Older adults learn less, but still reduce metabolic cost, during motor adaptation

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Huang HJ, Ahmed AA. Older adults learn less, but still reduce metabolic cost, during motor adaptation. *J Neurophysiol* 111: 135–144, 2014. First published October 16, 2013; doi:10.1152/jn.00401.2013.— The ability to learn new movements and dynamics is important for maintaining independence with advancing age. Age-related sensorimotor changes and increased muscle coactivation likely alter the trial-and-error-based process of adapting to new movement demands (motor adaptation). Here, we asked, to what extent is motor adaptation to novel dynamics maintained in older adults ($\geq$65 yr)? We hypothesized that older adults would adapt to the novel dynamics less well than young adults. Because older adults often use muscle coactivation, we expected older adults to use greater muscle coactivation during motor adaptation than young adults. Nevertheless, we predicted that older adults would reduce muscle activity and metabolic cost with motor adaptation, similar to young adults. Seated older ($n = 11$, 73.8 $\pm$ 5.6 yr) and young ($n = 15$, 23.8 $\pm$ 4.7 yr) adults made targeted reaching movements while grasping a robotic arm. We measured their metabolic rate continuously via expired gas analysis. A force field was used to add novel dynamics. Older adults had greater movement deviations and compensated for just 65% of the novel dynamics compared with 84% in young adults. As expected, older adults used greater muscle coactivation than young adults. Last, older adults reduced muscle activity with motor adaptation and had consistent reductions in metabolic cost later during motor adaptation, similar to young adults. These results suggest that despite increased muscle coactivation, older adults can adapt to the novel dynamics, albeit less accurately. These results also suggest that reductions in metabolic cost may be a fundamental feature of motor adaptation.

aging; minimization; energy; energetic cost; central nervous system; motor control; internal model; neuromechanics; biomechanics

THE ABILITY TO LEARN TO GENERATE accurate movements under varying dynamic conditions is critical for maintaining a high quality of life with increasing age. When young adults adapt to novel movement dynamics (motor adaptation), they are thought to use movement errors to update a sensorimotor mapping of the dynamics, i.e., an internal model (Shadmehr and Mussa-Ivaldi 1994). By forming an accurate internal model, one can apply specific forces to compensate for the novel dynamics. Furthermore, muscle activity and metabolic cost are reduced as the novel dynamics are learned, which suggests that the reduction of metabolic cost may be an important feature of motor adaptation (Huang et al. 2012). Here, we asked, to what extent is this adaptation process maintained with increasing age? Do healthy older adults retain the ability to form an accurate internal model of novel dynamics? Do they reduce muscle activity and metabolic cost during motor adaptation, similar to young adults?

Several age-related sensorimotor changes occur that may compromise the adaptation process. With increasing age, there is a reorganization of motor units (Brooks and Faulkner 1994) and also more variable motor-unit firing rates (Laidlaw et al. 2000), which amplifies motor variability (Christou 2011). Older adults have sensory deficits such as declines in vision (Lord and Dayhew 2001) and proprioception (Goble et al. 2009). Furthermore, declines in cerebellar morphology and function (Eckert et al. 2010; Hogan 2004) and impaired sensorimotor integration (Degardin et al. 2011) also occur with increasing age. These age-related changes often result in decreased motor performance, but the effect on motor adaptation is task-specific, dependent on task structure, complexity, difficulty, and familiarity (Voelcker-Rehage 2008).

When older adults move, they often use muscle coactivation (Darling et al. 1989; Hortobágyi et al. 2009; Schmitz et al. 2009; Seidler-Dobrin et al. 1998). Potential benefits of increased muscle coactivation are reduced movement variability (Osu et al. 2009; Seidler-Dobrin et al. 1998) and improved accuracy (Gribble et al. 2003). However, greater muscle coactivation may also be costly. In locomotion, older adults have higher metabolic costs compared with young adults, presumably in part due to increased muscle coactivation (Hortobágyi et al. 2011; Mian et al. 2006; Ortega and Farley 2007). Increased coactivation in older adults, whether voluntary or involuntary, may lead to reduced motor adaptation since it can be an effective yet costly means to reject perturbations and reduce movement deviation in lieu of forming a model of the novel dynamics.

The primary purpose of this study was to determine how well older adults learn novel dynamics compared with young adults. Because of age-related sensorimotor changes and increased muscle coactivation, older adults may not form accurate internal models as well as young adults. Therefore, we hypothesized that older adults would learn the novel dynamics less well than young adults. Based on previous observations of increased coactivation in older adults during movement tasks, we expected older adults to use greater muscle coactivation during a motor-adaptation task as well. Last, we predicted that older adults would demonstrate a reduction in muscle activity and metabolic cost with motor adaptation, similar to young adults. A portion of the young adult data has been previously reported (Huang et al. 2012).

METHODS

Subjects. Eleven older adults (means $\pm$ SD, age 73.8 $\pm$ 5.6 yr, mass 73.2 $\pm$ 15.0 kg, 5 females, 6 males) and 15 young adults (age 23.8 $\pm$ 4.7 yr, mass 66.9 $\pm$ 12.6 kg, 13 females, 2 males) participated in this study. Subjects had no physical injuries, known pathologies, or factors that affected their neurological, musculoskeletal, and cardiorespiratory health. With respect to neurological medications, none of the subjects was taking antidepressants, medications to prevent seizures, antipsychotics, sedatives, hypnotics, or pain medications such as Vicodin/hydrocodone, oxycodone, or Demerol. All subjects were right-handed. The University of Colorado Institutional Review Board

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approved the study protocol, and all subjects gave informed, written consent.

Task. Subjects grasped the handle of a robotic arm (Shoulder-Elbow Robot 2; Interactive Motion Technologies) to move a circular cursor from a green home circle to a red target circle displayed on a vertically mounted computer screen at the subject's eye level (Fig. 1*A*). Subjects were seated in a chair. Bilateral shoulder straps and a lap belt limited torso movement. The right forearm rested in a cradle attached to the robot handle so that the cradle supported the arm against gravity and restricted movement of the wrist. The radius of the cursor was 0.3 cm, whereas the radii of the home and target circles were 0.8 cm. The reaching distance was 20 cm. The red target turned gray if subjects moved too slowly (>600 ms) and turned green if subjects moved too fast (<300 ms). If subjects reached the target within 300–600 ms, a large yellow ring around the target flashed. An auditory metronome was used to try to pace subjects to initiate a movement every 2 s. On odd trial numbers, the home circle was a few centimeters in front of the torso so that subjects reached out anteriorly to the target (in the *y*-direction of the robot space, Fig. 1*B*). The home and target circles were then switched so that on even trial numbers, subjects began from an extended elbow position and reached inward toward their torso.

Muscle activity. We recorded surface electromyographic (EMG) data from six upper limb muscles: pectoralis, posterior deltoid, biceps brachii, long head of the triceps, lateral head of the triceps, and the brachioradialis. Electrodes were placed according to published guidelines (http://seniam.org) on the muscle belly after excess hair was removed and the skin was abraded lightly and cleaned with rubbing alcohol. Self-adhesive tape was wrapped around the electrode and arm to minimize motion artifact and to ensure good contact with the skin.

The EMG system (Delsys Trigno) collected EMG data at 2,000 Hz with a hardware band-pass filter (20–450 Hz). A signal from the robotic arm system was used to trigger the start and stop of the EMG recording. Because of delays in resetting the EMG system, we collected EMG data for every outward reach (i.e., every odd trial number).

