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J Neurophysiol 112:2264-2274, 2014. First published 6 August 2014; doi:10.1152/jn.00014.2014

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Reductions in muscle coactivation and metabolic cost during visuomotor adaptation

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Submitted 6 January 2014; accepted in final form 3 August 2014

Huang HJ, Ahmed AA. Reductions in muscle coactivation and metabolic cost during visuomotor adaptation. *J Neurophysiol* 112: 2264–2274, 2014. First published August 6, 2014; doi:10.1152/jn.00014.2014.—We often have to adapt our movements as we interact with a variety of objects in various conditions on a daily basis. Evidence suggests that motor adaptation relies on a process that minimizes error and effort; however, much of this evidence involved adapting to novel dynamics with physical perturbations to counteract. To examine the generality of the process of minimizing error and effort during motor adaptation, we used a visuomotor adaptation task that did not involve dynamic perturbations. We investigated the time courses of muscle activity, coactivation, and metabolic cost as subjects reached to a target with a visuomotor rotation. We wanted to determine whether subjects would modulate muscle activity, coactivation, and metabolic cost during a visuomotor adaptation task. Interestingly, subjects increased muscle coactivation early during visuomotor adaptation when there were large cursor-trajectory errors but no physical perturbations to reject. As adaptation progressed, muscle activity and coactivation decreased. Metabolic cost followed a similar time course. When the perturbation was removed, typical after-effects were observed: trajectory error increased and then was reduced quickly. This was accompanied by increases in muscle activity, coactivation, and metabolic cost, along with subsequent rapid reductions. These results demonstrate that subjects modulate muscle activity, coactivation, and metabolic cost similarly across different forms of motor adaptation. Overall, our findings suggest that minimization of error and effort may be a general process underlying various forms of motor adaptation.

motor adaptation; motor learning; internal model; visuomotor; effort minimization; metabolic cost

HUMAN MOVEMENT REQUIRES INTERACTING and adapting to a changing environment. This process of motor adaptation is thought to involve the minimization of both error and effort. When subjects learn to reach in a force-field, studies have shown that muscle activity and coactivation increase initially upon first exposure to the force-field and are reduced with adaptation (Darainy and Ostry 2008; Franklin et al. 2003; Franklin et al. 2012; Huang and Ahmed 2014; Huang et al. 2012; Thoroughman and Shadmehr 1999). The initial increase in muscle activity and coactivation could reflect an early reliance on musculoskeletal viscoelasticity to resist perturbations and minimize errors, since the central nervous system has not been able to learn the specific properties of the novel dynamics (i.e., internal model). As an improved internal model is formed during adaptation, the viscoelastic component of the response can be tuned down and reduced (Osu et al. 2002) perhaps to minimize effort and metabolic cost (Franklin et al. 2004). Measurement of actual metabolic cost during a force-field adaptation task has confirmed that such reductions in muscle coactivation lead to concomitant reductions in metabolic cost (Huang and Ahmed 2014; Huang et al. 2012). Taken together, these findings indicate that adaptation to novel dynamics involves a process that minimizes both effort and error (Emken et al. 2007). Whereas strong evidence for this has been observed in force-field learning, evidence for a similar process in visuomotor adaptation is less clear.

When subjects adapt to a visuomotor transformation, it is not clear if muscle coactivation may be beneficial. It is possible that there may be no increase in muscle activity and coactivation, as there are no mechanical perturbations for which to compensate. However, increases in muscle coactivation to modulate joint viscoelasticity could help to reduce kinematic variability that arises from neuromotor noise (Selen et al. 2009). Thus there may be increased muscle coactivation in visuomotor rotation tasks. Indeed, a number of studies indirectly suggest that this may the case. Increased coactivation was observed in a novel motor-learning task, where subjects learned to trace an unusual trajectory (Osu et al. 2002). There were no force perturbations in this task, yet subjects increased muscle coactivation, presumably to increase viscoelasticity and reduce performance errors. Interestingly, increased muscle activity has been observed in monkeys performing a visuomotor adaptation task (Paz et al. 2003). The monkeys increased muscle activity early during visuomotor adaptation but then rapidly decreased muscle activity within the first 25 adaptation trials. They also found that muscle activity and error were temporally correlated. However, they did not examine muscle coactivation. Furthermore, the monkeys performed the two-dimensional task bimanually (one hand controlling each direction independently), making it difficult to generalize to traditional visuomotor tasks.

In this study, we investigated the time course of muscle activity, coactivation, and metabolic cost in a visuomotor adaptation task. We sought to determine whether increased muscle coactivation would also be observed in a task where greater limb viscoelasticity was relatively less helpful for task performance and whether this would manifest as increases in metabolic cost. We also asked whether there would be reductions in muscle activity, coactivation, and metabolic cost as adaptation progressed. If reductions were observed during visuomotor adaptation, then it would provide strong support for the overall hypothesis that the reduction of error and effort is a general process underlying multiple forms of motor adaptation.

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MATERIALS AND METHODS

Subjects

Seven right-handed adults (mean ± SD, age 26 ± 5.3 yr; mass 67.8 ± 14.4 kg; four women, three men), with no known physical injuries or pathologies, participated in the main study. An additional three subjects (age 27.7 ± 7.1 yr; mass 66.7 ± 12.6 kg; one woman, two men) were recruited to participate in a control experiment. All subjects provided written, informed consent, and the protocol had the approval of the University of Colorado Institutional Review Board.

Task

Seated subjects grasped the handle of a robotic arm (Shoulder-Elbow Robot 2; Interactive Motion Technologies, Watertown, MA) and made out-and-back movements to a target, 20 cm away from the subject's torso (Fig. 1*A*). Visual feedback of the home circle (radius = 0.8 cm), target circle (radius = 0.8 cm), and cursor (radius = 0.3 cm) was displayed on a computer monitor mounted vertically in front of the subject. To initiate a trial, subjects had to hold the cursor within a ring (radius = 1.5 × cursor radius) in the center of the home circle for 50 ms. We instructed subjects to try to hit the target with a single smooth out-and-back movement and not to correct their trajectories within a trial to hit the target. As a result, subjects did not always hit the target. If subjects missed the target, then they could adjust their trajectories on the next trial. If subjects hit the target within 500–700 ms, then the target would "explode" to signal that the subject was successful. The end of the trial occurred when subjects returned to the home circle. Within each batch of five trials, there was a catch trial during which the cursor was invisible, removing visual feedback of the cursor. The purpose of the catch trial was to capture the planned out-and-back trajectory without potential corrections using visual feedback. During the visuomotor rotation trials, the cursor was rotated 30° clockwise (Fig. 1*B*). Thus to hit the target, subjects had to reach across their body to their left by 30°. The time from the start of one trial to the start of the next trial was ~2.25 s but could be longer if subjects had difficulty finding the home circle on catch trials. A physical horizontal barrier was placed roughly at the subject's chin height that prevented subjects from seeing their hand. The starting position of the hand was anterior to the sternum, due to the physical constraints required for using the metabolic system (Fig. 1*A*). Even though subjects actively grasped the handle of the robot, their arm rested in a cradle connected to the robot that supported the subject's forearm against gravity.

Protocol

Main experiment. There were six blocks in the experimental protocol (Fig. 1*C*). During the first block, subjects sat quietly for 10 min to establish a baseline resting metabolic rate. Subjects then performed four reaching blocks: 200 trials without the visuomotor rotation (Null 1; trials 1–200), 200 trials with the visuomotor rotation (VM 1; trials 201–400), another 200 visuomotor trials (VM 2; trials 401–600), and then 200 null trials (Null 2; trials 601–800). Each reaching block was ~8 min. Metabolic rate was measured continuously using expired gas analysis during the four reaching blocks. After a brief rest, where the subjects were able to remove the mouthpiece, we had subjects reach to a target at the adapted location, 30° counterclockwise from the target location, for 150 trials, while measuring their metabolic rate (Control; trials 801–950).

Control experiment. The control experiment was identical to the main experiment except for two differences. First, metabolic rate was not measured in these subjects. Second, the control block was placed at the start of the protocol rather than at the end. Subjects reached to targets rotated counterclockwise at 0°, 30°, and −30°, relative to the original target location, for 150 trials. Targets were randomized in blocks. The placement of the control block at the start of the protocol allowed subjects to familiarize themselves with the passive robot dynamics experienced when reaching to the adapted location. Thus any changes observed in muscle activity later in the protocol, during adaptation, could not be attributed to adaptation to inexperienced passive robot dynamics.

