

Heteronymous reflex responses in a hand muscle when maintaining constant finger force or position at different contraction intensities

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ABSTRACT

Objective: This study compared heteronymous reflex responses evoked in the first dorsal interosseus muscle by electrical and mechanical stimuli during force and position tasks performed at different target torques.

Methods: Twenty-two healthy human participants contracted the first dorsal interosseus muscle either to produce a constant force against a rigid restraint (force task) or to maintain a constant position of the index finger (position task) against a constant load of 20, 40, and 60% of maximum.

Results: The amplitude of the short-latency reflex evoked by electrical stimulation of the median nerve was significantly greater when maintaining finger position, whereas no difference was present for the long-latency responses. In contrast, the reflex responses (short- and long-latency) did not differ between tasks when elicited by tendon-taps.

Conclusions: Task difference in reflex responsiveness depended more on the type of stimulus applied than the reflex pathway and was consistent across three voluntary contraction forces.

Significance: The results suggest that afferent input from homonymous and heteronymous pathways is modulated similarly at the spinal level during such tasks, and implies the significance of presynaptic inhibition during motor performance.

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1. Introduction

When an individual performs a submaximal isometric contraction with the first dorsal interosseus (FDI) either to produce a constant force against a rigid restraint (force task) or to maintain the position of the index finger against a constant load (position task), the amplitude of the stretch reflex (Doemges and Rack, 1992a; Maluf et al., 2007) and the tendon-tap reflex (T-reflex) (Maluf et al., 2007; Jordan et al., 2007) are similar during both tasks. In contrast, when a reflex was elicited in the FDI by electrical stimulation of the median nerve (heteronymous H-reflex), the amplitude of the reflex response was larger during the position task than during the force task (Maluf et al., 2007; Jordan et al., 2007). Similar results have been observed with single motor units recorded in FDI in response to the T-reflex and median nerve H-reflex (Jordan et al., 2007).

These divergent results for electrically and mechanically induced reflexes might be attributable either to the reflex pathway involved (i.e., homonymous for the stretch and T-reflexes and heteronymous for the median nerve stimulation) or to the type of stimulus applied (mechanical and electrical stimulus). Previous work, however, suggests similar modulation of the afferent input

onto the motor neuron pool from the homonymous and heteronymous pathways (Meunier and Pierrot-Deseilligny, 1989). Moreover, the electrically induced reflex response is more sensitive to presynaptic inhibition compared with stretch and tendon-tap reflexes (Morita et al., 1998). If the different adjustments in the T- and H-reflexes during the force and position tasks are attributable to presynaptic inhibition, the greater amplitude of the heteronymous H-reflex during the position task should be present during contractions performed at different contraction intensities as presynaptic inhibition does not change with contraction force (Meunier and Pierrot-Deseilligny, 1989). Similarly, the absence of a difference in the T-reflex across tasks should not change with contraction force. If confirmed, these results suggest that changes in the efficacy of presynaptic inhibition, as observed in elderly adults (Butchart et al., 1993; Earles et al., 2001; Tsuruike et al., 2003), stroke patients (Aymard et al., 2000), individuals with spasticity (Morita et al., 2001), and in healthy subjects after a few weeks of limb immobilization (Lundbye-Jensen and Nielsen, 2008) and the consumption of ethanol (von Dincklage et al., 2007), could compromise motor performance.

The aim of the study was to compare heteronymous reflex responses evoked in the FDI by electrical and mechanical stimuli when the force and position tasks were performed at three target forces. These results indicate a similar modulation of homonymous and heteronymous afferent input onto the motor neuron pool of

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the agonist muscle, but a different adjustment of presynaptic inhibition during the force and position tasks. In addition, our results underscore that the use of the H-reflex method appears as a better tool to investigate fine differences in the afferent synaptic input onto the motor neuron pool between tasks compared with the mechanically evoked reflex.

2. Materials and methods

After informed consent was obtained, experiments were conducted on 22 subjects (9 women) aged between 18 and 37 yr (25.0 ± 5.7 yr; mean \pm SD). None of the participants reported any signs of neurological disorder or cardiovascular disease. Subjects were all right-handed and were asked to refrain from exercising the arm muscles for 24 h before testing. The Human Subjects Committee at the University of Colorado in Boulder approved the experimental procedures.

2.1. Experimental apparatus

The subject was seated in a modified dental chair with the left arm supported to minimize activity in shoulder and arm muscles. The upper arm was slightly abducted ($\sim 20^\circ$) and the elbow joint was flexed to $\sim 95^\circ$. The left hand was placed in a vertical position midway between supination and pronation and supported by means of a custom-made apparatus. The index finger was splinted in full extension at the proximal and distal interphalangeal joints and attached to a torque transducer (TRT-25, Transducer Techniques, Temecula, CA). The transducer was mounted on the shaft of an electrical torque motor (PMA44Q, Pacific Scientific, Rockford, IL). The metacarpophalangeal joint of the index finger was aligned with the shaft of the torque motor, which enabled abduction–adduction movements about the joint. The thumb was abducted by 45° and fixed in the same plane as the palm of the hand (Fig. 1).

