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J Neurophysiol 110:1323-1332, 2013. First published 3 July 2013;
doi: 10.1152/jn.00216.2013

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J Neurophysiol 110: 1323–1332, 2013.
First published July 3, 2013; doi:10.1152/jn.00216.2013.

Feedback responses rapidly scale with the urgency to correct for external perturbations

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Submitted 25 March 2013; accepted in final form 28 June 2013

Crevecoeur F, Kurtzer I, Bourke T, Scott SH. Feedback responses rapidly scale with the urgency to correct for external perturbations. *J Neurophysiol* 110: 1323–1332, 2013. First published July 3, 2013; doi:10.1152/jn.00216.2013.—Healthy subjects can easily produce voluntary actions at different speeds and with varying accuracy requirements. It remains unknown whether rapid corrective responses to mechanical perturbations also possess this flexibility and, thereby, contribute to the capability expressed in voluntary control. Paralleling previous studies on self-initiated movements, we examined how muscle activity was impacted by either implicit or explicit criteria affecting the urgency to respond to the perturbation. Participants maintained their arm position against torque perturbations with unpredictable timing and direction. In the first experiment, the urgency to respond was explicitly altered by varying the time limit (300 ms vs. 700 ms) to return to a small target. A second experiment addresses implicit urgency criteria by varying the radius of the goal target, such that task accuracy could be achieved with less vigorous corrections for large targets than small target. We show that muscle responses at ~60 ms scaled with the task demand. Moreover, in both experiments, we found a strong intertrial correlation between long-latency responses (~50–100 ms) and the movement reversal times, which emphasizes that these rapid motor responses are directly linked to behavioral performance. The slopes of these linear regressions were sensitive to the experimental condition during the long-latency and early voluntary epochs. These findings suggest that feedback gains for very rapid responses are flexibly scaled according to task-related urgency.

motor control; flexible feedback control; long-latency reflex; upper limb

A HALLMARK OF VOLUNTARY CONTROL is our ability to adjust the vigor of our motor patterns to consider temporal or spatial constraints of a motor task. For instance, musicians can easily change the tempo of a tune, and sport instructors often slow down or speed up movements for educational purposes. This flexibility in how we perform a given motor action has led to studies exploring how the agonist burst of arm muscle activity to initiate movements, such as reaching, exhibit considerable flexibility in its rate of increase, overall height, and duration. Changes in these initial motor patterns of muscle activity reflect the interplay of implicit parameters like movement amplitude and target size along with explicit criteria of intended movement speed (Brown and Cooke 1981; Corcos et al. 1989; Gottlieb et al. 1990; Gribble and Ostry 1999).

Feedback also plays an important role in voluntary control (Scott 2004; Todorov 2004), leading to increased interest in understanding the complexity present in corrective responses to changes in the visual or mechanical environment. A clear candidate to express flexible feedback control relative to the urgency to correct for a perturbation is the long-latency response (~50–100 ms, for review, see Pruszynski and Scott 2012). Muscle responses in this time window are known to reflect categorical changes in a subject's intention or "central set". For instance, an increase in long-latency activity is observed when participants are instructed to resist the impending perturbation compared with when instructed "do not intervene" (Calancie and Bawa 1985; Crago et al. 1976; Rothwell et al. 1980). Long-latency responses are also modulated by body, task, and environmental dynamics (David et al. 2009; Kimura et al. 2006; Kimura and Gomi 2009; Krutky et al. 2010; Kurtzer et al. 2008; Perreault et al. 2008) and are sensitive to changes in the spatial location (or structure) of the behavioral goal (Dimitriou et al. 2012; Nashed et al. 2012; Omrani et al. 2013; Pruszynski et al. 2008). Although these studies emphasize a very rich repertoire, the sensitivity of these responses to the urgency to correct for external disturbances has not been thoroughly investigated.

A modulation of long-latency responses with temporal constraints is expected as a consequence of the spatial tuning of these responses. Indeed, Pruszynski and colleagues (2008) highlighted that muscle responses to perturbations at ~60 ms increased when the spatial location of the goal target imposed more vigorous corrections. However, the effect of timing constraints cannot be directly deduced from these results because altering the goal target induced large differences in end-point hand location. To address the influence of timing constraints specifically, it is necessary to vary the time available to respond to the perturbation while keeping the same location of the goal target.

A recent observation was made in the context of bimanual control, where reducing the time available to respond to the perturbations increased the muscle agonist response (Omrani et al. 2013). These results make a more direct link between long-latency responses and temporal constraints, but leave unanswered the question of whether such an increase resulted from a nonspecific modulation of the peripheral apparatus, altering the mechanical impedance of the limb and the gain of the stretch reflex (Matthews et al. 1986), or from internal changes in feedback gains. Hence, the mechanism underlying response modulation remains unclear, and its actual contribution to the movement kinematics has not been quantified.

In this study, we present a detailed investigation of these issues. We use a posture task against mechanical perturbations

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applied at the shoulder and elbow joints. We hypothesized that the urgency to correct for external perturbations imposed by the task is also reflected in long-latency motor responses. The first experiment examined the impact of explicit time constraints on feedback corrections; subjects were instructed to return their hand within a moderate (700 ms) or brief (300 ms) amount of time to the same goal target. The change in response time allowed us to examine the influence of prior intent to perform quicker corrections while keeping the spatial constraints constant. Feedback responses were examined under two conditions of background load that either preactivated or preinhibited the stretched muscle. The second experiment examined the impact of implicit time constraints on feedback corrections; subjects were presented with goal targets having different radii, enabling more relaxed feedback actions for larger sized targets. By not enforcing a specific speed criterion and using targets with similar position, in contrast to Pruszynski et al. (2008), we could examine the subject's preferred strategy of motor correction. Hence this approach more closely parallels previous studies examining the preferred strategies in self-initiated reaching movements (Corcos et al. 1989; Gribble et al. 2003). We used the same approach to address the effect of accuracy constraints on the pattern of muscle response following the perturbation.

We show that muscle responses exhibited scaling with both explicit and implicit constraints altering the time available to respond to the perturbations. We further determined that the reversal time of the perturbation-evoked motion varied with the size of the long-latency response on a trial-by-trial basis, suggesting that the muscle activity in this time window is meaningfully linked to the temporal aspects of the corrective movement. This was also evident in the steep slopes of regressions between long-latency and movement reversal time, which were sensitive to the task constraints. Together our results suggest that long-latency motor responses contribute to the flexibility of voluntary behavior required by different urgency demands.