Muscle Activity Measurement

Surface electromyographic (EMG) data of six upper-limb muscles in the right arm were recorded. The EMG system (Trigno; Delysis,

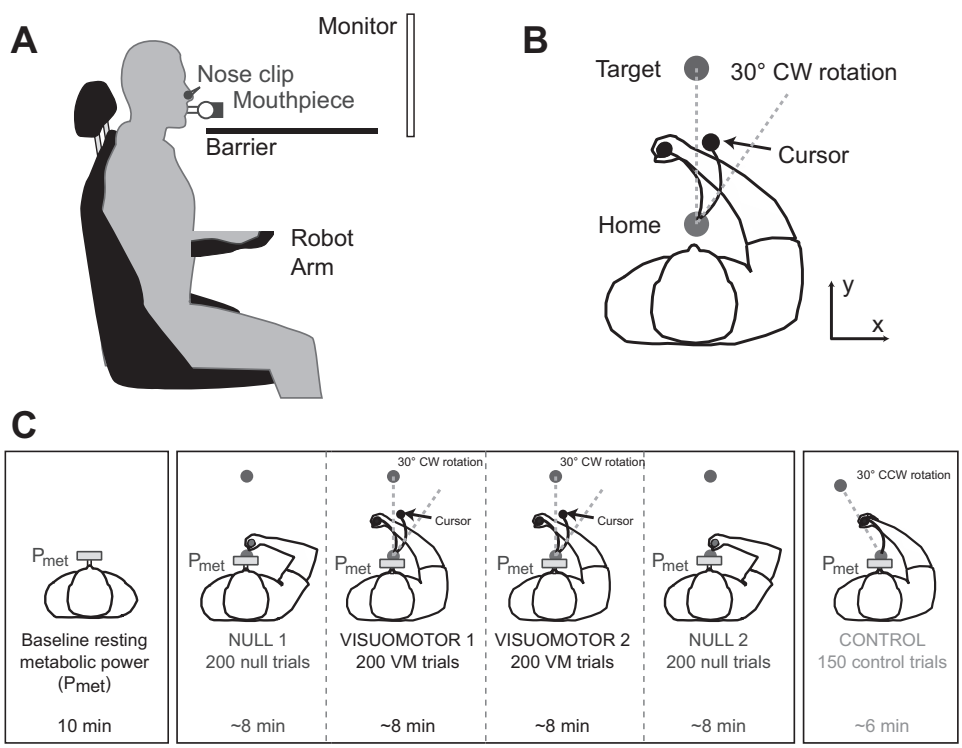

Fig. 1. Robot and experimental setup. *A*: subjects sat grasping the handle of a robot arm, while breathing through a mouthpiece for measuring metabolic rate. A vertically mounted monitor was set at eye level, and a horizontal barrier was placed above the plane of the robot arm to prevent subjects from viewing their hand. *B*: a top view of the robot plane during a visuomotor rotation. The cursor position was rotated 30° clockwise (CW). *C*: the experimental protocol consisted of 6 blocks: Resting (quiet sitting), Null 1, Visuomotor (VM) 1, Visuomotor 2, Null 2, and Control. Gray, dashed lines represent continuous transitions among blocks. Gaps between blocks represent moments when subjects were able to remove the mouthpiece. CCW, counterclockwise.

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Natick, MA) sampling rate was 2,000 Hz, and there was a hardware bandpass filter with cutoff frequencies of 20–450 Hz. The six muscles were the pectoralis, posterior deltoid, biceps brachii, long head of the triceps, lateral head of the triceps, and brachioradialis muscles. We followed the http://SENIAM.org (Enschede, the Netherlands) guidelines and placed the electrodes on the muscle belly after prepping the skin, by removing excess hair and lightly abrading the skin with an alcohol wipe. We wrapped self-adhesive tape around the electrode and arm to help secure the electrode placement and minimize motion artifact. We only recorded EMG data for every odd trial because of reset delays in the EMG system. We sent a trigger signal from the robotic arm system to sync EMG data with robot data.

Metabolic Measurement

Subjects breathed in and out of a mouthpiece and wore a nose clip so that we could measure the rates of oxygen consumption ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$; TrueOne 2400; Parvo Medics, Sandy, UT). Before each data collection, we calibrated the metabolic system using certified gas mixtures and a 3-liter calibration syringe to simulate a range of flow rates. The metabolic data were corrected with standard temperature and pressure, dry. The sampling rate of the metabolic system was set to be every ~5 s. We asked subjects to fast overnight, performing the experiment early in the morning to mitigate potential variability due to food digestion.

Movement Kinematics

Because metabolic rate was measured continuously, we needed to consider whole-movement trajectory, including both the outward movement and the return path to the home circle. The outward movement was the initial single bell-shaped velocity profile portion of the movement trajectory. The return path was the rest of the movement trajectory. Onset of the outward movement occurred when the tangential velocity exceeded 0.02 m/s, and the end of the outward movement occurred when the tangential velocity decreased to 0.02 m/s following the peak velocity. The return path started at the end of the outward movement and ended when the cursor first touched the home circle. Maximum tangential velocity, mean tangential velocity, and movement times were calculated for the outward movement, excluding the return path.

Motor Adaptation Metrics

The robot handle position and velocity were recorded at 200 Hz. We quantified motor adaptation using two metrics: movement deviation and initial reach angle. Movement deviation was the maximum perpendicular deviation of the cursor position from a line connecting the home and target circles during the outward movement. Initial reach angle was the angular difference between the direction of the target and the direction of the cursor when it had moved out, 4 cm away from the center of the home circle.

Muscle Activity Metrics

We calculated the mean activity for each muscle and muscle coactivation pair as our muscle activity metrics. We first digitally smoothed and normalized the EMG data using MATLAB; (MathWorks, Natick, MA). To smooth the EMG data, we applied a high-pass, fourth-order Butterworth filter at 20 Hz to remove motion artifact, rectified the EMG data, and then applied a low-pass, fourth-order Butterworth filter at 50 Hz to smooth the EMG data. We calculated the mean EMG data between the onset and end of the outward movement. We normalized the EMG data to the average mean EMG for late Null 1 for each muscle. For muscle coactivation, we had three muscle pairs: pectoralis-posterior deltoid, biceps brachii-triceps long head, and brachioradialis-triceps lateral head. We created a muscle coactivation profile, "wasted contraction" by taking the minimum normalized EMG activity between the two muscles in the muscle pair at each time point in the trial (Gribble et al. 2003; Thoroughman and Shadmehr 1999). Similar to muscle activity, we calculated the mean activity of the coactivation profile between the onset and end of the outward movement.

Metabolic Metrics

We first assessed whether our metabolic data were mostly a product of aerobic metabolism, because expired gas analysis does not measure anaerobic metabolism. We only used subjects with metabolic data that had respiratory exchange ratio (RER = $\dot{V}CO_2/\dot{V}O_2$) values <1.0 and generally <0.85 over the course of the whole experiment. A RER value <1.0 indicates that $\dot{V}O_2 > \dot{V}CO_2$, suggesting that oxidative metabolism was primarily involved (Brooks et al. 1996). RER values between ~0.75 and ~0.90 are normal and can vary, in part, due to diet and other factors (Seidell et al. 1992; Short and Sedlock 1997).

We quantified metabolic cost using two metrics: net metabolic power and net cost per movement. We used "net" metabolic metrics, because we were interested in the metabolic energy expended to perform just the task and not the overall energy that included a baseline resting metabolic rate. We measured rates (liter/min) of $\dot{V}O_2$ and $\dot{V}CO_2$, which we then converted to metabolic power (J/s) using the Brockway equation (Brockway 1987). We also normalized metabolic power to the subject's body weight ($J \cdot s^{-1} \cdot kg^{-1}$). To get the net metabolic power, we subtracted the baseline resting metabolic power, which was quiet sitting in this experiment. We also linearly interpolated the metabolic power data to get a metabolic power data point per reach. Our other metabolic metric was net cost per movement, the metabolic energy expended per movement (i.e., reach). We calculated the net cost per movement by multiplying the net metabolic power by the movement duration (δ; s/movement) associated with each reach, yielding the metabolic energy expended per reach [$J \cdot s^{-1} \cdot kg^{-1} \times$ s/movement = $J \cdot kg^{-1} \cdot$ movement $(mvt)^{-1}$]. If there were differences in movement durations, possibly from reaching more slowly or having longer movement trajectories, net cost per movement could detect these differences, whereas net metabolic power may not. That is, for the same net metabolic power, performing fewer reaches for a given time period would result in higher net cost per movement than performing more reaches for the same given time period.