We also obtained maximum voluntary contractions (MVCs) from a series of maximal effort isometric contractions against manual resistance. The four MVC movements were elbow flexion, elbow extension, medial rotation of the shoulder, and lateral rotation of the shoulder while the subject was seated with the right arm flexed at 90° by the side of the subject. Subjects gradually increased their effort over 3 s until they reached their maximum effort and then sustained this maximum effort for another 3 s until instructed to relax. We verbally encouraged subjects to provide maximal effort.

Metabolic cost. Subjects wore a nose clip and breathed in and out of a mouthpiece as they made the reaching movements so that we could measure their rates of oxygen consumption ($\dot{V}o_2$) and carbon dioxide production ($\dot{V}co_2$) using expired gas analysis (TrueOne 2400; Parvo Medics). We calibrated the metabolic system before each data collection using certified gas mixtures and with a range of flow rates using a 3-l calibration syringe. All metabolic data were corrected with standard temperature and pressure, dry (STPD).

Curl force field. To add novel dynamics to the arm-reaching task, we used a curl force field. When reaching in the curl force field, the subject's hand experienced a perturbing force that was proportional and perpendicular to the hand velocity, according to *Eq. 1* (Fig. 1*B*):

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = b \begin{bmatrix} 0 & 1 \\ -1 & 0 \end{bmatrix} \begin{bmatrix} V_x \\ V_y \end{bmatrix}, \text{ where } b = -20 \text{ Ns/m.} \quad (1)$$
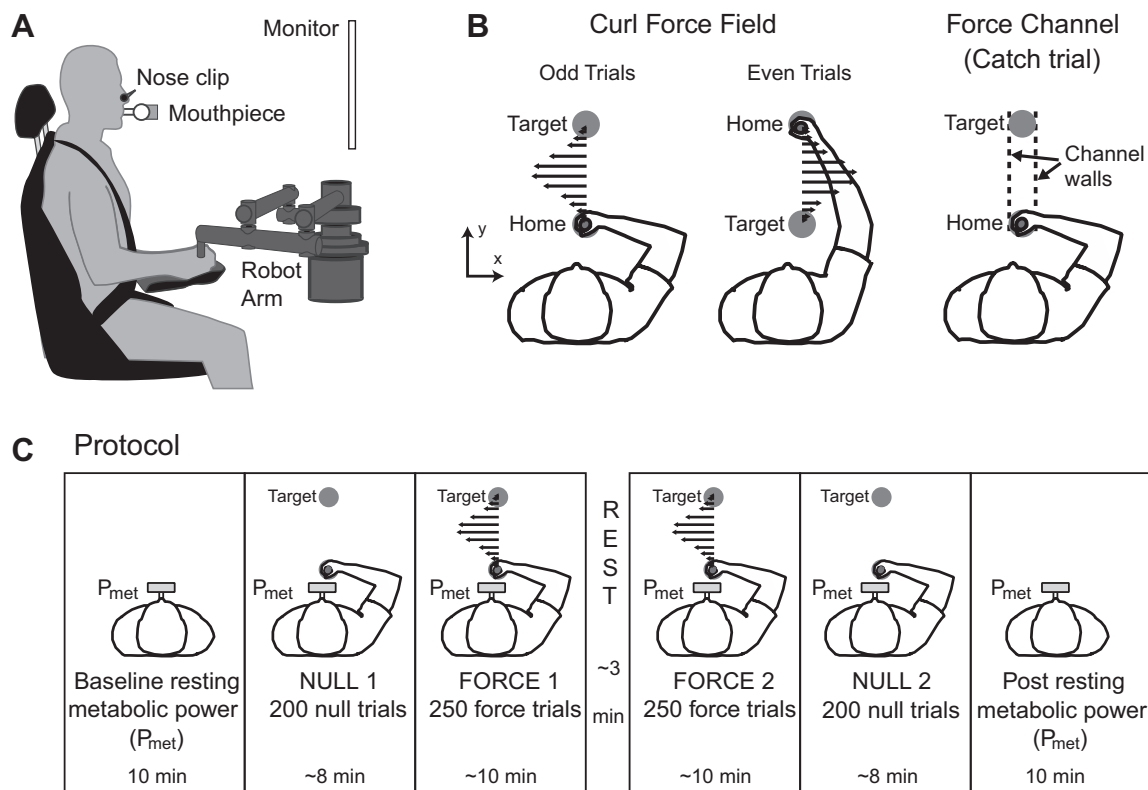

Fig. 1. Experimental setup and protocol. *A*: schematic of the robotic arm and mouthpiece for measuring metabolic cost. *B*: depiction of the curl force field and force channel. In the curl force field, when subjects extended their arm (on odd-numbered trials), they were perturbed to the left. When subjects flexed their arm (on even-numbered trials), they were perturbed to the right. During a catch trial, a force channel constrained subjects to move along a straight line. *C*: the experimental protocol consisted of 6 blocks: 10 min of quiet sitting (baseline resting metabolic power), 200 reaches in no force field (*null 1*), 250 reaches in the curl force field (*force 1*), another 250 reaches in the curl force field (*force 2*), another 200 reaches in no force field (*null 2*), and another 10 min of quiet sitting (postresting metabolic power). There was a brief rest halfway through the protocol when subjects could remove the mouthpiece. P$_{met}$ indicates that metabolic power was being measured.

Protocol. The experiment consisted of 6 blocks (Fig. 1*C*). During the 1st block, subjects sat quietly for 10 min to establish a baseline resting metabolic rate. Subjects then made 200 reaches (*null 1*) followed by 250 reaches in a curl force field (*force 1*). After a brief rest when the subjects did not have to breathe through the mouthpiece, subjects made another 250 reaches in the curl force field (*force 2*). The curl force field was then removed for the last 200 reaches (*null 2*). The experiment ended with another 10 min of quiet sitting.

Motor-adaptation analysis. We defined movement onset as the time when the *y*-velocity was ≥0.03 m/s in the direction of the target and movement end as the time when the *y*-velocity was ≤0.03 m/s and the hand position was within the target. Movement time was the duration of time between movement onset and end.

Our first motor-adaptation metric was movement deviation, defined as the maximum perpendicular deviation of the hand from the straight line path between the home and target circles. Even though subjects were not explicitly told to reach in a straight line, previous research suggests that people naturally tend to reach in relatively straight lines during goal-directed movements (Flash and Hogan 1985; Franklin et al. 2004; Shadmehr and Mussa-Ivaldi 1994). We consider movement deviation to reflect the subject's movement strategy. In this study, we were primarily interested in comparing movement strategies between older and young adults. Furthermore, a metric similar to movement deviation has been used to quantify differences in adaptation between young adults and children as well as older adults and individuals with Parkinson's disease (Krebs et al. 2001; Takahashi et al. 2003).

