Presynaptic Modulation of Ia Afferents in Young and Old Adults When Performing Force and Position Control

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Baudry S, Maerz AH, Enoka RM. Presynaptic modulation of Ia afferents in young and old adults when performing force and position control. J Neurophysiol 103: 623–631, 2010. First published November 25, 2009; doi:10.1152/jn.00839.2009. The present work investigated presynaptic modulation of Ia afferents in the extensor carpi radialis (ECR) when young and old adults exerted a wrist extension force either to support an inertial load (position control) or to achieve an equivalent constant torque against a rigid restraint (force control) at 5, 10, and 15% of the maximal force. H reflexes were evoked in the ECR by stimulating the radial nerve above the elbow. A conditioning stimulus was applied to the median nerve above the elbow to assess presynaptic inhibition of homonymous Ia afferents (D1 inhibition) or at the wrist (palmar branch) to assess the ongoing presynaptic inhibition of heteronymous Ia afferents that converge onto the ECR motor neuron pool (heteronymous Ia facilitation). The young adults had less D1 inhibition and greater heteronymous Ia facilitation during the position task (79 and 132.1%, respectively) compared with the force task (69.1 and 115.1%, respectively, P < 0.02). In contrast, the old adults exhibited no difference between the two tasks for either D1 inhibition (~72%) or heteronymous Ia facilitation (~114%). Contraction intensity did not influence the amount of D1 inhibition or heteronymous Ia facilitation for either group of subjects. The amount of antagonist coactivation was similar between tasks for young adults, whereas it was greater in the position task for old adults (P = 0.02). These data indicate that in contrast to young adults, old adults did not modulate presynaptic inhibition of Ia afferents when controlling the position of a compliant load but rather increased coactivation of the antagonist muscle.

INTRODUCTION

The existence of presynaptic inhibition of Ia afferents has been known for several decades (Frank and Fuortes 1957) and is assumed to be responsible for depressing the Ia afferent input received by motor neurons (Rudomin and Schmidt 1999). The mechanism underlying Ia presynaptic inhibition involves a reduction in the release of neurotransmitter from the Ia afferents due to their depolarization by primary afferent depolarization (PAD) interneurons (Rudomin and Schmidt 1999). Since the seminal work of Mizuno and colleagues (1971) on presynaptic depression of the triceps surae H reflex after stimulation of the common peroneal nerve, presynaptic inhibition of Ia afferents has been studied in a range of muscles and conditions in humans (Aimonetti et al. 1999; Aymard et al. 2001; Berardelli et al. 1987; Hultborn et al. 1987a; Nielsen and Kagamihara 1993).

Previous work has demonstrated that the strength of Ia presynaptic inhibition, which is largely controlled by supraspinal centers (Meunier and Pierrot-Deseilligny 1998; Stein 1995), can be modulated across tasks (Aimonetti et al. 1999; Aymard et al. 2001; Hultborn et al. 1987a). We recently reported that presynaptic inhibition of the Ia afferents in the extensor (ECR) and flexor carpi radialis (FCR) muscles was reduced when subjects controlled hand position while supporting a mass (position control) compared with exerting an equivalent constant torque against a rigid restraint (force control) (Baudry and Enoka 2009). These results indicate that the excitability of the PAD interneurons varies with load compliance and modulates the contribution of Ia afferent input to the net synaptic input received by motor neuron pool of wrist muscles.

Several studies have found that old adults are less able than young adults to modulate presynaptic inhibition of Ia afferents converging onto the soleus motor neuron pool when exerting plantar flexion forces to match different target forces (Butchart et al. 1993; Earles et al. 2001) and when going from a supine to a standing position (Koceja and Mynark 2000). The reduced capacity of older adults to modulate Ia presynaptic inhibition in the lower limb, however, may not generalize to the upper limb where the modulation appears to be stronger. For example, corticospinal projections to PAD interneurons differ for lower and upper limbs as presynaptic inhibition has been found to be greater in upper limb muscles in response to cortical stimulation (Meunier and Pierrot-Deseilligny 1998). Furthermore, presynaptic inhibition of Ia afferents from the flexor carpi radialis decreased at the onset and during a tonic contraction with the wrist flexors (Aymard et al. 2001), whereas the decrease was only observed at the onset of the contraction in lower leg muscles (Hultborn et al. 1987b). The purpose of the current study was to quantify the modulation of Ia presynaptic inhibition in extensor carpi radialis as young and old adults exerted torques against two types of loads that young adults manage with different levels of Ia presynaptic inhibition. Two independent methods were used to assess the level of presynaptic Ia inhibition as participants either supported a compliant load or pushed against a rigid restraint. Some of these data have been presented previously in abstract form (Baudry et al. 2009).