The electrical torque motor was used to simulate an inertial load in a gravitational field for the position task by using a Labview Real Time system (2PCs using a PCI-6029 and a PCI-6021, National Instruments, Austin, TX). The torque transducer signal, analog signals of the simulated mass, and motor shaft position and angular velocity were A/D sampled at 200 samples/s (Power 1401, 16-bit resolution, Cambridge Electronic Design, Cambridge, UK) and stored on computer for subsequent analysis.

2.2. EMG recordings

The surface EMG from the FDI and abductor pollicis brevis (APB) muscles were recorded using bipolar surface electrodes (silver–silver chloride; 4-mm electrode diameter; 12-mm interelectrode distance; In Vivo Metric, Healdsburg, CA). The electrodes were placed parallel to the radial border of the second metacarpal over FDI, just proximal to the junction with the distal tendon (Maluf et al., 2007), and over the muscle belly of the APB, close to the proximal insertion. The EMG activity from the antagonist muscle for FDI, second palmar interosseous (SPI), was recorded with a bipolar intramuscular electrode that comprised two Formvar-insulated stainless steel wires (50 μ m diameter), with 1 mm of insulation removed from the distal tip of the two wires to increase the recording volume of the electrode. Reference electrodes were placed over bony prominences on the left elbow. The EMG signals were amplified (500–5000) and filtered (13–1000 Hz) prior to sampling at 2000 samples/s (Coulbourn Instruments, Allentown, PA) and storage on a computer.

2.3. Reflex responses

Heteronymous reflexes were evoked in FDI by electrical stimulation of the median nerve (H-reflex) and with tendon-taps applied to the distal tendon of the APB (T-reflex). Electrical stimulation (0.5-ms pulse; Grass S88K, Astra-Med, West Warwick, RI) of the

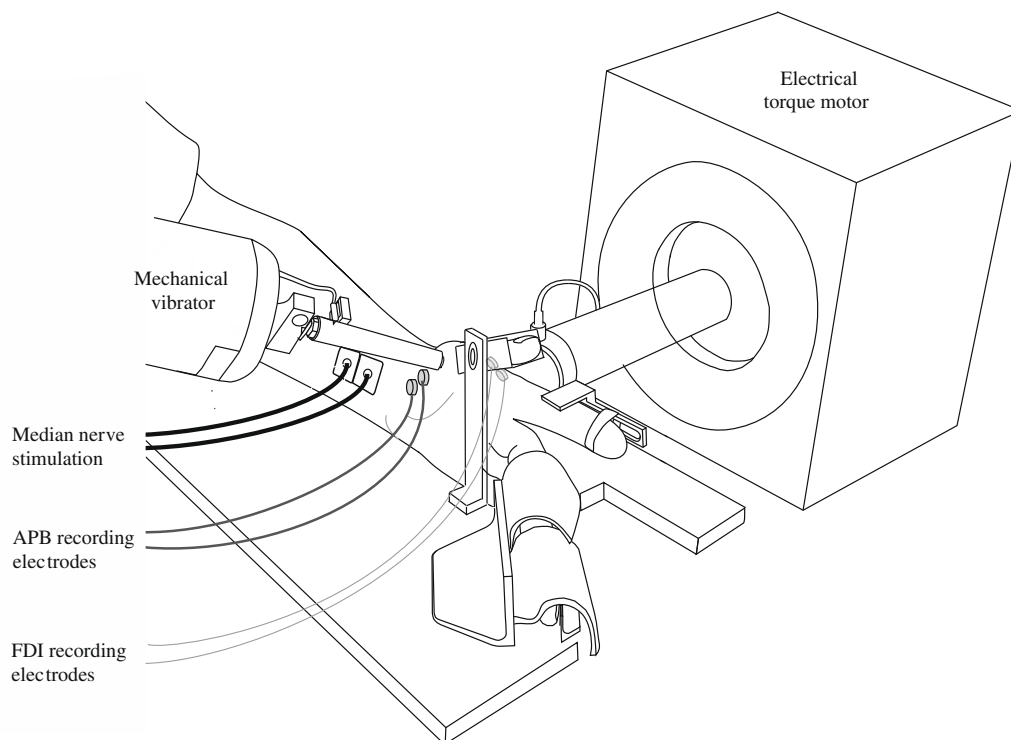


Fig. 1. Illustration of the experimental set-up. The index finger of the left hand is extended and contacts the lever attached to the shaft of the torque motor. The recording electrodes for the FDI are indicated in grey because they cannot be seen directly in this image.

median nerve was delivered at the level of the wrist. A constant-current unit (Model CCU1, Astra-Med, West Warwick, RI) was used to minimize the effect of time-dependent changes in the impedance of the electrodes attached to the skin (Zehr, 2002). Because it is difficult to evoke an H-reflex in FDI when the muscle is relaxed (Schieppati, 1987), the reflex was evoked and adjusted during a submaximal contraction (20% MVC) to obtain a response that was 50% of the maximal H-reflex (Zehr and Stein, 1999; Butler et al., 1993); the intensity was below the motor threshold of the APB, except for 5 subjects where a small M-wave (<10% of the maximal compound muscle potential) was observed.

