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Fatigue-induced adjustment in antagonist coactivation by old adults during a steadiness task

Christopher J. Arellano,[1,4] David Caha,[4] Joseph E. Hennessey,[4] Ioannis G. Amiridis,[3] Stéphane Baudry,[2] and Roger M. Enoka[4]

[1]*Department of Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island;* [2]*Laboratory of Applied Biology, Neurosciences Institute, Université Libre de Bruxelles, Brussels, Belgium;* [3]*Department of Physical Education and Sport Sciences, Aristotle University of Thessaloniki, Serres, Greece; and* [4]*Department of Integrative Physiology, University of Colorado, Boulder, Colorado*

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Arellano CJ, Caha D, Hennessey JE, Amiridis IG, Baudry S, Enoka RM. Fatigue-induced adjustment in antagonist coactivation by old adults during a steadiness task. *J Appl Physiol* 120: 1039–1046, 2016. First published February 4, 2016; doi:10.1152/japplphysiol.00908.2015.—The purpose of this study was to determine the adjustments in the level of coactivation during a steadiness task performed by young and old adults after the torque-generating capacity of the antagonist muscles was reduced by a fatiguing contraction. Torque steadiness (coefficient of variation) and electromyographic activity of the extensor and flexor carpi radialis muscles were measured as participants matched a wrist extensor target torque (10% maximum) before and after sustaining an isometric contraction (30% maximum) with wrist flexors to task failure. Time to failure was similar ($P = 0.631$) for young (417 ± 121 s) and old (452 ± 174 s) adults. The reduction in maximal voluntary contraction torque (%initial) for the wrist flexors after the fatiguing contraction was greater ($P = 0.006$) for young (32.5 ± 13.7%) than old (21.8 ± 6.6%) adults. Moreover, maximal voluntary contraction torque for the wrist extensors declined for old (−13.7 ± 12.7%; $P = 0.030$), but not young (−5.4 ± 13.8%; $P = 0.167$), adults. Torque steadiness during the matching task with the wrist extensors was similar before and after the fatiguing contraction for both groups, but the level of coactivation increased after the fatiguing contraction for old ($P = 0.049$) but not young ($P = 0.137$) adults and was twice the amplitude for old adults ($P = 0.002$). These data reveal that old adults are able to adjust the amount of antagonist muscle activity independent of the agonist muscle during steady submaximal contractions.

aging; electromyogram; fatigue; steadiness; wrist torque

NEW & NOTEWORTHY

Old adults tend to coactivate agonist and antagonist muscles more often than young adults when performing various voluntary actions. The present study compared the amount of coactivation during steady agonist submaximal contractions before and after the antagonist muscle performed a fatiguing contraction. The findings reveal that old adults, similar to what has been found for young adults, are able to independently adjust the relative activity in a pair of antagonistic muscles when performing submaximal contractions.

ADVANCING AGE IS ACCOMPANIED by functional declines in the neuromuscular system and changes in the control strategies used to perform voluntary actions (34, 41, 45). One of these adaptations is the tendency of old adults to use greater levels of agonist and antagonist muscle activity than young adults during the performance of various tasks (3, 20, 22, 28, 30), despite the greater metabolic cost associated with such a strategy (21, 35, 40). The concurrent activation of agonist and antagonist muscles, defined as coactivation, is often controlled by feedforward signals that arise from supraspinal centers (11, 32, 42). Compared with young adults, for example, Baudry et al. (3) discovered that old adults used a different neuromuscular control strategy when performing constant-torque, submaximal isometric contractions with the wrist extensor muscles under two load conditions: *1*) pushing against a rigid restraint; or *2*) supporting an inertial load. To accommodate the transition from pushing against a rigid restraint to supporting an inertial load, young adults increased the contribution of the group Ia afferent pathway to the synaptic input received by spinal motoneurons (feedback control), whereas old adults increased the level of coactivation by augmenting the synaptic input provided by descending pathways [feedforward control (32)].

The question addressed in the present report was whether the reliance on coactivation by old adults when performing a steadiness task with the wrist extensors (agonist) would be compromised after a fatigue-induced reduction in the torque-generating capacity of the wrist flexors (antagonist). The hypothesis was that old adults would increase the amplitude of electromyographic (EMG) activity in both the agonist and antagonist muscles during the torque-matching task performed after the fatiguing contraction, and this would compromise torque steadiness. The rationale underlying this hypothesis was that old adults do not have the ability to adjust the level of activity in agonist and antagonist muscles independently, hence a fatigue-induced reduction in the torque-generating capacity of the antagonist muscle would be accompanied by a corresponding increase in agonist activity. Because young adults rely less on modulating the level of coactivation when performing steady contractions, a fatigue-induced reduction in the torque-generating capacity of the antagonist muscle would not require them to adjust antagonist muscle activity during steady contractions performed after the fatiguing contraction. The outcomes were expected to indicate whether or not old adults could uncouple the common activation of agonist and antagonist muscles (8, 42), which has been demonstrated for young adults (11, 32).