METHODS

Twelve young (25.9 ± 4.8 yr, 5 women) and 12 old (74.0 ± 2.8 yr, 7 women) adults volunteered to participate in the study after informed consent was obtained. None of the subjects reported any neurological disorder. Participants reported to the laboratory for two separate sessions separated by ≥48 h and were asked to refrain from exercising the arm muscles for 24 h before testing. The Human Research Committee for the University of Colorado at Boulder approved the protocol.
**Experimental setup**

Subjects were seated in a chair with the left arm abducted by −1.3 rad, the elbow flexed to 1.57 rad, and the forearm in a neutral posture (midway between pronation and supination). The left wrist joint was aligned with the shaft of a servo-controlled torque motor (PMA44Q, Pacific Scientific, Rockford, IL, and PCI-7352, National Instruments, Austin, TX). The extension force exerted by the hand was applied against a padded metal plate (2 × 10 cm) that was attached to the torque motor; the plate was located at the middle of the metacarpus (Fig. 1A). The torque motor used a Labview Real Time system (2 PCs using a PCI-6029 and a PCI-6021, National Instruments) to simulate an inertial (compliant) load in a gravitational field, which was required for the position task. The torque transducer signal, analog signals of the simulated mass, motor shaft position, and angular velocity were A/D sampled at 200 Hz (Power 1401, 16-bit resolution, Cambridge Electronic Design, Cambridge, UK) and stored on a computer for subsequent analysis.

**Electromyographic recordings**

Electromyographic (EMG) signals were recorded from extensor carpi radialis (ECR), flexor carpi radialis longus (FCR), brachioradialis, and abductor pollicis brevis with surface electrodes (silver-silver chloride electrodes 8-mm diam for FCR and brachioradialis, 4 mm for ECR and abductor pollicis brevis, Coulbourn Instruments, Allentown, PA) placed in a bipolar configuration. The EMG signals were amplified (500–5,000 times) and band-pass filtered (13–1,000 Hz) prior to sampling at 2 kHz (Coulbourn Instruments) and storage on a computer. Voluntary contractions in the directions of wrist extension, radial deviation of the wrist, and elbow flexion were used to determine the correct placement of the surface electrodes.

**MVC force**

The wrist extension maximal voluntary contraction (MVC) involved a gradual increase in torque from zero to maximum over 3 s and sustaining the maximal torque for ∼3 s. Subjects were instructed to use only the wrist extensor muscles and to avoid contracting the elbow flexors. At least two trials were performed, with subjects resting for 90–120 s between trials to minimize fatigue. If the peak torques were within 5% of each other, the greater value was taken as the maximum and used as a reference for the submaximal contractions. Otherwise, additional trials were performed until the 5% criterion was achieved. In addition, single MVCs were performed with the wrist and elbow flexors for EMG normalization of FCR and brachioradialis activity, respectively.

**Electrical stimulation**

Electrical stimuli were used to elicit test H reflexes and to provide conditioning stimuli that produced either D1 inhibition (Mizuno et al. 1971) or heteronymous Ia facilitation (Hultborn et al. 1987a,b). The stimuli were elicited by electrical stimulation (Grass S88K, Astra-Med, West Warwick, RI; 1-ms rectangular pulse) of the target nerve via a constant current unit (Model CCU1, Astra-Med) that was connected to adhesive surface electrodes (Conmed, Utica, NY) placed in a bipolar configuration. The radial nerve (H reflex) was stimulated from the lateral side of the upper arm between the brachialis and triceps brachii muscles. The median nerve (D1 inhibition) was stimulated from the medial side of the upper arm just above the distal tendon of biceps brachii. The palmar branch of the median nerve (heteronymous Ia facilitation) was stimulated from the median side of the forearm at the level of the wrist. Stimulation locations were determined at rest (median nerve, palmar branch of the median nerve) and during a contraction at 5% MVC force (radial nerve).

The motor threshold was determined by checking both the occurrence of an M wave and a twitch response in the FCR with stimulation of the median nerve at the arm level and in abductor pollicis brevis with stimulation of the palmar branch of the median nerve. The intensity for the conditioning stimulation was expressed relative to the motor threshold (× MT) for comparisons between subjects.