The T-reflex from APB was evoked by a tap applied to the distal tendon of the APB with a mechanical vibrator (LDS V203 vibrator and PA25E power amplifier, Ling Dynamic System Ltd., Royston, UK). The tendon-tap was applied during a submaximal contraction (20% MVC) at an intensity that elicited a response in FDI with similar amplitude to that of the H-reflex at the same contraction force. The reaction force against the skin was measured continuously with a MLP-10 force transducer (Transducer Techniques, Temecula, CA) and kept at a similar level across the different conditions (~1 N).

The stimulation set-up was established during the force task for both H- and T-reflexes. In addition to the reflex responses, a maximal direct motor response (M-wave) was recorded by stimulating the ulnar nerve. The intensity of the stimulation was determined by gradually increasing the intensity of stimulus until the M-wave reached its maximal value (M_{\max}).

2.4. Testing procedure

The experimental session began with the performance of a maximal voluntary contraction (MVC) of FDI as the subject exerted an abduction force with the index finger. The MVC involved an increase in force from zero to maximum over 3 s and then holding the force for ~3 s. At least two trials were performed, with subjects resting for 90–120 s between trials to minimize fatigue. If the MVC forces were within 5% of each other, the higher 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 for both SPI (index finger adduction) and APB (thumb abduction) for EMG normalization.

The stimulus characteristics required to evoke the reflexes were determined after the MVC trials. In a counterbalanced order for the task, reflex, and contraction intensity across and within subjects, the participants performed the force and position tasks to target forces of 20, 40, and 60% MVC force. Visual feedback was provided on a monitor during both tasks at a gain equal to 3%/cm of the maximal performance range, which was operationally defined as MVC force for the force task and the full range of motion about the metacarpophalangeal joint for the position task (Maluf et al., 2007). Subjects performed 6 trials of each task (force and position) at each contraction intensity (20, 40, and 60%), with H-reflexes recorded in 3 trials and T-reflexes in the other 3 trials. Within each trial, 8 stimuli were delivered with a randomized interval varying about 1 s for the median nerve stimulation and about 0.5 s for the tendon-tap. There was a rest period of 30, 45, and 60 s between trials for the 20, 40, and 60% MVC target forces, respectively. MVCs were measured at the beginning and at the end of the experimental session.

2.5. Data analysis

The average amplitude of the rectified EMG signal (aEMG) was calculated for a 0.5-s interval centered about the peak EMG of MVC trials for the FDI, SPI, and APB muscles. Background activation of

the intrinsic hand muscles during the reflex trials was determined by averaging the aEMG activity within the 50-ms period that preceded the onset of each stimulus.

The short-latency reflex (SLR) and long-latency reflex (LLR) in response to median nerve stimulation and tendon-tap on the APB were characterized by: (1) latency – time from the stimulus artifact to the beginning of the EMG response; (2) duration – the time interval between the onset of aEMG activity and the point at which it returned to the mean background aEMG level; (3) peak amplitude – distance from the tonic aEMG activity in the 20 ms following the stimulation artifact and the peak amplitude of the response; and (4) area – the area above the tonic aEMG activity between the onset and offset of the response.

2.6. Statistics

Latency, duration, peak amplitude, and area of the short- and long-latency reflexes for the H- and T-reflexes were analyzed with a repeated-measures 3-way ANOVA (reflex type \times task \times contraction intensity). The tonic aEMG activity was examined with a repeated-measures 3-way ANOVA. When a significant main effect was found, a Student–Newman–Keuls post hoc test was used to identify the significant differences among the selected means. Changes in MVC force and its associated EMG activity were analyzed using a paired *t*-test. The level of statistical significance was set at $P < 0.05$. Data are reported as means \pm SD within the text and displayed as means \pm SE in the figures.

3. Results

Nineteen of the 22 subjects who participated in the study were included in the statistical analysis of the reflex responses induced by the median nerve stimulation (11 men; 25.0 ± 5.7 years; 165.7 ± 12.7 cm; 65.8 ± 10.6 kg) and 18 were included in the analysis of the tendon-tap of APB (8 women; 25.2 ± 5.8 years; 167.9 ± 13.8 cm; 65.6 ± 10.9 kg). Data were excluded for the electrically induced reflex from three subjects. In two subjects, the difference in EMG activity between the force and position tasks exceeded 30% for either FDI or APB. In a third subject, there was no H-reflex during the 40 and 60% MVC contractions for the position and force tasks, respectively. Furthermore, 4 subjects exhibited no T-reflex at one or several contraction forces and their data were excluded from analysis.