METHODS

Nine young adults (mean ± SD; 23.6 ± 2.9 yr, 175.3 ± 9.3 cm, 72.4 ± 13.3 kg; 3 women) and nine old adults (76.3 ± 7.0 yr, 168.8 ± 10.7 cm, and 71.6 ± 15.4 kg; 5 women) participated in the study. Before participation, each candidate completed a phone interview to

Address for reprint requests and other correspondence: C. J. Arellano, Ecology and Evolutionary Biology, Brown Univ., Box G-W, 80 Waterman St., Providence, RI 02912 (e-mail: christopher_arellano@brown.edu).

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assess the inclusion-exclusion criteria, which included being healthy, free of any neurological disorders, and not taking any medication that would influence the ability to perform the experimental tasks. After arriving in the laboratory, the experimental protocol was explained to each volunteer, and informed consent was obtained. The Institutional Review Board for the University of Colorado Boulder approved the protocol for the study.

Experimental setup. Participants were seated in a padded chair with the left arm positioned so that the wrist joint was aligned with the shaft of a custom-built servo-controlled torque motor (Fig. 1*A*). Wrist extensor and flexor torques were applied against a padded metal plate rigidly connected to the shaft of the torque motor. The padded metal plate was adjusted in the horizontal plane until positioned at the middle of the metacarpus (Fig. 1*A*). The height of the monitor was adjusted to eye level, and each participant affirmed that the signals displayed on the monitor were clearly visible.

EMG recordings. Before attaching the surface EMG electrodes, the skin was shaved to remove any hair, scrubbed with an abrasive gel, and cleaned with alcohol. Surface EMG signals were recorded from the extensor carpi radialis (ECR), flexor carpi radialis (FCR), brachioradialis (BRD), and abductor pollicis brevis (ABP) muscles. Circular silver-silver chloride electrodes (8 mm diameter for FCR and BRD; 4 mm diameter for ECR and ABP; Coulbourn Instruments, Allentown, PA) were placed in a bipolar configuration over the belly of each muscle and secured to the skin with tape. The integrity of each EMG signal was confirmed by ensuring the noise level was <0.2 V when each muscle was relaxed, and the amplitude increased during wrist extension (ECR) and flexion (FCR), and for both muscles during radial deviation. Thumb abduction was used to assess the quality of the EMG signal for ABP. EMG signals were amplified (500-5,000 times) and band-pass filtered (13-1,000 Hz) before sampling at 2,000 Hz using Spike 2 software.

Maximal voluntary contraction torque. The protocol began with participants practicing the tasks by pushing up and down [$\leq$50% maximal voluntary contraction (MVC) torque] against the torque motor with the left hand. They were asked to focus their actions on the wrist extensors and wrist flexors, respectively. Subsequently, they performed MVCs with the wrist flexors and extensors. The MVC task involved increasing the wrist extensor/flexor torque gradually from zero to maximum over 3 s and maintaining the maximal value for ~3 s before relaxing. Participants performed two to four MVC trials with 5 min of rest between trials. Once peak torques for two MVC trials were within 5%, the greatest value was used as the MVC torque.

The torque transducer signal was sampled at 200 Hz (Power 1401, 16-bit resolution, Cambridge Electronic Design, Cambridge, UK) using Spike 2 software. The EMG and torque signals were displayed on a monitor (15 in. $\times$ 12 in.) during the experiment and stored on a computer for later analysis.

After the MVC trials, subjects performed six 45-s contractions that involved supporting an inertial load equivalent to 10% of wrist extensor MVC torque. The gain of the visual display was 5% MVC/cm. Subjects rested for ~60 s between contractions. The original experimental design involved a protocol developed in our laboratory to investigate the modulation of Ia presynaptic inhibition of the ECR motoneuron pool by randomly eliciting test and conditioned Hoffmann reflexes in sets of 10 responses during each contraction (3), which were applied equally to both groups. Due to technical issues, the present report focuses on the EMG activity of the ECR and FCR and fluctuations in torque during the steadiness task with the wrist extensors (Fig. 1*B*).

Fatigue protocol. After the initial set of six steady contractions, subjects performed a fatiguing contraction with the wrist flexor muscles. The target torque was 30% of the wrist flexor MVC value. The submaximal contraction was sustained for as long as possible, and task failure was defined as the moment when the participant reached a maximal rating of perceived exertion on a Borg scale from 6-20 (6) and was not able to match the target torque for 5 s. In some instances, however, participants simply could not continue the fatiguing contraction, and torque declined instantaneously. The EMG activity for the FCR was monitored during the fatiguing contraction, and participants were encouraged to maintain a steady torque by producing wrist joint flexion (Fig. 2). Careful attention was directed to the EMG activity for the FCR, because pilot experiments indicated that subjects tended to compensate for the progressive fatigue of the wrist flexors by pronating the wrist and increasing the contribution from BRD. When this was detected, subjects were asked to correct the action and focus the activity on the wrist flexors. Immediately after task failure, subjects performed wrist flexor and extensor MVCs and then another six 45-s contractions that involved supporting an inertial load with the wrist extensors (10% MVC torque). The time between the MVCs and the torque-matching task was $<$30 s.