**Test H reflexes and conditioned H reflexes**

H REFLEX. The recruitment curve for the H reflex and M wave for ECR was recorded as subjects contracted at 5% of MVC in the force task. Electrical stimuli were delivered to the radial nerve in trains of 10 pulses with an interval of 1.75 ± 0.25 s between pulses. The EMG activity in response to each stimulus within the train was averaged and monitored on an oscilloscope and simultaneously stored on a computer for subsequent analysis. The initial intensity was set below H-reflex threshold and gradually increased until the maximal value of the M wave (Mmax) was evoked. The stimulation was then adjusted to yield a test H-reflex amplitude of ∼10% of Mmax (∼57 and ∼65% of the H max for young and old adults, respectively) throughout the experimental protocol.

D1 INHIBITION. The test H reflex was conditioned by a stimulus applied to the median nerve to activate the PAD interneurons respon-
possible for presynaptic inhibition of the Ia afferents from the ECR (Aimonetti et al. 1999; Berardelli et al. 1987). The delay between median (conditioning stimulus) and radial (test stimulus) nerve stimuli that produced the greatest depression of the H-reflex amplitude was determined for each participant in 5-ms steps. The amplitude of the test H reflex and the conditioned H reflex were obtained by averaging ≥10 responses. The intensity of the conditioning stimulus applied to the median nerve was set at 0.8–1.0 × MT so that H-reflex amplitude was depressed by ~30% in both groups of subjects (Fig. 1B).

HETERONYMOUS IA FACILITATION. An electrical stimulus was applied to the palmar branch of the median nerve at the level of the wrist to evoke a monosynaptic (heteronymous) facilitation from Ia afferents in the median nerve to the motor neuron pool of the ECR (Marchand-Pauvert et al. 2000). The first 0.5 ms of the monosynaptic heteronymous facilitation arises only from Ia afferents (Hultborn et al. 1987b). Therefore the onset of heteronymous Ia facilitation of the H reflex in ECR by stimulating the palmar branch of the median nerve (1 × MT) was established by using 1-ms and then 0.2-ms steps between the conditioning stimulus and test stimulus. The delay was then set 0.2 ms later for the rest of the experiment to ensure adequate activation of heteronymous Ia afferents (Baudry and Enoka 2009) (Fig. 1B). Under these conditions, the reflex facilitation was assumed to depend only on the size of the excitatory postsynaptic potential elicited by the monosynaptic heteronymous stimulus.

Experimental procedure

Subjects participated in two experimental sessions to assess Ia presynaptic inhibition during the force and position tasks: the D1-inhibition method was used in one session, and the heteronymous Ia facilitation method was used in the other session. The order of the sessions was counterbalanced across subjects. Each experimental session began with the subject performing MVCs in the directions of wrist extension, wrist flexion, and elbow flexion. After the MVCs, the location of the stimulating electrodes for the radial nerve (test H reflex) was determined and the recruitment curve for the H reflex and M wave in ECR was established. Next the location of the electrodes for either the median nerve (D1 inhibition) or the palmar branch of the median nerve (heteronymous Ia facilitation) was located and the intensity and delay between the conditioning and test stimuli were established as subjects performed the force task at 5% MVC force.

The main part of the protocol involved evoking test H reflexes and conditioned H reflexes as subjects performed the force and the position tasks at 5, 10, and 15% of MVC force in a counterbalanced order. As the sensitivity of the H reflex to excitatory and inhibitory inputs depends on its amplitude (Crone and Nielsen 1989), the amplitude of the test H-reflex was adjusted to be the same in both tasks at all contraction intensities (~10% M-max). Test and conditioned H reflexes were then randomly alternated in sets of 20 reflexes evoked every 1.75 ± 0.25 s. Each contraction lasted ~35 s, and there was ≥60 s of rest between two successive contractions. The responses were averaged from a minimum of 20 H reflexes and 20 conditioned H reflexes (most subjects had ≥40 responses for each reflex) for each contraction intensity and load type.

Data analysis

Surface EMG signals were rectified and averaged (aEMG) over a 0.75-s epoch from the peak EMG during the MVCs. The aEMG during the submaximal contractions at 5, 10, and 15% MVC force was measured for a 0.75-s epoch that preceded the stimuli. The EMG activity recorded from each muscle was normalized to the maximal value recorded during the respective MVC. The coactivation ratio was calculated as the EMG amplitude for FCR muscle relative to that for ECR.

H-reflex responses were characterized by latency—time from the stimulus artifact to the beginning of the EMG response; duration—the time between the onset of EMG activity and the return to the mean background EMG level; peak-to-peak amplitude—distance between the positive and negative peaks. The coefficient of variation for force (SD divided by the mean) was calculated from 2-s intervals during each contraction that did not include any stimuli.

