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RESEARCH ARTICLE

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Short- and long-latency reflex responses during different motor tasks in elbow flexor muscles

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Abstract Stretch reflex responses in three elbow flexor muscles – the brachioradialis and the short and long heads of the biceps brachii – were studied during different motor tasks. The motor tasks were iso-velocity (8 deg/s) elbow flexion movements in which the muscles performed shortening or lengthening contractions, or were isometric contractions. Care was taken to maintain constant background electromyographic (EMG) activity in the brachoradialis muscle at a 50-deg elbow angle across the tasks by changing the magnitude of the initial load. During each task, mechanical perturbations (duration 170 ms) were applied at pseudorandom intervals when the elbow angle was 50 deg. The magnitude of the perturbation was varied across tasks in order to induce an elbow extension velocity of 80 deg/s over the first 50 ms after the onset of perturbation. The stretch reflex EMG responses in all muscles varied across the three tasks, despite a constant EMG level and similar perturbation-induced angular velocity in the direction of elbow extension. In particular, both the short- and long-latency reflex EMG components were reduced during the lengthening contractions. Further, the task-dependent variations in the early (M2) and the late (M3) components of the long-latency reflex were different, i.e., the magnitude of M3 was considerably enhanced during the shortening task as compared with that of M2. These findings suggest that central modification was responsible for the task-dependent modulation of late EMG responses.

Key words Reflex and voluntary control of movement · Shortening and lengthening contractions · Long-latency reflex · Elbow · Human

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Introduction

It is well recognized that modulation of reflex and volitional electromyographic (EMG) activities occurs in parallel during movement. This parallel modulation requires co-activation of alpha- and gamma-motoneurons, in which the intrafusal musculature is controlled by gamma activity to provide a reference signal for activation of extrafusal fibers. Although the stretch reflex and volitional EMG activity are generally coupled, several investigations have demonstrated that some degree of independent control exists during functional movements (Capaday and Stein 1986, 1987; Johnson et al. 1993; Dietz et al. 1994). For example, Capaday and Stein (1987) demonstrated that the relative amplitude of the H-reflex in triceps surae muscles is modulated in a phase-dependent manner during human walking. Similarly, Johnson et al. (1993) found uncoupling of the reflex and volitional EMG activity in wrist muscles during a sinusoidal pursuit tracking movement. Furthermore, Dietz et al. (1994) found that the magnitude of reflex EMG activity varied independently when different tasks were executed, even though the level of volitional EMG activity was relatively constant.

These studies suggested that there might be some neural mechanism that independently modulates the reflex gain with voluntary activation levels to match the movement requirement. One way to achieve such modulation would be to vary the central activation of alpha- and/or gamma-motoneurons according to the task, as has been proposed by Tax et al. (1989, 1990). They found that the recruitment threshold and firing patterns of motor units in the elbow flexors were different for force and movement tasks, which they attributed to changes in the central activation pattern of alpha- and/or gamma-motoneurons. Abbruzzese et al. (1994) observed task-dependent variation of the H-reflex and the motor-evoked potentials (transcranial magnetic/electric stimulation) during different kinds of elbow flexor contractions. They suggested that the activation levels of spinal alpha-motoneurons might be modified by a peripheral neural mechanism, and the role of the cortical motoneurons might be an appropriate “setting” for the excitability of the spinal neural circuit and/or the spinal motoneurons.

In the present study, subjects performed shortening, lengthening, and isometric contractions with the elbow flexor muscles against loads that required a similar level of EMG activity for a reference elbow angle during the three tasks. The purpose was to determine the similarity of the stretch-evoked EMG responses across the three tasks. We found that the responses differed across muscles and tasks, which meant that the reflex and volitional activity were modulated independently under these conditions.

Materials and methods

Subjects and apparatus

Experiments were performed on 13 normal subjects (eight men and five women) aged between 21 and 33 years and with no known history of neurological disorder, all of whom gave informed consent to the experimental procedures. They were all