Data analysis. All data were analyzed using customized code developed with commercial software (Spike2 6.09, Cambridge Electronic Design, Cambridge, UK; MATLAB R2014a, Mathworks, Natick, MA). The maximal EMG amplitude for ECR and FCR during MVCs measured before and after the fatiguing contraction was quan-

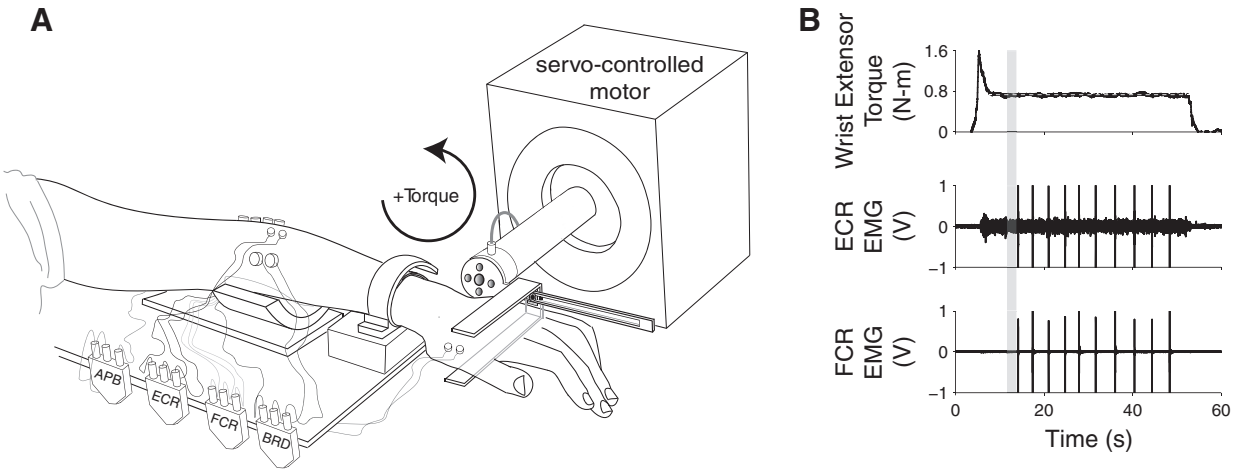

Fig. 1. Wrist extensor torque and electromyographic (EMG) activity of forearm muscles during a task that required a subject to support the position of an inertial load before and after a fatiguing contraction with the wrist flexor muscles. *A*: position of the left forearm relative to the servo-controlled torque motor. *B*: 10 electrical stimuli were applied to the radial nerve to elicit Hoffmann reflexes in the extensor carpi radialis (ECR) muscle as each participant performed a steady submaximal contraction [10% maximal voluntary contraction (MVC) torque] with the wrist extensors. EMG signals were also recorded for abductor pollicis brevis (APB), brachioradialis (BRD), and flexor carpi radialis (FCR). [Illustration in *A* adapted from Baudry et al. (3).]

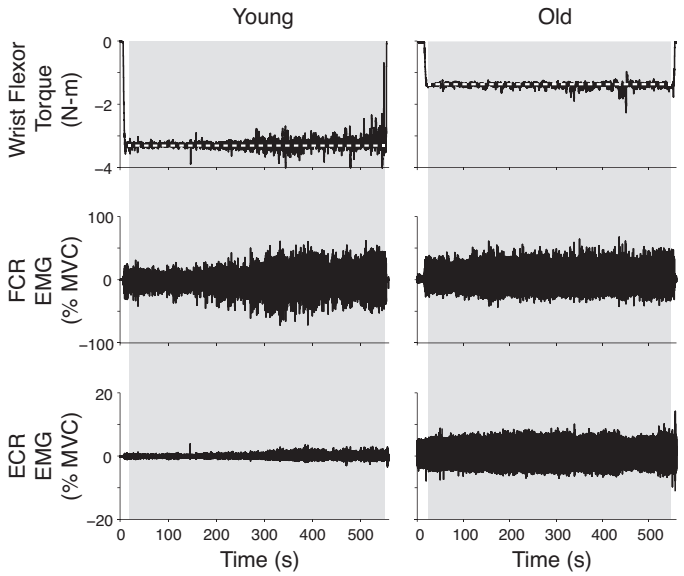

Fig. 2. Wrist flexor torque and EMG activity of forearm muscles during a fatiguing contraction for one young and one old adult. Young (*left*) and old (*right*) adults were provided visual feedback on a monitor during the fatiguing contraction and instructed to apply a constant wrist flexor torque equivalent to 30% MVC (dashed horizontal line). Surface EMG recordings are shown for FCR (agonist) and ECR (antagonist). Measurements of the coefficient of variation (CV) for wrist flexor torque, EMG amplitudes, and agonist-antagonist coactivation during the fatiguing contraction were calculated over 20-s intervals during the time period denoted by the shaded regions.

tified by averaging the rectified EMG (aEMG) over a 0.75-s window centered about the peak MVC torque. The aEMG amplitude for ECR and FCR during the six 45-s contractions performed before and after the fatiguing protocol was computed over a 2-s interval before the first electrical stimulus (emphasized by shaded region in Fig. 1*B*). Fluctuations in wrist extensor torque were characterized during the same intervals as the coefficient of variation for torque (SD torque/mean torque × 100). The aEMG and the coefficient of variation for wrist extensor torque were averaged across the six 45-s contractions for the same 2-s interval performed before and after the fatiguing protocol. These 2-s intervals were selected to avoid contamination by the first electrical stimulus applied to the radial nerve.