Statistics

Prior to comparing each dependent variable, the normality of the data were confirmed with the Kolmogorov-Smirnov test. The amplitude of the test H reflex (normalized to M-max) and the amount of inhibition and facilitation of the conditioned H reflex (expressed as a percentage of the test H-reflex amplitude) within the two age groups were compared with a two-way ANOVA with repeated measures (task × contraction intensity). The effect of age on the modulation of presynaptic inhibition (amplitude of the conditioned H reflex in the position task subtracted by the amplitude of the conditioned H reflex in the force task) was analyzed with a two-way ANOVA (age × contraction intensity) with repeated measures on contraction intensity. The latency and duration of the H reflexes were examined with a three-way ANOVA (age × task × contraction intensity) with repeated measures on task and intensity. Similarly, the EMG amplitude during the tasks (normalized to the MVC value) and the force fluctuations were analyzed with two (task × contraction intensity)- and three-way ANOVAs (age × task × contraction intensity) with repeated measures on task and contraction intensity.

When a significant main effect was found with an ANOVA, a Tukey post hoc test was used to identify the significant differences among the selected means. The delay between the conditioning and test stimuli, the MVC torque, and the MVC EMG were compared between young and old adults with unpaired t-test. The level of statistical significance was set at P < 0.05 for all comparisons. Unless otherwise specified, values are expressed by means ± SD in the text and means ± SE in the figures.

RESULTS

The maximal force exerted by the hand when contracting the wrist extensor muscles did not differ between young (102.0 ± 26.5 N) and old adults (83.4 ± 20.6 N, unpaired t-test, P = 0.20). Similarly, the absolute EMG amplitude recorded from the ECR did not differ (unpaired t-test, P = 0.24) between the young (0.326 ± 0.241 mV) and old adults (0.221 ± 0.102 mV).

TEST H REFLEX. The intensity of the test stimulus was adjusted to keep H-reflex amplitude constant across tasks and contraction intensities during D1 inhibition (task × contraction intensity: young, P = 0.28; old, P = 0.52) and heteronymous Ia facilitation experiments (young, P = 0.38; old, P = 0.24; Table 1). The latency of the H reflex in ECR was longer (age main effect, P < 0.001) for the old adults (19.0 ± 1.7 ms) than the young adults (16.7 ± 1.7 ms). In the absence of a difference in the height of the subjects (young: 175 ± 8.7 cm; old: 169 ± 10.0 cm; unpaired t-test, P = 0.12), this result suggests a slowing in the nerve conduction velocity (Brooke et al. 1989; Dorfman and Bosley 1979), a change synaptic transmission (Sant’Ambrogio et al. 1961; Wayner and Emmers 1958), or a combination of the two adaptations. In contrast, no difference was observed in the duration of the H reflex between young (12.3 ± 2.6 ms) and old adults (11.5 ± 2.4 ms; P = 0.16).

D1 INHIBITION. A conditioning stimulus was applied to the median nerve to investigate homonymous presynaptic inhibi-
tion of Ia afferents from ECR. Data from 12 young and 12 old subjects were obtained for this part of the study. The mean delay between the two stimuli did not differ (unpaired t-test, \( P = 0.83 \)) between the two age groups and was 17.7 ± 2.6 and 17.9 ± 2.6 ms for young old adults, respectively. Under these conditions, the amplitude of the conditioned H reflex was depressed to 68.5 ± 13.4, 69.2 ± 15.7, and 69.7 ± 16.8% of the test H reflex in young adults to 73.5 ± 13.6, 71.0 ± 14.6, and 71.2 ± 17.0% of the test H reflex in old adults during the force task at 5, 10, and 15% MVC force, respectively (Fig. 2). The amplitude of the conditioned H reflex during the position task ranged from 77.4 ± 11.6 to 80.5 ± 17.1% of the test H reflex in young adults and from 72.1 ± 18.2 to 75.2 ± 21.0% of the test H reflex in old adults across the three contraction intensities.

The amount of D1 inhibition was less (task main effect, \( P = 0.04 \)) in the position task (79.0 ± 12.6% of the test reflex) compared with the force task (69.1 ± 15.0%; Fig. 3A) for the young adults. In contrast, there was no statistical difference for the old adults in the amount of D1 inhibition between the force (72.7 ± 18.0% of the test reflex) and the position tasks (74.2 ± 19.0%; task main effect, \( P = 0.63 \); Fig. 3A). The amount of D1 inhibition was not influenced by contraction intensity for either the young (intensity main effect, \( P = 0.90 \)) or old adults (\( P = 0.87 \)).