Our second motor-adaptation metric was an adaptation index based on the subject's anticipatory forces. To measure the subject's anticipatory force learning, one in every five trials was a catch trial. During a catch trial, the hand moved along a straight line path to the target within a force channel (Fig. 1*B*). As subjects learned the curl force-field dynamics, they would anticipate encountering the perturbing force of the curl force field and therefore exert an anticipatory force to counter the perturbing force. As a result, during a catch trial, subjects would apply a force into the wall of the channel. This force was their anticipatory force. The anticipatory force provides a measure of how well subjects learned the internal model. We then performed a linear regression of the *y*-velocity, V_y, with the anticipatory force produced, F_a, to find an estimated gain, $b_{est} = F_a/V_y$, for each catch trial. The estimated gain accounts for potential differences in movement velocity because it normalizes the anticipatory force to the actual movement velocity. Finally, the adaptation index was the percentage of the magnitude of the estimated gain, $|b_{est}|$, relative to the magnitude of the actual gain, $|b| = 20$ (see *Eq. 2*):

$$\text{Adaptation index}(\%) = \frac{|b_{est}|}{|b|} \times 100 = \frac{F_a/V_y}{20} \times 100. \quad (2)$$

Muscle-activity analysis. EMG data were digitally smoothed and normalized relative to a MVC using MATLAB (MathWorks). EMG data were high-pass filtered at 20 Hz to remove motion artifact, rectified, and low-pass filtered at 50 Hz to smooth the EMG data using fourth-order Butterworth filters. For each reach, we quantified the root mean square (RMS) of the EMG data between movement onset and movement end, ~450 ms in young adults. For the MVC data, subjects attempted to sustain their MVC for ~3 s. Rather than calculate the RMS over ~3 s, we calculated the RMS of the MVC EMG data in 500-ms windows that incremented by 100 ms. Thus there were multiple RMS values for each MVC. We then used the maximum of these RMS EMG MVC values for each muscle to normalize the EMG data during the reaching trials.

To quantify muscle coactivation, we took the minimum normalized EMG activity level of the two muscles in the muscle pair at each time point to yield a coactivation profile for the trial. This coactivation profile represented the "wasted contraction" (Gribble et al. 2003; Thoroughman and Shadmehr 1999). We calculated RMS coactivation

amplitudes for three muscle pairs: pectoralis-posterior deltoid, biceps brachii-triceps long head, and brachioradialis-triceps lateral head.

For the muscle-activity analysis, we excluded 1 older adult subject's data because of technical issues during the data collection. Thus we analyzed EMG data from 10 older adults (4 females, 6 males). For the young adults, we only acquired EMG data from 7 of the subjects (5 females, 2 males), as reported in Huang et al. (2012).

Metabolic analysis. When people are uncomfortable and anxious, they often hyperventilate. In this experiment, some subjects appeared to be uncomfortable and anxious about breathing through the mouthpiece and/or about using the robot for the first time. Hyperventilating results in elevated respiratory-exchange-ratio (RER $= \dot{V}_{CO_2}/\dot{V}_{O_2}$) values because the person is "blowing off" excess CO_2 from the stores of the body. Hyperventilating also results in high ventilatory equivalent of oxygen values, $VEQ_{O_2} = \dot{V}_E/\dot{V}_{O_2}$, which relates the volumetric flow rate exhaled ($\dot{V}_E$, the expired minute ventilation in liters per minute) with the rate of oxygen consumption, $\dot{V}_{O_2}$ in liters per minute. The excess CO_2 that is blown off during hyperventilation distorts the calculation of metabolic power.

To ensure that the changes in metabolic power observed were related to the adaptation process, we excluded subjects whose RER and/or VEQ_{O_2} values suggested that they may have been hyperventilating during the experiment. We expected the RER values to be well below 1.0 and generally below 0.85, suggesting that oxidative metabolism was primarily involved (Brooks et al. 1996). Normal resting RER values range from 0.74 to 0.87, partly depending on diet and other factors (Seidell et al. 1992; Short and Sedlock 1997). We excluded subjects with maximum RER values during the experiment that were identified as statistical outliers. We defined an outlier as being $\geq Q_3 + 1.5 \times (Q_3 - Q_1)$, where Q_1 is the first quartile and Q_3 the third quartile for the data set. One young and one older subject with maximum RER values ≥0.96 were excluded. We also excluded subjects with average VEQ_{O_2} values during the experiment that were identified as statistical outliers. Using this VEQ_{O_2} criterion, we excluded 3 older adults with an average VEQ_{O_2} that was above the upper outlier boundary of 44.0. In the end, we included the metabolic data from 7 older adults and 14 young adults.

Our metabolic metric was net metabolic power, the rate of metabolic energy consumption. We used the Brockway equation to calculate metabolic power from the measured rates of oxygen consumption and carbon dioxide production (Brockway 1987). To obtain a metabolic power data point per trial, the metabolic power data were linearly interpolated at each trial time. We calculated the time-weighted average of the gross metabolic power for 60 trials (approximately 2–3 min) in each block and then subtracted out the baseline resting gross metabolic power to get the net metabolic power.

Adaptation phases and analysis. We quantified metrics at "early" and "late" phases within the block to assess adaptation throughout the protocol. We use the definition of adaptation to be changes in parameters of a movement that occur with practice that manifest within minutes to hours and requires a deadaptation period to eliminate aftereffects (Bastian 2008). For movement deviation, early referred to the 1st noncatch trial, and late referred to the 8 noncatch trials within the last 10 trials. For the adaptation index, early referred to the 1st catch trial, and late referred to the 2 catch trials within the last 10 trials. For metabolic metrics, we excluded the 1st 60 trials (approximately 2–3 min) in the analysis to account for any physiological and measurement delays. Early referred to the 60 trials after accounting for metabolic delays, and late referred to the last 60 trials in the block. Last, for the EMG data, early referred to the 1st 10 noncatch EMG trials, and late referred to the last 25 noncatch EMG trials. More EMG trials were included compared with the number of trials included for motor-adaptation metrics because EMG data had greater intertrial variability.

Statistics. Repeated-measures ANOVAs were used to determine whether age, phase (i.e., early and late of each block), and the interaction of age and phase had main effects. If phase had a main

effect, paired *t*-test comparisons between specific phases were then used to determine significant differences during adaptation. The primary comparison for quantifying adaptation was *early force 1* with *late force 2*, which assessed changes in our metrics over the entire adaptation period. We also compared *early force 1* with *late force 1* and *late force 1* with *late force 2* to determine whether adaptation occurred rapidly during the first half or later during the adaptation period, respectively. We also compared *late null 1* with *early force 1* to determine whether the novel dynamics of the force field resulted in a significant changes in our metrics and compared *late force 1* with *early null 2* to determine whether there were significant aftereffects after the force field was abruptly removed. Additionally, if the repeated-measures ANOVA indicated that there was a significant interaction effect of age and phase, we made comparisons within each age group and used paired *t*-tests at phases of interest (*late null 1*, *early force 1*, *late force 1*, *late force 2*, and *early null 2*). We also used independent *t*-tests to determine which phases had significant differences between age groups. The level of significance was set at $\alpha = 0.05$. Exact *P* values are reported for values greater than $P = 0.0001$.

RESULTS

We first characterized the movement trajectories between older and young adults. Reaching trajectories of older adults were similar to young adults with the greatest differences emerging at the transitions when the force field was turned on (*late null 1* to *early force 1*) and turned off (*late force 2* to *early null 2*; Fig. 2*A*). At these transitions, the older adult trajectories were perturbed less, having smaller perpendicular deviations in the *x*-direction. Furthermore, the older adult trajectories ini-

tially followed the young adult trajectories but then decelerated earlier than young adults, thus restricting their perpendicular deviation.