The aEMG for ECR and FCR during the fatiguing contraction was computed by averaging the rectified EMG over the first and last 20 s and for 20-s intervals centered at 20, 40, 60, and 80% of task duration (43, 44). The rectified aEMG amplitude for ECR and FCR at each time interval was expressed relative to the rectified aEMG amplitude recorded during maximal wrist extensor and wrist flexor MVCs performed before the fatiguing contraction. Similar to the EMG analysis, the coefficient of variation for wrist flexor torque was calculated over the first and last 20 s and for 20-s intervals centered at 20, 40, 60, and 80% of task duration.

The changes in aEMG for each muscle and the coefficient of variation for wrist flexor torque during the fatiguing contraction were quantified with single-term exponential functions for individual trials (43, 44). The initial value for each outcome variable was indicated by a constant coefficient, and the rate of change during the fatiguing contraction was quantified with an exponential term. All single-term exponential fits were performed in MATLAB (R2014a, Mathworks, Natick, MA) using a robust, nonlinear least squares fitting method by minimizing the least absolute residuals.

The level of coactivation during the submaximal wrist extensor contractions was calculated as the ratio of the aEMG values for FCR and ECR (FCR aEMG/ECR aEMG × 100). Similarly, the level of coactivation at the start and end of the fatiguing contraction with the wrist flexors was calculated as the ratio of the aEMG values for the ECR and FCR (ECR aEMG/FCR aEMG × 100). Based on the approach developed by Lévénez et al. (33), the aEMG values for ECR and FCR were normalized to their respective maximal EMG values measured during the MVCs performed before and after the fatiguing wrist flexor contraction.

Statistical analysis. A general linear model was used to examine the influence of age (young and old) and fatigue (before and after) on wrist flexor and extensor MVCs, the level of wrist extensor coactivation (FCR/ECR), and the coefficient of variation for wrist extensor torque during the steady contractions. A similar approach was used to examine the influence of age (young and old) and fatigue (start and end) on the aEMG amplitudes of the ECR and FCR, the level of wrist flexor coactivation (ECR/FCR), and the coefficient of variation for wrist flexor torque during the fatiguing contraction. In these analyses, age (young and old) was a between-subjects fixed factor, and fatigue was a within-subjects fixed factor.

A general linear model was also used to determine the influence of age on time to failure and the exponential functions for the coefficient of variation for wrist flexor torque, ECR aEMG, and FCR aEMG during the fatiguing contraction. Age was again a between-subjects fixed factor, and significance was assessed with tests of between-subjects effects.

Statistical significance was set at 0.05 for all tests (SPSS, Chicago, IL). When significant main and interaction effects were detected, appropriate univariate ANOVAs and planned comparisons between young and old adults were performed. Values are reported as means ± SD in the text and Tables 1 and 2 and as means ± SE in the Figs. 3–5.

The normality of the data was confirmed for all but two dependent variables with the Kolmogorov-Smirnov test. The two exceptions (the level of antagonist coactivation at the start of the fatiguing contraction for young adults and aEMG for ECR during the steady wrist extensor contractions for old adults) were evaluated with nonparametric statistics (Friedman and Mann-Whitney tests) to test or significant differences between groups and before and after the fatiguing contraction.

RESULTS

The MVC torques for the wrist extensors ($F_{1,16} = 7.95$, $P = 0.012$) and flexors ($F_{1,16} = 8.65$, $P = 0.010$) were greater for young than for old adults (age main effect; Table 1). When expressed as a ratio of the MVC extensor torque relative to the MVC flexor torque before the fatiguing contraction, the values were 1.12 ± 0.24 (range: 0.86–1.57) for young adults and 1.07 ± 0.23 (range: 0.85–1.45) for old adults.

Steady wrist extensor contractions. The coefficient of variation for torque during the steadiness task (10% MVC torque) was similar before and after the fatiguing contraction for both young (1.23 ± 0.42 and 1.18 ± 0.29% MVC) and old (1.37 ± 0.29 and 1.43 ± 0.20% MVC) adults (fatigue main effect; $F_{1,16} = 0.02$, $P = 0.901$); however, there was no difference between groups (age main effect: $F_{1,16} = 1.99$, $P = 0.177$; young: 1.21 ± 0.35% MVC; old: 1.4 ± 0.25% MVC; Fig. 3, *A* and *B*).

Although both groups performed steady wrist extensor contractions at the same relative net torque, old adults exhibited greater aEMG amplitudes for the agonist (ECR, age main effect; $F_{1,16} = 3.46$, $P = 0.041$) and antagonist (FCR; age main effect; $F_{1,16} = 10.90$, $P = 0.003$) muscles. The aEMG amplitude for the agonist (ECR) was 16.7 ± 4.8 and 24.8 ± 12.6% MVC for young and old adults, respectively, whereas that for the antagonist (FCR) was 1.3 ± 0.8 and 3.9 ± 2.4% MVC, respectively.