The MVC torque recorded prior to reflex measurements was 1.36 ± 0.5 Nm and decreased ($P < 0.05$) by 4.7% at the end of the experiment. In contrast, there was no change in EMG amplitude of the FDI during the MVC (start: 0.478 ± 0.149 mV, end: 0.469 ± 0.192 mV). FDI background activity during the 50 ms prior to each stimulus did not differ between reflex types and tasks (ANOVA, $P = 0.82$ and 0.54 , respectively), but increased significantly with contraction force (ANOVA, $P < 0.001$; Fig. 2). The post hoc test indicated that the aEMG activity differed between each contraction force (Student–Newman–Keuls, $P < 0.01$). Similar results were obtained for the aEMG of APB (intensity main effect, $P < 0.001$; Student–Newman–Keuls, $P < 0.05$), but differences were only observed between 20 and 40% MVC and 60% MVC forces. AEMG for the SPI muscle also did not differ between reflex and task ($P = 0.72$ and 0.45 , respectively) but increased with contraction force (main effect, $P < 0.001$) and the post hoc test indicated significant differences between the 20% and 40–60% forces ($P < 0.01$).

Fig. 3 illustrates the responses to the electrical (left column) and mechanical stimuli (right column) at the different contraction forces for a single subject. The latency for the H-reflex (29.9 ± 3.0 ms) averaged across all subjects was less than that for the T-reflex (32.1 ± 3.6 ms; $P < 0.001$), whereas there was no signif-

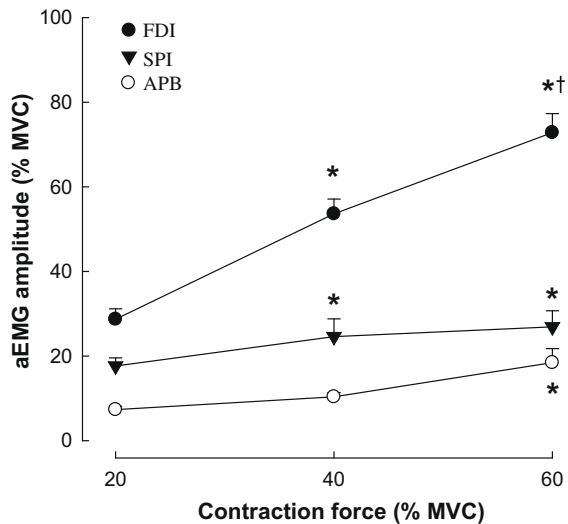


Fig. 2. Average EMG (aEMG) amplitude in the 50 ms prior to the onset of the stimulus for the FDI (●), APB (○) and SPI (▼). Data for each muscle are collapsed across task and expressed as percentage of the value recorded during the MVC for each muscle. * $P < 0.05$ compared with 20% and 40% MVC contraction, respectively.

icant difference for the mean duration of the response (11.0 ± 5.0 ms and 12.1 ± 8.3 ms, respectively). The amplitude of the H- and T-reflexes did not differ significantly (116 ± 84.5 μ V and 122 ± 52.7 μ V, respectively) during a 20% MVC trial for the force task. When the reflex amplitude was expressed relative to the maximal direct motor response, the H- and T-reflexes were $2.7 \pm 1.3\%$ and $2.8 \pm 1.2\%$ of the M_{max} , respectively. The long-latency reflex evoked by median nerve stimulation occurred earlier and was briefer in duration (53.6 ± 6.9 ms and 10.1 ± 4.2 ms, respectively) than that elicited by tendon-tap (65.2 ± 13.4 ms and 14.4 ± 16.2 ms; $P < 0.001$). The amplitude of the long-latency reflex evoked by median nerve stimulation and tendon-tap were similar (59.9 ± 45.3 μ V and 50.4 ± 25.8 μ V, respectively) during a 20% MVC trial of the force task. The latency and duration of the short- and long-latency reflexes did not differ between the force and position tasks for the two types of stimuli (median nerve stimulation and tendon-tap).

The amplitude of the H-reflex increased with contraction force; the reflex amplitude was significantly greater at 40% and 60% compared with the 20% contraction ($P < 0.05$). When the amplitude of the H-reflex was compared across contraction forces between the force and position tasks, a significant task main effect ($P < 0.01$) indicated that the amplitude of the H-reflex was greater during the position task at all forces (Fig. 4A). Although all subjects showed a greater H-reflex for the position task than for the force task, four subjects did not exhibit any differences in H-reflex amplitude between the 40 and 60% contractions. In contrast to the H-reflex, the amplitude (Fig. 4B) and area of the T-reflex did not differ between the two tasks, but increased with contraction intensity (main effects for amplitude and area, $P < 0.01$ and 0.05 , respectively) and the reflex amplitude was significantly greater at 40% and 60% compared with the 20% contraction ($P < 0.01$).