The *y*-velocity profiles indicate that older adults moved more slowly, having slower peak velocities (Fig. 2*B*). Older adult *y*-velocity profiles were also right-skewed compared with the more bell-shaped *y*-velocity profiles of young adults. In older adults, the peak velocity occurred earlier and was followed by a prolonged deceleration period. Age ($P < 0.0001$) and phase ($P = 0.0010$) had main effects on average *y*-velocity; however, there was not a significant interaction between age and phase ($P = 0.2043$). The average *y*-velocity for older adults was 0.21 ± 0.0037 m/s (mean $\pm$ SE), which was 13% slower than 0.24 ± 0.0036 m/s observed in young adults ($P < 0.0001$; Fig. 2*C*). The average velocity at the end of adaptation, *late force 2*, was 0.22 ± 0.0057 m/s, which was statistically slower than 0.23 ± 0.0046 m/s, at *late force 1* ($P = 0.0485$).

Can older adults learn the novel arm-reaching dynamics? Both older and young adults learned the novel dynamics, but older adults learned the dynamics less well based on movement deviation, our first motor-adaptation metric (Fig. 3*A*). Interestingly, during *null 1* and *null 2*, older adults had similar movement deviations as young adults. As a result, age did not have a significant main effect on movement deviation ($P = 0.3991$). Phase had a main effect ($P < 0.0001$), and there was a significant interaction between age and phase ($P = 0.0004$). At *late null 1*, movement deviations were 1.44 ± 0.10 cm for older adults and 1.31 ± 0.08 cm for young adults (older vs.
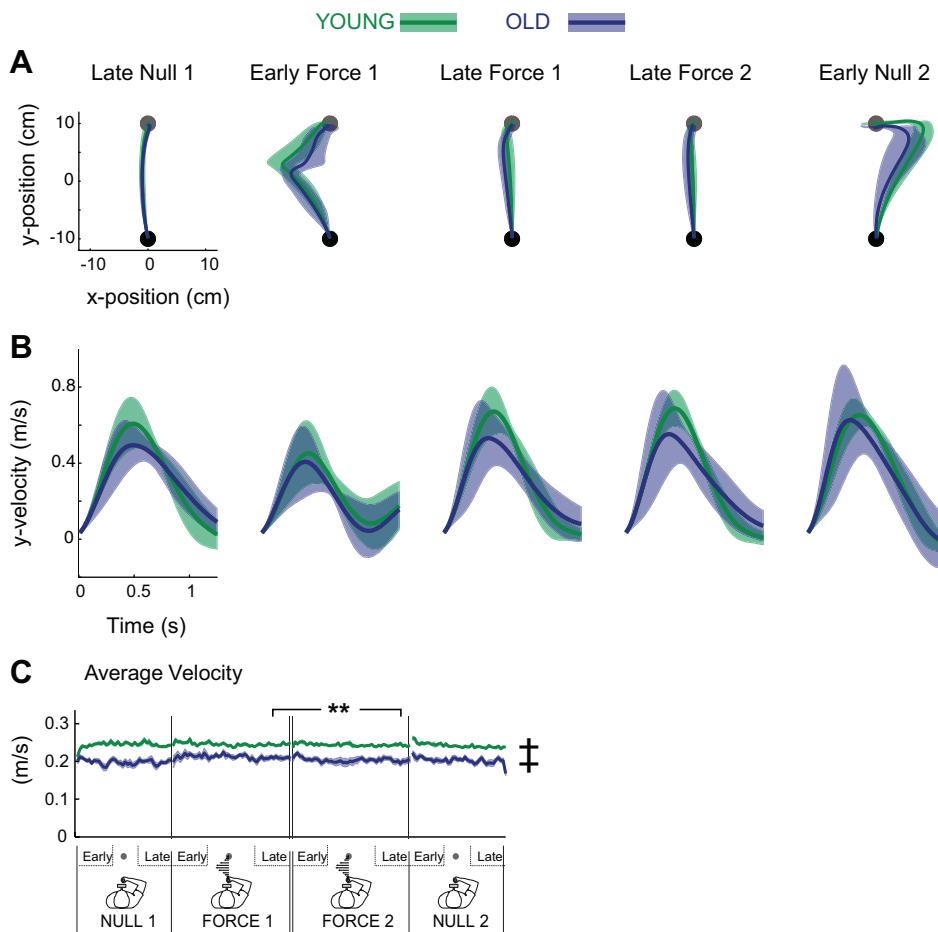

Fig. 2. Group-averaged movement trajectories (*A*), *y*-velocity profiles (*B*), and average *y*-velocity throughout the protocol (*C*). *A*: the movement trajectories illustrate that older adults (blue) had similar trajectories as the young adults (green) except during *early force 1* and *early null 2*, when older adults had smaller excursions in the *x*-direction. *B*: the *y*-velocity profiles illustrate that older adults had asymmetrical profiles with prolonged deceleration phases. *C*: the average *y*-velocities show that older adults moved more slowly than young and that there was a slight but significant reduction in average *y*-velocity from *late force 1* to *late force 2*. ‡Age effect, $P < 0.05$. **Differences between phases for all subjects, $P < 0.05$.
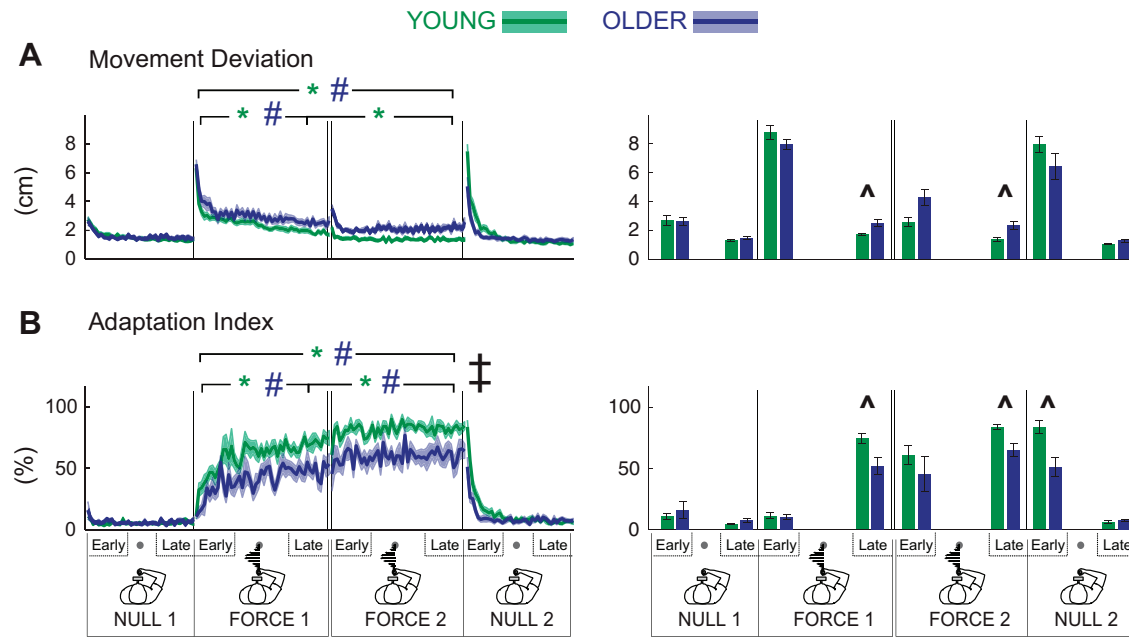
Fig. 3. Group-averaged movement deviation (*A*) and adaptation index (*B*) results plotted over the time course of the protocol and at specific phases. The time courses are by batches. A batch is the average of every 5 trials. Shaded areas and error bars are ±SE. ‡Age effect, *P* < 0.05. # And * indicate *P* < 0.05 between phases for older and young adults, respectively. ^*P* < 0.05 between older and young adults. *A*: older adults (blue) had similar movement deviations during *null 1* as young adults (green). On 1st exposure to the force field (*early force 1*), older adults were less perturbed. Both older and young adults had significant reductions in movement deviation with adaptation (#, *). Older adults had larger movement deviations during adaptation at *late force 1* and *late force 2* than young adults (^). *B*: older adults had lower adaptation indices than young adults (‡). Both older and young adults increased their adaptation indices with dynamics adaptation, indicating that they compensated for the novel dynamics more with adaptation (#, *). Older adults had lower adaptation indices at *late force 1* and *late force 2* (^), reaching a peak adaptation index of 65% compared with 84% for young adults.