The aEMG amplitude of the agonist muscle (ECR) during the torque-matching steadiness task remained similar after the

Table 1. *MVC torques (before and after) and aEMG amplitudes (start and end) for young and old adults performing a fatiguing contraction sustained at 30% MVC wrist flexor torque*

	Young		Old	
	Wrist flexors	Wrist extensors	Wrist flexors	Wrist extensors
MVC torque, N·m				
Before	9.0 ± 2.3	8.6 ± 3.3	5.9 ± 1.2†	5.7 ± 1.5†
After	6.2 ± 2.3*	7.8 ± 2.2	4.6 ± 0.7*†	4.9 ± 1.4*†
%Δ	−32.5 ± 13.7	−5.4 ± 13.8	−21.8 ± 6.6	−13.7 ± 12.7
ΔMVC aEMG, %before	−14.9 ± 31.0	−3.4 ± 23.6	−16.2 ± 27.2	−5.3 ± 20.0
aEMG, %MVC				
Start	29.1 ± 10.6	2.3 ± 0.8	30.9 ± 7.4	6.4 ± 3.8
End	57.3 ± 20.6‡	4.6 ± 3.2‡	48.2 ± 9.8‡	8.0 ± 3.0‡

Values are means ± SD. The change (Δ) in maximal voluntary contraction (MVC) average rectified electromyographic (aEMG) values indicates the percent decline during the MVC performed after the fatiguing contraction relative to the MVC performed before the fatiguing contraction. The aEMG values for the wrist flexors were obtained from flexor carpi radialis (FCR), and those for the wrist extensors were recorded from extensor carpi radialis (ECR). $P < 0.05$ compared with *before the fatiguing contraction, †young adults, and ‡the start of the fatiguing contraction.

fatiguing contraction (fatigue main effect; $F_{1,16} = 2.08$, $P = 0.169$) for both young [before: 16.2 ± 4.8% MVC; after: 17.1 ± 5.0% MVC; $t(8) = -0.641$, $P = 0.54$] and old [before: 23.2 ± 13.2% MVC; after: 26.4 ± 12.6% MVC; $t(8) = -1.294$, $P = 0.12$] adults. This was confirmed by a Friedman nonparametric test, which revealed that the aEMG amplitude of the ECR during the torque steadiness task was similar before and after fatiguing contraction for young [$\chi^2(1) = 1.00$, $P = 0.31$] and old [$\chi^2(1) = 0.11$, $P = 0.73$] adults. The aEMG of the antagonist muscle (FCR) during the torque steadiness task did not change after the fatiguing contraction (fatigue main effect; $F_{1,16} = 9.84$, $P = 0.006$) for young adults [before: 1.1 ± 0.6% MVC; after: 1.5 ± 1.0% MVC; $t(8) = -1.773$, $P = 0.11$], but increased significantly for old adults [before: 3.3 ± 2.1% MVC; after: 4.6 ± 2.7% MVC; $t(8) = -2.637$, $P = 0.02$]. As a result, the level of coactivation when supporting the inertial load during the torque steadiness task was significantly greater (age main effect: $F_{1,16} = 13.01$, $P = 0.002$) for old (15.9 ± 6.1%) than young adults (7.8 ± 4.5%), and it was greater after the fatiguing contraction for old [before: 14.3 ± 4.1%; after: 17.6 ± 7.5%; $t(8) = -1.877$, $P = 0.049$] but not for young adults [before: 6.9 ± 4.1%; after: 8.6 ± 5.0%; $t(8) = -1.176$, $P = 0.137$].

Fatiguing contraction. Young and old adults sustained the submaximal fatiguing contraction with the wrist flexors for a similar duration (young: 417 ± 121 s; old: 452 ± 174 s; $F_{1,16} = 0.24$, $P = 0.631$). The ratings of perceived exertion at task failure did not differ statistically ($F_{1,16} = 0.84$, $P = 0.372$) for the young (19.67 ± 0.50) and old (19.44 ± 0.53) adults. Although the average coefficient of variation for wrist flexor torque did not differ between groups ($F_{1,16} = 3.27$, $P = 0.089$), the rate of exponential increase in the coefficient of variation for torque was greater for young than for old adults ($F_{1,16} = 16.30$, $P = 0.001$; Table 2). By the end of the fatiguing contraction, the coefficient of variation for torque was 1.6 times greater for young than for old adults (Fig. 4*A*).

When expressed as a percentage of the initial MVC, the constant coefficient (initial value) and rate of exponential increase in aEMG for the FCR muscle during the fatiguing contraction (Fig. 4*C*) were similar for young and old adults ($F_{1,16} = 2.15$, $P = 0.162$ and $F_{1,16} = 2.03$, $P = 0.173$, respectively; Table 2). The constant coefficient in aEMG for the antagonist muscle (ECR) during the fatiguing contraction with the wrist flexors was greater for old than for young adults ($F_{1,16} = 6.94$, $P = 0.018$; Fig. 4*B*), whereas the rate of exponential increase in aEMG for this muscle was similar for the two groups ($F_{1,16} = 3.58$, $P = 0.077$; Table 2).

