/3  
504 was stable over the course of the experiment (see Table 2).

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

518 We also examined whether linear summation was present at the level of  
519 individual subjects by regressing each subject's predicted R2/3 activity against their  
520 observed R2/3 activity (Fig. 7C). We found a high correlation ( $r = 0.88$ ,  $P < 0.01$ ,  $df = 25$ )  
521 and a linear regression that did not differ from unity (95% confidence interval). Note



522 that this same pattern continued when we examined the predicted and observed R2/3  
523 within each torque perturbation ( $r > 0.62$ ,  $P < 0.05$ ,  $df = 7$ ).

524 *Experiment 2: Behaviour and muscle activity evoked by elbow displacement*

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

533 The induced motion is grouped into 10 combinations of background torque and  
534 target size (Fig. 8). Multi-joint torque perturbations and targets led to a similar pattern  
535 described in Experiment 1. The combined flexor torque initially displaced the elbow into  
536 flexion whereas the combined extension torque initially displaced the elbow into  
537 extension. Neither perturbation caused much shoulder displacement; across all targets  
538 and background loads, the initial shoulder displacement was  $2 \pm 1\%$  the size of the initial  
539 elbow displacement. The different background torques led to minimal changes in the  
540 movement trajectories. In contrast, the two targets led to dramatically different  
541 movement trajectories. With the small target subjects reversed their outward

542 movement at  $209 \pm 17$ ms and obtained a final positional error of  $1 \pm 1^\circ$  whereas the  
543 large target often led to movement reversal and a final positional error of  $27 \pm 6^\circ$ .

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

560 To ascertain whether the task-dependent component had a constant  
561 contribution of knowledge of limb dynamics across different background torques, we  
562 focused on the combined flexion torque perturbation since it evokes an excitatory  
563 response; otherwise, the inhibitory response to combined extensor torque would have a

564 floor effect with low pre-perturbation activity. Background extension torque resulted in  
565 weak shoulder extensor activity whereas increased flexion torque resulted in increased  
566 shoulder extensor activity (Fig. 10A), a trend confirmed by a main effect of background  
567 torque ( $F_{(4,20)} = 158, P < 0.001$ ). Evoked activity in the R2/3 epoch largely paralleled this  
568 pattern – increasing activity with increasing flexion torque – and exhibited a main effect  
569 of background torque ( $F_{(4,20)} = 11.2, P < 0.001$ ). Importantly, the small target led to  
570 consistently larger responses than the large target ( $F_{(1,20)} = 33.6, P < 0.005$ ), yet the  
571 interaction of target size and background torque failed to reach significance ( $F_{(4,20)} =$   
572  $0.83, P > 0.5$ ) indicating that the two variables had independent affects. As a final  
573 analysis, we conducted a regression of task-dependent activity against background  
574 torque to test for a systematic relation not flagged by the ANOVA. A linear regression  
575 failed to achieve significance ( $P > 0.5, df = 28$ ) consistent with a constant contribution  
576 from the task-dependent component and independent use of knowledge of limb  
577 dynamics.

578         Similar findings were obtained with the shoulder flexor, pectoralis major,  
579 collected in the same session (Fig. 10B). Its excitatory R2/3 was evoked by combined  
580 extension torque and showed a main effect of background torque ( $F_{(4,20)} = 9.4, P <$   
581  $0.001$ ) – greater activity when the subject countered greater background extension  
582 torque. The small target resulted in larger R2/3 to this perturbation than the large  
583 target ( $F_{(1,20)} = 22.5, P < 0.01$ ), however, target size did not show a significant interaction  
584 with background torque ( $F_{(4,20)} = 1.7, P > 0.19$ ) indicating independent effects of the two  
585 variable. As a final analysis we examined whether the task-dependent difference in

586 activity had a systematic change with the level of background torque. The linear  
587 regression failed to achieve significance ( $P > 0.13$ ,  $df = 28$ ) consistent with a constant  
588 contribution from the task-dependent component and independent use of knowledge  
589 of limb dynamics.

## 590 Discussion

591 The present study dissected a key capability of the arm's stretch-evoked R2/3  
592 response – knowledge of limb dynamics. Our paradigm involved three experimental  
593 manipulations: 1) background torque to modify the level of pre-perturbation muscle  
594 activity, 2) target size to modify the level of voluntary reaction, 3) and two pairs of  
595 perturbations to probe if the shoulder response utilized elbow motion appropriate for  
596 the arm's dynamics. In Experiment 1 we observed that background torque and target  
597 size scaled the evoked shoulder muscle activity indicative of knowledge of limb  
598 dynamics and these two factors had a combined impact akin to linear summation. In  
599 Experiment 2 we found that background torque and target size had an independent  
600 impact on the evoked shoulder muscle activity indicative of knowledge of limb  
601 dynamics. This pattern of results is consistent with a separate “activity-dependent” and  
602 “task-dependent” component contributing knowledge of limb dynamics to the R2/3  
603 response.

604 A number of previous studies have argued that activity within the R2/3 epoch  
605 reflected the overlap of two components, one automatic and the other linked to the  
606 voluntary goal (Capaday et al. 1994; Lewis et al. 2006; Manning et al. 2012; Pruszynski et

607 al. 2011a; Rothwell et al. 1980; Shemmell et al. 2009). This hypothesis is supported by  
608 the shared features of voluntary reactions and task-dependent changes in R2/3 activity.  
609 Both are impacted by stimulus predictability, where greater uncertainty in perturbation  
610 onset or perturbation direction leads to weaker task-dependent changes (Rothwell et al.  
611 1980; Pruszynski et al. 2008). An even stronger association of the R2/3 and voluntary  
612 reaction is the trial-by-trial correlation in their magnitude of activity (Pruszynski et al.  
613 2011a). The highest correlation occurs when the subject generates a vigorous response  
614 from a low activity background which primarily recruits the task-dependent component;  
615 a significant but lower correlation occurs when the subject generates a vigorous  
616 response from a high activity background which recruits both the task-dependent and  
617 activity dependent components.

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

626         Several previous studies have identified that the activity-dependent and task-  
627 dependent components have different properties. During a “do not intervene”  
628 instruction, Lewis et al. 2006 abolished R2/3 activity when the perturbing displacement

629 lasted less than 35 ms whereas Shemmell et al. 2009 attenuated the R2/3 by increasing  
630 the stiffness of the robotic interface. In both cases, the manipulation had a powerful  
631 effect on the automatic aspect of the R2/3 activity and little impact on the additional  
632 evoked activity occurring with a “resist” instruction. Here we demonstrated that the  
633 activity-dependent and task-dependent components share a similar and notably  
634 sophisticated capability.