young, *P* = 0.3081). At *early force 1*, when first exposed to the curl force field, movement deviation in older adults increased to 7.95 ± 0.37 cm (*P* < 0.0001) and to 8.78 ± 0.51 cm in young adults (*P* < 0.0001), but there was no age effect (*P* = 0.2332). By *late force 1*, movement deviation decreased by 69% for older adults from 7.95 ± 0.37 to 2.48 ± 0.24 cm (*P* < 0.0001) and by 81% for young adults from 8.78 ± 0.51 to 1.71 ± 0.09 cm (*P* < 0.0001), indicating that older adults reduced deviations to a lesser degree than young adults. At *late force 1*, there was an age effect as older adults had larger movement deviations than young adults (*P* = 0.0023). By the end of adaptation, older adults reduced movement deviation by just an additional 2%, 2.32 ± 0.25 cm (*late force 1* to *late force 2*, *P* = 0.4287), whereas young adults continued to reduce movement deviation significantly by an additional 4% to 1.36 ± 0.11 cm (*late force 1* to *late force 2*, *P* = 0.0021). At *late force 2*, older adults still had larger movement deviations than young adults (*P* = 0.0007) despite their slower movement velocities. When the force field was removed, older and young adults exhibited significant movement deviation aftereffects of 6.41 ± 0.89 cm (*late force 2* to *early null 2*, *P* = 0.0023) and 7.96 ± 0.54 cm (*P* < 0.0001), respectively, suggesting that all subjects adapted to the novel dynamics.

Adaptation index, our second motor-adaptation metric, also indicated that both older and young adults adapted their movements to the novel dynamics but that older adults adapted less well (Fig. 3*B*). Age (*P* = 0.0156) and phase (*P* < 0.0001) had main effects on adaptation index. There was also a significant interaction between age and phase. At the beginning of adaptation, *early force 1*, older and young adults had similarly low adaptation indices, 10.45 ± 1.87 and 11.26 ± 2.60% (*P* =

0.8177). By *late force 1*, older adults increased their adaptation indices by 42% to 52.18 ± 7.00% (*P* = 0.0002). Young adults increased their adaptation indices by 63% to 74.69 ± 4.19% (*P* < 0.0001). The adaptation indices of older adults were significantly less than young adults at *late force 1* (*P* = 0.0076). By the end of adaptation, *late force 2*, older adults had learned an additional 13%, settling to a final adaptation index of 65.01 ± 5.16% (*late force 1* to *late force 2*, *P* = 0.0363). Young adults learned an additional 9% during the second half of adaptation, settling to a final adaptation index of 83.78 ± 2.33% (*late force 1* to *late force 2*, *P* = 0.0223). At the end of adaptation, older adults had only learned ~65%, whereas young adults had learned ~84% (older vs. young, *P* = 0.0013), indicating that older adults had learned less than the young adults. When the curl force field was removed at *early null 2*, both older and young adults continued to exert anticipatory forces and thus had adaptation indices of 51.36 ± 7.91 and 84.05 ± 5.48%, respectively, suggesting that both groups had updated their internal models to account for the novel dynamics. Older adults had a smaller adaptation index aftereffect than young adults (*P* = 0.0018).

Do older adults use a muscle coactivation strategy during motor adaptation? Older adults used greater muscle activity than young adults during adaptation to novel dynamics (Fig. 4). Age had a main effect on the EMG activity of both heads of the triceps muscle (long head, *P* = 0.0320; lateral head, *P* = 0.0254). In the triceps long head, the group-averaged EMG activity over the whole experiment was 17.4 ± 1.0% MVC for older adults compared with 8.2 ± 0.7% MVC for young adults. In the triceps lateral head, the group-averaged EMG activity was 24.6 ± 1.1% MVC for older adults compared with 11.4 ±
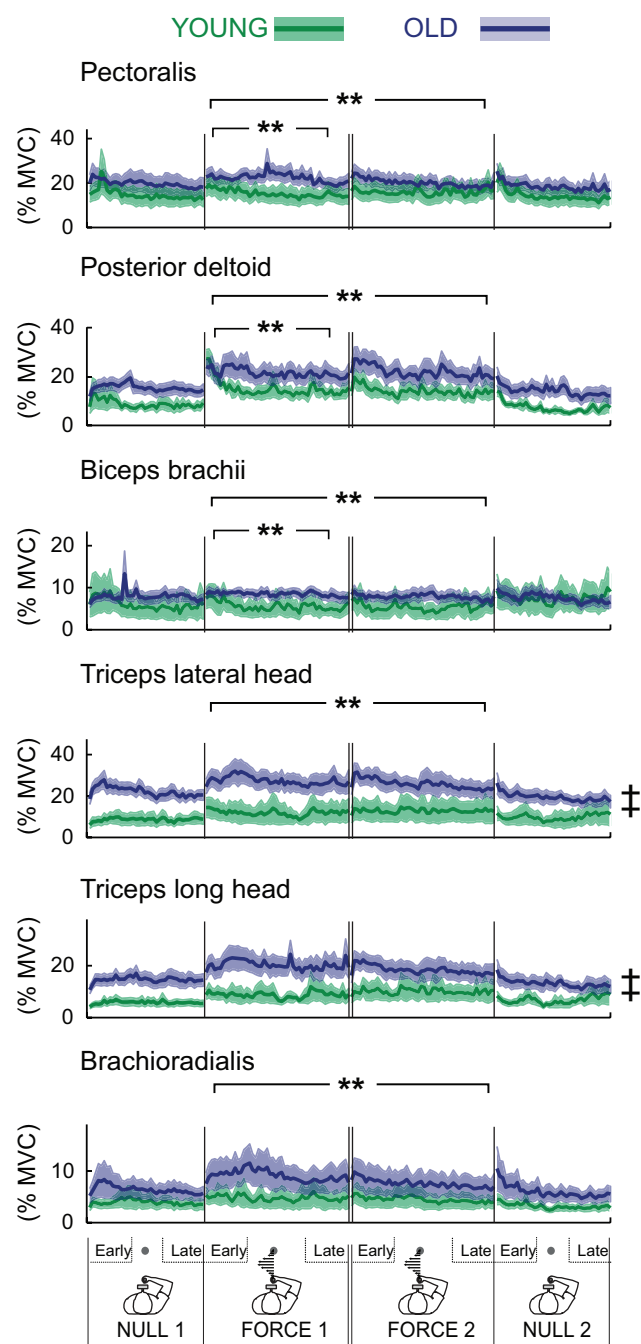
Fig. 4. Group-averaged muscle activity plotted over the time course of the protocol. The *x*-axis is by batches, where each batch is the average of every 5 trials. Shaded areas are ±SE. ‡Age effect, *P* < 0.05. **Differences between phases for all subjects, *P* < 0.05. Older (blue) and young (green) adults reduce muscle activity in 5 of the 6 muscles over the entire adaptation period, *early force 1* to *late force 2* (**). There are rapid reductions in muscle activity in the pectoralis, posterior deltoid, and biceps brachii from *early force 1* to *late force 2* (**). There was an age effect in the triceps lateral and long heads (‡). MVC, maximum voluntary contraction.