An age main effect indicated that the level of coactivation during the fatiguing contraction was greater for old (18.6 ± 8.1%) than young (8.8 ± 6.1%, $F_{1,16} = 11.99$, $P = 0.003$) adults. This was confirmed by a Mann-Whitney nonparametric test, indicating that the level of coactivation at the start ($U = 11.00$, $P = 0.009$) and end ($U = 10.00$, $P = 0.007$) was significantly greater for old than young adults. A fatigue main effect revealed that aEMG values for both FCR (start: 30.0 ± 8.9% MVC; end: 52.7 ± 16.3% MVC, $F_{1,16} = 52.80$, $P < 0.001$) and ECR (start: 4.4 ± 3.4% MVC; end: 6.3 ± 3.5% MVC, $F_{1,16} = 12.66$, $P = 0.003$) were greater at the end of the fatiguing contraction (Fig. 5, *A* and *B*). The similar increases in aEMG for the agonist (FCR) and antagonist (ECR) resulted in no statistically significant difference in the level of coactivation

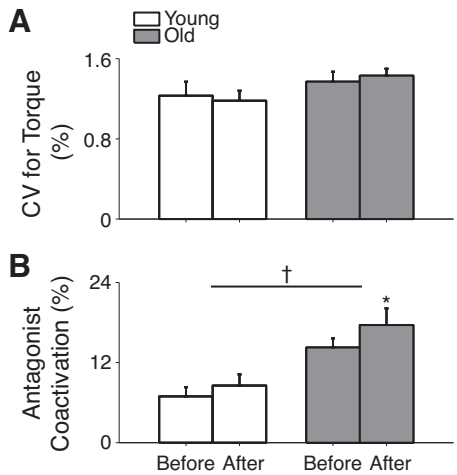

Fig. 3. Influence of a fatiguing contraction with the wrist flexors on the CV for wrist extensor torque (*A*) and agonist-antagonist coactivation (*B*) during steady submaximal contractions performed by young and old adults. The level of antagonist coactivation values derived from the average amplitude of the rectified EMG signal (aEMG) for ECR and FCR were normalized to the respective MVC values measured before and after the fatiguing contraction. Values are means ± SE. *$P < 0.05$ before vs. after the fatiguing contraction. †$P < 0.05$ between young and old (age main effect).

Table 2. *Single-term exponential fits underlying the change in CV for torque and aEMG amplitude for the ECR and FCR muscles during a fatiguing contraction sustained at 30% MVC torque with the wrist flexors by young and old adults*

	CV for Torque, %		ECR aEMG, %		FCR aEMG, %	
	a	exp^b	*a*	exp^b	*a*	exp^b
Young	1.37 ± 0.43	1.004 ± 0.001	3.28 ± 2.10	1.001 ± 0.001	25.31 ± 7.58	1.002 ± 0.002
Old	1.66 ± 0.58	1.002 ± 0.001*	5.87 ± 3.55*	1.001 ± 0.001	30.30 ± 8.78	1.001 ± 0.001

Values are means ± SD. The term *a* denotes the initial value (constant coefficient), and the term exp^b indicates the rate of change (exponential) during the fatiguing contraction. CV, coefficient of variation. *$P < 0.05$ between young and old adults.

(fatigue main effect; $F_{1,16} = 0.93$, $P = 0.349$) at the start (14.6 ± 9.7% MVC) and end (12.8 ± 7.5% MVC) of the fatiguing contraction for both groups (Fig. 5*C*). This was confirmed by a Friedman nonparametric test, which revealed that the level of coactivation was similar at the start and end of the fatiguing contraction for young [$\chi^2(1) = 0.11$, $P = 0.74$] and old [$\chi^2(1) = 1.00$, $P = 0.32$] adults.

Immediately after the fatiguing contraction, wrist flexor MVC torque decreased for both groups (fatigue main effect; $F_{1,16} = 78.09$, $P < 0.001$), but the reduction was greater for young (−32.5 ± 13.7%) than old (−21.8 ± 6.6%) adults ($F_{1,16} = 9.93$, $P = 0.006$, Table 1). In contrast, planned comparisons due to the finding of a fatigue main effect ($F_{1,16} = 7.15$, $P = 0.17$) indicated that wrist extensor MVC torque did not change after the fatiguing contraction for young adults [−5.4 ± 13.8%; $t(8) = 1.52$, $P = 0.167$], whereas it decreased significantly for old adults [−13.7 ± 12.7%; $t(8) = 2.63$, $P = 0.030$, Table 1].

DISCUSSION

The purpose of the current study was to determine the adjustments in the level of coactivation during a steadiness task performed by young and old adults after the torque-generating capacity of the antagonist muscle was reduced by a fatiguing contraction. Steadiness (coefficient of variation for torque) during a torque-matching task with the wrist extensors was similar before and after a wrist flexor fatiguing contraction for both young and old adults (Fig. 3*A*). The primary finding was that old adults were able to maintain torque steadiness after the fatiguing contraction by independently adjusting the EMG amplitude for the agonist (ECR) and antagonist (FCR) muscles (Fig. 3*B*). The results broadens our understanding of previous work on young adults (32, 33) by demonstrating that the level of coactivation exhibited by old adults is not constrained by the common activation of an antagonistic set of muscles (8, 11, 42).