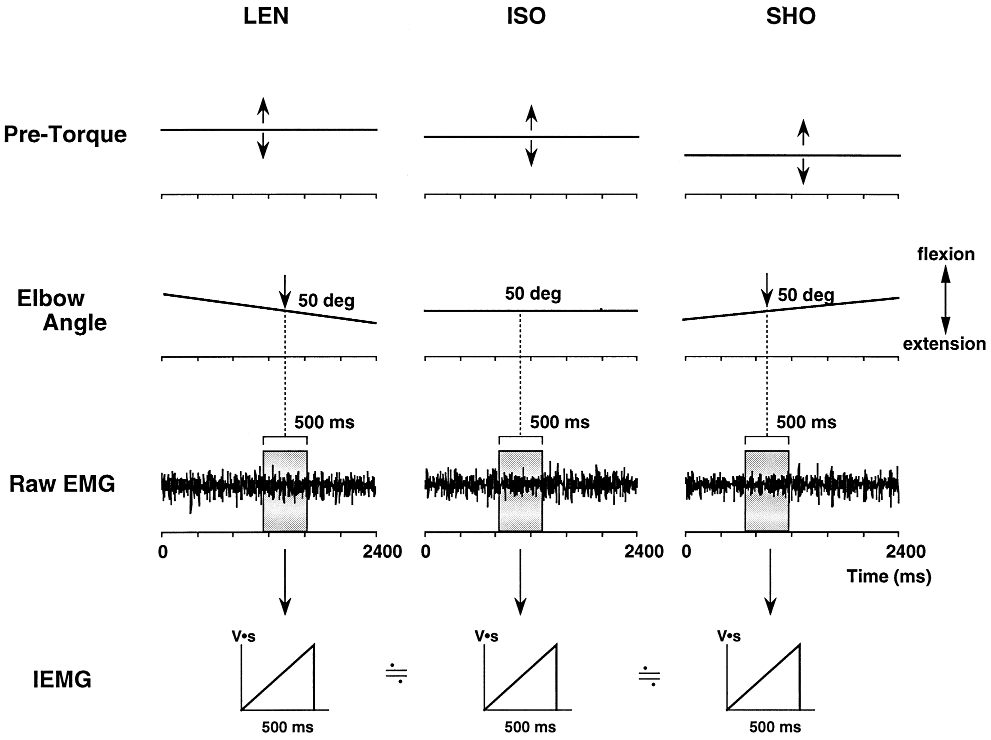


Fig. 1 A schematic representation of the experimental procedure to set the integrated electromyographic (*EMG*) activity (*IEMG*) of the three tasks at a similar level by changing the pre-load torque (*Pre-Torque*). *LEN*, *ISO* and *SHO* represent lengthening, isometric and shortening tasks, respectively

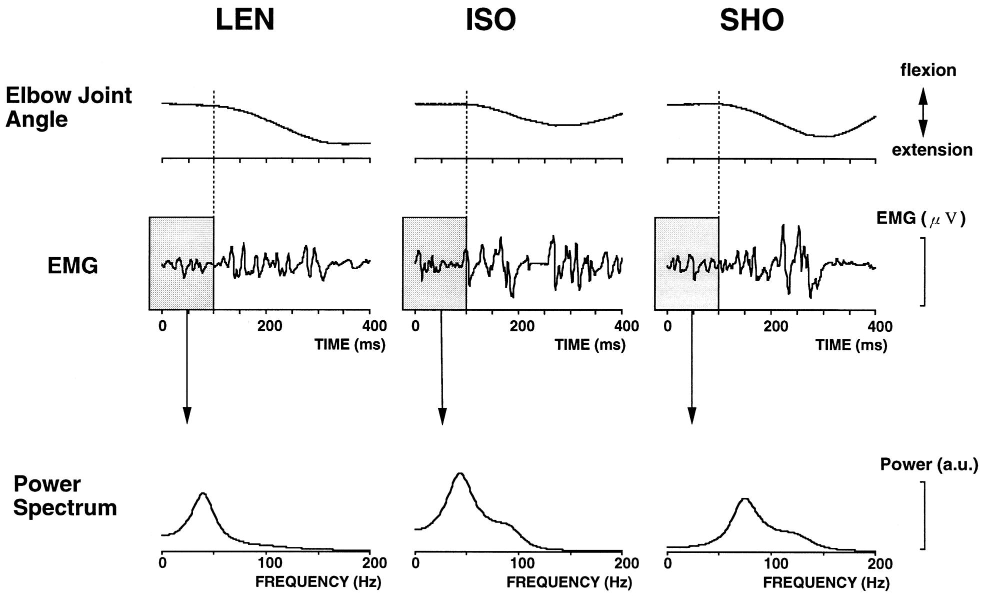


Fig. 2 A typical example of the EMG power spectrum, elbow joint angular displacement, and raw EMG responses during each task. The *shaded areas* represent the time interval when data for the calculation of power spectra were sampled

right-handed, and their right arms were tested. The subjects were seated in a heavy chair with the trunk fixed by a strap, and their right arms attached at the wrist to the shaft of a torque motor such that joint rotation was in a horizontal plane. The forearm was in the neutral position between full supination and full pronation, so that the palm faced downward. The shoulder angle was about 45 deg (0 deg: upper arm in frontal plane). The torque motor was used to apply constant pre-load torques and perturbation torques to the subject's forearm in the extension direction. Perturbation torques were applied in a pseudorandom order at a target angle of 50 deg, which was detected by means of a rotary encoder mounted on the axis of the torque motor. The duration of the perturbation torque was 170 ms. The torque exerted about the joint was measured with a torque sensor (Torque-Ducer, K22015, Kubota).