0.8% MVC in young adults. Phase had a main effect on all muscles (biceps brachii, *P* = 0.0486; brachioradialis, *P* = 0.0003; all other *P*s < 0.0001). Muscle activity increased significantly from *late null 1* to *early force 1* (*P*s < 0.05). With motor adaptation, muscle activity decreased from *early force 1* to *late force 2* for all muscles (*P*s < 0.05) except the triceps long head (Fig. 4). During the first half of adaptation, *early*

force 1 to *late force 1*, significant reductions occurred in the pectoralis, posterior deltoid, and biceps brachii muscles (*P*s < 0.05). There were no significant reductions from *late force 1* to *late force 2* for any muscle. There was not a significant interaction of age and phase for any muscles.

Older adults also used greater muscle coactivation than young adults when adapting to the novel dynamics (Fig. 5). Age had a main effect on the biceps brachii-triceps long-head (*P* = 0.0136) and pectoralis-posterior deltoid (*P* = 0.0147) muscle pairs. Older adults showed greater levels of muscle coactivation in the pectoralis-posterior deltoid (9.4 ± 0.4 vs. 5.0 ± 0.4% MVC) and biceps brachii-triceps long-head (5.9 ±
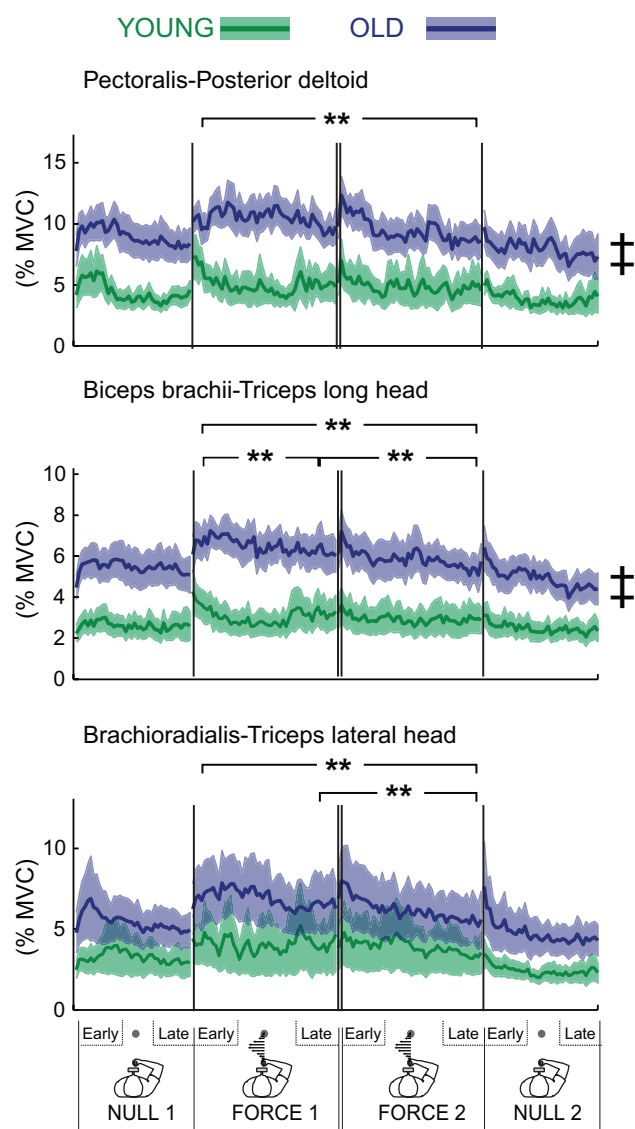

Fig. 5. Group-averaged muscle coactivation plotted over the time course of the protocol. The *x*-axis is by batches, where each batch is the average of every 5 trials. Shaded areas are ±SE. ‡Age effect, *P* < 0.05. **Differences between phases for all subjects, *P* < 0.05. Older (blue) adults had greater muscle coactivation than young (green) adults (‡). Older and young adults reduced muscle activity in all 3 muscle pairs over the entire adaptation period, *early force 1* to *late force 2* (**). The biceps brachii-triceps long-head biarticular elbow muscle pair had significant reductions from *early force 1* to *late force 1* and also *early force 2* to *late force 2* (**). The brachioradialis-triceps lateral head muscle pair showed a reduction later during adaptation, *late force 1* to *late force 2*.
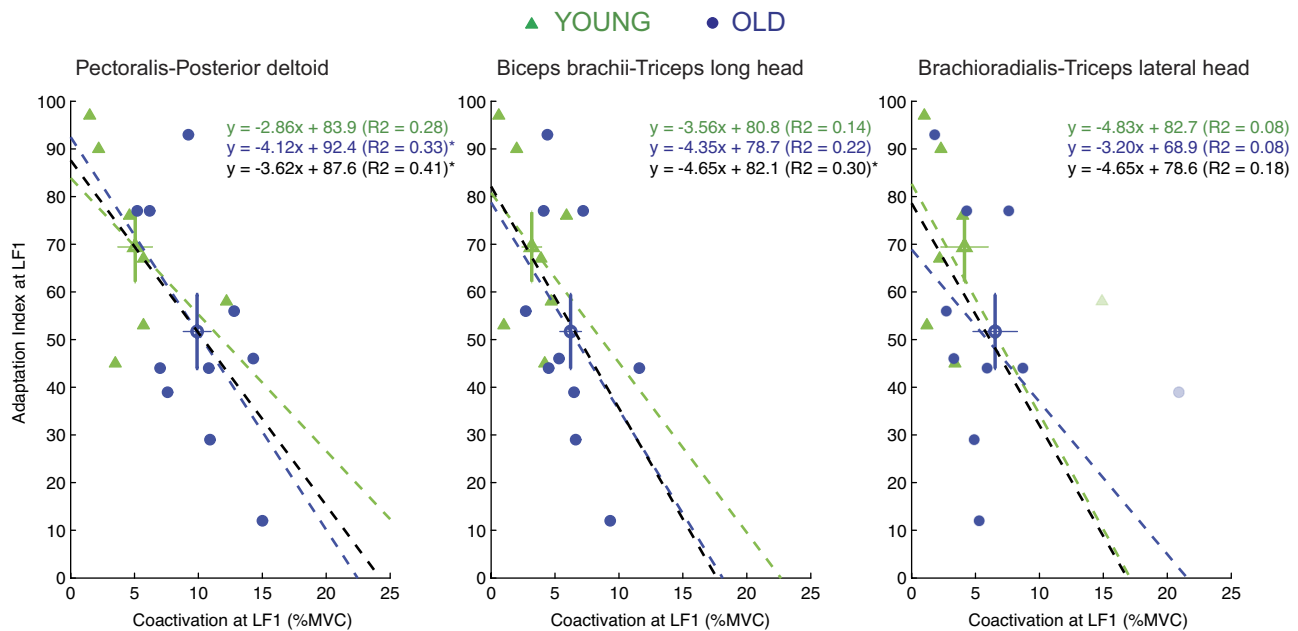
Fig. 6. Scatterplots and linear regressions of adaptation index as a function of muscle coactivation for the 3 muscle pairs. The bold, open symbols are the average coactivation and adaptation index for the young (green triangles) and older adults (blue circles). The dashed lines are the linear regressions when using just the young adult data (green dash), just the older adult data (blue dash), and young and older adult data combined (black dash). * Indicates that the slope is significantly different from 0, $P < 0.05$. The light, filled symbols in the *rightmost* plot (Brachioradialis-Triceps lateral head) were outliers and excluded from the regression analysis. These plots indicate a negative correlation between adaptation index and muscle coactivation. LF1, *late force 1*.