Steady wrist extensor contractions. In the present study, the coefficient of variation for wrist extensor torque when matching a target value of 10% MVC was similar for young and old adults both before and after the fatiguing contractions. Baudry et al. (3) also found similar values for young and old adults

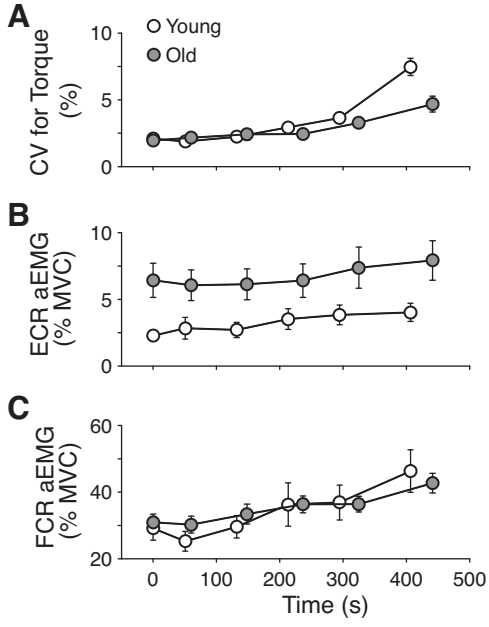

Fig. 4. Changes in the CV for wrist flexor torque (*A*) and aEMG for the ECR (*B*) and FCR (*C*) during the fatiguing contraction performed by young and old adults. Values are means ± SE.

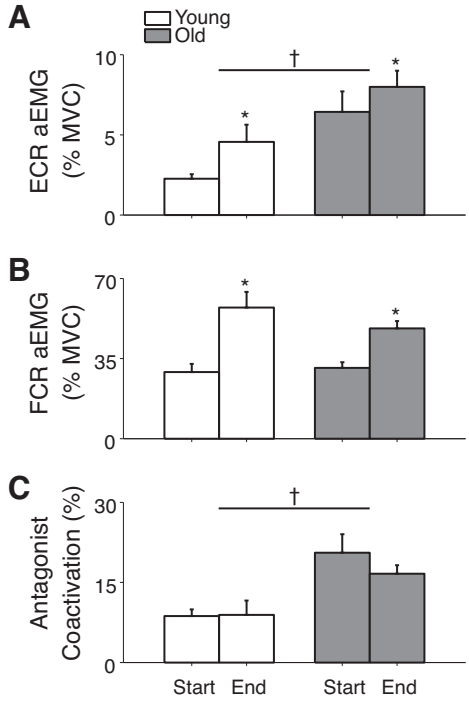

Fig. 5. Young and old adults modulated the agonist and antagonist EMG activity of the upper limb during the fatiguing contraction. Values are means ± SE for aEMG of the ECR (*A*) and FCR (*B*) muscles and antagonist coactivation (*C*) measured at the start and end of the fatiguing contraction. Note that the aEMG amplitude for the ECR and FCR was normalized to the respective MVC values measured before and after the fatiguing contraction. *$P < 0.05$ start vs. end of fatiguing contraction. †$P < 0.05$ between young and old (age main effect).

when they performed torque-matching steady contractions at 10 and 15% MVC torque with the wrist extensors, but the coefficient of variation were greater for old than young adults when the target torque was matched to 5% MVC.

The fluctuations in muscle torque during steady, submaximal contractions are attributable to the proportion of common synaptic input received by the involved motor units (12, 13). The magnitude of the fluctuations, and hence the relative amount of common input, varies with target torques (15, 16), is greater for muscles with fewer motor units (17), is often greater for old relative to young adults (7, 15, 29), and differs with load compliance (37). The data in the present study suggest that the proportion of common synaptic input to the motoneurons activated during the steady contraction at 10% MVC torque with the wrist extensors was similar for both age groups before and after the fatiguing contraction, despite differences in aEMG amplitude between the two groups.

Fatigue task. Time to failure when sustaining an isometric contraction at 30% MVC wrist flexor torque and the rating of perceived exertion at task failure were similar for both groups. Immediately after task failure, however, the decline in MVC torque for the agonist (wrist flexors) was greater for young than old adults. Furthermore, the coefficient of variation for torque at the end of the fatiguing contraction was greater for young adults (Fig. 4*A*). Together, these two outcomes suggest that old adults did not sustain the fatiguing contraction with the wrist flexors to the same final intensity as young adults (26, 44).

The two groups, nonetheless, exhibited similar adjustments in antagonist and agonist muscle activity during the fatiguing contraction (9). The exponential rate of increase (Fig. 4 and Table 2) in aEMG for the agonist (FCR) and antagonist (ECR) muscles were similar, resulting in levels of coactivation (Fig. 5*C*) that remained constant at the start and end of the fatiguing contraction for the two groups. Although the average level of coactivation was greater for old adults (Fig. 5*C*), the aEMG for the antagonist muscle (ECR; Fig. 4*B*) seems rather low to have been responsible for the reduction in MVC torque for the antagonist muscle (Table 1) immediately after the fatiguing contraction. Despite young adults sustaining the fatiguing contraction to a greater level of fatigability (decline in MVC torque and increase in the coefficient of variation for torque), MVC torque for their wrist extensors was not reduced after the fatiguing contraction. These results suggest the control of activation in a set of antagonistic muscles changes with advancing age.