Adaptation Phases

We analyzed adaptation using two phases: early and late within each reaching block. For movement kinematics and motor adaptation metrics, early was the first regular (noncatch) trial in the block, whereas late was the average of the regular trials in the last 10 trials of the block. For net metabolic power, we calculated the time-weighted average for specific sets of trials. We used the first 20 trials in the block for early and the last 50 trials for late (see DISCUSSION for comments regarding the number of trials used for early for the metabolic metrics). We used trials 51–70 for early Null 1 and trials 851–870 for early Control. We did not include the first 50 trials in the metabolic average for these phases, because subjects started breathing into the mouthpiece beginning with trial 1, and the air flow into the metabolic system was still accumulating for the first ~50 trials. For the muscle activity and muscle coactivation amplitudes, early was the average of the first five odd-numbered null trials of each block, whereas late was the last 20 odd-numbered null trials of each block. EMG data were only recorded for every odd-numbered trial.

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Statistics

We use repeated-measures ANOVA to determine if phase (i.e., early and late of the Null 1, VM 1, VM 2, Null 2, and Control blocks) had main effects. If phase had a main effect, then two-tailed paired *t*-tests between specific phases were used to determine significant differences during adaptation. The primary specific phase comparisons were the following: *1*) late Null 1 to early VM 1 to determine whether there was a significant perturbation as a result of the introduction of the visuomotor rotation, *2*) early VM 1 to late VM 2 to assess overall adaptation, *3*) early to late VM 1 to assess whether adaptation occurred rapidly during the first half of the visuomotor trials, and *4*) late VM 2 to early Null 2 to determine whether there was a significant after-effect when the visuomotor rotation was removed. For the control block, we compared late Control with late VM 2 to determine whether the metabolic cost of reaching in the adapted direction was the same, regardless of the presence of the visuomotor rotation. We also compared late Control with late Null 2 to determine whether reaching in different directions had different metabolic costs. Additionally, we performed linear regressions between movement deviation and each individual muscle and coactivation muscle pairs during the adaptation period (early VM 1 to late VM 2). For the control experiment, we used one-sided paired *t*-tests to compare movement deviation, muscle activity, and coactivation between late Null 1 and early VM 1, early VM 1 and late VM 2, and late VM 2 and early Null 2. The level of statistical significance was set at $\alpha = 0.05$.

RESULTS

Overview

All subjects learned the visuomotor rotation, demonstrating typical movement deviation reduction over the course of the adaptation and after-effects during the washout period. Interestingly, muscle activity, coactivation, and metabolic cost all increased at the start of adaptation and were reduced quickly as adaptation progressed. Moreover, when the perturbation was removed, increases in these three metrics were again observed and followed by rapid reductions.

Movement Kinematics

Hand trajectories for regular trials with visual feedback of the cursor and catch trials without visual feedback illustrated that subjects adapted to the visuomotor rotation (Fig. 2). Overall, subjects made relatively straight outward movements (Fig. 2) out to the target (0°) and during the return path to the

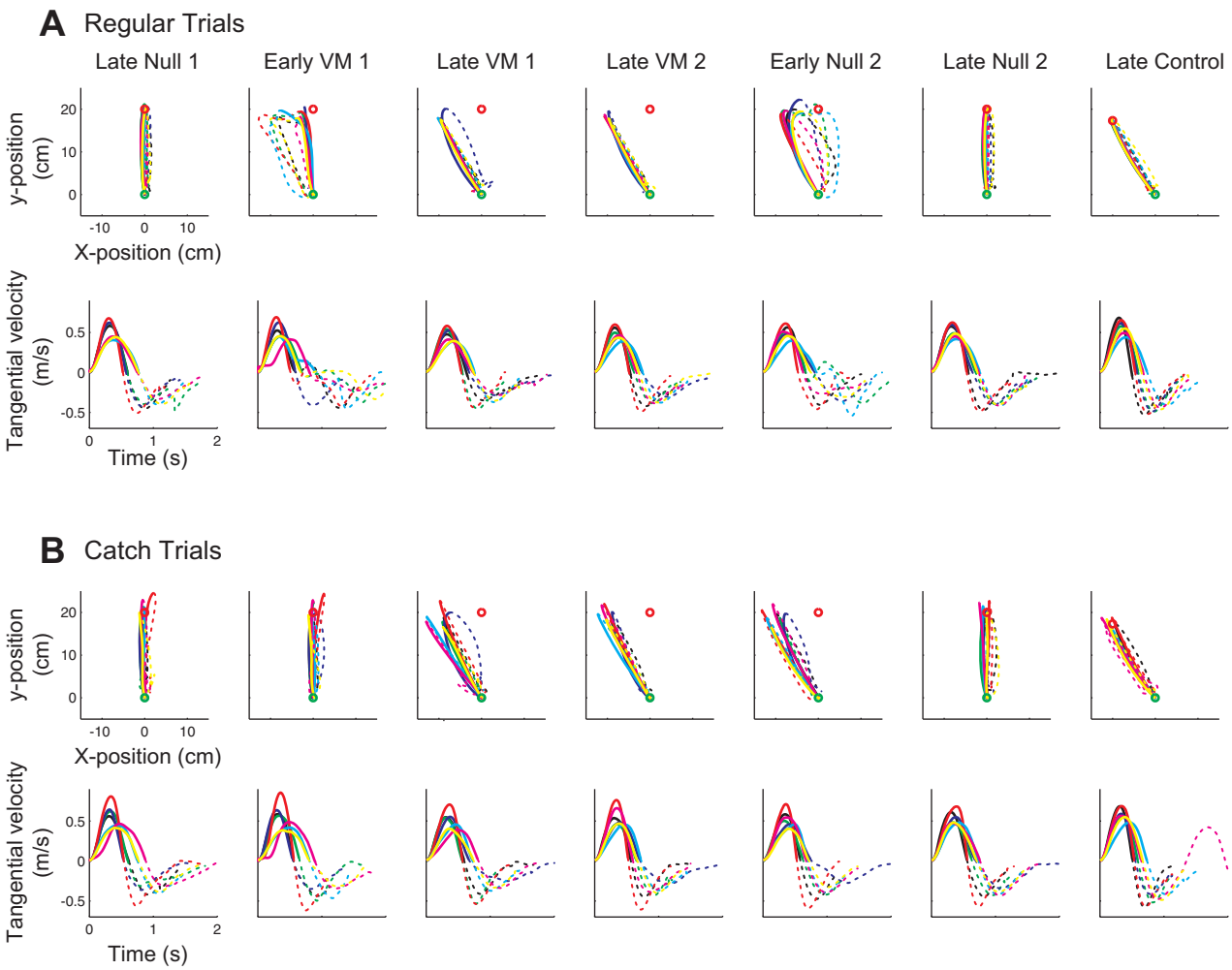

Fig. 2. Hand trajectories and tangential velocity profiles of regular (*A*) and catch trials (*B*) for different phases during the protocol. Different colors represent individual subjects. Solid lines are the outward movement, and dotted lines are the return path. Red and green circles represent the target and home circles, respectively. Overall, subjects made relatively straight out-and-back movements, except immediately after transitions (early VM 1 and early Null 2), where corrections were evident during the return path.

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home circle (Fig. 2), particularly late in the blocks. These relatively straight movement trajectories were observed during the regular trials (Fig. 2*A*) and the catch trials (Fig. 2*B*). The noticeable exceptions were the regular trials during the transitions, when the visuomotor rotation was added (early VM 1) and removed (early Null 2). Without visual feedback of the cursor, the catch trial for early VM 1 indicated that subjects did not expect the visuomotor rotation and planned to move out and back to the target, which caused the cursor to travel straight along the rotated direction (30° clockwise). With visual feedback of the cursor, the regular trials for early VM 1 revealed that subjects made corrective movements to hit the target during the return path, despite being instructed not to correct (Fig. 2). The outward movements of the hand during late Null 1 and early VM 1 were the same, both relatively straight trajectories in the direction of the target (Fig. 2). The catch trials in early Null 2 indicated that subjects had adapted their movement trajectories to account for the visuomotor rotation, directing their movement trajectories 30° counterclockwise. Again, the regular trials revealed that subjects made corrective movements to hit the target during the return path when the visuomotor rotation was removed. The outward movements of the hand during late VM 2 and early Null 2 were the same, both relatively straight trajectories in the adapted rotated direction (Fig. 2).