The amplitude of the long-latency reflex evoked in FDI in response to median nerve stimulation increased ($P < 0.05$) with contraction force (Fig. 5A). However, there was no difference between the two tasks for either the amplitude (Fig. 5A) or area (data not shown). Similar results were observed for the long-latency reflex in response to tendon-tap of the APB (Fig. 5B), with reflex amplitude being significantly greater for the 40–60% contractions compared with the 20% contraction ($P < 0.01$).

4. Discussion

The main finding of this study was the greater response for the heteronymous H-reflex during the position task compared with the force task performed at the three contraction forces. In contrast, there was no difference between tasks in the size of the heteronymous T-reflex at any contraction force. In combination with previous work, these results indicate that the task difference in reflex responsiveness depends more on the type of stimulus applied than the reflex pathway used, and are consistent with a similar modulation of homonymous and heteronymous afferents at the spinal level during submaximal isometric contractions. Moreover, the findings suggest less presynaptic inhibition when the task involved maintaining a constant finger position than when exerting a constant force against a rigid restraint.

A critical feature of these studies is the specificity of the stimulus and the origin of the response. To avoid concurrent activation of FDI and its antagonist (SPI) and to limit contamination of the recording by F-waves (Fisher, 1992), investigators often use a heteronymous pathway to induce an H-reflex in the FDI (Duchateau and Hainaut, 1993; Maluf et al., 2007). Because the F-wave represents the response of motor neurons to an antidromic volley (Espirito et al., 2003; Mesrati and Vecchierini, 2004), it does not occur when activating a heteronymous pathway and could not have influenced the responses reported in the current study. The short-latency response to electrical stimulation of the heteronymous pathway is also unlikely to involve cross-talk because a short-latency response was not always observed in the APB muscle whereas it was always present in FDI. In addition, Duchateau and Hainaut (1993) reported that the short-latency response elicited in FDI by median stimulation decreased during a sustained fatiguing contraction, whereas the responses evoked in APB did not change. Furthermore, Jordan et al. (2007) found that electrical stimulation of the median nerve evoked both an H-reflex and single motor unit discharges in FDI.

Because FDI can receive some innervation from the median nerve in 6 to 44% of healthy subjects (Amoiridis and Vlachonikolis, 2003), the reflex responses observed in the current study could have been confounded by the presence of a median nerve anastomosis. A significant contribution by median nerve innervation of FDI, however, should result in the H-reflex amplitude first increasing and then decreasing (H-reflex recruitment curve) as stimulus intensity was increased. The recruitment curve did not exhibit this profile in the current study. It seems, therefore, that electrical stimulation of the median nerve activated a heteronymous pathway to produce an H-reflex in FDI.

Similarly, the mechanical tap to the tendon of APB could have provided a stimulus that resulted in the indirect activation of FDI (Lance and De Gail, 1965). This seems unlikely because an indirect response to the spread of the vibration would be delayed by 1 to 4 ms in the upper limb (Lance and De Gail, 1965), whereas the T-reflex latency in the current study (~ 32.1 ms) was slightly shorter (~ 34.3 ms) to that for a T-reflex evoked by an FDI tendon-tap (Jordan et al., 2007). These observations suggest that the short-latency responses evoked in FDI by electrical and mechanical stimuli originated in Ia afferents located in a heteronymous pathway.

The present results on the similar responsiveness of the heteronymous T-reflex during the force and position tasks are consistent with some previous work (Doemges and Rack, 1992a; Jordan et al., 2007; Maluf et al., 2007), but contrast with the results of others (Akazawa et al., 1983; De Serres and Milner, 1991; Doemges and Rack, 1992b). The discrepancy between these studies likely depends on the details of the task. For example, the amplitude of the short- and long-latency reflexes was greater when subjects attempted to maintain finger position as force was changed compared with keeping the force constant while small movements were imposed (Doemges and Rack, 1992a; Doemges and Rack,