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

650 Another important question is the neural substrates which underlie these  
651 functionally distinct components. Primary motor cortex (M1) certainly plays a key role  
652 in creating R2/3 activity (see Scott 2004 for review). Its physiological involvement in the  
653 arm's R2/3 is established by depressed hand and elbow muscular responses following  
654 sensori-motor stroke (Marsden et al. 1977; Trumbower et al. 2013), cortical responses  
655 preceding muscular responses of the wrist, elbow, and shoulder (Cheney and Fetz 1984;  
656 Evarts and Tanji 1976; MacKinnon et al. 2000; Herter et al. 2001), and altered hand,  
657 wrist, elbow, and shoulder muscle responses by transcranial magnetic stimulation (Day  
658 et al. 1990; Tsuji and Rothwell 2000; Lewis et al. 2005). By pairing our perturbation  
659 paradigm with transcranial magnetic stimulation in humans and single-unit recording in  
660 monkeys we also demonstrated that M1 contributes to the shoulder's R2/3's knowledge  
661 of limb dynamics (Pruszynski et al. 2011b). Accordingly, primary motor cortex appears  
662 to contribute to the R2/3 of all muscles of the upper limb. It is an open-question  
663 whether primary motor cortex contributes a similar amount to the R2/3 of different  
664 upper limb muscles since some neural disorders impact the R2/3s of distal more than  
665 proximal arm muscles (Thillman et al. 1991; Fellows et al. 1996) and the relative size of  
666 the R2/3 can vary across different arm muscles (Lenz et al. 1983).

667 In addition to primary motor cortex, several studies provide evidence that spinal  
668 and brainstem circuits contribute to some of the arm's R2/3 activity. R2/3s in elbow  
669 muscles continue to be expressed when primary motor cortex is temporarily blocked via  
670 cooling probes (Miller and Brooks 1981) or even following spinalization (Tracey et al.  
671 1980; Ghez and Shinoda 1978). Depressed R2/3s of wrist muscles are reported to occur

672 in the presence of anti-spastics which inhibit spinal processing (Lourenco et al. 2006;  
673 Meskers et al. 2010). However, direct recording of spinal and brainstem circuits during  
674 limb perturbations are currently lacking.

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

691         The particular capabilities expressed by activity-dependent and task-dependent  
692 component are not entirely distinct since we provide evidence that a notably  
693 sophisticated ability – knowledge of limb dynamics – is present in both. This fact is



694 novel and suggests that the highly parallel organization of descending neural control  
695 does not provide unique functions for each pathway but rather partially overlapping  
696 capabilities. The past 50 years has uncovered a wide range of capabilities in the R2/3  
697 epoch (see Pruszynski and Scott 2012 for review). Some examples include scaling with  
698 environmental instability (Doemges and Rack 1992; Kimura et al. 2006; Perrault et al.  
699 2008), habituating with repeated exposures (Rothwell et al. 1986), adapting to different  
700 perturbation durations (Christakos et al. 1983; Hore and Vilis 1984), and coordinating  
701 actions across the two limbs (Marsden et al. 1981; Dimitriou et al 2012; Omrani et al.  
702 2013). At the moment, these capabilities are a loose collection. Relating these diverse  
703 capabilities to the activity-dependent and task-dependent components will reveal which  
704 capabilities are shared, which are unique, and possibly a general logic which lumps  
705 capabilities together. In sum, an approach which examines partially overlapping sets of  
706 capabilities could help identify the parallel structures that underlie fast feedback  
707 control.

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## 715 Figure Legends

716 **Figure 1.** Contrasting models of the knowledge of limb dynamics expressed in the R2/3  
717 epoch. Note that these are didactic simplifications and do not show sensory inflow,  
718 descending commands, or feedback from action to sensory inflow. A. In model #1, the  
719 R2/3 is generated by an activity-dependent component and a task-dependent  
720 component, but only the task-dependent component has knowledge of limb dynamics.  
721 B. This model predicts that the knowledge of limb dynamics expressed by the R2/3  
722 would exhibit a particular pattern with changes in target size and background muscle  
723 activity. Bar height reflects the differential amount of shoulder R2/3 activity to the  
724 paired perturbations which is indicates the knowledge of limb dynamics (Experiment 1:  
725 shoulder flexion versus elbow extension torque; Experiment 2: combined flexion versus  
726 combined extension torque). Only the task-dependent component has knowledge of  
727 limb dynamics so differential activity only occurs with the small target and does not  
728 change with background muscle activity. C. In model #2 only the activity-dependent  
729 component has knowledge of limb dynamics. D. Predicted differential activity of  
730 model #2 only occurs with conditions having high background muscle activity and does  
731 not change with the target size. E. In model #3 both components have knowledge of  
732 limb dynamics. F. Predicted differential activity of model #3 occurs with either high  
733 background muscle activity or the small target and their combination causes the  
734 greatest differential.

735 **Figure 2.** Background torques, targets, and perturbation torques for Experiment 1. A. A  
736 constant flexor (2Nm) or extensor (-2Nm) torque was applied to the subject's shoulder  
737 joint to create a relatively high or low amount of steady-state activity by the shoulder  
738 extensor muscle. The small target (2 cm radius) required relatively vigorous responses  
739 to achieve task success whereas the large target (30 cm radius) required relatively weak  
740 responses. Four combinations of background muscle activity and target size were used  
741 with all four torque perturbations (16 conditions in total). B. The red-armed cartoon  
742 depicts arm motion following shoulder flexion torque whereas the blue-armed cartoon  
743 depicts arm motion following elbow extension torque. C. The four target  
744 size/background activity combinations are shown with the pair of perturbation torques  
745 selected to induce similar amounts of shoulder motion (corresponding to panel B in left  
746 column). D. The red-armed cartoon depicts arm motion following combined flexion  
747 torque whereas the blue-armed cartoon depicts arm motion following combined  
748 extension torque. E. The four target size/background activity combinations are shown  
749 with the pair of perturbation torques selected to induce motion of just the elbow joint  
750 (corresponding to panel C in left column).

751 **Figure 3.** Joint motion during Experiment 1. A. Group average of hand motion following  
752 the pair of single-joint torque perturbations (shoulder flexor torque indicated by red,  
753 elbow extensor torque indicated by blue). Data only shown for the high activity  
754 condition. B. Each panel displays the group's shoulder and elbow motion following the  
755 same torque perturbations; vertical lines indicate perturbation onset and 50ms after  
756 perturbation onset. Solid and dashed lines show the average shoulder and elbow

757 position, respectively. Red and blue outlines show the standard error for joint motion.  
758 Each panel is associated with a particular combination of target size and background  
759 muscle activity (same format as Fig 2 B). C. Group average of hand motion following the  
760 pair of multi-joint torque perturbations (flexor torque indicated by red, extensor torque  
761 indicated by blue). Data only shown for the high activity condition. D. The four panels  
762 display the group's shoulder and elbow motion following the same torque  
763 perturbations. Red and blue outlines show the standard error for joint motion.