METHODS

A total of 17 subjects participated in this study (10 men, between 22 and 48 yr of age). All subjects gave written, informed consent following standard procedures. The experimental protocol was approved by the local ethics committee at Queen's University. One subject participated in the two experiments presented below. Each participant's right arm was placed in an exoskeleton that can selectively apply torques at the shoulder and/or elbow joints (KINARM, BKIN Technologies, Kingston, Canada) (Scott 1999; Singh and Scott 2003). Arm motion was constrained to the horizontal plane, and direct vision of the arm was blocked. The visual targets and the hand-aligned cursor were presented in the horizontal plane. A background torque was initially applied at the shoulder (±2 Nm). Subjects were asked to stabilize their fingertip at the start target presented at 45° and 75° of shoulder and elbow angles, respectively. The return target was initially presented as an open circle concentric with the start target. Subjects were instructed to maintain postural control at the start target and to go back to the return target following the perturbation. The perturbation was applied after a random delay uniformly distributed between 2 and 4 s following stabilization in the start target. The hand-aligned cursor was extinguished at perturbation onset so that the corrective movements were only driven by limb afferent feedback. The two experiments presented below varied the perturbation direction, the radius of the return target, and the time constraint following the perturbation (Fig. 1).

Experiment 1. Subjects ($n = 8$) were instructed to return to the goal target (radius 1 cm) within 700 ms or 300 ms of perturbation onset, and to stay in the target for 2 s. The timing constraints were verbally communicated to the participants and constant within each block of trials. Feedback was given about movement success by displaying a green return target if subjects could return and stabilize within the prescribed time window, and a red return target otherwise. Exemplar hand paths are illustrated in Fig. 1*A* for each timing condition (700 ms in red and 300 ms in blue). Participants performed the task in the presence of an extensor or a flexor background load applied at the shoulder joint (±2 Nm). The background load was constant within each block of trials. Perturbation directions were randomized and included positive and negative shoulder torque relative to the background load (Fig. 1*A*, ±2 Nm). Perturbations and background loads were reduced by 25% for one subject who encountered difficulties to perform the task. We recorded 25 trials per timing condition × perturbation direction × background load direction, summing to a total of 200 trials per subject.

Experiment 2. Subjects ($n = 10$) performed the same postural task initiated from a 1-cm radius circle used as the start target. The radius of the return target was constant within each block of trials. The values of the return target radius were 2 cm (Fig. 1*B*, blue), 4 cm (green), 6 cm (black), and 30 cm (turquoise). The timing constraint was constant and set to 800 ms. In this experiment, we chose to apply an extensor background load (−2 Nm) to inhibit the shoulder extensor as we found no effect of the background load on the response scaling in the first experiment. The preinhibition allowed us to emphasize the response component that is related to the task (Pruszynski et al. 2011b). Four different perturbation directions were randomized within each block to avoid anticipation (Fig. 1*B*; positive shoulder torque, negative elbow torque, and positive or negative combined shoulder

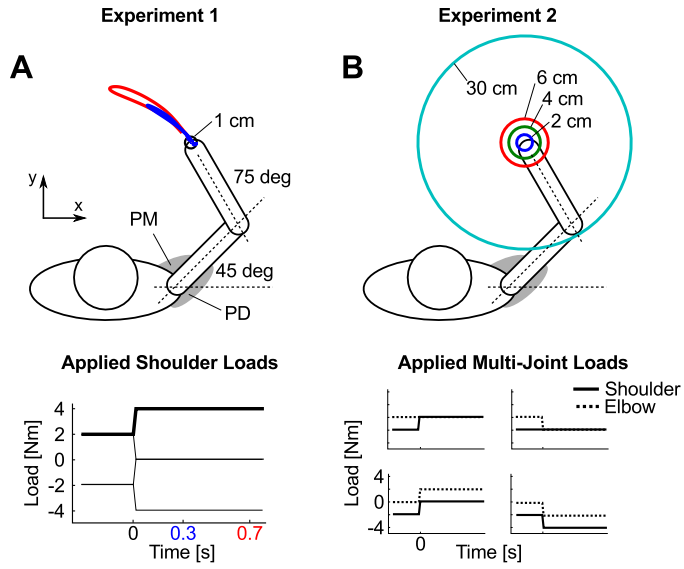


Fig. 1. *A*: overhead representation of the postural task and initial joint configuration. Hand paths following positive shoulder torque perturbations are illustrated in the two timing conditions: 700 ms in red and 300 ms in blue. Observe that changes in time constraints also induce variation in hand path, with shorter excursion for tighter constraints. Shoulder muscles are depicted in gray [posterior deltoid (PD); pectoralis major (PM)]. The *bottom* plot illustrates the time course of the load applied at the shoulder joint. The background load (time < 0) was positive or negative, and the perturbations were ±2 Nm relative to the background load. The thick trace emphasizes the perturbation load that generated the motion illustrated in the *top* panel. Deadlines to return to the target are shown with the same color code as in *A*. *B*: illustration of the different target radii used in *experiment 2*. *Bottom*: illustration of the multijoint perturbation loads used in the second experiment.

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and elbow torques). All perturbation magnitudes applied at the shoulder and/or elbow joints were equal to ±2 Nm relative to the background load (Fig. 1*B*). We recorded 30 perturbation trials per perturbation direction × return target radius (total of 480 trials per subject). As in the first experiment, a green or red return target was used to inform participants about the task success or failure. The only instruction given to participants was to get a green return target, meaning that they had to return to, and stay within, the target in the prescribed time window and remain in the target for 2 s.

In each experiment, the task was varied across the blocks, as previous studies have reported that a blocked design produced more consistent results compared with when the task is randomized within each block of trials (Nashed et al. 2012; Pruszynski et al. 2008).

Data collection and analysis. Shoulder and elbow angles were sampled at 1 kHz and digitally low-pass filtered (4th order, zero-lag Butterworth filter with 20-Hz cutoff frequency). The activity of shoulder flexor and extensor muscles [pectoralis major (PM) and posterior deltoid (PD)] was collected with surface electrodes (Delsys, Boston, MA) attached on the muscle belly after light abrasion of the skin. The signal was amplified (gain = 10^4), band-pass filtered (15–500 Hz), rectified, and normalized to the average activity evoked by 2 Nm background load collected prior to the perturbation for the first experiment, or on a separate set of trials for the second experiment (the value of 1.5 Nm was used for one subject in *experiment 1*). The binned analysis of muscle responses was based on the average activity across distinct epochs of time relative to perturbation onset. For each participant, the rectified electromyogram (EMG) was averaged across time and across trials using standard epochs (Pruszynski et al. 2008): preperturbation activity (−50 ms to 0 ms), R1 (20 ms to 45 ms), R2 (45 ms to 75 ms), R3 (75 ms to 105 ms), and early voluntary (Vol, 120 ms to 180 ms). Kinematic analyses concentrate on the reversal time, defined as the timing of the peak shoulder displacement, or equivalently the time when the joint velocity changed sign during the motor response. As presented below, this parameter is directly related to the timing of corrective movements, and it was sensitive to the change in strategy across conditions. We also determined the stabilization time for each individual trial as the time when the tangential hand velocity dropped below a fixed threshold set to 5 cm/s. Changing the threshold had qualitatively no influence on the results.