HETERONYMOUS IA FACILITATION. Due to the weak facilitation between the palmar branch of the median nerve and the motor neuron pool of ECR (Marchand-Pauvert et al. 2000), it was only possible to obtain data from eight young (3 women) and eight old adults (5 women) for this part of the study (Fig. 4). The onset of the heteronymous facilitation (see method) was briefer (unpaired t-test, \( P = 0.03 \)) in young adults (5.4 ± 0.5 ms; range: 4.8–6.2 ms) than in old adults (5.8 ± 0.2 ms; range: 5.6–6.2 ms).

As observed with the D1 inhibition method, contraction intensity did not influence the amount of facilitation for either the young (intensity main effect, \( P = 0.93 \)) or old adults (\( P = 0.80 \); Fig. 3B). When the data were collapsed across contraction intensities, the amplitude of the conditioned H reflex during the force task was 115.1 ± 29.7 and 114.0 ± 18.2% of the test H reflex in young and old adults, respectively. The amplitude of the conditioned H reflex during the position task increased to 132 ± 32.2% of the test reflex in young adults (task main effect, \( P = 0.02 \); Fig. 3B), whereas it did not change in old adults (115 ± 18.5% of the test reflex; task main effect, \( P = 0.89 \)).

AGE-DEPENDENT MODULATION OF IA PRESYNAPTIC INHIBITION. The results obtained with the two conditioning methods indicated a similar task effect within each group of subjects. To assess the influence of age on the presynaptic modulation of Ia afferents during the two tasks and to be able to combine data from the two methods, the amplitude of the conditioned H reflex (D1 inhibition and heteronymous Ia facilitation pooled together) obtained in the position task was expressed as a percentage of that obtained during the force task. Both age and task influenced the amplitude of the conditioned H reflex (age × task interaction, \( P < 0.05 \)). Young adults exhibited a significantly greater conditioned H-reflex amplitude in the position task compared with the force task (119.0 ± 21.2% of the conditioned H reflex recorded in the force task; Tukey post hoc test, \( P < 0.001 \)), whereas the amplitude of the conditioned H reflex did not increase in the position task for old adults (103.5 ± 16.9%; Tukey post hoc test, \( P > 0.05 \)). Moreover, the amplitude of the conditioned H-reflex was greater for young adults compared with old adults for the position task (Tukey post hoc test, \( P < 0.01 \); Fig. 3C).

EMG AMPLITUDE. The EMG amplitude (% MVC) recorded from the ECR increased with the contraction intensity (contraction intensity main effect, \( P < 0.001 \); Tukey post hoc test, \( P < 0.05 \)) and did not differ between age groups or tasks (age and task main effects, \( P = 0.07 \) and 0.69, respectively; Fig. 5A). The EMG activity from the FCR and brachioradialis did not change significantly across tasks and contraction intensities (main effects, \( P > 0.05 \)), but the old adults had greater EMG activity in FCR (9.8 ± 4.7% MVC; age main effect, \( P = 0.03 \)) compared with young adults (5.8 ± 3.8% MVC; Fig. 5B). The coactivation ratio did not differ between tasks for young adults (task main effect, \( P = 0.96 \)) but decreased with an increase in contraction intensity from 42.4 ± 31.3% (5% MVC force) to 32.0 ± 21.1% (10% MVC force, \( P = 0.014 \)) and 30.0 ± 23.9% (15% MVC force, \( P = 0.011 \)). Similarly, old adults exhibited a decrease in the level of coactivation with an increase in contraction intensity from 55.0 ± 32.8% (5% MVC force) to 43.3 ± 28.8% (10% MVC force, \( P = 0.003 \)) and 36.4 ± 22.8% (15% MVC force, \( P = 0.001 \)). Moreover the level of coactivation was greater in the position task (47.2 ± 30.3%) than in the force task (42.9 ± 27.8%; task main effect, \( P = 0.02 \)) for old adults. In addition, an age main effect (\( P = 0.04 \)) revealed that the level of coactivation was greater for old adults compared with young adults (Fig. 5C).

MECHANICAL OUTPUT. The force fluctuations recorded from the servo-controlled torque motor during the force and position tasks was expressed as the coefficient of variation for force (CV for force). The CV for force decreased with an increase in the contraction intensity during both tasks, and differed between groups (age × intensity, \( P = 0.003 \); Fig. 6). The CV for
DISCUSSION

The original findings of this study were the absence of a difference in the modulation of Ia presynaptic inhibition when old adults performed force and position control, which contrasted with the reduction in Ia presynaptic inhibition exhibited by the young adults during position control. Instead of modulating Ia presynaptic inhibition when maintaining the position of the compliant load, the old adults used greater antagonist coactivation.