764 **Figure 4.** Evoked muscle activity in Experiment 1a (torque perturbations which induce  
765 similar amounts of shoulder motion). A. The four panels display the shoulder extensor  
766 activity during the four combinations of target size and background muscle activity  
767 (same format as Fig 2 B,C). The black line with red outline depicts the group mean and  
768 standard error with the shoulder flexor torque. The black line with blue outline depicts  
769 the group's mean and standard error with the elbow extensor torque. Green line  
770 depicts the group's mean activity with no background torque. Vertical black lines in  
771 each panel indicate the onset of the step torque whereas the grey rectangles bracket  
772 the R2/3 epoch. B. Bar plots showing group mean and standard error of muscle activity  
773 with shoulder flexor torque (red) and elbow extensor torque (blue). Grey horizontal line  
774 indicates baseline muscle activity prior to perturbation; evoked activity is the bar height  
775 relative to the grey horizontal line. Bars are grouped according to the target size and  
776 background torque. Single and double asterisks indicate significant contrasts at  $P < 0.05$   
777 and  $P < 0.01$ .

778 **Figure 5.** Evoked muscle activity with torque perturbations induced no elbow motion.  
779 A. The four panels display the shoulder extensor activity during the four combinations of  
780 target size and background muscle activity (same format as Fig 2 B,C). The black line  
781 with red outline depicts the group mean and standard error with the combined flexor  
782 torque. The black line with blue outline depicts the group's mean and standard error  
783 with the combined extensor torque. Green line depicts the group's mean activity with  
784 no background torque. Vertical black lines in each panel indicate the onset of the step  
785 torque whereas the grey rectangles bracket the R2/3 epoch. B. Bar plot showing  
786 group mean and standard error of muscle activity with the combined flexor torque (red)  
787 and combined extensor torque (blue). Grey horizontal line indicates baseline muscle  
788 activity prior to perturbation; evoked activity is the bar height relative to the grey  
789 horizontal line. Bars are grouped according to the target size and background torque.  
790 Single and double asterisks indicate significant contrasts at  $P < 0.05$  and  $P < 0.01$ .

791 **Figure 6.** R2/3 activity for all conditions of Experiment 1. A . A. Group mean and  
792 standard error of the differential muscle activity between the shoulder flexor torque  
793 and elbow extensor torque conditions. B. Group mean and standard error of differential  
794 muscle activity between the combined flexor torque and combined extensor torque  
795 conditions. Single and double asterisks indicate significant contrasts at  $P < 0.05$  and  $P <$   
796 0.01.

797 **Figure 7.** Comparison of R2/3 responses across different conditions of Experiment 1. A.  
798 The high activity/large target combination should primarily engage the activity-

799 dependent component whereas the low activity/small target combination should  
800 primarily engage the task-dependent component. If the activity-dependent component  
801 and task-dependent component of the R2/3 are independent then a linear summation  
802 of evoked activity from the two conditions should accurately predict the evoked activity  
803 with the small target and extensor background torque. B. Bar plot showing group mean  
804 and standard error for the linear prediction (white) and observed response (black).  
805 Contrasts are shown for the shoulder flexor torque, elbow extensor torque and  
806 combined flexor torque perturbations. C. Each subject's predicted and observed  
807 activity for the shoulder flexor torque (grey circles), elbow extensor torque (grey  
808 triangles) and combined flexor torque perturbations (grey squares). Inset shows the  
809 linear correlation.

810 **Figure 8.** Joint motion during Experiment 2. A. Each panel displays the group's shoulder  
811 and elbow motion following the pair of multi-joint torque perturbations; vertical lines  
812 indicate perturbation onset and 50ms after perturbation onset. Solid and dashed lines  
813 show the average shoulder and elbow position, respectively. Red and blue outlines  
814 show the standard error for joint motion with shoulder flexor torque and elbow  
815 extensor torque, respectively. Each panel is associated with a particular combination of  
816 target size and background torque.

817 **Figure 9.** Evoked muscle activity with combined flexor torque and combined extensor  
818 torque perturbations: Experiment 2. Left column shows the shoulder muscle activity  
819 (group mean and sem) during the combined flexor torque (red) and combined extensor

820 torque (blue) and small target. Right column shows the shoulder muscle activity in the  
821 same format given the large target. The rows correspond to the background torque  
822 employed.

823 **Figure 10.** R2/3 activity for all conditions of Experiment 2. A. Background muscle  
824 activity (group mean and standard error) across different background torques. Activity  
825 with the small and large targets is depicted by the back and grey lines, respectively. B.  
826 Evoked activity (ground mean and standard error) in the R2/3 epoch to perturbation  
827 torque causing pure elbow flexion (for posterior deltoid) or pure elbow extension (for  
828 pectoralis major). C. Difference in evoked activity for the two different target sizes.

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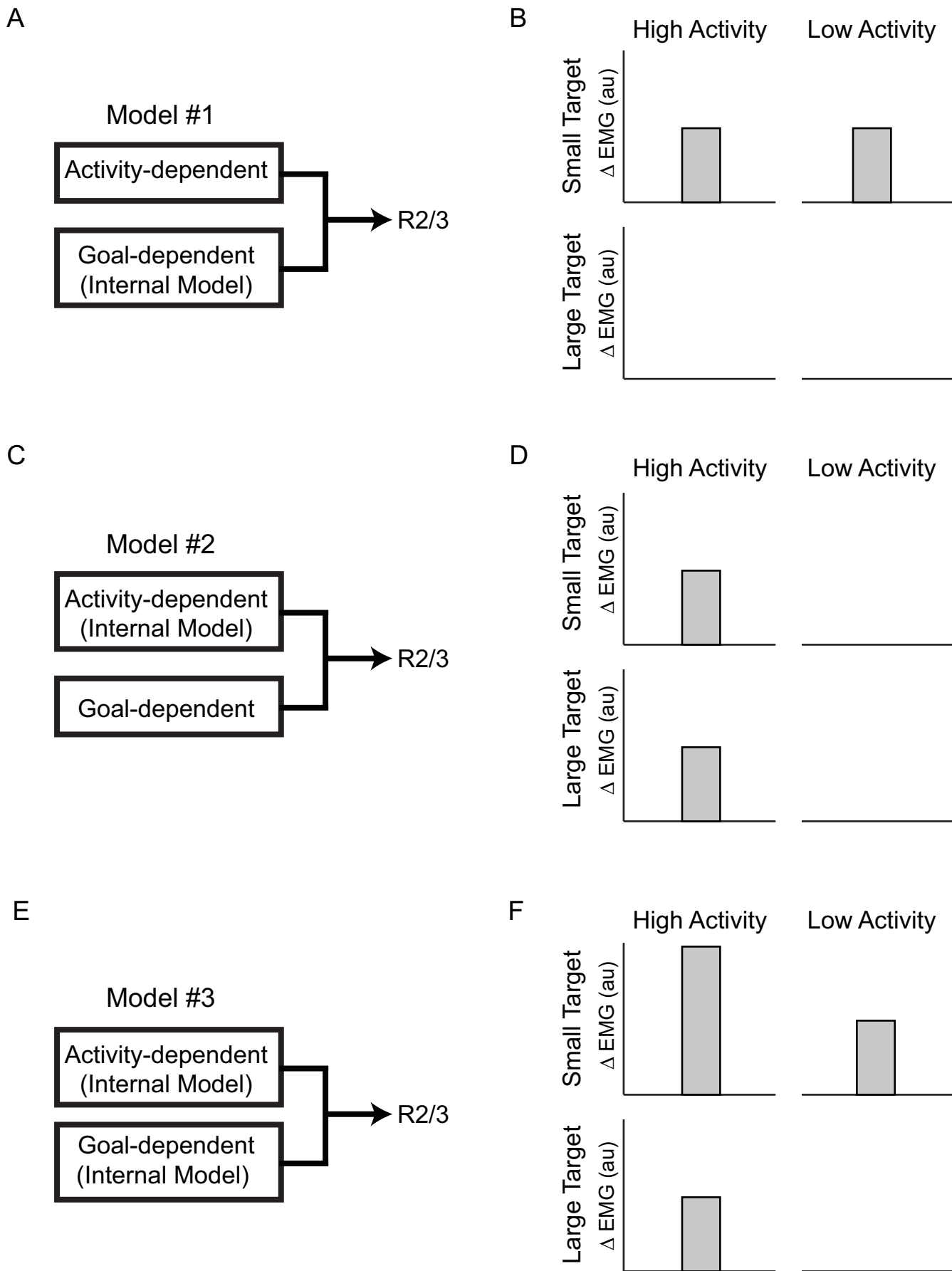