For each experiment, we performed statistical comparisons across trials from individual subjects. These analyses were based on Wilcoxon rank sum tests across fast and slow conditions in *experiment 1*, and on one-way analysis of variance (ANOVA) across the different conditions of target radius in *experiment 2*. Group comparisons were also performed using participants' individual means. These tests were based on paired *t*-test for *experiment 1* and ANOVAs for *experiment 2*. The ANOVAs were used to test the presence of main effects across the different values of return target radius, considering the measurements (kinematic parameter or binned EMG) as a random variable across subjects (39 or 29 degrees of freedom in total, corresponding to 10 participants × 4 or 3 target radii). ANOVAs were also performed for each subject to address the presence of main effects on individual trials (119 degrees of freedom, 30 trials from one perturbation direction × 4 target radii). The relationship between muscle responses and movement kinematics was based on linear regressions between the movement reversal times and the average muscle activity in each epoch of time. The regressions were computed for each participant, and the slope and correlations were compared across subjects using paired *t*-tests. The onset of divergence between muscle responses from the first experiment was estimated with receiver operating characteristics (Metz 1978). This technique quantifies the overlap between the distributions of EMG from the two timing conditions at each time step (1 or 0 indicating non-overlapping distributions, 0.5 indicates identical distributions). The time series is approximated with a linear regression over 15 time steps around the threshold corresponding to 0.75 and the divergence onset is defined as the time when the linear approximation crosses the value of 0.5 (Crevecoeur et al. 2012; Pruszynski et al. 2008).

RESULTS

Experiment 1. This experiment examines the effect of participants' prior intent to perform quicker corrective movements following the perturbation. The fastest timing condition (300 ms) was quite challenging, and most movements did not reach the target on time. However, subjects clearly generated quicker corrective movements. The effect of the timing condition on the movement kinematics is illustrated in Fig. 2*A* for one subject. When comparing individual trials across conditions for each subject, we found a significant effect of the timing condition for 7/8 subjects when both the background load and the perturbation induced shoulder flexion (Wilcoxon rank sum test, $Z > 2.9$, $P < 0.005$). The cumulative distributions from individual subjects are shown in Fig. 2*B*. For each subject, the median reversal time in the 300-ms condition was reduced compared with the median reversal time in the 700-ms condition (Fig. 2*C*). Similar results were obtained when the background load had opposite sign. In this case, all subjects displayed significantly lower reversal times in the 300-ms return condition ($Z > 3$, $P < 0.005$). Figure 2*D* represents the proportion of reversal times in the 300-ms condition smaller than a monotonically increasing value, plotted against the proportion of the reversal time from the 700-ms condition. Each curve corresponds to one subject. Integrating each curve

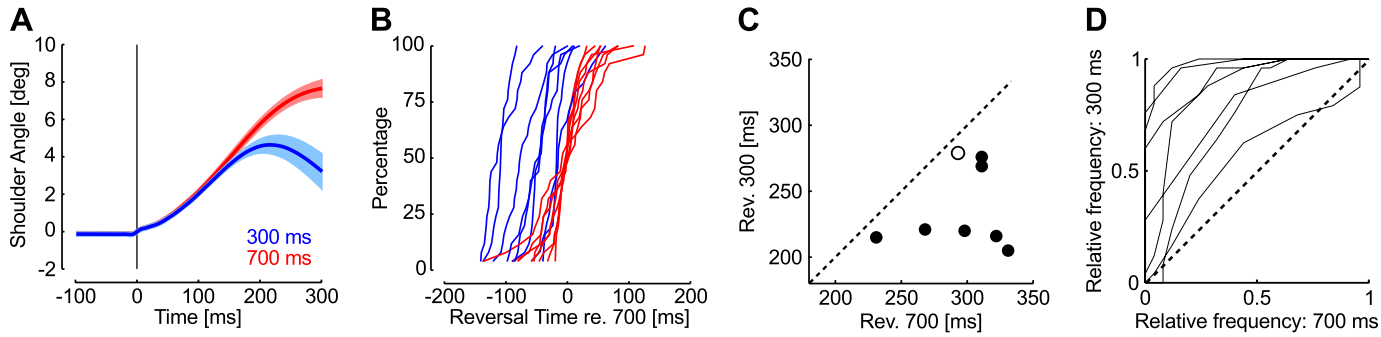


Fig. 2. *A*: perturbation-related shoulder displacement from one representative subject in the 300-ms (blue) and 700-ms (red) timing conditions (*experiment 1*). Solid traces and colored areas represent the average and SD across trials. *B*: individual cumulative distribution of reversal times in the two conditions of timing constraints relative to the mean from the 700-ms condition for each subject. *C*: individual median reversal times in the 300-ms condition plotted again the median reversal time in the 700-ms condition. The open circle corresponds to the subject for whom the comparison of individual trials across conditions was not significant. *D*: relative frequency of reversal times from individual trials in the 300-ms condition plotted against the 700-ms condition for each subject.

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would give a value > 0.5, which confirms the consistent effect of the timing instruction on the reversal times from individual trials. Statistical comparisons on group data based on participants' individual means confirmed a significant reduction in reversal times in the 300-ms condition, in the two preloading conditions [paired *t*-tests, $t_{(7)} > 4.2$, $P < 0.005$].

The motor responses are shown in Fig. 3, for both agonist (posterior deltoid PD, *top* panels) and antagonist (PM, *bottom* panels) muscles. In each condition of the agonist preactivation, we found that the preperturbation, R1, and R2 time windows were statistically similar across timing conditions [one-tail paired *t*-test, $t_{(7)} < 1.6$, $P > 0.14$]. Significant modulation was observed within the R3 [$t_{(7)} > 3.2$, $P < 0.05$], and Vol epochs of time [$t_{(7)} = 2.68$, $P < 0.05$]. Receiver operating characteristics analysis identified the onset of divergence between the two populations of response signals in the R2 time window (Fig. 3, *A* and *B*, vertical arrow), and it was approximately the same when the muscle was preexcited or preinhibited (60 ms when preexcited, and 55 ms when preinhibited, Fig. 3*C*). The linear regressions between these two signals indicate that they were similar [$R_I(t)$: preinhibited; $R_E(t)$: preexcited], suggesting a common underlying mechanism capable to modulate the motor response independently from the level of preactivation. Importantly, there was no difference in the antagonist response across timing conditions, independent from the preloading conditions [$t_{(7)} < 1.6$, $P > 0.17$, Fig. 3, *A* and *B*, *bottom*]. We found qualitatively similar results when looking at the shoulder flexor following the negative shoulder perturbation (PM), although the modulation observed in this muscle across conditions was smaller (peak ΔEMG across conditions was ~1.5 arbitrary units). For this muscle, muscle responses were significantly higher during the Vol time window when the muscle was preinhibited [$t_{(7)} = 2.45$, $P < 0.05$], and in the R3 time window when preexcited [$t_{(7)} = 2.17$, $P < 0.05$]. Although responses were more variable, we found similar onset of divergence between responses evoked in the two timing conditions (65 ms, signals were averaged across preloading conditions). The activity of PD was also statistically similar across timing conditions when this muscle acted as an antagonist [$t_{(7)} < 1.85$, $P > 0.1$].