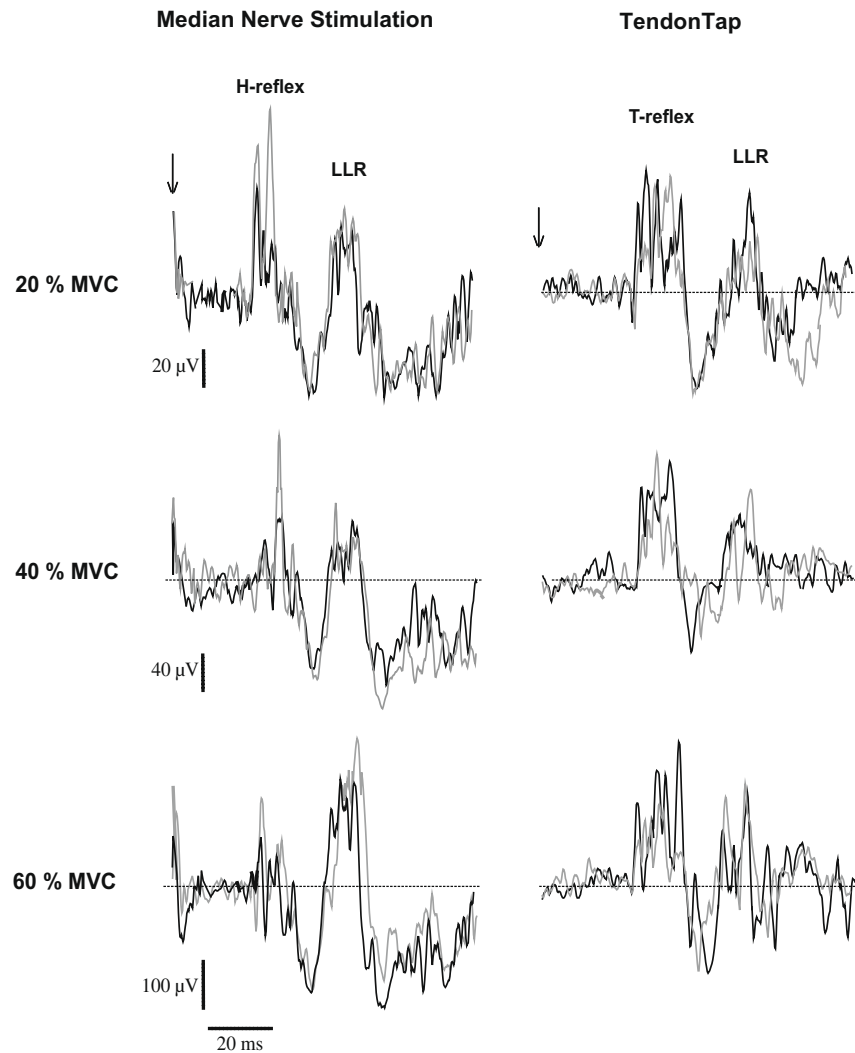


Fig. 3. Typical traces from one subject in response to median nerve stimulation (left column) and APB tendon-tap (right column) during the force (black lines) and position tasks (grey lines) during isometric contractions performed at 20% (upper row), 40% (middle row) and 60% MVC forces (lower row). The arrows indicate stimulus onset and the horizontal dashed lines represent aEMG amplitude for the 50 ms before the stimulus. LLR, long-latency reflex.

1992b). Similarly, the amplitude of the stretch reflex increased when the force varied during the position task (Akazawa et al., 1983). Conversely, reflex responsiveness was the same for both tasks in the absence of a perturbation (Doemges and Rack, 1992a; Maluf et al., 2007).

In contrast to the similar T-reflex in the force and position tasks, the amplitude of the H-reflex was greater during the position task compared with the force task, as reported previously (Jordan et al., 2007; Maluf et al., 2007). In these studies, the H-reflex was elicited in the FDI by median nerve stimulation (Duchateau and Hainaut, 1993; Maluf et al., 2007) to avoid contamination by antidromic activation of the homonymous motor axons (Fisher, 1992). Because the current results on the heteronymous T- and H-reflexes are similar to those for the homonymous T-reflex and heteronymous H-reflex, the findings suggest that the differences between the T-reflex and H-reflex during the force and position tasks do not depend on the reflex pathway that was activated (homonymous versus heteronymous), but rather argue for similar modulation of afferent inputs coming from homonymous or heteronymous muscles at the spinal level (Meunier and Pierrot-Deseilligny, 1989).

The different responsiveness of the T- and H-reflexes when individuals maintained finger position or exerted a constant force

against a rigid restraint persisted across the three contraction forces despite an increase in the size of the reflex response. To enhance the sensitivity of the reflex response to excitatory and inhibitory inputs that could differ between force and position tasks, the stimulus intensity was adjusted to elicit reflexes with moderate amplitudes (Crone et al., 1990). Under these conditions, an increase in the descending drive onto the FDI motor neuron pool with increased contraction intensity reduced the difference between the membrane potential and voltage threshold of motor neurons not already involved in the reflex response elicited at 20% MVC, and thereby increased the number of motor neurons activated by the afferent volleys (Stein et al., 2007) and the size of the reflex. Moreover, an increase in the level of background EMG activity can reduce the inhibitory input from Ib afferents onto alpha motor neurons (Fournier et al., 1983; Pierrot-Deseilligny and Burke, 2005) and enhance fusimotor drive (Hagbarth and Vallbo, 1968) by the activation of the gamma motor neurons (Burke et al., 1979). Although reflex gain and joint stiffness change with the level of EMG activity (Mirbagheri et al., 2000), the preceding EMG activity of FDI in the current study was similar between task and reflex type for all the contraction intensities tested (Fig. 2). The background level of EMG activity, therefore, did not play a major role in the different reflex responsiveness between tasks and reflex