The tangential velocity profiles were variable among subjects (Fig. 2), and tangential velocity metrics revealed that subjects tended to have slower mean velocities when the visuomotor rotation was added. Movement times also tended to increase at the transitions, when the visuomotor rotation was introduced and removed. The greater intersubject variability in tangential velocity profiles was most likely because movement speed was not rigorously controlled, in that subjects did not have to stop at the target within the specified time window (500–700 ms), A repeated-measures ANOVA indicated that phase did not have a main effect on maximum tangential velocity [$F(9,54) = 1.569$, $P = 0.1712$] but did have a significant effect on mean tangential velocity [$F(9,54) = 5.542$, $P = 0.0001$]. There were only significant differences in mean tangential velocity at the transitions. Mean tangential velocity decreased significantly from late Null 1 to early VM 1 [0.25 ± 0.01–0.22 ± 0.01 m/s (mean ± SE)] when the visuomotor rotation was introduced ($P = 0.0144$) and increased slightly from late VM 2 to early Null 2 (0.22 ± 0.01–0.23 ± 0.01 m/s) when the visuomotor rotation was removed ($P = 0.0139$). Over the course of adaptation, early VM 1 to late VM 2 mean tangential velocity did not change significantly, remaining at 0.22 ± 0.01 m/s ($P = 0.8511$). Phase also had a main effect on movement times [$F(9,54) = 2.367$, $P = 0.0392$, repeated-measures ANOVA]. When the visuomotor rotation was first introduced, movement times at late Null 1 (622 ± 39 ms) and early VM 1 (644 ± 53 ms) were not significantly different ($P = 0.4729$). Movement times decreased to 616 ± 30 ms by the end of adaptation (late VM 2) but were not significantly different than early VM 1 ($P = 0.5208$). The only significant difference was an increase in movement times from 616 ± 30 ms at late VM 2 to 661 ± 38 ms at early Null 2 ($P = 0.0262$).

Motor Adaptation

Subjects rapidly adapted to the visuomotor rotation, as evident from adjustments in reaching trajectories during the visuomotor rotation trials that led to after-effects that required a de-adaptation period (Fig. 3). The repeated-measures ANOVA indicated that phase had a main effect on movement deviation [$F(9,54) = 132.56$, $P < 0.0001$] and initial angle [$F(9,54) = 51.77$, $P < 0.0001$]. Movement deviation decreased from 6.9 ± 0.4 cm to 1.1 ± 0.3 cm during the first half of learning (early to late VM 1, $P < 0.0001$). Similarly, initial angle decreased from 22.7° ± 1.3° to −4.4° ± 1.8° ($P < 0.0001$), where 0° was the target direction, and positive initial angles indicated that the cursor deviated clockwise of the target. Movement deviation continued to decrease to 0.9 ± 0.1

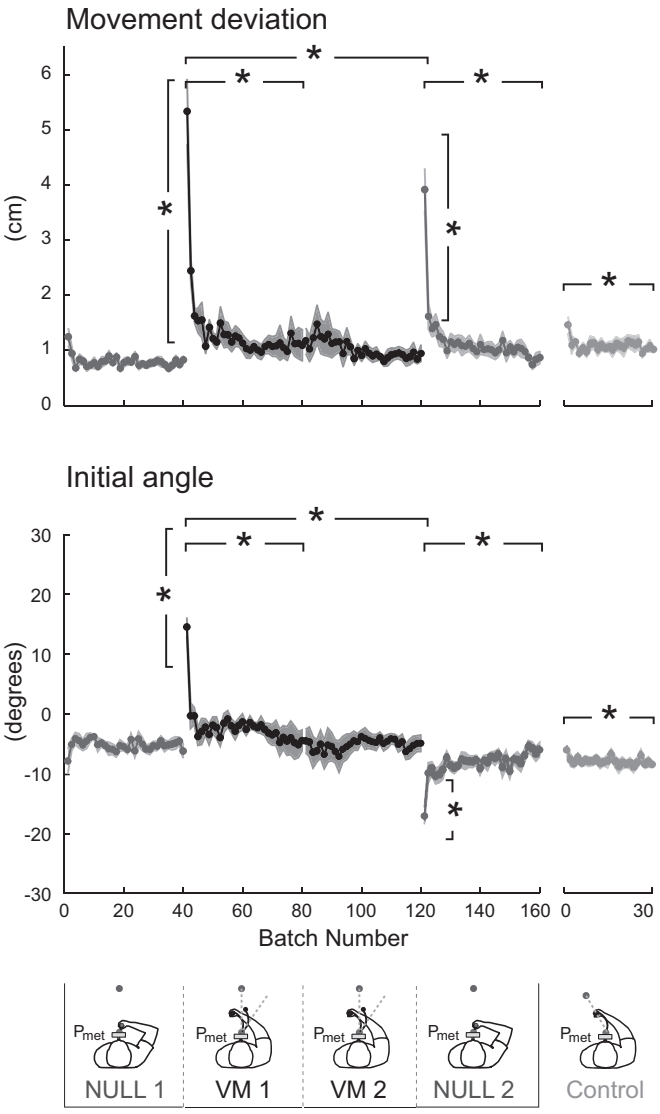

Fig. 3. Movement deviation and initial angle adapted over the course of the reaching protocol and control block. Each point of the thick line is the average of the regular (noncatch) trials within a batch of 5 trials averaged over all subjects. Shaded area is ± SE. Asterisks (*) within vertical brackets represent significant differences at the transitions, whereas asterisks within horizontal brackets represent significant changes over the course of adaptation or within a block ($P < 0.05$). Subjects reduced movement deviation and initial angle during adaptation, and after-effects occurred when the visuomotor rotation was removed.

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cm, and initial angle continued to shift counterclockwise to −4.9° ± 1.4° at late VM 2, but neither was a significant improvement ($P = 0.3074$, and $P = 0.5242$, respectively), suggesting that adaptation had stabilized. Overall, from early VM 1 to late VM 2, there was a significant reduction in movement deviation ($P < 0.0001$) and reorientation of initial angle of the cursor toward the target ($P < 0.0001$). When the visuomotor rotation was removed, after-effects were evident, indicating that adaptation had occurred. From late VM 2 to early Null 2, movement error increased to 7.5 ± 0.4 cm ($P < 0.0001$), and initial angle deviated 32.4° ± 1.1° ($P < 0.0001$) away from the target. Subjects quickly de-adapted, reducing movement deviation to 0.9 ± 0.1 cm (early Null 2 to late Null 2, $P < 0.0001$), and initial angle reoriented to −6.0° ± 1.2° (early Null 2 to late Null 2, $P < 0.0001$).

Muscle Activity and Coactivation

Muscle activity amplitudes peaked when the visuomotor rotation was introduced and exhibited reductions with motor adaptation (Fig. 4). The repeated-measures ANOVA indicated that phase had a main effect on the posterior deltoid [$F(9,54) = 6.55$, $P < 0.0001$], biceps brachii [$F(9,54) = 5.92$, $P < 0.0001$], triceps long head [$F(9,54) = 3.69$, $P = 0.0012$], brachioradialis [$F(9,54) = 10.26$, $P < 0.0001$], and triceps lateral head [$F(9,54) = 5.92$, $P < 0.0001$], except the pectoralis [$F(9,54) = 1.58$, $P = 0.1454$]. Even though there was a small spike in muscle activity when the visuomotor rotation was applied (late Null 1 to early VM 1), this increase was only significant for the triceps long head ($P = 0.0244$). As subjects adapted from the beginning to the end of the visuomotor trials, early VM 1 to late VM 2, significant reductions occurred in all muscles except the pectoralis (posterior deltoid $P = 0.0107$; biceps brachii $P = 0.0147$; triceps long head $P = 0.0007$; brachioradialis $P = 0.0185$; and triceps lateral head $P = 0.0103$). The reductions occurred rapidly in the first half of the adaptation, early VM 1 to late VM (posterior deltoid $P = 0.0262$; biceps brachii $P = 0.0271$; triceps long head $P = 0.0058$; brachioradialis $P = 0.0278$; and the triceps lateral head $P = 0.0291$). During the latter half of adaptation, late VM 1 to late VM 2, only the posterior deltoid and triceps long head demonstrated a significant reduction ($P = 0.0151$, and $P = 0.0246$, respectively). When the visuomotor rotation was removed, late VM 2 to early Null 2, the posterior deltoid ($P = 0.0130$), the triceps long head ($P = 0.0202$), and the brachioradialis ($P = 0.0390$) activity increased, but only the posterior deltoid decreased during Null 2 (early to late Null 2, $P = 0.0301$).