Figure 1

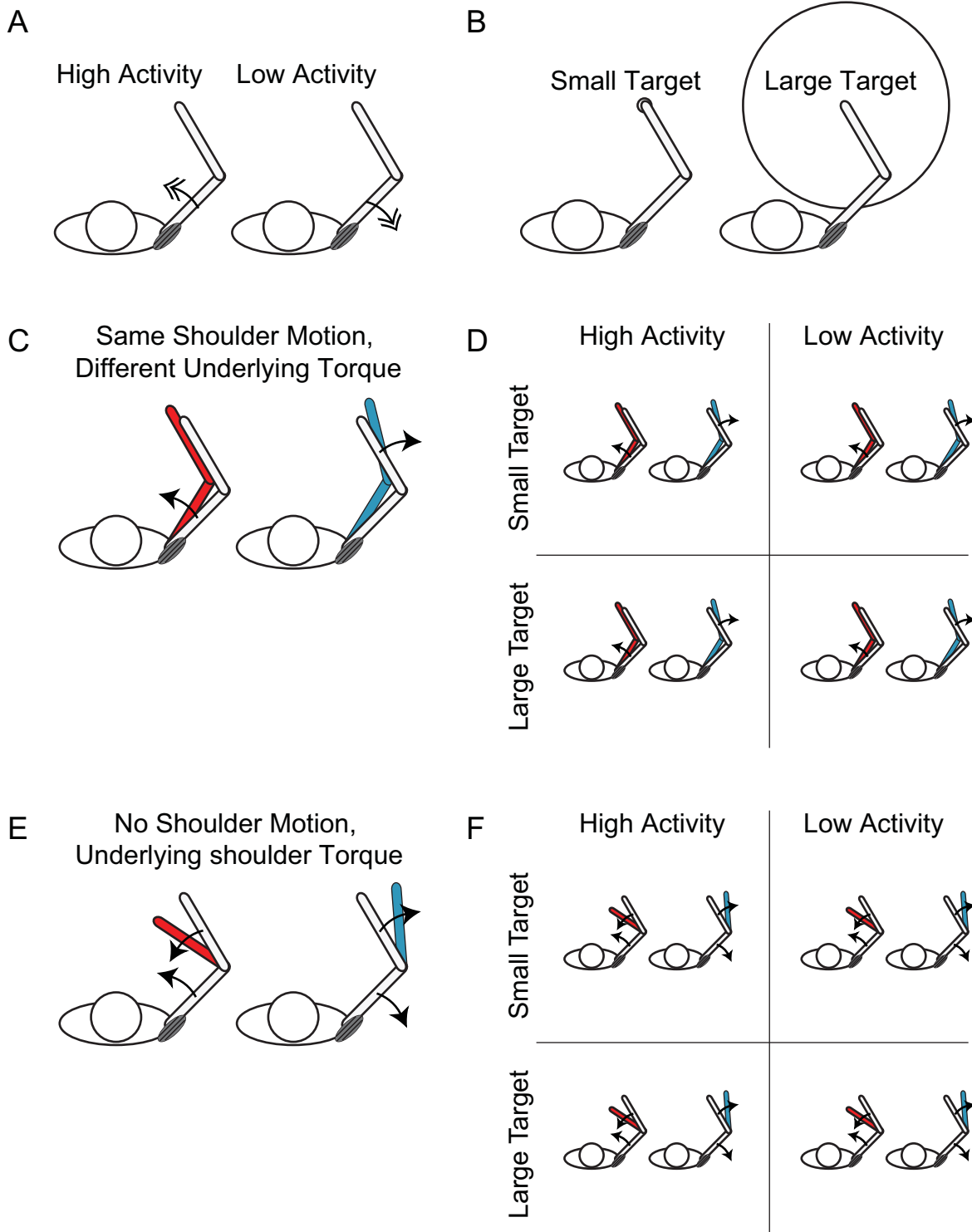


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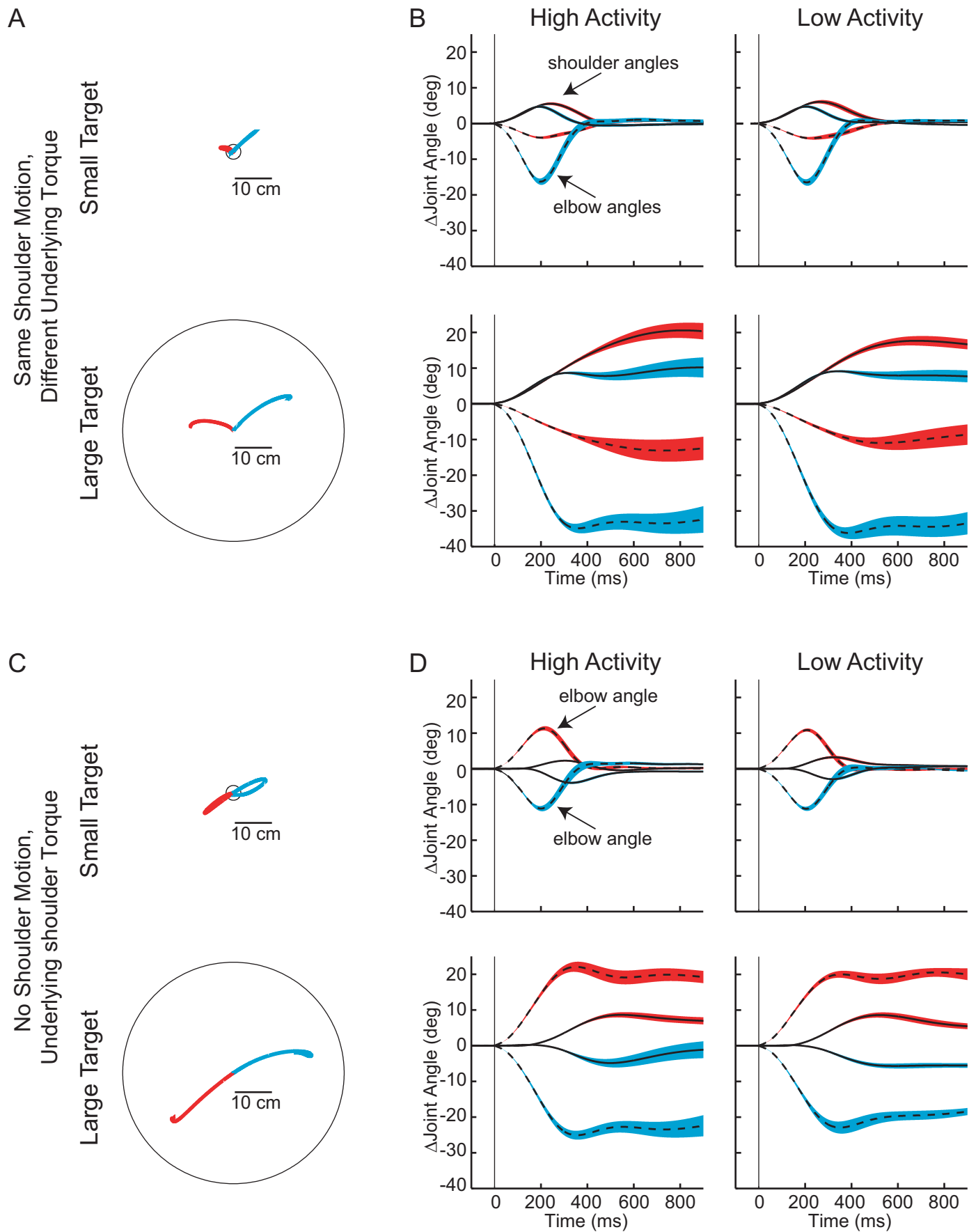