Procedures

Three motor tasks were performed, in random order, and the mechanical perturbations were applied during each task. The magnitude of pre-load torque was determined for each subject so that the integrated EMG activity in the brachioradialis was similar across the three tasks (6% of maximum voluntary contraction, 6%MVC) at the elbow joint angle of 50 deg. The integrated EMG activity for the time interval from 250 ms before to 250 ms after the moment when the elbow joint angle passed the target angle of 50 deg was measured as an index of the EMG activity level (Fig. 1). Similarly, the magnitude of the perturbation torque was adjusted so that the resultant angular displacement for the first 50 ms after the onset of perturbation during the three tasks was about 4 deg (80 deg/s).

Shortening and lengthening contractions

The subjects were requested to rotate their forearms about the elbow joint at a constant angular velocity of 8 deg/s between 10 and 80 deg (full extension = 0 deg). Mechanical stops were used to prevent hyper-extension or -flexion, although the subject could stop the shortening and the lengthening contractions at near 10 deg and 80 deg, respectively. The desired angular displacement was displayed as a horizontal target line on an oscilloscope placed 1.0 m away from the subject's face. The subjects were requested to track accurately the target line with the display of the actual elbow angle. In particular, the lengthening contraction was performed by gradually decreasing the activities of elbow flexor muscles. Some practice were given to the subjects before the measurement.

Isometric contractions

For the isometric contraction task, the subjects were requested to keep the elbow angle at 50 deg against the constant pre-load torque. The perturbation was applied 30 times at pseudorandom intervals between 1 s and 6 s. The subjects were requested to resist the perturbation and the constant pre-load torque.

Recording and analysis of EMG activities

EMG activities of the long and short heads of biceps brachii, the brachioradialis, and the long head of triceps brachii were measured by means of bipolar surface electrodes (Ag/AgCl, diameter 0.7 cm) placed over the bellies of all muscles with a center-to-center interelectrode distance of 1.5 cm. The EMG signals were amplified and band-pass filtered (5.3 Hz–1.5 kHz) with a conventional bioamplifier (EEG 1A97, NEC San-ei). The EMG, force, and position signals were simultaneously stored on computer memory for off-line analysis. The digitized EMG signals were full-wave rectified after subtraction for the DC component. Then, the rectified EMG and the other signals were averaged over a period of 100 ms before and 400 ms after the onset of the perturbation for 30 trials of each task. From the ensemble-averaged EMG waveforms, the average background activity level occurring in the 100 ms before the onset of perturbation was established. The areas of the reflex (M1, M2 and M3) and voluntary (VOL) responses above this level were measured. With respect to the reflex activity during the shortening and lengthening contractions, it might have been reasonable to evaluate the reflex EMG activity as an EMG magnitude over the voluntary activity levels during unperturbed shortening and lengthening contractions. However, no significant difference in the mean voluntary EMG activities was observed between two periods, i.e., approximately –100–0 ms and 20–100 ms, namely the "reflex period", after the expected onset of perturbation (at the elbow angle of 50 deg)