When the visuomotor rotation was introduced and removed, there were significant increases in muscle coactivation (Fig. 5). The repeated-measures ANOVA indicated that phase had a main effect on all muscle pairs [pectoralis-posterior deltoid $F(9,54) = 2.09$, $P = 0.0466$; biceps brachii-triceps long head $F(9,54) = 4.78$, $P = 0.0001$; brachioradialis-triceps lateral head $F(9,54) = 11.66$, $P < 0.0001$]. When the visuomotor rotation was added, there were significant increases in coactivation early during visuomotor adaptation (late Null 1 to early VM 1) in the biceps brachii-triceps long head and brachioradialis-triceps lateral head muscle pairs ($P = 0.0165$, and $P = 0.0280$, respectively) but not in the pectoralis-posterior deltoid ($P = 0.1231$). When the visuomotor rotation was removed (late VM 2 to early Null 2), there were also increases in coactivation for the biceps brachii-triceps long head ($P = 0.0002$) and brachioradialis-triceps lateral head ($P = 0.0254$) but not for the pectoralis-posterior deltoid ($P = 0.4656$).

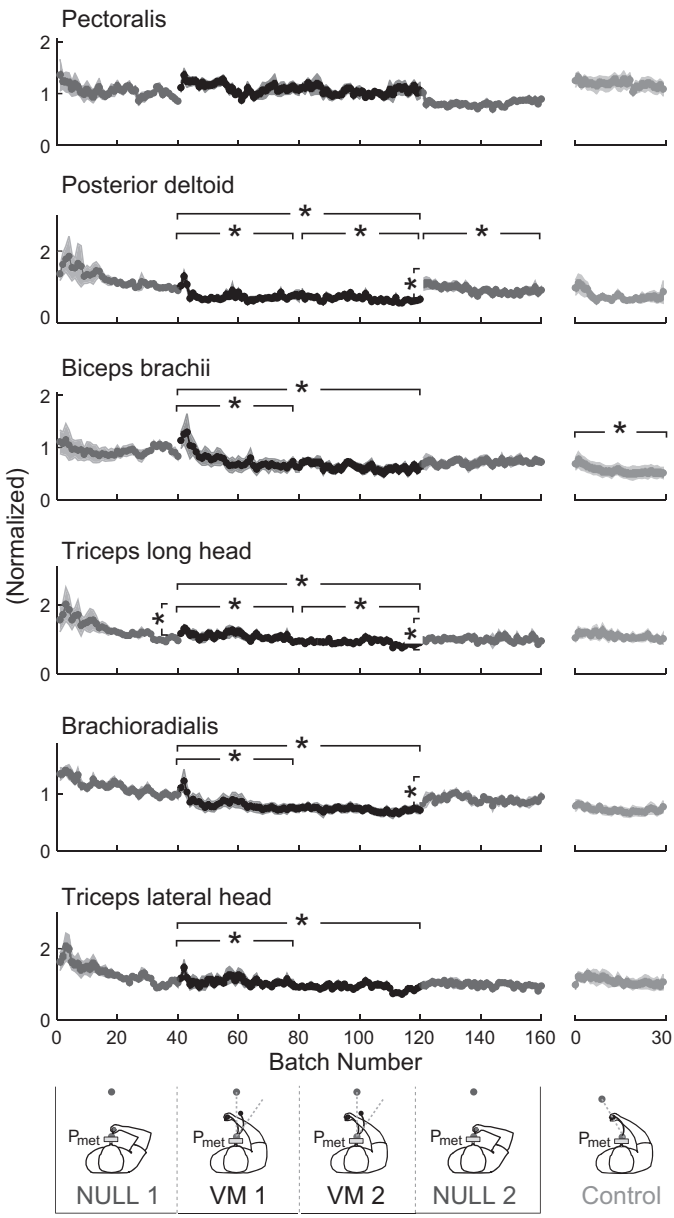

Fig. 4. Muscle activity time course during adaptation to a visuomotor rotation and during the control block. Each point of the thick line is the average of the electromyographic (EMG) trials within a batch of 5 trials averaged over all subjects. Shaded area is ± SE. Asterisks (*) within vertical brackets represent significant differences at the transitions, whereas asterisks within horizontal brackets indicate significance ($P < 0.05$). Activity in 5 of the 6 muscles decreased within the first half and over the whole course of adaptation.

Similar to muscle activity, muscle coactivation amplitudes reduced with visuomotor adaptation (Fig. 5). For the biceps brachii-triceps long head and brachioradialis-triceps lateral head pairs, there were significant reductions in coactivation over the whole visuomotor adaptation period (early VM 1 to late VM 2, $P = 0.0001$, and $P = 0.0009$, respectively). Both muscle pairs demonstrated clear, significant reductions during the first half of adaptation (early to late VM 1, biceps brachii-

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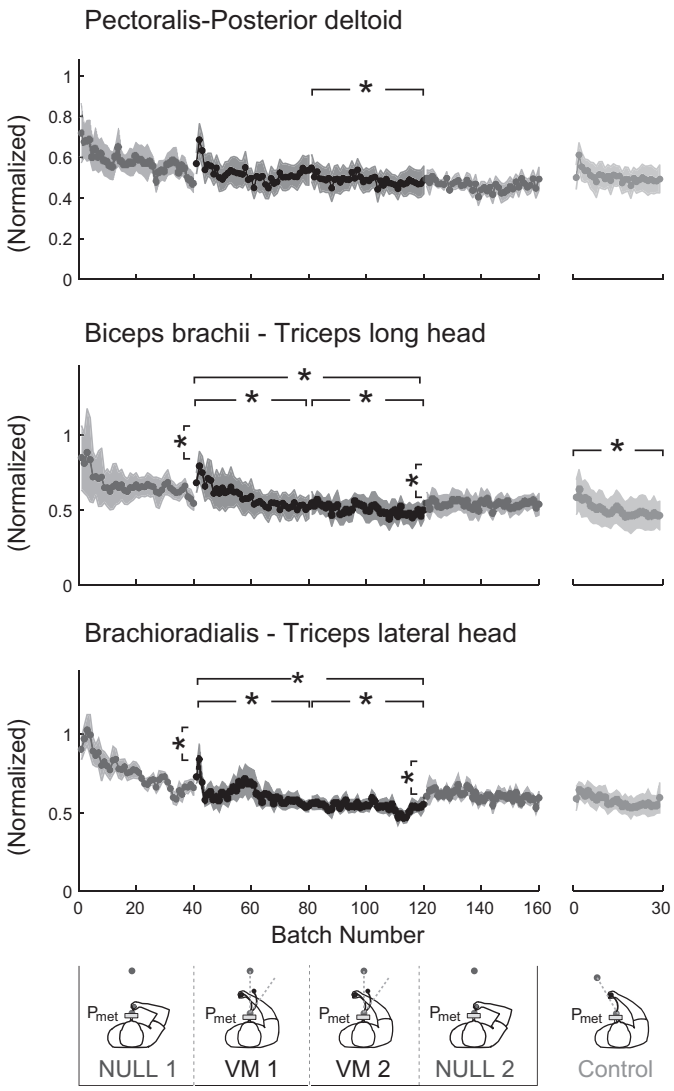

Fig. 5. Coactivation time course during adaptation to a visuomotor rotation and during the control block. Each point of the thick line is the average of the EMG trials within a batch of 5 trials averaged over all subjects. Shaded area is ± SE. Asterisks (*) within vertical brackets represent significant differences at the transitions, whereas asterisks within horizontal brackets represent significant changes over the course of adaptation or within a block ($P < 0.05$). The introduction of the visuomotor rotation resulted in increased muscle coactivation in the elbow muscle pairs that decreased rapidly and over the whole course of adaptation.

triceps long head $P = 0.0002$; brachioradialis-triceps lateral head $P = 0.0027$) and continued to decrease slightly during the latter half (late VM 1 to late VM 2, biceps brachii-triceps long head $P = 0.0171$; brachioradialis-triceps lateral head $P = 0.0023$). The pectoralis-posterior deltoid pair also showed a significant reduction during the later half of adaptation ($P = 0.0107$). During Null 2, coactivation for all muscle pairs did not change (pectoralis-posterior deltoid $P = 0.0539$; biceps brachii-triceps long head $P = 0.4061$; brachioradialis-triceps lateral head $P = 0.1804$).