ASSESSMENT OF IA PRESYNAPTIC INHIBITION. The goal of this study was to assess the modulation of presynaptic inhibition of Ia afferents as young and old adults performed isometric contractions with the wrist extensor muscles either to push against a rigid restraint to match a target force or to maintain a constant wrist angle while supporting an equivalent inertial load. The level of Ia presynaptic inhibition was assessed with two methods: D1 inhibition and heteronymous Ia facilitation. The D1-inhibition method (Mizuno et al. 1971) tests the excitability of the PAD interneurons by stimulating the Ia afferents originating from the antagonist muscle (conditioning stimulation) before applying the test stimulus to the nerve supplying the agonist muscle (test stimulation; H reflex). The heteronymous Ia facilitation method provides a measure of the ongoing presynaptic inhibition imposed on heteronymous Ia afferents that synapse with the target motor neuron pool (Hultborn et al. 1987a,b).

Although the heteronymous Ia facilitation and D1-inhibition methods assess different Ia afferent pathways converging onto the ECR motor neuron pool, previous work suggests that presynaptic inhibition of homonymous and heteronymous Ia afferents to ECR motor neurons are modulated by the same subset of PAD interneurons (Aymard et al. 2001; Baudry and Enoka 2009). As a consequence, a change in the level of presynaptic inhibition should induce similar changes in the amplitude of the conditioned H reflexes recorded with the two methods, providing the conditioning stimulus elicits a monosynaptic excitatory postsynaptic potential of constant size in PAD interneurons (D1 inhibition) or motor neurons (heteronymous Ia facilitation). A decrease in presynaptic Ia inhibition, for example, will increase the amplitude of the conditioned H reflexes for both D1 inhibition and heteronymous Ia facilitation methods.

As the sensitivity of the monosynaptic reflex to excitatory and inhibitory inputs depends on the size of the test reflex (Crone and Nielsen 1989), it was necessary to adjust the intensity of the test stimulation to keep the amplitude of the test H reflex constant (Table 1). Although such adjustments in the stimulus intensity likely change the Ia afferents and motor units that contribute to the H reflex (Pierrot-Deseilligny and Mazevet 2000), it is the recommended approach for assessing Ia presynaptic inhibition in different conditions (Pierrot-Deseilligny 1997). In the absence of a difference in the amplitude of the test H reflex across the two tasks and the three contraction intensities, the present results were likely not influenced by a differential sensitivity of the test reflex across conditions. Therefore the concurrent depression of D1 inhibition and augmentation of heteronymous Ia facilitation observed in young adults during the position task relative to the force task provide evidence of a lower level of presynaptic inhibition of Ia afferents converging onto the ECR when they maintained the position of the compliant load. In contrast, the absence of a change in the amount of depression (D1 inhibition) and facilitation (heteronymous Ia facilitation) between the force and the position tasks in old adults indicates that Ia afferent...
modulation by the PAD network did not differ between the two tasks.

**TASK-DEPENDENT MODULATION OF IA PRESYNAPTIC INHIBITION.** The decrease in presynaptic inhibition of Ia afferents during the position task in young adults is consistent with previous results from our laboratory (Baudry and Enoka 2009). The present findings, however, did not show any change in the amount of Ia presynaptic inhibition during contractions performed at 5, 10, and 15% MVC force, which contrasts with previous studies that have found a decrease in the amount of Ia presynaptic inhibition in the soleus muscle with an increase in contraction strength of the plantarflexor muscles (Butchart et al. 1993; Earles et al. 2001). The divergent findings are likely attributable to differences in how the target torque was determined for each contraction: Earles et al. (2001) used the amplitude of the surface EMG to set the intensity of the contraction, whereas Butchart et al. (1993) used the same absolute torques across subjects. Accordingly, Meunier and Pierrot-Deseilligny (1998) reported no change in the amount of soleus Ia presynaptic inhibition across different contraction intensities when the target torque was set relative to the MVC torque (12, 25, and 50% MVC force). In the current study, the increase in target force from 5 to 15% MVC force should be accompanied by an increase in fusimotor drive (α-γ linkage) and greater Ia afferent input from the ECR muscle (Vallbo et al. 1979) onto PAD interneurons. If the level of presynaptic inhibition is modulated by peripheral input from Ia collaterals, therefore it should increase with the target force. Rather the absence of a change in the amplitude of the conditioned H reflex across the different contraction intensities suggests that Ia presynaptic inhibition was not modulated by Ia afferent input but rather controlled by