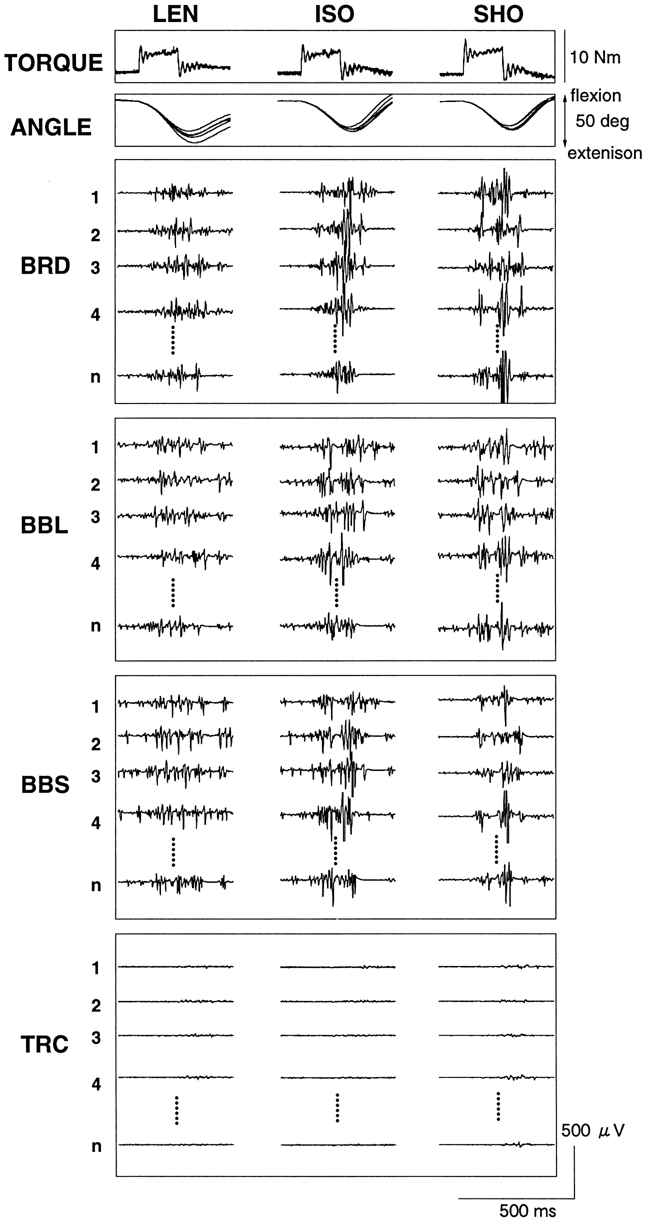


Fig. 3 A typical example of raw EMG responses in the brachioradialis (*BRD*), the long and short heads of biceps brachii (*BBL, BBS*), and the triceps brachii (*TRC*), torque and angle changes during the three tasks (*LEN, ISO, SHO*). Each raw EMG trace is a single response to a perturbation, and torque and angle traces are superimposed for responses to five perturbations

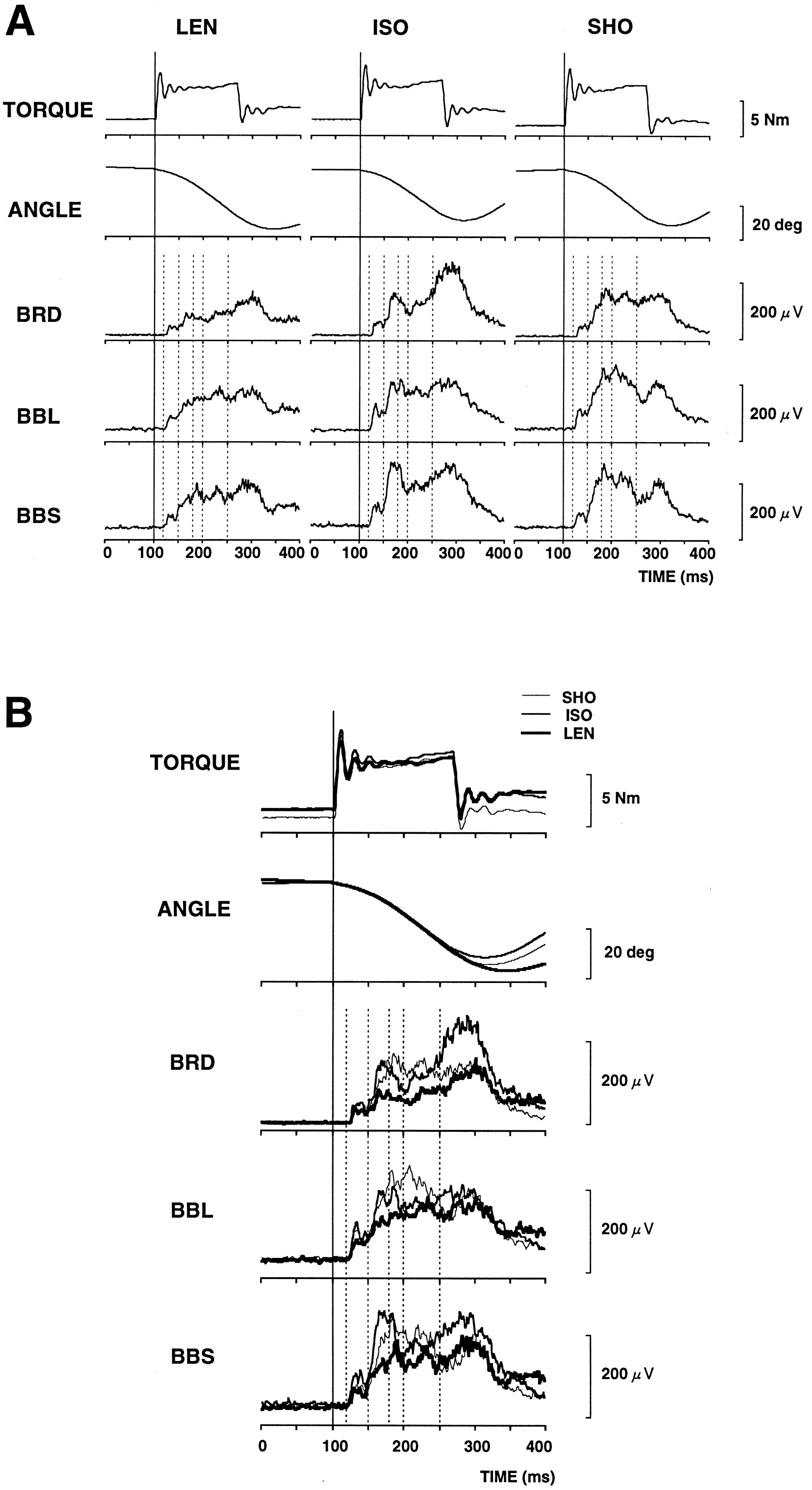


Fig. 4 **A** Group means of EMG responses during each task. **B** The superimposed traces for the same data in **A**, i.e., the isometric task (*thin lines*), the shortening task (*medium lines*), and the lengthening task (*thick lines*). Each trace represents the group means for the 13 subjects. The *thick vertical line* represents the onset of perturbation, and the *broken lines* on the *left* represent the onset and/or offset of the reflex EMG components, M1, M2, M3 and VOL, respectively

during the unperturbed contractions examined preliminarily (n = 2). This might be due to the slow movement velocity (8 deg/s) in our experiment. We therefore defined the background activity as the EMG activity in the 100 ms before the onset of perturbation.