We examined the relationship between the motor responses and the behavioural performance by relating the EMG from individual trials to the joint reversal time. We computed the partial correlation between these variables relative to the preperturbation activity. Figure 4*A* shows the evolution of the relationship between each epoch of the stretch response and the reversal times for one subject who best illustrated the general tendency (data from preinhibited condition). Linear fits are displayed when significant. In some cases, we measured significant correlations between the reversal times and the preperturbation activity (Fig. 4*B*, 6/32 computed regressions, $R = -0.12 \pm 0.19$, mean ± SD across subjects), or the short latency response (10/32 regressions, $R = -0.14 \pm 0.18$). However, the slope of these linear regressions indicated a marginal link between the response in these time windows and the movement kinematics. Significant correlations appeared in greater proportion during R2 and even more clearly during the R3 time window (Fig. 4*B*, percentages refer to 8 subjects × 2 timing conditions × 2 preloading conditions). Figure 4*B* displays the raw correlation, as well as the partial correlations, after removing the contribution of the preperturbation epochs in the linear fits. Interestingly, the raw and partial correlations

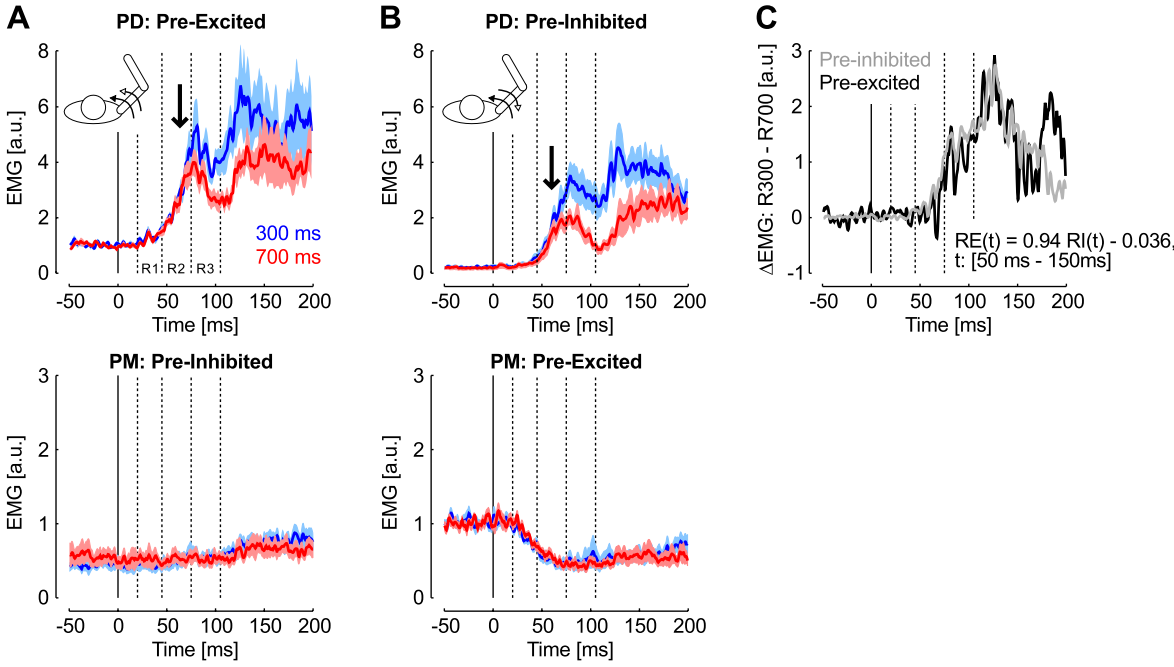


Fig. 3. *A*: muscle response from *experiment 1*, in the two timing constraint conditions when the PD was preactivated (mean ± SE across subjects). Perturbation (filled arrow) and background loads (open arrow) are illustrated on the stick diagram. The *top* panels show the agonist response from the PD, and the *bottom* panels illustrate the antagonist activity from the PM. The vertical arrow indicates the estimated onset of divergence between the two response signals obtained from the receiver operating characteristics analysis. The different epochs of rapid motor responses are illustrated with vertical dashed lines. *B*: same as *A* when PD was preinhibited. *C*: differences (Δ) between perturbation-evoked responses in the 300-ms (R300) and 700-ms conditions (R700) when the muscle was preexcited (black) and preinhibited (gray). The linear regression estimated the relationship between the difference signals in the preexcited (R_E) and preinhibited (R_I) conditions from 50 ms to 150 ms. EMG, electromyogram; au, arbitrary units.

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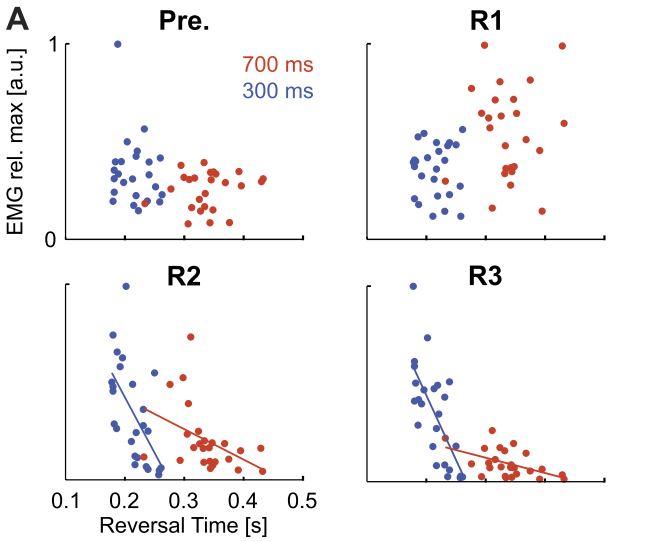


Fig. 4. *A*: EMG activity in each epoch of time (Pre, R1, R2, R3) as a function of the joint reversal time from one representative subject (*experiment 1*). Each dot corresponds to one single trial. EMG values were normalized to their maximum in each subplot for illustration purpose. Red and blue correspond to the 700-ms and 300-ms conditions, respectively, as in Figs. 2 and 3. Linear fits are illustrated when significant ($P < 0.05$). *B*, *top*: raw (dashed) and partial (solid) correlation between average EMG and reversal times relative to the preperturbation activity with identical color code as in *A* (mean ± SE across subjects). The percentages indicate the proportion of significant fits across subjects and preloading condition. *Bottom*: slopes of the linear regressions (mean ± SE across subjects). *Significant changes from paired *t*-tests at the level $P < 0.05$.