0.2 vs. 3.0 ± 0.2% MVC) muscle pairs. Phase had a main effect on all muscle pairs ($Ps < 0.0001$). On first experiencing the force field, subjects increased muscle coactivation in all muscle pairs, from *late null 1* to *early force 1* ($Ps < 0.05$). With adaptation, muscle coactivation decreased in all muscle pairs, from *early force 1* to *late force 2* (Fig. 5; $Ps < 0.05$). There was a rapid reduction in coactivation in the biceps brachii-triceps long-head pair from *early force 1* to *late force 1* and also a reduction in coactivation in the elbow muscle pairs from *late force 1* to *late force 2* ($Ps < 0.05$). There was not a significant interaction between age and phase for any muscles or muscle pairs.

Interestingly, we also found that individuals with greater muscle coactivation demonstrated lower adaptation indices at *late force 1* (Fig. 6). A linear regression including young and older adult data indicated a significant negative correlation for the pectoralis-posterior deltoid, $y = -3.62x + 87.6$ ($r^2 = 0.41$, $P = 0.0029$, 1-sided paired t-test) and the biceps brachii-triceps long head, $y = -4.65x + 82.1$ ($r^2 = 0.30$, $P = 0.0109$; Fig. 6). Linear regressions using just the older adult data or young adult data also indicated negative correlations between muscle coactivation in the pectoralis-posterior deltoid and adaptation indices (older: $r^2 = 0.41$, $P = 0.0410$, young: $r^2 = 0.41$, $P = 0.1125$).

Do older adults reduce metabolic cost with motor adaptation? Older and young adults reduced net metabolic power with motor adaptation (Fig. 7A). The gross metabolic power during the quiet sitting baseline period was 1.04 ± 0.03 W/kg for older adults and was less than 1.31 ± 0.04 W/kg for young adults, which was expected due to decreased muscle mass in older adults. Phase had a main effect on net metabolic power ($P < 0.0001$), whereas age did not have a main effect on net metabolic power. There was also no interaction effect between age and phase. Reaching in the force field during early adaptation was more metabolically costly than reaching in the null field ($P < 0.0001$). When initially reaching in the force field, older adults increased net metabolic power by 74%, from 0.31 ± 0.03 W/kg when reaching in the null field (*late null 1*, *trials 141-200*) to 0.54 ± 0.05 W/kg at *early force 1* (*trials 261-320*). Young adults also increased net metabolic power but
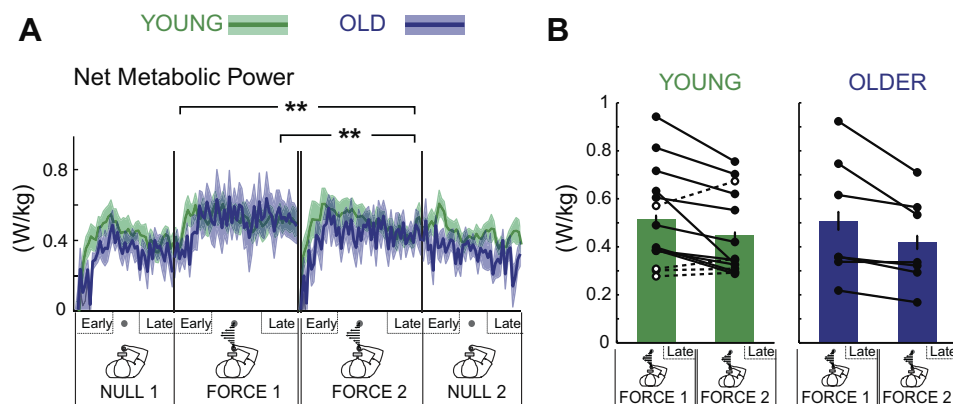

Fig. 7. Group-averaged net metabolic power plotted over the time course of the protocol (A) and net metabolic power changes from *late force 1* to *late force 2* in individual subjects (B). A: the x-axis is by batches, where each batch is the average of every 5 trials. Shaded areas are ±SE. **Differences between phases for all subjects, $P < 0.05$. Older (blue) and young (green) adults reduced net metabolic power over the entire adaptation period, *early force 1* to *late force 2*, and also later during adaptation, *late force 1* to *late force 2* (**). B: there were also consistent reductions in net metabolic power among older and young adults from *late force 1* to *late force 2* (solid lines). Only 4 subjects showed an increase in net metabolic power (dashed lines).

by 41%, from 0.39 ± 0.01 W/kg at *late null 1* to 0.55 ± 0.02 W/kg at *early force 1*. Over the entire adaptation period, both older and young adults reduced net metabolic power ($P = 0.0068$). Older adults reduced net metabolic power from 0.54 ± 0.05 W/kg at *early force 1* to 0.42 ± 0.03 W/kg at *late force 2* (*trials 641-700*); young adults reduced net metabolic power with adaptation from 0.55 ± 0.02 to 0.45 ± 0.01 W/kg at *late force 2*. Both older and young adults demonstrated consistent reductions in net metabolic power during the second half of adaptation, *late force 1* (*trials 391-450*) to *late force 2* (Fig. 7B; $P = 0.0015$). Older adults reduced net metabolic power from 0.51 ± 0.04 W/kg at *late force 1* to 0.42 ± 0.03 W/kg at *late force 2*. Similarly, young adults reduced metabolic power from 0.51 ± 0.01 W/kg at *late force 1* to 0.45 ± 0.01 W/kg at *late force 2*.

DISCUSSION

Our primary purpose was to determine whether older adults adapt to novel dynamics as well as young adults. We found that older adults did adapt their movements the novel dynamics but less well compared with young adults. As expected, older adults used greater muscle activity and coactivation, which correlated with an impaired ability to form an accurate internal model of the novel dynamics. Despite adapting less well and using greater muscle coactivation, older adults also reduced muscle activity and metabolic power with motor adaptation, similar to young adults. These findings suggest a decline in the ability to form accurate internal models with increasing age. These findings also suggest that metabolic cost is reduced during motor adaptation even with advancing age.

Interestingly, older adults had greater movement deviations during motor adaptation than young adults despite using greater muscle coactivation and reaching more slowly. Previous studies have shown that increasing muscle coactivation may help reduce movement variability (Gribble et al. 2003; Osu et al. 2009; Seidler-Dobrin et al. 1998). Therefore, by employing a coactivation strategy, older adults could have reductions in movement deviations similar to young adults. Older adults could also improve accuracy by moving more slowly, based on the speed-accuracy tradeoff (Fitts 1954). Indeed, we observed that older adults had similar movement deviations to young adults during *null 1* and *null 2* (Fig. 3A), which suggests that older adults successfully used increased coactivation and slower velocities when just reaching (i.e., no force field) to perform similarly as young adults. However, when reaching in the force field, the coactivation and slower movement strategy of older adults was not sufficient to reduce movement deviations as much as young adults. The larger movement deviations in the older adults also occurred despite encountering smaller perturbing forces from the force field as a result of the slower movement speeds.