The latencies and durations of each EMG component were determined on the basis of previous (Yamamoto and Ohtsuki 1989) and preliminary studies. The following time periods were used for each component: M1, 20–50 ms; M2, 50–80 ms; M3, 80–100 ms; VOL, 100–150 ms after perturbation onset. The magnitude of each component was expressed as the mean EMG activity during each period.

It has been demonstrated that the motor unit (MU) activities during the lengthening contraction are different from those during the shortening contraction. For example, Nardone and Schieppati (1988) and Nardone et al. (1989) have shown that the higher-threshold MUs are selectively recruited. At the same time, Moritani et al. (1988)

have shown that the mean power frequency of the EMG power spectrum shifts to a lower frequency. This is probably due to lower firing frequencies and/or derecruitment of the MUs which were earlier discharging at a high frequency. However, it was less clear whether the MU activities differed among the three contractions despite the standardized EMG level. In our study, the frequency characteristics of the background EMG activities were analyzed by applying the maximum entropy method to the four subjects in question.

For this measurement, EMG signals were sampled at 2 kHz for 256 ms before the perturbation onset 10 times during each task, and the power spectrum of each set of EMG data was calculated and ensemble averages determined for the ten power spectra (Fig. 2). The details for calculating the EMG power spectrum by this method have been described previously (Nakazawa et al. 1993). From each power spectrum, the mean power frequency (MPF) was calculated by the following equation:

$$\mathrm{MPF} = \sum_{f=0}^{256} f \cdot P(f) \,/\, \sum_{f=0}^{256} P(f)$$

where f is frequency and $p(f)$ is power.

Statistical data analysis

An analysis of variance (ANOVA) was used to test for differences in the EMG responses of the three tasks. When the ANOVA detected a significant difference among tasks, Scheffe's test was used to locate specific differences. Significance was accepted at $P<0.05$.

Results

Figure 3 shows an example of raw EMG responses to perturbations during the three tasks. During all experiments the EMG activity of the triceps brachii was monitored. There was minimal activity in this muscle during the three tasks, i.e., the background EMG activities were 1.7 ± 0.32, 1.8 ± 0.28 and 1.9 ± 0.39 (mean ± SE)

Table 1 The mean and s.e. of the background EMG magnitude in each muscle and the joint angular velocity ($\dot{\theta}$) induced by the perturbations during the three motor tasks

	$\dot{\theta}$ (deg/s)		Background EMG (%MVC)					
	Mean	SE	BRD		BBL		BBS	
			Mean	SE	Mean	SE	Mean	SE
SHO	83.11	0.75	5.77	1.16	17.25	1.89	10.80	1.78
ISO	82.40	1.14	6.99	1.36	15.85	1.61	13.19	2.30
LEN	82.61	1.32	6.90	1.36	17.14	2.34	11.72	2.56