were similar in the R2/3 time window and Vol, which suggests that long-latency responses override the relationship between the preperturbation activity and the reversal times. The activity in the early-voluntary epoch (120–180 ms) is relatively close to the reversal times (240 ± 24 ms, mean ± SD across subjects), but also displayed a good correlation (partial correlations: −0.32 ± 0.13, mean across conditions ± SD, see also second experiment). Significant differences in regression slopes were observed in the R2 and R3 time window [Fig. 4*B*, $t_{(7)} > 2.5$, $P < 0.05$]. In this analysis, the correlations and the slopes for each subject were averaged across the two conditions of muscle preactivation. All results were similar when looking at each condition independently. In all, the statistical relationship between the perturbation-related EMG and the performance of the corrective movement is gradually stronger as the underlying process becomes a contributor of the movement kinematics. The slope of the relationship indicates a gradually greater sensitivity to the evoked motion, which reaches significance in the long-latency time window (R2/3).

Experiment 2. Perturbation related motion is illustrated in Fig. 5*A*. Changes in return target size produced combined changes in movement timing with variation in end-point distribution. Figure 5*A* shows that the stabilization time tended to increase with the radius of the return target, as well as the end-point *x*- and *y*-coordinates. Group data confirm that the subjects performed slower feedback corrections when the target radius increased (Fig. 5*B*). Participants also took advantage of the relaxation of spatial constraints and allowed small changes in end-point coordinates (Fig. 5*B*). Interestingly, they responded in the 30-cm radius condition before hand displace-

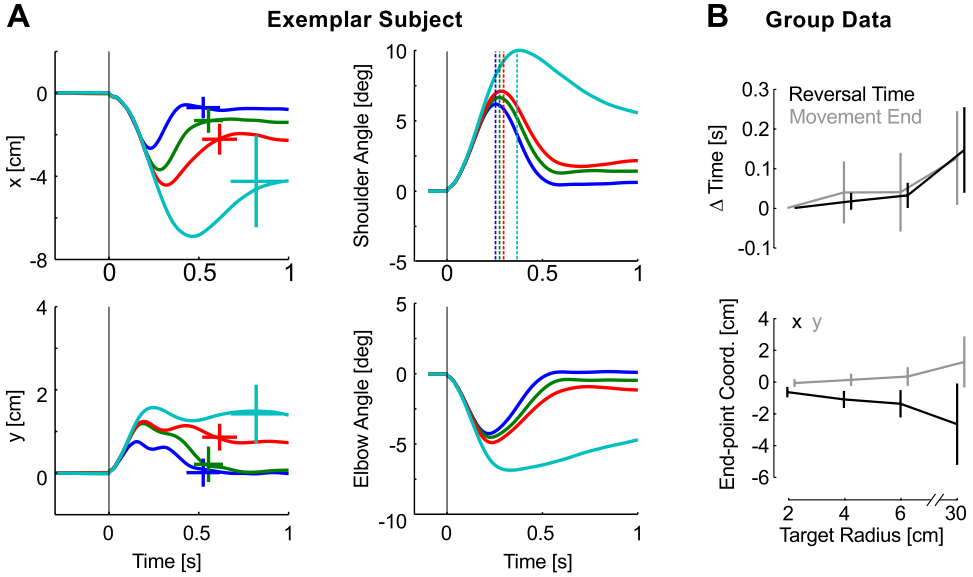


Fig. 5. *A*, *left*: perturbation-induced displacements along the *x*-axis as a function of time for the different return target radii from one representative subject (*experiment 2*). The color code corresponds to Fig. 1*C*: 2 cm in blue, 4 cm in green, 6 cm in red, and 30 cm in turquoise. Horizontal and vertical bars represent the stabilization time and corresponding end-point coordinate, respectively (mean ± SD across trials). Zero corresponds to each participant's fingertip location with 45° and 75° of initial shoulder and elbow angles, respectively. The panels on the *right* show the corresponding shoulder and elbow angle. The vertical dashed lines illustrate the time of maximum joint displacement. *B*, *top*: reversal times (black) and movement end (gray) for the different sizes of return target radius. Displays are the difference between each condition and the data from the 2-cm target for each subject. *Bottom*: end-point *x* (black) and *y* (gray) coordinates at the stabilization time following the perturbation that involves a pure shoulder torque. Vertical bars indicate 1 SD across subjects (*top* and *bottom* panels).

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ment exceeded 30 cm. The average radial distance between the hand end-point and the start target was 7.3 ± 5 cm (mean ± SD across subjects, all perturbation directions pooled). Step torque perturbations require a response because the load is constantly pushing participants' hand. How soon subjects had to respond was open ended, allowing participants to rely on their preferred strategy. Our data indicate that they preferred to break the movement early, even if their hand was still far from the target boundary.

The reversal time as well as the movement end varied significantly with the target radius [one-way ANOVA, $F(3,36) > 3.2$, $P < 0.05$]. The effect of the radius on the reversal time persisted even after removing the 30-cm radius from the analysis [$F(2,27) > 3.4$, $P < 0.05$]. The effect of the target radius on the reversal times was also present across trials for 9/10 subjects [one-way ANOVA on individual trials, $F(3,116) > 5$, $P < 0.01$]. This is important because it confirms that this parameter captures the small variations in reversal time across small and intermediate target radii. Changes in end-point coordinates were also analyzed after excluding the data from the 30-cm radius condition, as they were clearly distinct from the small and intermediate target radii. For the perturbation direction illustrated in Fig. 5 (pure shoulder torque), changes in end-point coordinates were significant along the *x*-axis [$F(2,27) = 3.63$, $P < 0.05$], but not along the *y*-axis [$F(2,27) = 2.26$, $P > 0.12$]. Overall, corrective movements following the other perturbation directions displayed similar variations in temporal parameter with only small changes in end-point coordinates. In particular, perturbation-related joint motion for the first 100 ms were virtually equal, regardless of the target radius.

Average shoulder responses following the two perturbations that include a shoulder torque are depicted in Fig. 6, *A* (pure shoulder torque) and *B* (combined shoulder and elbow torque). We observed a small modulation of preperturbation activity across the different conditions of target radii that reached significance for PM that was preexcited [one-way ANOVA, $F(3,36) = 5.12$, $P < 0.01$]. The modulation observed for PD was not significant [$F(3,36) = 2.09$, $P = 0.12$]. As in the first experiment, differences between antagonist responses in the different epochs were not significant [$F(3,36) < 2.42$, $P > 0.08$, Fig. 6, *A* and *B*, PM]. The binned analysis confirmed a strong modulation of the agonist response (PD) within the R3 and Vol time windows for these two perturbation directions [Fig. 6, *C* and *D*, $F(3,36) > 3.3$, $P < 0.05$].