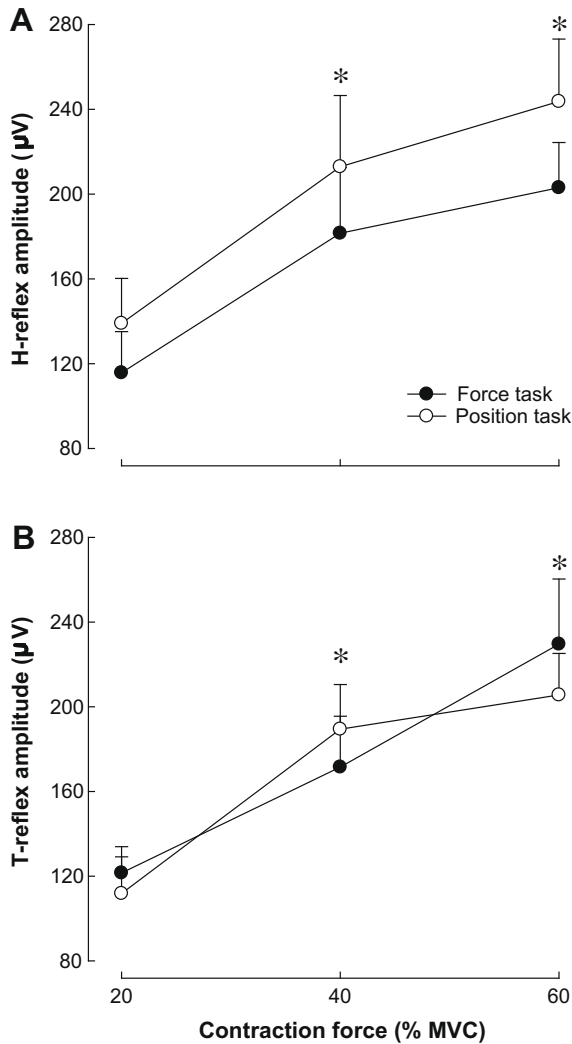


Fig. 4. Amplitude of the H-reflex (A) and T-reflex (B) during the force (●) and position tasks (○). There was a significant task main effect for the H-reflex. * $P < 0.05$ compared with 20% MVC contraction.

types. Furthermore, the H-reflexes evoked in FDI do not appear to have been influenced by post-synaptic depression because this effect was abolished with increasing stimulus repetition rates (up to 4 Hz) in the tibialis anterior and APB muscles during voluntary contractions (Burke et al., 1989).

Although the electrically evoked H-reflex and mechanically elicited T-reflex both recruit motor neurons in the order of increasing size (Burke, 1981), electrical stimulation of the nerve evokes a more synchronous afferent volley (Burke et al., 1983) from a larger number of Ia afferents than the tendon-tap (Morita et al., 1998). Such characteristics likely underlie the greater sensitivity of the H-reflex to presynaptic inhibition (Morita et al., 1998) and could explain the different responses of the H-reflex between the force and position tasks, whereas no difference was observed for the T-reflex. As suggested by Maluf et al. (2007), the amount of presynaptic inhibition might be less during the position task compared with the force task. This possibility is consistent with the greater H-reflex amplitude during the position task across the three contraction forces as the amount of presynaptic inhibition does not change with the level of the voluntary contraction (Meunier and Pierrot-Deseilligny, 1989).

Electrical stimulation applied over the skin, however, might also confound the results. For example, digital nerve stimulation of the