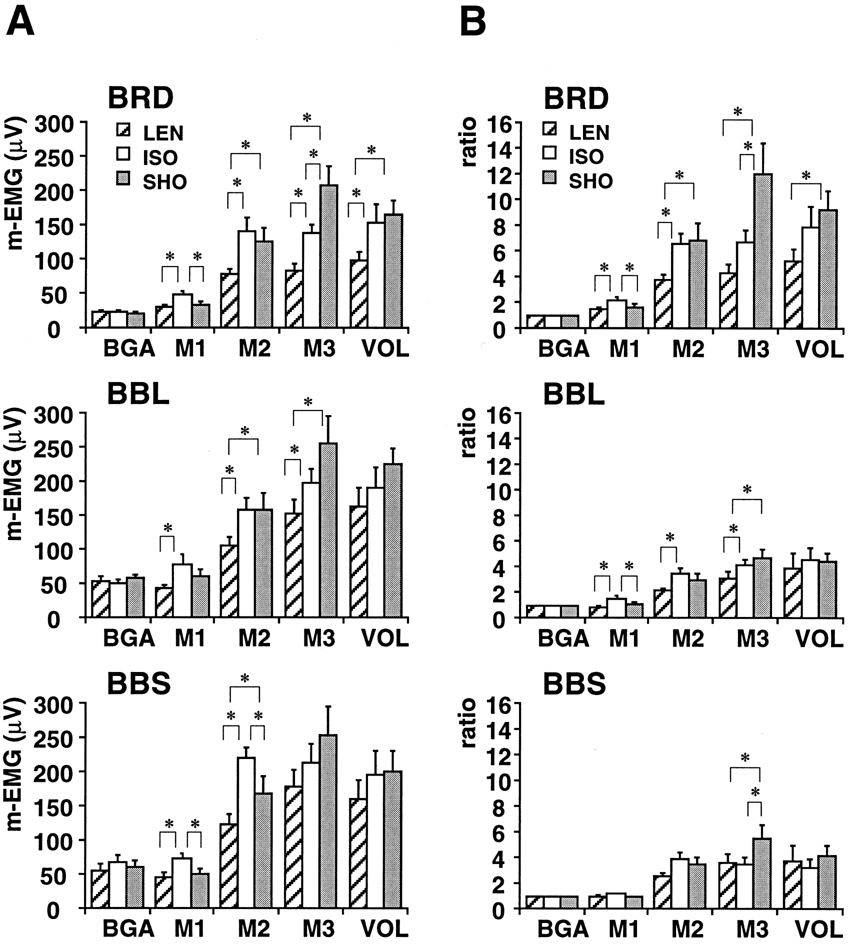
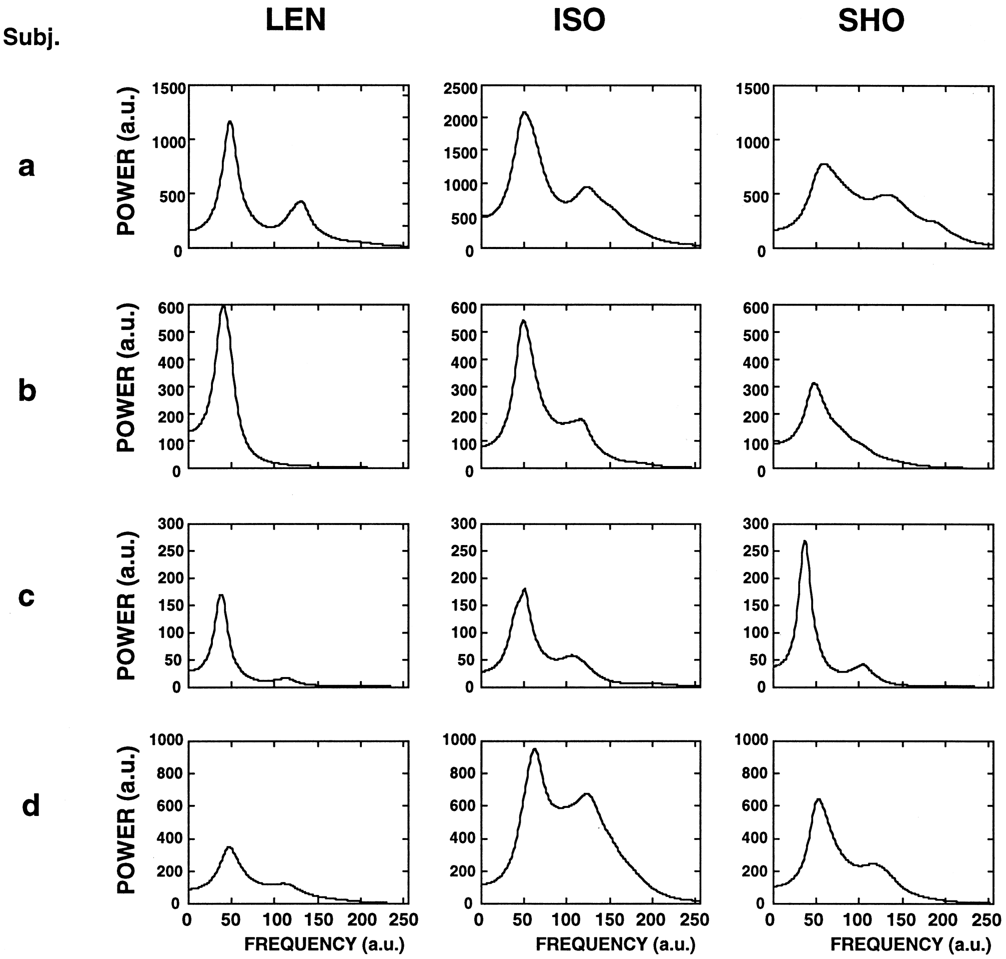


Fig. 5 **A** Comparison of the magnitude of each reflex component among the motor tasks. **B** The data in **A** presented as the ratio to the corresponding background activity (*BGA*) value. Each *bar* represents the mean and standard error (SE) for the 13 subjects. * Significantly different at $P<0.05$

Fig. 6 EMG power spectra for the background EMG activities during the three motor tasks from four subjects. Each spectrum is the average for 10 cases in which perturbations were applied during each motor task



%MVC, during the shortening, the lengthening, and the isometric contractions, respectively.