A linear regression was performed to determine the relation between movement deviation and individual muscle activation and muscle coactivation pairs during the adaptation period. The analysis for each subject revealed significant, positive slopes ($P < 0.05$). Larger movement deviations corresponded with greater muscle activity and muscle coactivation. The regression between movement deviation and muscle activity was significant for the pectoralis (seven of seven, $R^2 = 0.15 \pm 0.04$), posterior deltoid (six of seven, $R^2 = 0.27 \pm 0.05$), biceps brachii (six of seven, $R^2 = 0.24 \pm 0.04$), triceps long head (five of seven, $R^2 = 0.16 \pm 0.04$), and brachioradialis (six of seven, $R^2 = 0.27 \pm 0.04$). Similarly, the regression was significant for all seven subjects for the biceps brachii-triceps long head ($R^2 = 0.07 \pm 0.04$) and for five of seven of the subjects for the brachioradialis-triceps lateral head ($R^2 = 0.11 \pm 0.04$).

Metabolic Reduction

Net metabolic power and net cost per movement spiked at the beginning of the visuomotor rotation block and rapidly reduced as subjects adapted (Fig. 6). For reference, the average resting metabolic cost of sitting in this study was 1.21 ± 0.04 W/kg. The repeated-measures ANOVA indicated that phase had a main effect on net metabolic power [$F(9,54) = 4.75$, $P = 0.0001$] and net cost per movement [$F(9,54) = 6.12$, $P < 0.0001$]. At the end of Null 1, net metabolic power was 0.38 ± 0.02 W/kg. During the first min of the visuomotor rotation (early VM 1), net metabolic power spiked to 0.56 ± 0.04 W/kg (late Null 1 to early VM 1, $P = 0.1296$). As subjects adapted, there was a reduction in net metabolic power by 36% to 0.36 ± 0.02 W/kg at late VM 1 (early VM 1 to late VM 1, $P = 0.0739$). As subjects continued to refine their movement trajectories, net metabolic power leveled off at 0.33 ± 0.02 W/kg at late VM 2 (late VM 1 to late VM 2, $P = 0.3407$). There was a significant overall reduction of 41% from the initial spike at early VM 1 to the last visuomotor rotation trials at late VM 2 ($P = 0.0433$). When the visuomotor rotation was first removed, there was a modest increase in net metabolic power to 0.37 ± 0.02 W/kg (late VM 2 to early Null 2, $P = 0.0951$), which quickly settled to an apparent steady-state rate of 0.32 ± 0.02 W/kg (early to late Null 2, $P = 0.1196$).

Net cost per movement, which accounts for differences in movement times, indicated a similar time course as net metabolic power. After an initial spike from 0.88 ± 0.03 $J \cdot kg^{-1} \cdot mvt^{-1}$ to 1.39 ± 0.10 $J \cdot kg^{-1} \cdot mvt^{-1}$ (late Null 1 to early VM 1, $P = 0.0828$), net cost per movement decreased significantly to 0.85 ± 0.05 $J \cdot kg^{-1} \cdot mvt^{-1}$ (39%; early to late VM 1, $P = 0.0438$). With more practice, net cost per movement decreased modestly to 0.74 ± 0.04 $J \cdot kg^{-1} \cdot mvt^{-1}$ (late VM 1 to late VM 2, $P = 0.2110$). The overall reduction from the initial spike to the end of the visuomotor trials was significant (47%; $P = 0.0257$). Upon removing the visuomotor rotation, there was a significant increase in net cost per movement to 0.91 ± 0.05 $J \cdot kg^{-1} \cdot mvt^{-1}$ (late VM 2 to early Null 2, $P = 0.0346$) that settled down to 0.73 ± 0.04 $J \cdot kg^{-1} \cdot mvt^{-1}$ by the end of Null 2 (early to late Null 2, $P = 0.0206$). Additionally, the regression analyses of movement deviation with metabolic power and with net cost per movement were not significant.

Control Block

Movement deviation and initial angle indicated that subjects were able to reach in the expected adapted direction accurately (30° counterclockwise of the original target). At the end of the control block, the average movement deviation was small (1.0 ± 0.06 cm), and the initial angle was −8.1° ± 0.6°.

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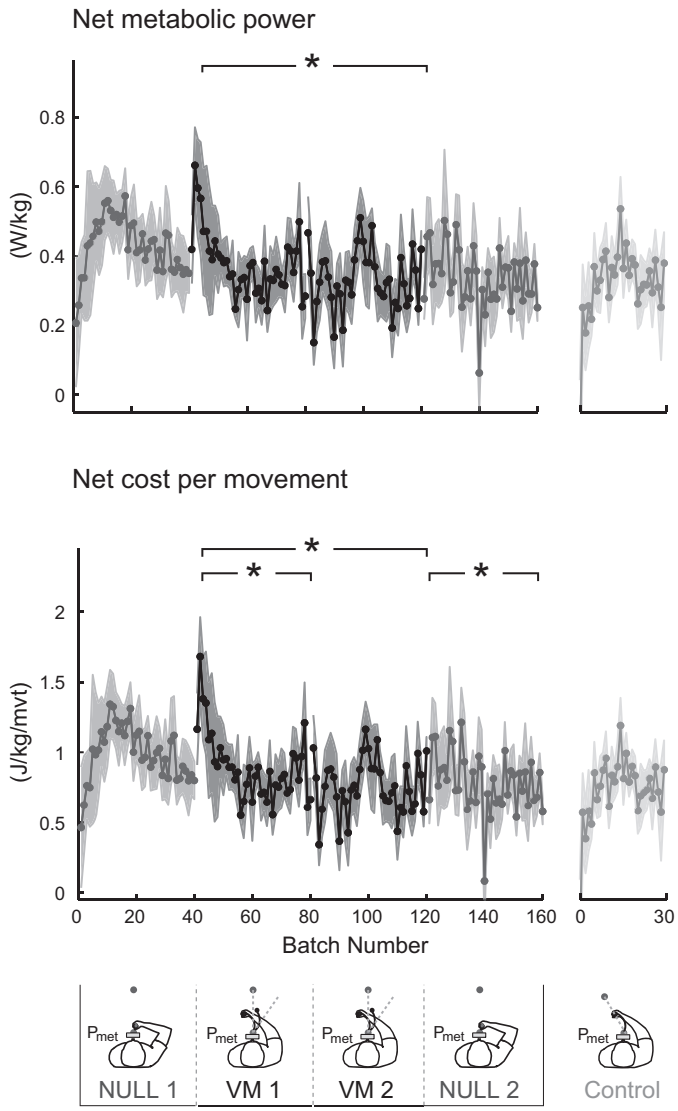

Fig. 6. Net metabolic power and net cost per movement (mvt) time courses during adaptation to a visuomotor rotation and during the control block. Each point of the thick line is the average of a batch of 5 trials averaged over all subjects. Shaded area is ± SE. Asterisks (*) within horizontal brackets represent significant changes over the course of adaptation or within a block ($P < 0.05$). Both net metabolic power and net cost per movement increased sharply after the introduction of the visuomotor rotation and reduced with visuomotor adaptation.

Similar levels of muscle activity and coactivation were used when reaching in the adapted direction during the visuomotor rotation and control block. There were no significant differences in muscle activity or coactivation when reaching in the adapted direction during the visuomotor rotation (late VM 2) and during the control block (late Control; pectoralis $P = 0.6000$; posterior deltoid $P = 0.3274$; biceps brachii $P = 0.1623$; triceps long head $P = 0.0970$; brachioradialis $P = 0.9981$; triceps lateral head $P = 0.2456$; pectoralis-posterior deltoid $P = 0.3849$; biceps brachii-triceps long head $P = 0.8106$; brachioradialis-triceps lateral head $P = 0.4825$). When reaching in the adapted direction during late Control, the biceps brachii and brachioradialis activities were less than reaching straight during late Null 2 ($P = 0.0171$, and $P = 0.0392$, respectively). For the other muscles and three coactivation muscle pairs, there were no significant differences between late Null 2 and late Control (pectoralis $P = 0.0624$; posterior deltoid $P = 0.5572$; triceps long head $P = 0.7890$; triceps lateral head $P = 0.7843$; pectoralis-posterior deltoid $P = 0.6804$; biceps brachii-triceps long head $P = 0.1738$; brachioradialis-triceps lateral head $P = 0.6391$).