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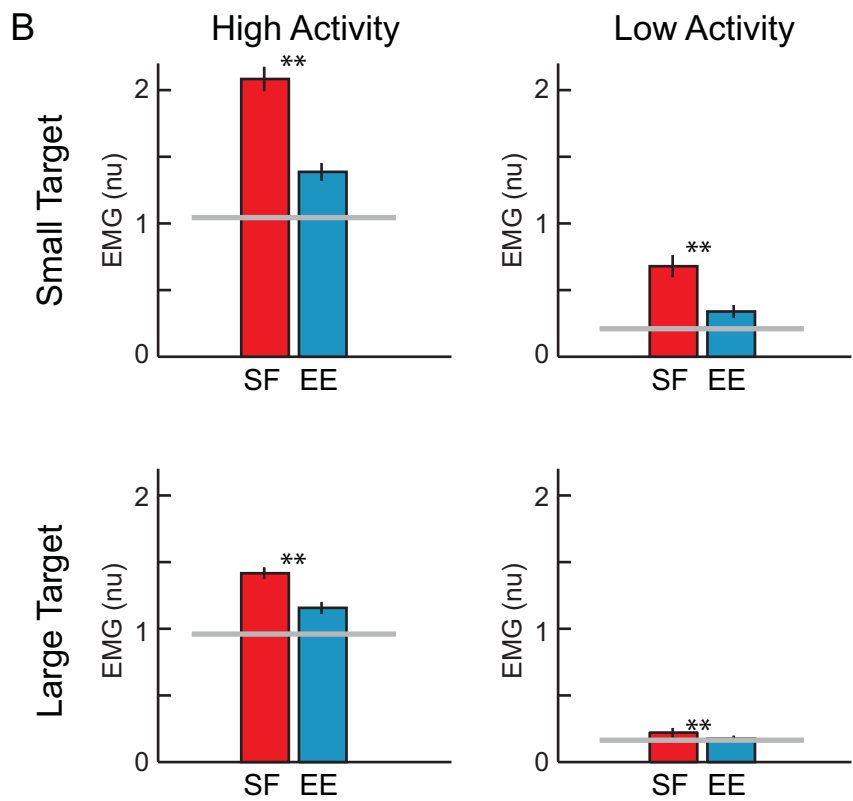
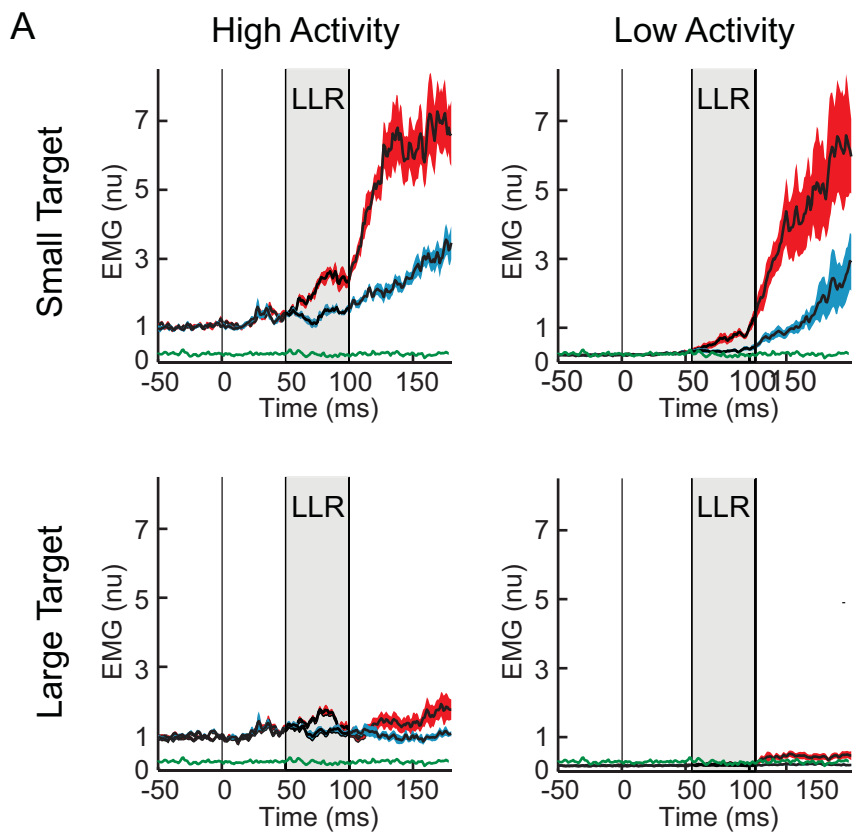