![FIG. 3. Modulation of Ia presynaptic inhibition during force and position control in young and old adults. The amplitude of the conditioned H reflex (% test H reflex; means ± SE) in young and old adults during the force (■) and position tasks (□) for the D1-inhibition (A) and the heteronymous Ia facilitation (B) methods. Data are collapsed across intensities. C: the amplitude of the conditioned H reflex (expressed as percentage of the conditioned H reflex during the force task) collapsed across D1 inhibition and heteronymous Ia facilitation. Data are expressed as means ± SE. *, P < 0.05 compared with lower contraction force. §, P < 0.05 compared with force task. †, P < 0.05 compared with old adults.](http://jn.physiology.org/doi/abs/10.1152/jn.00888.2009)

![FIG. 4. Amount of heteronymous Ia facilitation during force and position control in young and old subjects during contractions at 5, 10, and 15% MVC force. The amplitude of the conditioned H reflex (% test H reflex) recorded in each young (left) and old subject (right) during the force and position tasks performed at the 3 contraction intensities. Each thin line corresponds to the 2 measurements for 1 subject and the thick line denotes the mean value of the group. Each point represents the mean of ≥20 H-reflex amplitudes for each subject.](http://jn.physiology.org/doi/abs/10.1152/jn.00888.2009)
descending input onto spinal interneurons (Hultborn et al. 1987a,b; Meunier and Pierrot-Deseilligny 1998).

In addition to the absence of a change in the amount of Ia presynaptic inhibition across contraction intensities, old adults did not modulate the level of Ia presynaptic inhibition between force and position control (Fig. 3). Similarly, Koceja and Mynark (2000) found no change in the level of Ia presynaptic inhibition in the lower leg of old adults with an increase in task complexity. The absence of modulation in Ia presynaptic inhibition in old adults during various tasks has been interpreted as a reduced ability to adjust Ia presynaptic inhibition to match changing task requirements (Koceja and Mynark 2000). However, the similar level of D1 inhibition for young and old adults in the present study shows that young and old adults can depress Ia afferent input via PAD interneurons to a comparable level (force task: 69.1 ± 15.0 and 72.7 ± 18.0% of the test H reflex, respectively). This result indicates that the capacity of the PAD network to depress the Ia afferents in the upper arm is not altered in old adults, which differs from results obtained in the lower leg. The divergent results may be a consequence of age-related differences in the adaptations experienced by upper and lower limb muscles, as suggested by the greater loss of muscle mass in the lower limb compared with the upper limb (Janssen et al. 2000). One might hypothesize that more frequent activation of a muscle in targeted movements may limit the age-related decrease in the capacity to modulate the synaptic input received by the motor neuron pool, which is consistent with the observation that practice improves the ability of young and old adults to modulate the H reflex (Mynark and Koceja 2002; Perez et al. 2007). Moreover, the absence of a change in Ia presynaptic inhibition across contraction intensities in old adults indicates that supraspinal centers modulated the excitability of the PAD interneurons similarly to that for young adults. Rather the current findings suggest that the difference between young and old adults has more to do with the strategy used to control a compliant load than an inability to modulate Ia presynaptic inhibition.

**FIG. 5.** Averaged electromyograph (aEMG) for the ECR and FCR muscles and the coactivation ratio during the force and position tasks at 5, 10, and 15% MVC force for the young and old adults. The average rectified EMG (% MVC) for the extensor carpi radialis (A) and the flexor carpi radialis (B) during the force (●) and position (○) tasks performed at 5, 10, and 15% MVC force for young (●, ○) and old adults (■, □). EMG amplitude for ECR increased similarly in both groups with the increase in the contraction intensity. EMG amplitude for FCR was greater for the old adults (age main effect, P = 0.04). C: coactivation ratio (FCR/ECR amplitude × 100) during the force (●) and position (○) tasks (data collapsed across intensities) in young and old adults. Old adults had greater antagonist coactivation than young adults and in the position task compared with the force task. †, P < 0.05 compared with 5% MVC. §, P < 0.05 compared with force task. *, P < 0.05 compared with old adults (age main effect).