Metabolic power and net cost per movement were not different after adapting to reaching with the visuomotor rotation compared with the control block. The net metabolic power was 0.32 ± 0.02 W/kg, and the net cost per movement was $0.72 \pm 0.05\ \mathrm{J \cdot kg^{-1} \cdot mvt^{-1}}$ at late Control. After subjects adapted to the visuomotor rotation, late VM 2, the net metabolic power ($P = 0.7215$) and net cost power movement ($P = 0.7526$) were not significantly different than reaching in the adapted direction without the visuomotor rotation, late Control. Compared with late Null 2, which involved reaching directly to the target and did not require processing a visuomotor rotation, there were no significant differences with late Control (net metabolic power $P = 0.9472$; net cost per movement $P = 0.8770$).

For the most part, there were no significant differences from the beginning to the end of the control block. Neither metabolic power ($P = 0.3761$) nor net cost per movement ($P = 0.4018$) demonstrated a reduction from early to late Control. Only movement deviation ($P = 0.0086$), initial angle ($P = 0.0148$), the biceps brachii ($P = 0.0015$), and the biceps brachii-triceps long head ($P = 0.0021$) had significant reductions over the course of the control block. If we used early Control rather than late Control, metabolic power and cost per movement were still not significantly different from either late VM 2 or late Null 2. Similarly, there were no significant differences between early Control and late VM 2 for any muscle or muscle coactivation pair, and only the pectoralis was significantly different between early Control and late Null 2 ($P = 0.0099$).

Control Experiment

To ensure that the increase in muscle coactivation was not a result of adaptation to novel robotic passive dynamics in the untrained direction, we ran an additional control experiment. In the control experiment, subjects were first familiarized with reaching in both the initial and adapted directions, before exposure to the visuomotor rotation. All subjects exhibited error patterns similar to those observed in the main experiment (Fig. 7). Specifically, error increased when the visuomotor perturbation was introduced (late Null 2 to early VM 1, $P = 0.0011$), decreased over the course of the adaptation period (early VM 1 to late VM 2, $P = 0.0049$), and increased again when the perturbation was removed (late VM 2 to early Null 2, $P = 0.0019$). Muscle activity and coactivation followed similar trends. Perturbation onset led to increases in activity in at least five out of six muscles in each subject (Fig. 7). This increase reached significance in the triceps long head and triceps lateral head ($P = 0.0389$, and $P = 0.0322$, respectively). For comparison, in the main experiment, a significant increase was only observed in the triceps lateral head. Activity was then reduced over the course of adaptation and once again, increased upon perturbation removal in at least five out of six muscles in each subject. Muscle coactivation from late Null 2 to early VM 2 increased significantly in two muscle pairs and approached

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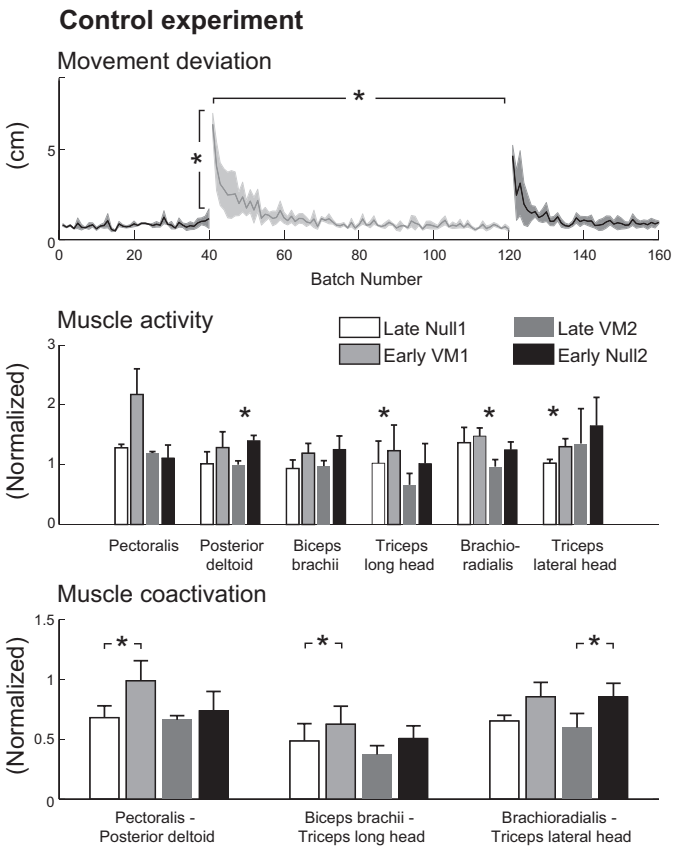

Fig. 7. Control experiment. *Top*: movement deviation time course during adaptation to visuomotor rotation (Null 1, black; VM 1–VM 2, gray; Null 2, black), following 150 familiarization trials (not shown). Each point of the thick line is the average of 5 trials (1 batch) averaged over all subjects. Shaded area is ± SE. Asterisk (*) within vertical brackets represents significant differences at the transitions, whereas asterisk within horizontal brackets represents significant changes over the course of adaptation or within a block ($P < 0.05$). *Middle*: average muscle activity in each of 6 muscles during the phases of interest. Asterisks indicate a significant difference between phases ($P < 0.05$). *Bottom*: average coactivation in each of 3 muscle pairs during the phases of interest. Error bars represent ± SE. Asterisks within horizontal brackets indicate a significant difference between phases ($P < 0.05$).

significance in the third pair (pectoralis-posterior deltoid $P = 0.0383$; biceps brachii-triceps long head $P = 0.0060$; brachioradialis-triceps lateral head $P = 0.0583$; Fig. 7). For comparison, significant increases in coactivation were observed in the main experiment for two out of the three muscle pairs. Coactivation decreased over the course of adaptation from early VM 1 to late VM 2, approaching significance (pectoralis-posterior deltoid $P = 0.0713$; biceps brachii-triceps long head $P = 0.0541$; brachioradialis-triceps lateral head $P = 0.1033$). Upon removal of the perturbation in early Null 2, coactivation increased once again (pectoralis-posterior deltoid $P = 0.3028$; biceps brachii-triceps long head $P = 0.0636$; brachioradialis-triceps lateral head $P = 0.0073$). Together, the results of the control experiment suggest that increases in muscle activity and coactivation are observed upon exposure to a visuomotor perturbation, independent of prior familiarization with passive robot dynamics. Therefore, we feel that it is unlikely that the increased muscle activity observed in the main experiment is a result of adaptation to the novel robot dynamics involved in reaching to the adapted direction.

DISCUSSION

We found that during visuomotor adaptation, muscle activity and coactivation increased initially but then decreased rapidly, along with metabolic cost. These results suggest that increasing muscle coactivation early during adaptation is a common feature of motor adaptation across a variety of sensorimotor perturbations. The general pattern seems to be to increase muscle coactivation when the perturbation is first introduced and then rapidly reduce muscle coactivation as adaptation progresses. Reductions in metabolic cost also appear to be a common observable feature across multiple forms of motor adaptation, suggesting that minimization of effort is part of the adaptation process. Overall, these findings highlight that the modulation of muscle activity, muscle coactivation, and metabolic cost is remarkably consistent across various forms of motor adaptation.