Age-associated differences in the ability to control a pair of antagonistic muscles were demonstrated in a study that examined steadiness during the concurrent contraction (cocontraction) of the dorsiflexor and plantar flexor muscles (19). The task was to match a dorsiflexor target force (10% MVC) and then cocontract the plantar flexor muscles to reduce the net torque to zero while maintaining EMG amplitude for the dorsiflexor muscles. Young, middle-aged, and old adults practiced the task for 50 min with the goal of improving steadiness. Young adults improved steadiness (~19%) after practicing the task, whereas there was no change in steadiness for middle-aged adults, and old adults actually became less steady. Moreover, MVC torque for the plantar flexors declined significantly for middle-aged (~17%) and old (~20%) adults after the practice session, but not for young adults. Similar age-group changes were reported for ratings of perceived exertion during the steady contractions performed at the beginning and end of the practice session. Since there was no difference in MVC force for the plantar flexors between young and middle-aged subjects, the findings indicated that the decline in the ability to control the voluntary actions of antagonistic muscles precedes the reduction in muscle strength.

Coactivation of agonist and antagonist muscles. Both the present study and its precursor (3) found that the level of coactivation during the same 10% MVC torque steadiness task was greater for old than young adults. The present study discovered that the level of coactivation increased, due to a relatively greater increase in aEMG for the antagonist (FCR) muscle, after the fatiguing contraction for old but not for young adults (Fig. 3*B*). The difference in the role of the antagonist muscle during the torque steadiness task for the two groups is underscored by the observation that the decrease in wrist flexor MVC torque after the fatiguing contraction was greater for young adults (Table 1). Yet young adults did not exhibit a statistically significant change in aEMG for the FCR during the subsequent torque-steadiness task with the wrist extensors. Thus young and old adults achieved similar values for torque steadiness by recruiting relatively different amounts of agonist and antagonist muscle activity.

Compared with young adults, old adults often use elevated levels of coactivation when performing such tasks as downward stepping (20, 23), walking (14, 21), maintaining balance while standing (5, 31), performing a functional reach test (38), during MVCs with the arm muscles (28), and when learning novel arm-reaching movements (24). These observations beg the question of why old adults tend to increase the level of coactivation during such tasks rather than engaging sensory feedback pathways (3).

One likely explanation is that aging reduces the responsiveness of spinal reflex pathways (2, 27, 39). Consistent with this finding is that proprioceptive acuity (1, 10) and processing of visual information (4) are also reduced in old adults. Together, these effects of aging may require old adults to shift from a feedback- to a feedforward-dominated control strategy. The feedforward control of coactivation also involves supraspinal pathways (11). In addition, declines in corticospinal function may contribute to a greater reliance on coactivation by old adults (1, 2). Although coactivation can increase joint stiffness and thereby augment stability (11, 18), the trade-off is an increase in the metabolic cost of the prescribed task (18, 21, 25, 35, 36, 40).

Nonetheless, the adaptations underlying the greater levels of coactivation observed in old adults seem difficult to reverse. After practicing a novel arm-reaching task, for example, old adults reduced the level of muscle activity and the metabolic cost of the task, as did young adults, but old adults continued to exhibit greater amounts of coactivation (24), representing a greater reliance on feedforward control. Old adults in this study also exhibited a greater reliance on feedforward control by independently adjusting the level of EMG activity in agonist and antagonist muscles during a steady contraction performed after a fatiguing contraction reduced the torque-generating capacity of the antagonist muscle. It has been demonstrated that young adults are capable of such independent control of antagonistic muscles (11, 32), but it now appears that old adults also possess this ability. However, the range of conditions

under which the independent control of antagonist muscles can be observed remains to be examined.

Conclusion. Previous work found that the adjustments used to accommodate a change in load compliance while performing a steady, submaximal contraction differed for young and old adults (3). Whereas young adults increased the level of sensory feedback provided by Ia afferents to perform the task, old adults increased the level of coactivation. The results of the present study demonstrate that, when the torque-generating capacity of the antagonist muscle is comprised, old adults are able to modulate the amount of activity in agonist and antagonist muscles independently and maintain the same level of torque steadiness. Contrary to the hypothesis, the findings indicate that old adults are able to adjust the relative activity in a pair of antagonistic muscles when performing steady, submaximal contractions.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

Author contributions: C.J.A., S.B., and R.M.E. conception and design of research; C.J.A., D.C., J.E.H., and I.G.A. performed experiments; C.J.A., D.C., and J.E.H. analyzed data; C.J.A., S.B., and R.M.E. interpreted results of experiments; C.J.A. prepared figures; C.J.A. drafted manuscript; C.J.A., D.C., I.G.A., S.B., and R.M.E. edited and revised manuscript; C.J.A., D.C., J.E.H., I.G.A., S.B., and R.M.E. approved final version of manuscript.

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