**FIG. 6.** Coefficient of variation (CV) for force at 5, 10, and 15% MVC force for the young and old adults. Average coefficient of variation for force (CV for force; collapsed across tasks and expressed as means ± SE) for young (●) and old adults (■) during tasks performed at 5, 10, and 15% MVC force. †, P < 0.05 compared with 5% MVC. *, P < 0.05 compared with old adults.
FORCE AND POSITION CONTROL. When asked to match a target force by pushing against a rigid restraint, the level of Ia presynaptic input was similar for young and old adults. When the task was to maintain the position of a compliant load, however, the young adults reduced the level of Ia presynaptic inhibition but the old adults did not. Rather the old adults increased the amount of antagonist coactivation to manage the more compliant load.

The strategy adopted by the young adults is consistent with earlier reports of how they tend to manipulate the responsiveness of stretch-related reflexes when load compliance varies (Akazawa et al. 1983; Baudry et al. 2009; Doemges and Rack 1992; Maluf et al. 2007). The functional significance of modulating Ia presynaptic inhibition during motor tasks remains unclear. In the present study, the decrease in Ia presynaptic inhibition during the position task should increase the responsiveness of the segmental reflex and increase the reflex-induced stiffness of the muscle to augment joint stability. This interpretation, however, is challenged by previous observations showing that an increase in the responsiveness of the short-latency reflex (segmental pathway) has only a minor influence on muscle stiffness (Akazawa et al. 1983; Hasan 2005; Mirbagheri et al. 2000). Rather longer latency responses appear to provide a more significant contribution to the ongoing EMG activity during position control (Hasan 2005; Perreault et al. 2008). A change in the contribution of the Ia afferent input to the net synaptic input converging to the motor neuron pool of active muscles, however, may occur even in the absence of typical short- and long-latency responses. Subtle changes in the amount of ankle dorsiflexion during the stance phase of stepping, for example, activated homonymous Ia afferents that modulated the level of EMG activity in soleus even in the absence of stretch-evoked responses (Mazzaro et al. 2005).

Although presynaptic inhibition of Ia afferents has been shown to increase during walking compared with sitting, it is less during the stance phase than during the swing phase (Faist et al. 1996). The lower Ia presynaptic inhibition during the stance phase may represent a strategy to heighten the contribution of Ia afferent input to the muscle activation in the phase of the step that requires rapid and subtle adjustments. Accordingly, the lower level of Ia presynaptic inhibition during the position task in the present study likely denotes a strategy in which supraspinal centers choose to enhance the contribution of muscle afferents to the synaptic input that converges onto spinal motor neurons (Nielsen 2004) to provide reactive responses to small variations in wrist angle. In association with adjustments in the descending drive, such modulation would enhance the efficacy of the segmental Ia afferent pathway in providing position feedback.

In contrast to young adults, the old adults did not modulate the level of Ia presynaptic inhibition across tasks but instead increased antagonist coactivation to maintain the stability of the limb (Fig. 3 and 5). This alternative strategy may represent a compensatory adjustment to the greater mechanical fluctuations experienced by the old adults (Fig. 5, bottom) (Enoka et al. 2003). In the presence of a high reflex gain, for example, the greater mechanical fluctuations experienced by old adults could induce reflex-mediated joint oscillations (Hasan 2005; Stein and Ögütörel 1976) that would compromise the ability of an individual to sustain the required position. Moreover the slower conduction along the spinal reflex pathway, which was observed as an increase in reflex latency for the old adults, would delay any correction based on Ia afferent feedback (Matthews 1986). The preference of old adults to use greater levels of antagonist coactivation to increase joint stiffness has also been reported by others (Hortobágyi and DeVita 2000) and may represent a greater reliance on feedforward control during the performance of tasks that involve the position control.

The results obtained in the current study on voluntary activation of extensor carpi radialis likely generalize to the wrist flexor muscles and to muscles that contribute to radial deviation of the hand. Indeed, Aymard et al. (2001) reported a similar modulation of Ia afferent input in flexor carpi radialis when subjects produced either a wrist flexion or wrist extension force. Moreover we recently reported a similar presynaptic modulation of Ia afferents in the flexor and extensor carpi radialis when they acted as synergists (Baudry and Enoka 2009). These results are consistent with a similar subset of PAD interneurons projecting on the motor neuron pools of both extensor and flexor carpi radialis.

In conclusion, young adults used a differential presynaptic modulation of the Ia afferent input to the motor neuron pool of a wrist muscle when performing force and position control, whereas old adults did not modulate the amount of Ia presynaptic inhibition across the two tasks but rather increased the activity in the antagonist muscle. These results suggest that aging may be accompanied by a preference for feedforward control rather than feedback control when maintaining the position of the hand while supporting a compliant load.

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REFERENCES