Responses of the joint torque, angle, and EMG activity to mechanical perturbations during the different motor tasks

Figure 4A shows the group means for the responses of torque, elbow joint angle, and EMG activity of the three muscles during the three motor tasks. Figure 4B shows superimposed traces for the same data as shown in Fig. 4A. The background EMG levels and the angular displacements for the first 50 ms after the onset of perturbation were qualitatively similar for the three tasks. Table 1 shows the mean and standard errors for the background EMG activity (0–100 ms in Fig. 4) and the joint angular velocity induced by the perturbation during the three tasks. There were no significant differences in background EMG activity among the tasks, i.e., the difference was less than 2% of the maximum voluntary EMG activity. Despite the similar background EMG activities and mechanical perturbation, EMG responses to the stretch were found to be different among the three motor tasks. It was clear that the earlier reflex responses (the period from the first to the third broken lines in Fig. 4) were larger during the isometric tasks, while the later responses (from the third to the fifth broken lines) were larger during the shortening task. The earlier and later responses correspond to the M1–M2 and the M3–VOL components, respectively. The EMG responses were markedly reduced during the lengthening tasks for all three muscles.

Figure 5A compares the magnitude of the EMG component for the three tasks and the three elbow flexor muscles. There were statistically significant differences ($P < 0.05$) for all reflex EMG components (M1, M2, and M3) among tasks, although the variation within each task was different for the three components. For the M1 and M2 components, the largest EMG activities appeared during isometric contraction, while the largest activity during shortening was observed in the M3 component (and VOL). For all reflex EMG components the reflex EMG activity was considerably reduced during lengthening. However, it is worth noting that there were relatively small differences for the M1 component between shortening and lengthening as compared with the M2 and M3 components, in which significant differences ($P<0.05$) between those tasks were observed.

Although the variation patterns of reflex EMG components among the three motor tasks were generally similar in the three elbow flexors, the rate of changes in the long-latency reflex components, M2 and M3, were dif-

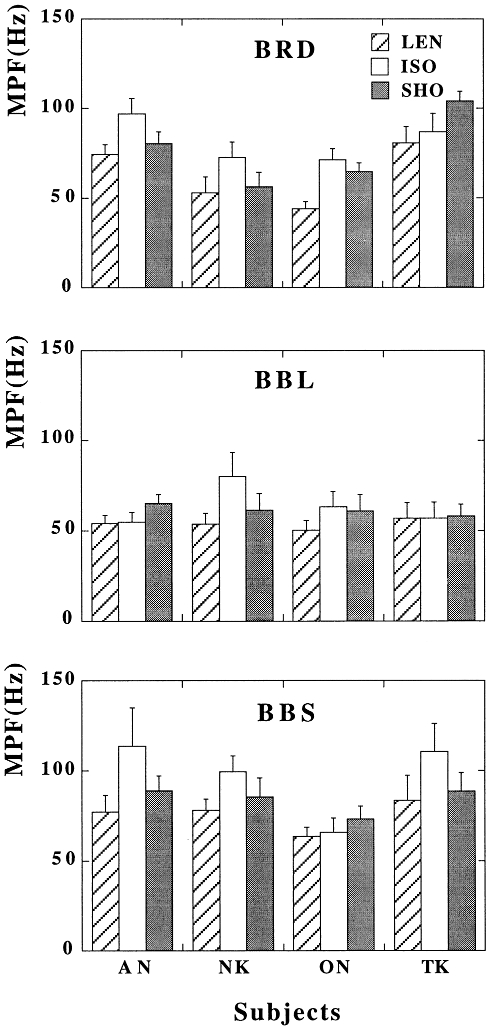


Fig. 7 Comparison of the mean power frequency (*MPF*) for the EMG power spectra for the three motor tasks. Each *bar* represents the mean and standard error (SE) for the 10 cases during each task

ferent in different muscles, i.e., the long-latency components of brachoradialis were more dramatically reduced during lengthening than during the other tasks.

In Figure 5B the magnitude of each EMG component has been normalized as the ratio to the corresponding background EMG value. Generally, the ratios of all EMG components of brachoradialis were higher than those of the other two muscles, indicating the higher reflex responsibility of brachoradialis than the other muscles. Moreover, the task-dependent differences of each EMG component were larger in brachoradialis than in the other muscles.

Comparison of frequency characteristics in background EMG activity

If motor unit activities varied across the tasks despite the same level of integrated EMG, the frequency characteristics of the surface EMG waveforms would be different.

Figure 6 shows power spectra calculated for the background EMG activities of BRD during the three motor tasks from four subjects. There was a general tendency for the high-frequency content of the power spectra to be reduced during the lengthening contraction. This was evident in a comparison of the mean power frequency for the three muscles and the task (Fig. 7). For almost all muscles and subjects, the mean power frequency was lowest during the lengthening contraction.