It is intriguing that subjects would increase muscle coactivation, because muscle coactivation does not help reject the visuomotor perturbation, as there are no perturbing forces to counteract. We observed increases in coactivation whenever there were large cursor trajectory errors, which occurred when the visuomotor rotation was introduced and also when it was removed. One reason that subjects may increase muscle coactivation is to modulate joint viscoelasticity to help reduce kinematic variability that arises from neuromotor noise (Selen et al. 2009). Increases in viscoelasticity via coactivation can also help to reduce performance errors initially during adaptation, and as performance of the task improves, viscoelasticity can be attenuated (Osu et al. 2002). These results complement the motor adaptation model proposed by Franklin et al. (2008), which updated muscle activation and coactivation based on error, and our results also suggest that their adaptation model may be applicable to visuomotor adaptation, as well novel dynamics. The initial increase and subsequent reduction of viscoelasticity may also play a role in the facilitation of internal model learning. A recent study found that the amount of internal model learning observed in a force-field adaptation task was negatively correlated with muscle coactivation, suggesting that reductions in viscoelasticity can aid internal model learning (Huang and Ahmed 2014). In addition, our regression analyses indicated that larger movement deviations corresponded with greater muscle activity and coactivation. Whereas the present study does not provide causal evidence for this hypothesis, it highlights the prevalence of a coactivation-based strategy in motor adaptation and hence, the need for future research on the role of coactivation in learning internal model-based control.

The initial spike in metabolic cost was also unexpected, as additional forces were not required for adapting to the visuomotor rotation. From our control block, we found that reaching in the adapted direction and reaching to the original target had the same net metabolic power of 0.32 ± 0.02 W/kg and similar net cost per movement (0.72 ± 0.04 $J \cdot kg^{-1} \cdot mvt^{-1}$ vs. 0.73 ± 0.05 $J \cdot kg^{-1} \cdot mvt^{-1}$; late Control and late Null 2, respectively). Furthermore, subjects actually reached more slowly when the visuomotor rotation was first introduced (mean tangential velocity at early VM 1 < late Null 1). We have data from our laboratory that metabolic power increases with faster reaching speeds (Huang and Ahmed 2012), which suggests that we might not observe an

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increase in metabolic power early during visuomotor adaptation when subjects reached more slowly. The increases in muscle activity and coactivation provide a probable, partial explanation for the metabolic spike observed early during adaptation to the visuomotor rotation. Another possible explanation is an increased load of neural processing in the brain. Processing information and increases in neural firing patterns in the brain require energy (Attwell and Laughlin 2001; Magistretti 2009), which could contribute to the increased metabolic cost.

An interesting difference in the metabolic reductions between visuomotor adaptation and force-field adaptation was when the significant metabolic reductions occurred. For the visuomotor rotation, significant reductions in metabolic cost (net cost per movement, early to late VM 1) were observed during the first half of the adaptation trials, when there were also clear, significant reductions in muscle activity and coactivation. For the visuomotor adaptation task, muscle coactivation decreased slightly during the second half (late VM 1 to late VM 2); however, no significant reductions in metabolic cost were observed. For the curl force-field task, significant reductions in metabolic cost were observed during the second half of the adaptation trials, after muscle activity and biomechanics had apparently stabilized (Huang and Ahmed 2014; Huang et al. 2012). This difference may be because reaching in the adapted direction for the visuomotor adaptation task did not require more metabolic power than reaching straight forward in a null field, and thus further reductions later during adaptation were unobservable or unlikely. Additionally, the lack of difference may be due to a faster learning time course in visuomotor adaptation that prevented us from dissociating different time scales of muscle activity and metabolic reductions. Nevertheless, the overall degree of similarity and consistency in the metabolic data for adapting to a visuomotor rotation vs. a curl force-field was surprising. In this study, we found that the net metabolic power for reaching to the target was 0.38 ± 0.02 W/kg (at late Null 1, $n = 7$), which matched what we measured previously when a different set of healthy, young adults reached to a target at the same location, which was 0.38 ± 0.05 W/kg (at late Null 1, $n = 15$) (Huang et al. 2012). Interestingly, in both adaptation tasks, the initial increase in net metabolic power in response to the perturbation was nearly identical. For the visuomotor rotation, net metabolic power spiked to 0.56 ± 0.04 W/kg, whereas for the curl force-field, net metabolic power increased to 0.54 ± 0.06 W/kg. In both adaptation tasks, there were significant reductions in metabolic power from the initial to the last adaptation trials.

Minimization of effort may be a general feature of motor adaptation, as reductions in effort have also been observed during locomotor adaptation tasks. When learning to walk on a split-belt treadmill, where one belt moves faster than the other, subjects reduced asymmetry, muscle activity, and metabolic cost as they adapted to the novel locomotor task (Finley et al. 2013). With the use of a computational approach, a mathematical model of motor adaptation, which minimized both error and muscle activation, predicted learning dynamics of subjects adapting to walk in a robotic device that could apply novel dynamics that perturbed stepping (Emken et al. 2007). Although not directly measured, we predict that similar reductions would also be observed in postural adaptation (Ahmed and Wolpert 2009; Manista and Ahmed 2012; Pienciak-Siewert et al. 2014). However, an additional cost of coactivation in these tasks may be a reduction in maneuverability. In a recent study of whole-body movements, it was observed that increased coactivation led to reduced maneuverability, as evidenced by a slower response to a change in direction (Huang and Ahmed 2011). Thus there may be multiple reasons motivating a reduction in muscle activity, coactivation, and ultimately effort.

Some limitations of this study were that we could not prevent corrective submovements, and the measurement of metabolic cost, using expired gas analysis, is inherently variable. Even though subjects were instructed to reach in a single out-and-back movement, when visual feedback of the cursor was provided, subjects tended to alter their movement trajectories to hit the target during the return path. These corrective submovements and longer path trajectories could contribute to the increased metabolic cost. However, since these corrections were observed during the return path, and muscle activity amplitude was only calculated during the outward movement, the corrections should not influence the observation of increased muscle activity and coactivation. Another potential limitation is that the passive robot dynamics experienced when reaching to the adapted direction may have led to increased coactivation, independent of the visuomotor perturbation. However, increases in coactivation are even observed when the perturbation is removed, at which point, the subjects have been familiarized with reaching in both the trained and adapted directions. Additionally, the results of the control experiment suggest that increased coactivation and muscle activity are observed even when subjects are familiarized with reaching in multiple directions, including the adapted direction. Furthermore, typically, metabolic data are averaged over a specified period of time (1–3 min) when biomechanics are assumed to be at a steady state (Brooks et al. 1996). In this study, we were interested in metabolic changes before settling to steady state. Because visuomotor adaptation occurred rapidly, within the first ~20 trials, we chose to average over a relatively short period of time (~50 s) to attempt to capture these metabolic changes. Times as short as 1 min have been published in metabolic studies during standing (Houdijk et al. 2009, 2010). We chose to calculate early VM 1 as the average of the first 20 trials, which was ~50 s in duration, to try to capture this metabolic spike. Additionally, metabolic variability due to limitations in the resolution of expired gas analysis may provide an explanation for why the metabolic spikes were not statistically significant, even though they were clearly evident in the time-course plots (Fig. 6). The lack of a statistical increase may also be due, in part, to the number of subjects ($n = 7$); however, the focus of the study was to observe reductions in metabolic cost during adaptation, which were indeed observed.

In conclusion, we have shown that the time courses of muscle activity, muscle coactivation, and metabolic cost during a visuomotor adaptation task were similar to other motor-adaptation tasks. Initially, muscle activity and coactivation increased when the visuomotor rotation was introduced, along with a spike in metabolic cost. As subjects quickly adapted, muscle activity, coactivation, and metabolic cost were reduced. These data suggest that increasing muscle coactivation, presumably to reduce large performance errors or neuromotor noise, is a common feature of motor adaptation. Furthermore, the time courses of muscle activity and coactivation and the

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reduction of metabolic cost observed in this study suggest that minimization of error and effort may be a general underlying process in motor adaptation.

ACKNOWLEDGMENTS

The authors thank Rodger Kram for use of his metabolic cart and Stefan Garcia, Alison Pienciak-Siewert, and Ali Nikooyan for their help with data collections.

GRANTS

Support for this work was provided by National Science Foundation Grants CMMI 1200830, SES 1230933, and SES 1352632 (to A. A. Ahmed).

DISCLOSURES

The authors declare no competing financial interests.

AUTHOR CONTRIBUTIONS

Author contributions: H.J.H. and A.A.A. conception and design of research; H.J.H. and A.A.A. performed experiments; H.J.H. and A.A.A. analyzed data; H.J.H. and A.A.A. interpreted results of experiments; H.J.H. and A.A.A. prepared figures; H.J.H. and A.A.A. drafted manuscript; H.J.H. and A.A.A. edited and revised manuscript; H.J.H. and A.A.A. approved final version of manuscript.

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