This experiment reproduced a strong correlation between the muscle response and the time of maximum shoulder displacement as observed in *experiment 1*. The largest target radius (30 cm) was excluded from this analysis, as most trials did not exhibit a clear reversal time. For the small and intermediate target radii, we found a strong relationship between the integrated EMG and the reversal time across individual trials, which confirms that the long-latency response is directly linked to the kinematics of the corrective movement. Figure 7*A* illustrates the evolution of the regressions between integrated EMG and the reversal times for one representative subject (target size = 2 cm), and a summary of regression results is shown in Fig. 7, *B* and *C*, across subjects. The changes in return target radius reproduced the same tendency as observed in *experiment 1*: the correlation between motor responses and reversal times increased across the different epochs of time, and the change in regression slopes started in the long-latency

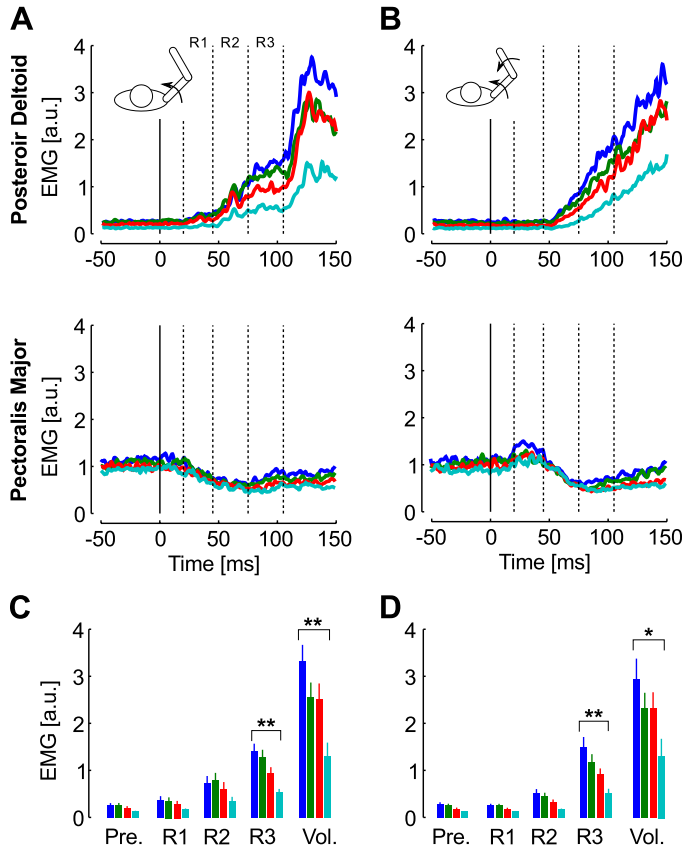


Fig. 6. *A*, *top*: perturbation evoked response averaged across subjects following pure shoulder torque perturbation (*experiment 2*). The color code corresponds to the different return target radii. The solid vertical line (time = 0) illustrates the perturbation onset, and the dashed vertical lines illustrate the different epochs of rapid motor responses (see METHODS). *Bottom*: activity from the antagonist muscle (PM). *B*: same as *A* for the combined shoulder and elbow torques. *C* and *D*: binned analysis of EMG from the PD, averaged across the different epochs of time. Vertical bars indicate 1 SE across subjects. Significant effect of the return target on the response based on one-way ANOVA at the level $*P < 0.05$ or $**P < 0.01$ is illustrated.

time window. Figure 7*B* shows the partial correlations across the different epochs of time after controlling for the correlation present in the preperturbation activity. The correlation between reversal times and preperturbation activity displayed similar values as those found in the first experiment (raw correlation: $R = -0.12 \pm 0.19$, mean ± SD across subjects). The small modulation of baseline activity and short-latency response correlated with the reversal times in ~30% of the 30 regressions (10 subjects × 3 return target radii). However, as observed in *experiment 1*, the corresponding slopes (Fig. 7*C*) revealed that these relationships were weak. In the subsequent epochs of time, the number of significant fits increased, and the correlation gradually accounted for greater proportion of the reversal time variability.

For each target radius, the slopes measured in the R3 and early-voluntary epochs were significantly different from those measured in the preperturbation and R1 time windows [$t_{(9)} > 2.6$, $P < 0.05$]. Importantly, significant changes across target radii were observed in later epochs of time, as indicated with asterisks on Fig. 7*C* (one-tail paired *t*-tests). These results reproduce the effect observed in the first experiment, even with the more subtle variation in behavior induced by the changes in target radius.

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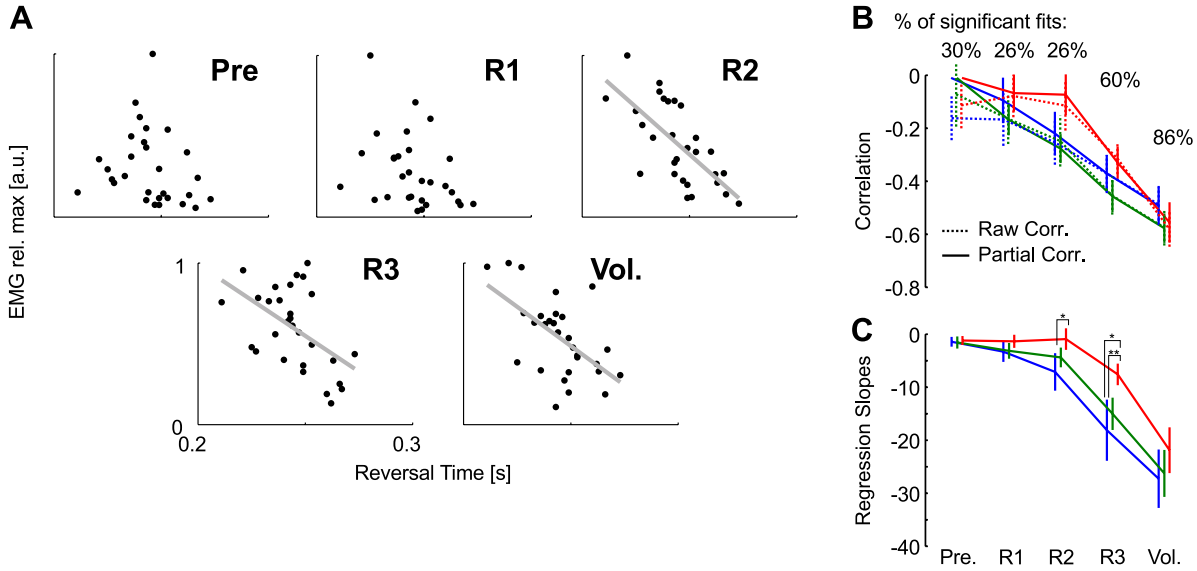