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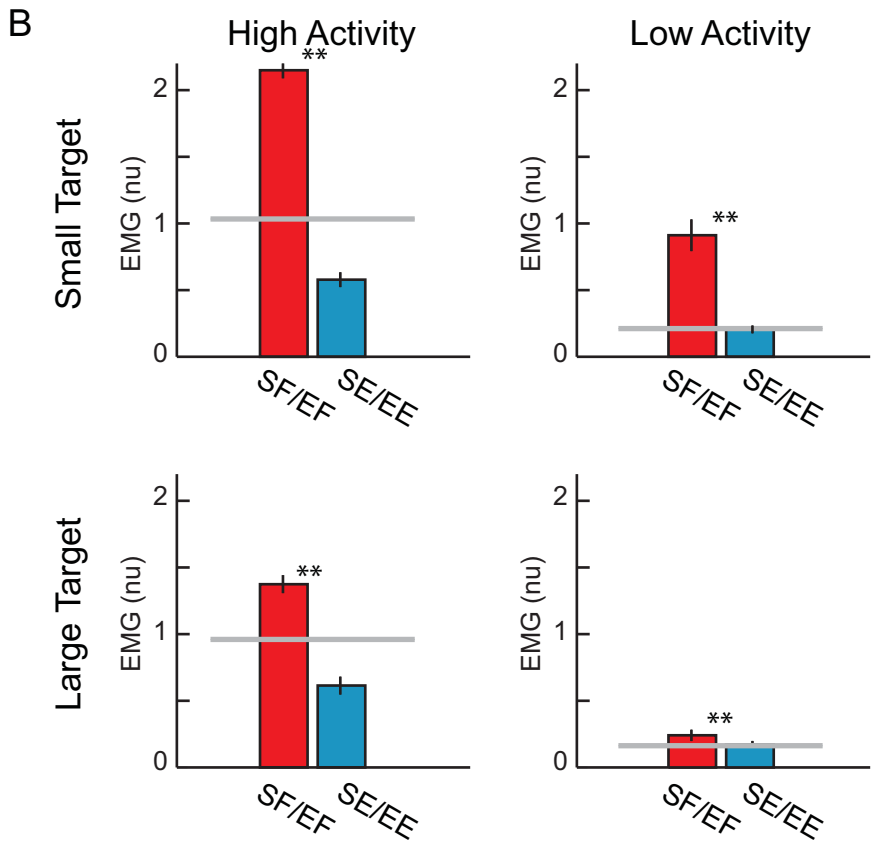
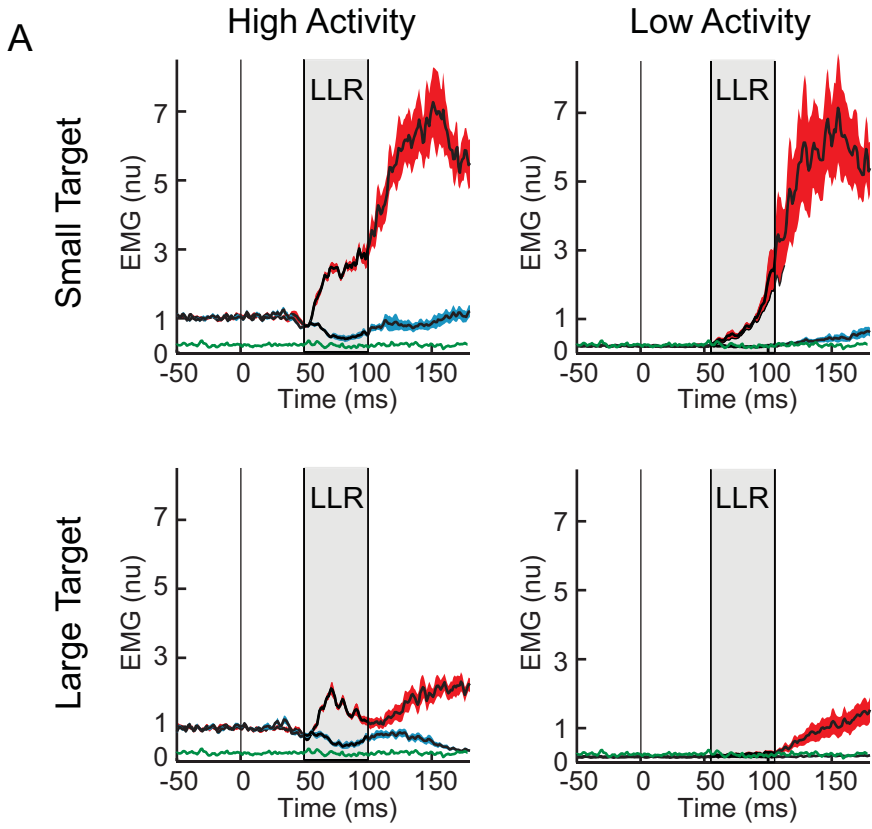


Figure 5

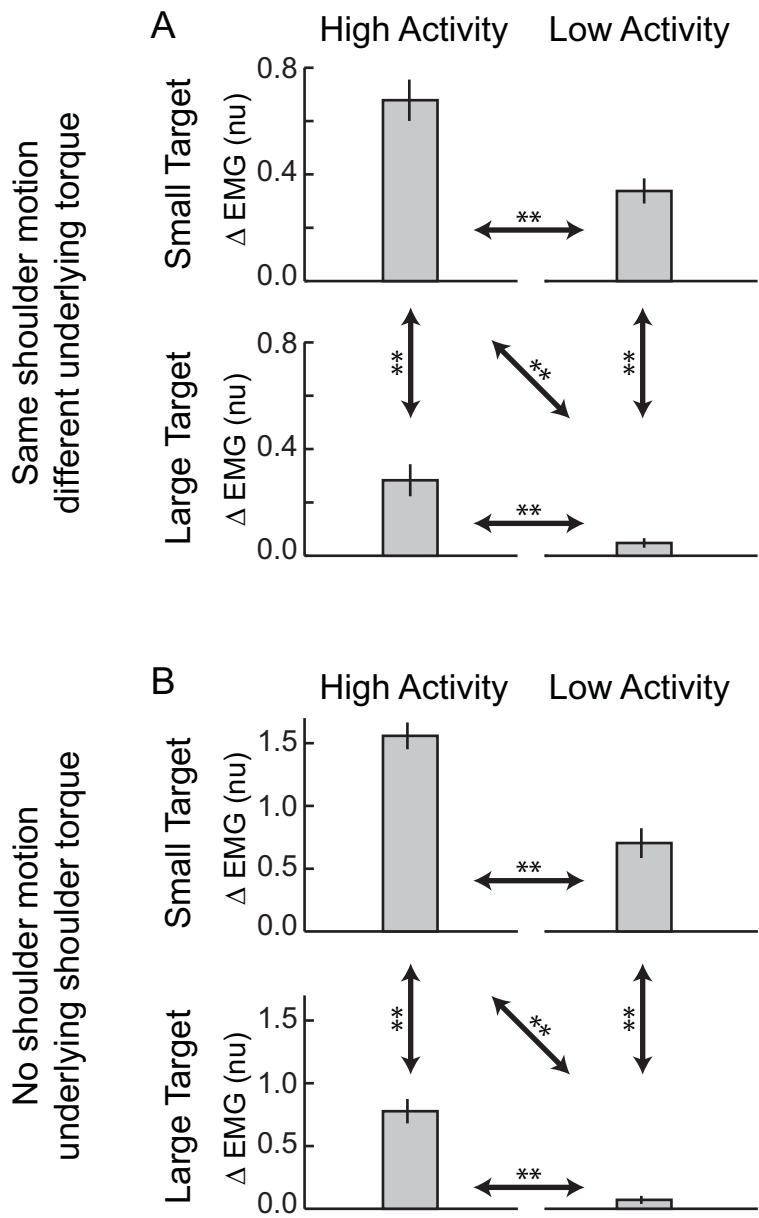
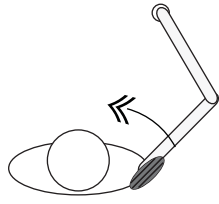
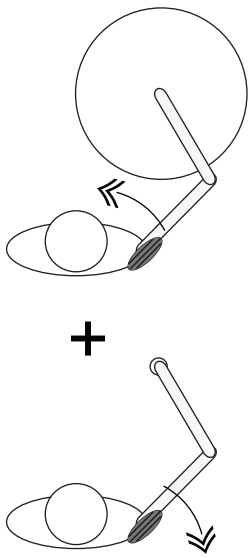