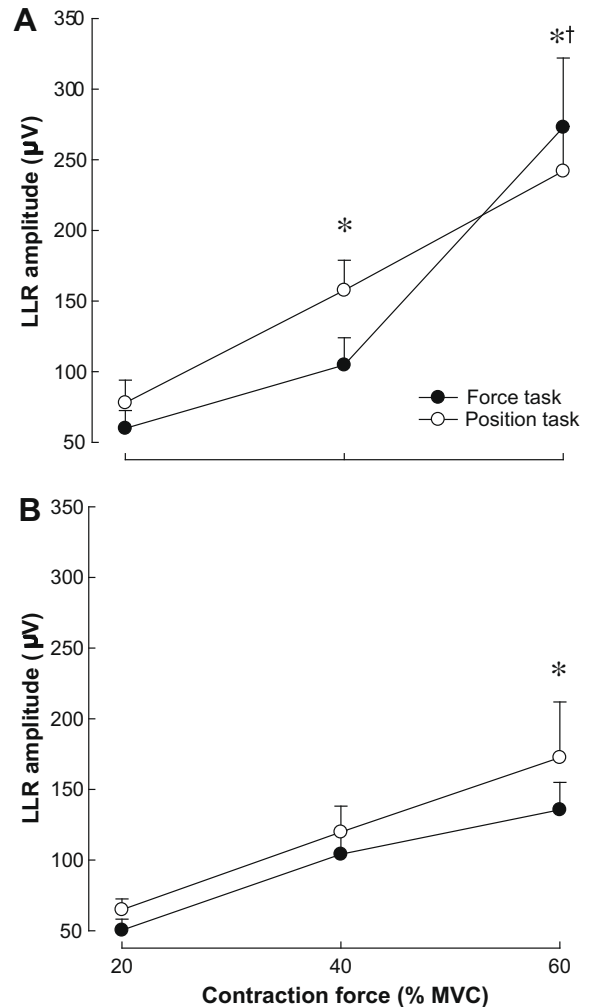


Fig. 5. Amplitude of the long-latency reflex (LLR) evoked by median nerve stimulation (A) and APB tendon-tap (B) during the force (●) and position tasks (○). * $P < 0.05$ compared with 20% and 40% MVC contraction, respectively.

index finger evokes reflex responses in the FDI (Tarkka, 1986) that can change the recruitment gain of the FDI motor neuron pool (Garnett and Stephens, 1981) and reduce the amount of presynaptic inhibition (Aimonetti et al., 2000). Furthermore, cutaneous stimulation associated with median nerve stimulation can alter the discharge rate of single motor units. However, the responses evoked by digital nerve stimulation of the index finger did not differ during the force and position tasks (Barry et al., 2007). Therefore, differences in H-reflex amplitude between the force and position tasks are likely not caused by input from cutaneous afferents but indicate differences in control by corticospinal inputs (Meunier and Pierrot-Deseilligny, 1998).

These results argue for a reduction in presynaptic inhibition to the FDI muscle during the position task compared with the force task. This reduction in presynaptic inhibition could heighten reflex responsiveness during the unstable task of maintaining finger position. However, the greater responsiveness of the H-reflex contrasted with the influence of task on the long-latency reflex (Fig. 5A). Soechting and Lacquaniti (1988) reported that short- and long-latency responses to multidirectional load perturbations of the human arm could differ and change direction from an increase to a decrease of the rectified EMG activity during the first 120 ms after the onset of the perturbation. Compared with the short-latency response, which depends on the monosynaptic excitation of the motor neurons from homonymous Ia afferents, the

long-latency response involves a transcortical pathway of the peripheral afferents (Deuschl et al., 1991). This transcortical pathway of the peripheral afferents has been suggested to play a role in motor control by modulating the motor output in response to sudden limb perturbations, as suggested by the optimal feedback control theory (Scott, 2004, 2008). Therefore, the absence of a task difference in the long-latency response evoked by electrical nerve stimulation likely involved modulation of the afferent volleys by cortical areas to maintain a constant motor output during the two tasks despite a higher sensitivity of the motor neuron pool to Ia afferents. If confirmed, such differences in modulation of short- and long-latency responses likely enhance motor control for a wide range of conditions.

The results of these studies suggest that the ability to exert a constant force against a rigid restraint and to maintain the position of the index finger while supporting a constant load requires a differential modulation of the presynaptic inhibition of Ia afferents in homonymous and heteronymous pathways. Changes in the efficacy of presynaptic inhibition could compromise performance. For example, older adults appear less capable of modulating presynaptic inhibition (Earles et al., 2001; Tsuruike et al., 2003), which could contribute to their reduced ability to perform steady contractions (Enoka et al., 2003). Similarly, stroke patients exhibit a decrease in presynaptic inhibition of Ia terminals (Aymard et al., 2000) that likely alters their ability to perform fine movements (McCombe Waller and Whittall, 2004). Furthermore, the influence of operant conditioning on H-reflex amplitude (Thompson et al., 2006) might be mediated by changes in presynaptic inhibition input of Ia afferents. In addition, our results imply the greater sensitivity of the H-reflex method to fine differences in the afferent synaptic input onto the motor neuron pool between tasks compared with the mechanically evoked reflex.

In conclusion, the present study found greater responsiveness of the H-reflex at three contraction forces during the position task compared with the force task, whereas there was no task effect for the T-reflex. Moreover, the long-latency reflex was not influenced by task for either the electrical or mechanical stimulus. Therefore, the difference in reflex responsiveness depends on the type of stimulus and not on the reflex pathway (homonymous vs. heteronymous). The findings suggest a similar modulation of the inputs coming from homonymous and heteronymous afferents onto the motor neuron pool of FDI, and are consistent with a reduction in presynaptic inhibition when the task involves maintaining limb position compared with exerting a constant force against a rigid restraint.

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