Fig. 7. *A*: average EMG from individual trials in the different epochs of time as a function of the reversal time from one representative subject (data from the small target radius condition of *experiment 2*). We normalized the EMG to the maximum value in each epoch for illustrative purposes. *B*: raw (dashed) and partial (solid) correlations from the regressions of the average EMG as a function of the reversal time (mean ± SE), after removing the correlations between the reversal times and the preperturbation activity. Percentages represent the proportion of significant linear fits ($P < 0.05$) across subjects and return target radii (30 regressions). As above, blue, green, and red correspond to 2 cm, 4 cm, and 6 cm return target radii, respectively. *C*: mean slope of linear regressions in each epoch of time (average across subjects ± SE). Significant changes in the sensitivity of the relationship between the evoked response and the reversal time at the level $*P < 0.05$ or $**P < 0.01$ are displayed.

We performed a similar analysis after replacing the reversal times with shoulder end-point angle and maximum shoulder displacement. The shoulder end-point angle was poorly predicted by the response variability across the different epochs of time (≤6/30 significant fits across epochs, the mean absolute correlation was < 0.23). The maximum shoulder displacement displayed better correlation, which is expected as it clearly covaries with the reversal time. However, the overall number of significant fits and correlation values (≤21/30 significant fits, mean absolute correlation < 0.42) were lower than those obtained with the reversal times (Fig. 7*B*, ≤26/30 significant fits, mean absolute correlation < 0.54). Although spatial and temporal parameters are clearly related by the laws of motion, this analysis suggests that, in these experiments, the joint reversal time is the best parameter to capture the correlation between muscle responses and movement kinematics.

Finally, we investigated the effect of changes in muscle baseline activity to address possible effects of cocontraction. We concentrated on the small target radius (2 cm) and separated responses to positive shoulder torques based on the preperturbation activity. The movement kinematics and muscle responses are illustrated in Fig. 8, *A* and *B* (black, baseline > median; gray, baseline ≤ median). It can be observed that, on average, trials associated with higher baseline displayed quicker reversal times. The muscle response was qualitatively the same. In fact, trials with higher baseline activity further increased across the following response epochs. Figure 8*C* shows the partial correlation between muscle responses and reversal times for the two subsets of trials. Qualitatively, there was no difference between higher and lower baseline trials. Figure 8 shows that participants relied on a concomitant modulation of preperturbation activity with feedback gains, rather than one or the other strategy. Therefore, the correlations and regression slopes from individual trials provide important information to quantify how much each strategy contributes to the movement kinematics: on average, the regression slopes

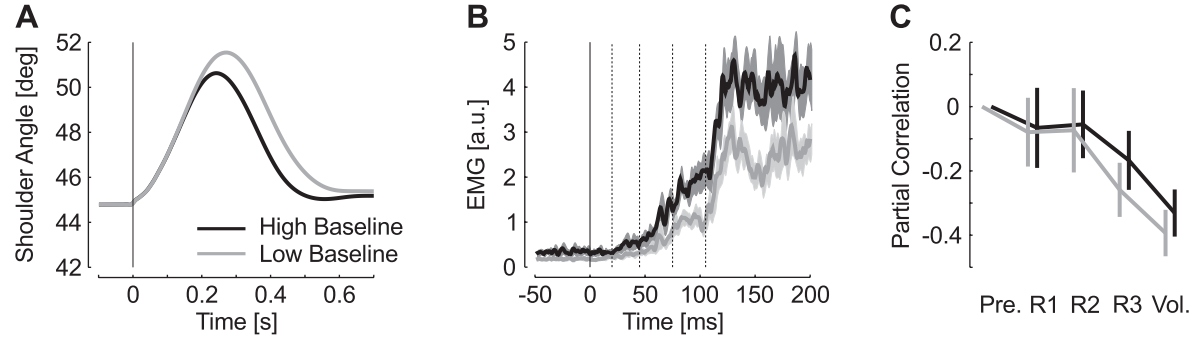


Fig. 8. *A*: shoulder displacement following the positive shoulder torque perturbation averaged across subjects (data from *experiment 2*). The black and gray traces represent the trials associated with higher or lower muscle preperturbation activity (baseline). Trials were separated based on the median average preperturbation activity across trials for each subject. *B*: muscle responses for trials with higher or lower preperturbation activity averaged across subjects with the same color code as in *A*. Shaded areas represent the SE; vertical lines represent the perturbation onset (solid) and the different epochs of feedback responses. *C*: partial correlations between the movement reversal times and muscle responses across epochs of time for the two subsets of trials.

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during the preperturbation epoch and R1 were ~10% and ~18% of those found in R3, respectively (5% and 10% compared with Vol).

DISCUSSION

Rapid feedback responses to mechanical perturbation are sensitive to spatial constraints during both postural control and reaching (Nashed et al. 2012; Pruszynski and Scott 2012). In addition, we may also encounter situations where the time available to respond to a perturbation varies, or where the accuracy constraint imposes more vigorous corrections for a similar spatial goal. We investigated feedback responses in these situations by varying the urgency to respond to the perturbations either explicitly (*experiment 1*) or implicitly (*experiment 2*). We showed that muscle responses scaled with the urgency to respond imposed by time or accuracy constraints, with higher responses for tighter constraints consistently starting in the long-latency epoch. Muscle responses in this time window were a good predictor of movement kinematics. We investigated the relationship between the muscle activity and the reversal times, which correspond to the moment when sufficient joint torque has been produced to reverse the motion toward the target. We suggest that this relationship between muscle responses and motor behavior can be used as an indicator of the feedback response strategy as it captures the effect of changes in motor response across conditions on the movement kinematics. Our results emphasize that changes in feedback control strategy start to influence the response in the long-latency epoch and display similar scaling properties with the task demand, as previously reported for self-initiated movements (Corcos et al. 1989).

Our analyses concentrate on the reversal times because the motor response variability captured a greater proportion of its variance compared with other tested parameters, such as the maximum joint angle. Also, the reversal time was a natural choice following the design of *experiment 1*, as we explicitly constrained the time available to return to the target. However, we cannot completely disentangle the temporal aspects of the corrective movement from spatial parameters, such as the joint displacement, or from the joint velocity, because these variables are all related by the laws of motion. Our analyses revealed that the reversal time was a good parameter for our analyses, capturing well the relationship between muscle responses and motor behavior.