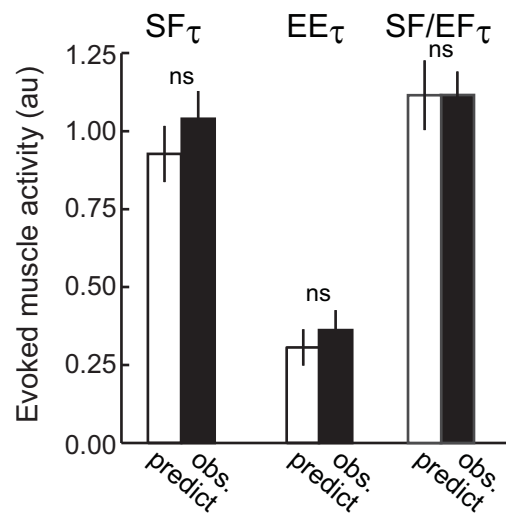
Figure 6

A Predict

Observe



B



C

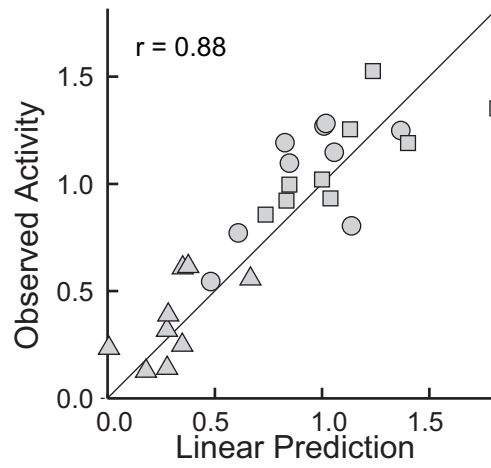


Figure 7

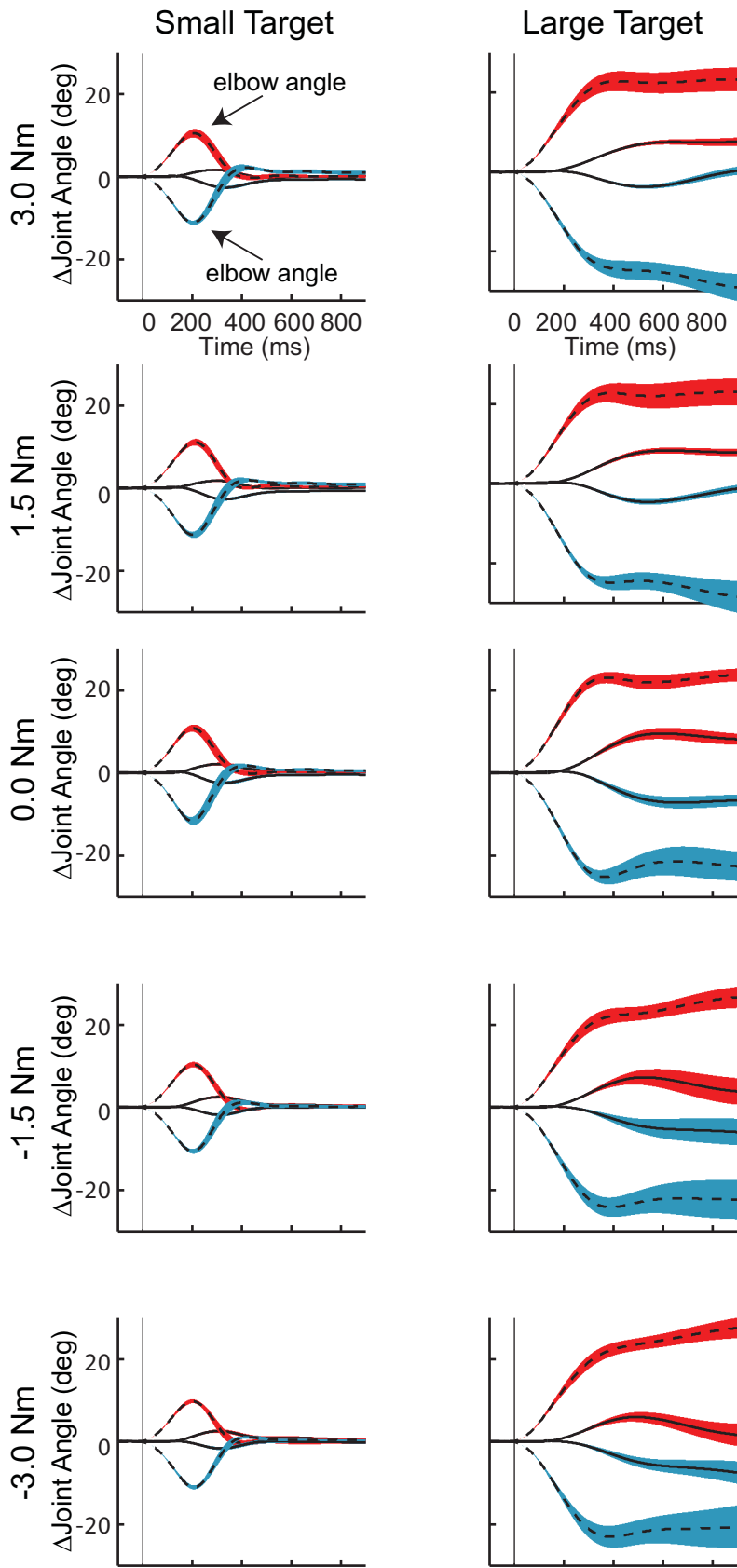


Figure 8

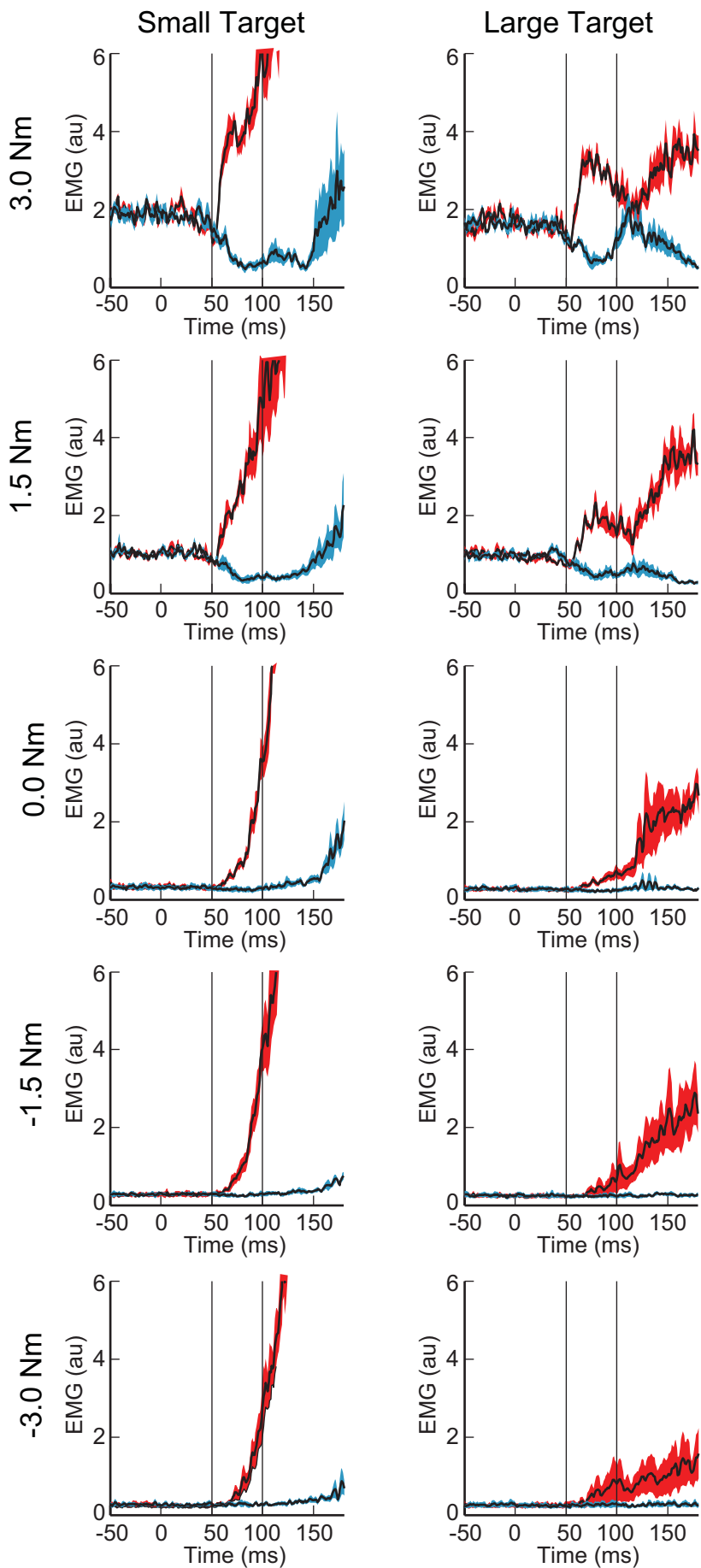


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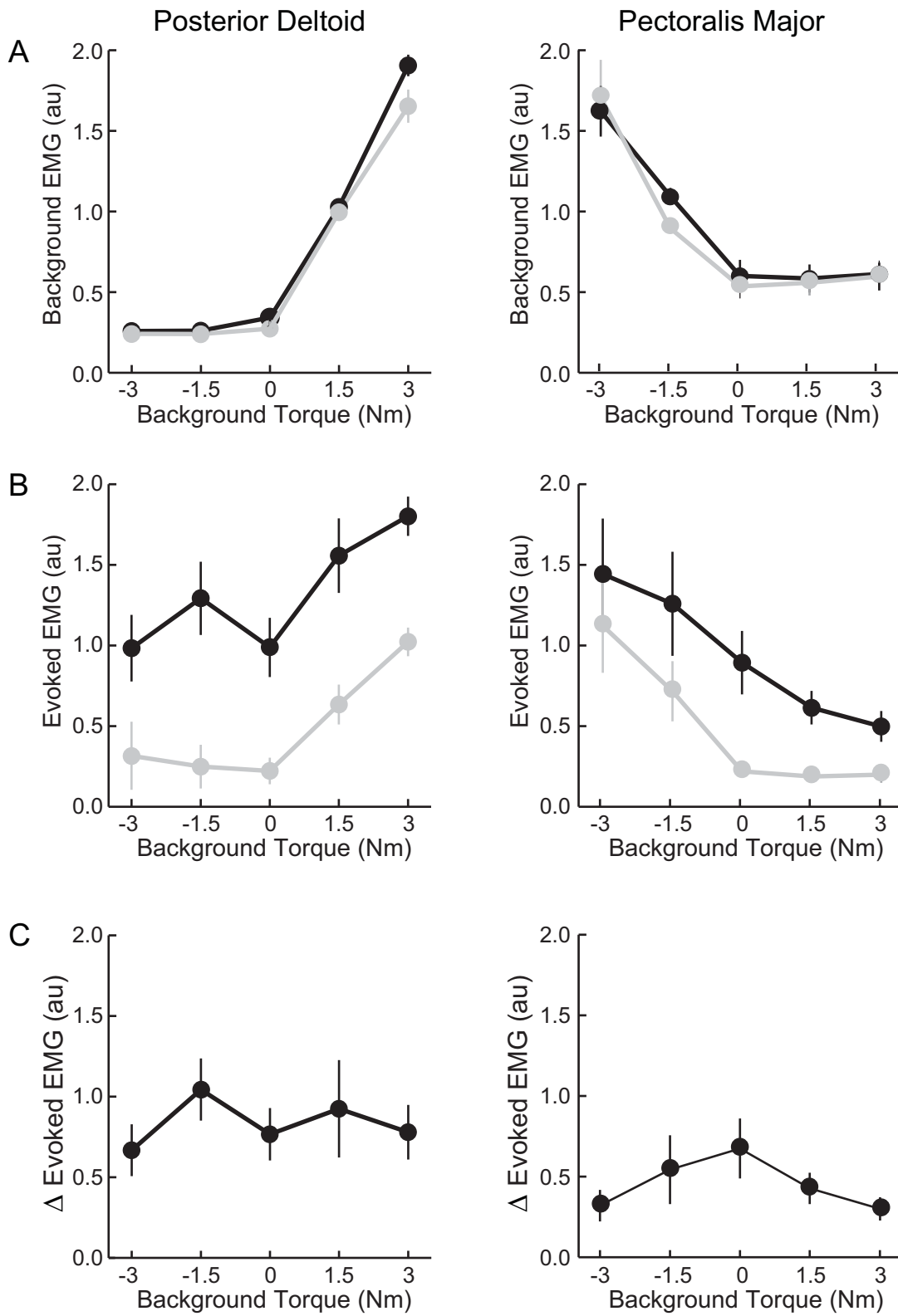


Figure 10

	<b>Target Size</b>	<b>Background Torque</b>	<b>Perturbation Torques</b>
<b>Experiment 1</b>	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
<b>Experiment 2</b>	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

Table 1



<b>Muscle Activity</b>	<b>Target Size</b>	<b>Perturbation Torque</b>	<b>Early R2/3</b>	<b>Late R2/3</b>
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)

Table 2