Another strategy for reducing movement errors during motor adaptation is to form an accurate internal model of the novel dynamics and apply specific forces to compensate for the force field. We quantified internal model adaptation by measuring anticipatory forces to calculate an adaptation index. According to the adaptation index, older adults only compensated for $\sim$65% of the curl force-field dynamics by the end of adaptation, *late force 2*, compared with $\sim$84% in young adults. This could explain why older adults had greater movement devia-

tions than young adults. The lower adaptation indices in older adults also suggest that they may have formed a less-accurate internal model of the force-field dynamics.

Our results clearly indicated that older adults adapt less well, unlike previous studies that reported no difference or only a moderate decrement in adaptation in older adults. A previous force-field study found no differences in hand path error aftereffects between young and older adults and concluded that aging did not affect the ability to adapt (Cesqui et al. 2008). However, they did not measure anticipatory forces, which better reflect internal model adaptation. Furthermore, the effects of age on visuomotor learning are not clear (Buch et al. 2003; Heuer and Hegele 2008b), as both preservation of adaptation (Bock and Schneider 2002; Heuer and Hegele 2008a; Roller et al. 2002) and degradation of adaptation with increasing age (Bock 2005; Bock and Girgenrath 2006; McNay and Willingham 1998; Seidler 2006) have been reported.

More difficult tasks appear to exacerbate age-related adaptation deficits (Heuer and Hegele 2008b; Voelcker-Rehage 2008). Our protocol was challenging (gain $= -20$ Ns/m, reach distance $= 20$ cm) and designed to produce large enough changes in metabolic power that could be measured using expired gas analysis in young adults (Huang et al. 2012). We used a longer reach distance than Cesqui et al. (2008), which may explain why we observed less adaptation in older adults, whereas they did not. Additionally, during split-belt walking, which involves whole body coordination, older adults were less able to return to symmetry than young adults, suggesting impaired adaptation (Bruijn et al. 2012).

We observed that older adults used greater muscle coactivation than young adults but maintained the ability to reduce muscle activity and coactivation during motor adaptation. The increased muscle activity and coactivation during adaptation were expected since older adults generally tend to use muscle coactivation during movement (Darling et al. 1989; Hortobágyi et al. 2009; Schmitz et al. 2009; Seidler-Dobrin et al. 1998). A novel finding in this study is that increased muscle coactivation correlated with reduced adaptation. This increased muscle coactivation may have hindered adaptation since lower adaptation indices negatively correlated with greater muscle coactivation (Fig. 6). However, the increased coactivation may be a compensatory mechanism to ameliorate the consequences of a potentially impaired ability to adapt to the novel dynamics.

During motor adaptation, young adults typically increase muscle activity and coactivation initially but then rapidly reduce muscle activity and coactivation within 50–100 trials (Darainy and Ostry 2008; Franklin et al. 2003; Huang et al. 2012; Thoroughman and Shadmehr 1999). We also observed significant reductions in EMG activity during the 1st half of motor adaptation (*early force 1* to *late force 1*) and over the entire adaptation period (*early force 1* to *late force 2*; Figs. 4 and 5). In this analysis, we normalized EMG data to the MVC, whereas previously we normalized EMG to the task (i.e., *late null 1*; Huang et al. 2012). Normalizing to MVC allowed us to detect differences in EMG between older and young adults even during *null 1*. If we normalized EMG to *late null 1*, we would have observed similar trends in reductions with motor adaptation but would not have observed that older adults used statistically greater muscle activity or coactivation than young adults.

Despite using a coactivation strategy, older adults reduced metabolic cost with motor adaptation, similar to young adults. Furthermore, both young and older adults demonstrated consistent reductions in net metabolic power later during adaptation (*late force 1* to *late force 2*; Fig. 7*B*). These metabolic data support our finding that reductions in metabolic power occurred later during adaptation, when movement biomechanics and muscle activity were being fine-tuned (Huang et al. 2012).

We did not compare net metabolic power between older and young adults because older adults did not perform the exact same task as young adults. Typically, metabolic power is averaged over a specific amount of time such as the last 2 min, assuming steady-state biomechanics and metabolics. Therefore, to compare metabolic power between individuals or groups, subjects should be performing the same task. In this experiment, subjects would have had to make the same number of reaches, at the same frequency, and at the same speed. Older adults reached with ~13% slower velocities than young adults and also reached at a slower reaching frequency despite the auditory metronome. Therefore, we cannot directly compare net metabolic power between older and young adults.

A limitation of this study was that older adults had slower movement speeds even though we used an auditory metronome and provided visual feedback. A previous force-field study also reported that older adults moved with slower velocities than young adults (Cesqui et al. 2008). Although we accounted for the slower reaching speeds by using the adaptation index for our motor-adaptation analysis, we could not fairly compare metabolic power between older and young adults. We have preliminary unpublished data that indicate that net metabolic power increases with faster reaching speeds. It seems likely that older adults would have higher net metabolic power than young adults if they were moving at the same speed, which is what we would expect based on locomotion studies (Hortobágyi et al. 2011; Mian et al. 2006; Ortega and Farley 2007).

More studies are needed to determine the underlying neural mechanisms that lead to an impaired ability to form an accurate internal model with advancing age. In particular, to what extent does increased muscle coactivation affect error detection and sensory prediction errors? By increasing muscle coactivation and stiffening up, older adults can reduce the size of errors and perhaps their sensitivity to the errors. There is some evidence from a visuomotor discrimination task that older adults likely have a reduced sensitivity to visual perception and proprioception (Rand et al. 2013). Age-related declines in sensitivity to errors may lead to more gradual updates to the internal model. Additionally, to compensate for an impaired ability to form an internal model, older adults may rely more on nonspecific forms of control such as coactivation and sensory feedback during the movement. Indeed, we observed that older adults used a muscle coactivation strategy and also had prolonged deceleration phases, which may reflect an increased reliance on feedback control during the movement. Alternatively, age-related cerebellar dysfunction (Cooke et al. 1989; Eckert et al. 2010) may also lead to less adaptation. The cerebellum has been shown to encode sensory prediction errors that are critical for adaptation (Schlerf et al. 2012). Furthermore, cerebellar patients have difficulty adapting to novel dynamics because of impairment in predicting sensory outcomes (Morton and Bastian 2006; Smith and Shadmehr 2005; Tseng et al. 2007). It is also important to note that the reduced adaptation observed in the older adults may have reflected a choice rather than an explicit inability to adapt to the novel dynamics. In the interest of creating as natural a movement as possible, subjects were never explicitly told to minimize movement deviations (i.e., reach in a straight line). This leaves open the possibility that older adults may have had a larger tolerance for movement deviation. Understanding the age-related neural mechanisms that influence the formation of accurate internal models may help guide the design of interventions for preserving mobility and independence among the aging population.

In summary, older adults adapted to the novel dynamics less well than young adults. Unlike young adults, older adults employed a coactivation strategy, but, similar to young adults, older adults also reduced muscle activity and coactivation with motor adaptation. Last, older adults exhibited consistent metabolic reductions later during motor adaptation, similar to young adults. These results suggest that there is an impaired ability to form accurate internal models with advancing age and that reducing metabolic cost may be a fundamental feature of motor adaptation.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

H.J.H. and A.A.A. conception and design of research; H.J.H. 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. 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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