Previous studies have suggested that the long-latency response result from functionally distinct processes that overlap in time (Rothwell et al. 1980; Shemmell et al. 2009), with distinct sensitivity to the reloading condition or task requirements (Pruszynski et al. 2011b). Following this study, we recently showed that motor responses are sensitive to perturbation loads across a range of magnitudes, including small joint displacement comparable to the natural variability of postural control and reaching tasks (Crevecoeur et al. 2012). In addition to the ability to scale the response with a range of perturbations, the present paper shows that the response component that is more sensitive to the task requirements is likely continuous with respect to constraints at hand. Altogether, these findings indicate that the scaling properties of long-latency responses, with both task and load requirements, enables rapid and flexible feedback control.

The effect of prior intent on feedback responses has been addressed mostly with categorical instructions such as "resist/let go", "intervene/don't intervene" (Calancie and Bawa 1985; Capaday et al. 1994; Colebatch et al. 1979; Crago et al. 1976; Rothwell et al. 1980; Shemmell et al. 2009), or by altering the spatial location of the goal target (Mutha et al. 2008; Pruszynski et al. 2008, 2011b). These studies reported a strong modulation of the long-latency response imposed by distinct task goals. Because the spatial location of the goal targets was varied across experiments, none of these studies could disambiguate temporal from spatial factors influencing the response modulation. To address this concern, we varied the timing of corrective movements while minimizing changes in the endpoint location. This approach allowed us to emphasize the relationship between the response modulation and the temporal aspects of the movement kinematics imposed by the urgency to respond. Our results show that the response modulation was tightly linked to the timing of the corrective movement captured in the reversal time, while participants were intending to return to the same spatial goal. These results emphasize a direct relationship between long-latency responses and the subsequent corrective movement generally ascribed to voluntary corrections, as reversal times typically occurred after 200 ms following the perturbation.

Previous studies suggested that the variability of long-latency responses made them unreliable and required adjustments of the early-voluntary responses to achieve consistent corrective responses across trials (Marsden et al. 1981; Rothwell et al. 1982). We also observed variability of the long-latency activity for any one subject. This variability must clearly be compensated in later epochs of time (>100 ms), as corrective movements return broadly to the same spatial goal (Rothwell et al. 1982). To our knowledge, the underlying compensation mechanism remains unexplored. Although the response variability requires online adjustments in later epochs, we showed that the long-latency variability was a good predictor of the reversal time, and this relationship could be influenced by prior intent or by implicit changes in the control strategy. The correlation between the long-latency responses and the subsequent reversal times highlights that, although EMG is generally assumed to be noisy, such measurements still capture an important proportion of the response variability. We expect that the consistent success of corrective movements in spite of the response variability is maintained with online adjustments of motor commands following the long-latency time window, as observed during unperturbed movements (Todorov and Jordan 2002).

A possible mechanism to alter perturbation responses is the increase of joint stiffness, such that a given joint displacement elicits a larger torque response (Burdet et al. 2001; Franklin et al. 2007, 2008; Houk 1979; Mussa-Ivaldi et al. 1985; Selen et al. 2009). Stiffness modulation can be achieved by increasing the level of cocontraction prior to the perturbation, which is also known to increase the stretch response via "gain-scaling" properties of the motoneuron pool (Marsden et al. 1976; Matthews 1986; Pruszynski et al. 2009). Compatible with this strategy, we observed a small absolute increase in partial correlations measured during the R1 time window relative to preperturbation activity (Figs. 4*B* and 7*B*). It can also be observed from the second experiment that participants modulated slightly their preperturbation activity (reaching signifi-

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cance for the preexcited shoulder flexor), likely to increase the joint stiffness and the short-latency response. However, the slopes of the corresponding relationship between the EMG and reversal times across the preperturbation and short-latency epochs suggested that these changes had a limited impact on the performance of the corrective movement. In addition, the relative increase in stretch response attributed to gain-scaling disappears near the end of the long-latency time window [R3 (Pruszynski et al. 2009)], where we observed higher sensitivity of the response relative to perturbation-related displacement, as well as differences in feedback strategies across conditions (Figs. 4*B* and 7*C*). These observations suggest that, in the experimental conditions presented above, possible influence of the intrinsic joint stiffness was not a significant component of the corrective response.

An alternative mechanism is the modulation of feedback gains as a result of changes in task demand. Previous studies on visually guided reaching have reported such task-dependent feedback mechanism following sudden jumps of the goal target or hand-aligned cursor (Franklin and Wolpert 2008; Knill et al. 2011; Liu and Todorov 2007). These observations are compatible with optimal feedback control models that suggest a direct link between accuracy constraints and feedback gains (Bryson and Ho 1975; Todorov and Jordan 2002). Accuracy constraints can be captured by a cost-function penalizing deviations from the goal target, and varying the cost of position errors directly modulates the feedback gains. Also, increasing the penalty on position errors evoke quicker corrective movements, providing a common mechanism to handle time and accuracy constraints. In this framework, the changes in the control strategy modulate the response through the estimated state of the limb that is perceived from delayed and noisy sensors. Our data are compatible with this prediction as the effect of changes in the control strategy across conditions started to influence the response in the long-latency time window, where a corrected estimate of the joint displacement may be available (Ariff et al. 2002; Crevecoeur and Scott 2013). Also, note that, in the second experiment, the participants' strategy was open ended. They could have used the same motor corrections across small and intermediate target radii while stopping as soon as the hand entered the target. Such a strategy would have produced a systematic shift of movement end-point without any modulation of the movement speed. Instead, our data clearly indicate that participants relaxed the intensity of motor command while returning broadly to the same location. This aspect of the data is compatible with the hypothesis that motor commands have a cost, and that altering the task demand directly impacts the feedback control strategy (Scott 2004; Todorov and Jordan 2002).

We suggest that the flexible sensorimotor strategies observed in voluntary control (Diedrichsen 2007; Liu and Todorov 2007) and following mechanical perturbations (Nashed et al. 2012; Pruszynski and Scott 2012) emanate from shared neural pathways, including primary motor cortex (Matthews 1991; Palmer and Ashby 1992; Pruszynski et al. 2011a; Scott 2012). At the implementation level, neural circuits must, therefore, have the capability to generate multiple outputs for a given sensory input according to the ongoing task. In agreement with this prediction, we demonstrated that the urgency to correct for perturbations evokes changes in feedback gains at latency compatible with the contribution of the transcortical pathway.

ACKNOWLEDGMENTS

The authors thank K. Moore, H. Bretzke, and J. Peterson for technical and logistic support.

GRANTS

This work was supported by the Natural Sciences and Engineering Research Council of Canada. F. Crevecoeur is supported by a fellowship from the Canadian Institute of Health Research-Instituts de Recherche en Santé du Canada.

DISCLOSURES

S. H. Scott is associated with BKIN Technologies, commercializing the robotic apparatus used in the experiment.

AUTHOR CONTRIBUTIONS

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

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