Discussion

The results of the present study have shown that: (1) the reflex responses varied in a task-dependent manner despite similar background EMG and stretch velocities, and (2) the task-dependent patterns differed across the EMG components and muscles.These results have important implications for the understanding of reflex and voluntary motor control during human movement, which will be discussed in more detail in the following section.

Differences in modulation of the reflex EMG components during the three motor tasks

The lowered reflex EMG responses during the lengthening contraction were common observations across components and muscles in the present study. Similar results have been reported for the H-reflexes evoked in the triceps surae (Romano and Schieppati 1987) and brachioradialis (Abbruzzese et al. 1994) muscles. These studies have demonstrated that the EMG amplitude of the H-reflex decreased during the lengthening contraction as compared with those during the shortening and the isometric contractions. Since the joint angular velocities employed in these studies were higher (12 deg/s, 25 deg/s and 50 deg/s; Romano and Schieppati 1987, 50–150 deg/s; Abbruzzese et al. 1994) than that (8 deg/s) in our study, the decreased reflex responses during the lengthening contractions observed in our study suggest that the stretch reflex activity which involves the excitability of both alpha- and gamma-motoneurons is suppressed irrespective of contraction velocities during the lengthening contraction. However, there was little difference in M1 between the shortening and the lengthening contractions in contrast with the large reduction of the long latency component during the lengthening contraction in our results. This may be due to the lower contraction velocity employed in our experiment because the reduction of the H-reflex has been shown to be more pronounced as the contraction velocity increases (Romano and Schieppati 1987).

Our results further showed that the task-dependent variations of reflex EMG responses were more pronounced in the long-latency reflex components (M2 and M3) than in the short-latency component (M1). Such pronounced variability of the long-latency stretch reflex agrees with recent observations concerning the task-dependent modulation of stretch reflex activities (Doemges and Rack 1992a,b; Dietz et al. 1994), and might indicate that the long-latency reflex is modulated in an appropriate way to match the motor requirements. As regards the neural mechanisms underlying the task-dependent modulation of the long-latency stretch reflex, Dietz et al. (1994) have proposed two possibilities: (1) modulation of the gamma-motoneurons, and (2) selection of appropriate afferent information, according to motor tasks which might change the stretch reflex responses. These neural mechanisms can also explain our results. Nevertheless, we have to consider another possibility, that is, that the different motor unit activity during different contractions may alter the stretch reflex response. In our experiment we paid particular attention to the background EMG activity and adjusted it to about same level across tasks. However, by examining the frequency characteristics of the background EMG waveforms it was shown that the mean power frequency during the lengthening contraction was reduced when compared with the other contractions, suggesting a different motor unit activity pattern. It has been well recognized that changes in motor unit recruitment and/or firing patterns should cause changes in surface EMG waveforms, and power spectra (Basmajian and De Luca 1985; Moritani et al. 1988). Further, such differences in motor unit activity patterns according to the muscular contraction mode have been demonstrated (Moritani et al. 1988; Nardone and Schieppati 1988; Nardone et al. 1989; Nakazawa et al. 1993). Moritani et al. (1988) have indicated that the reduced mean power frequency during the lengthening contraction might be due to lower firing frequencies and/or derecruitment of the MUs that were discharging at higher frequency. Therefore, the observed lower mean power frequency during the lengthening contraction in our results suggests that the MU activity pattern varied despite the standardized background EMG level. However, the similar magnitude of M1 between the shortening and the lengthening contractions may indicate that the different MU activity pattern might have little influence on the short latency reflex response. Thus, to the extent to which the MU activity pattern influences the stretch reflex EMG responses is less clear. Further studies are necessary to elucidate this.

Differences in the modulation patterns of M2 and M3

Although the greater variability of the long-latency reflexes due to tasks has been demonstrated in several studies, it was noteworthy in our results that the pattern of variation of M2 across tasks was not consistent with that of M3. These different behaviors observed in the patterns of M2 and M3 suggest that the early and late parts of the long latency EMG components have different neural mechanisms, as reported by Balestra et al. (1992). They found that the effects of fatigue on medium latency (M2) and long latency (M3) reflex responses in the human first dorsal interosseous were different, and on the basis of this and additional experiments they concluded that the medium- and long-latency components were mediated by different peripheral afferents, possibly muscle spindles and cutaneous receptors, respectively. Our data might agree with those of Balestra et al. (1992) in that the early and late part of the long-latency reflex EMG complex showed different behavior in different conditions, and this probably indicates a different neural origin and/or pathway for generating those parts in the long-latency reflex.

Differences in the reflex responses across muscles

The graphs in Fig. 5B shows that the reflex ratios (relative to the corresponding background EMG activity) in the brachioradialis were generally higher than those in both the short and long heads of the biceps brachii. This means a higher stretch reflex activity in the brachioradialis with respect to the same background activity. The higher reflex ratio in the brachioradialis might in large part be due to the longer moment arm of the muscle compared with those of the other elbow flexor muscles (Murray et al. 1995). The longer moment arm would result in a greater change in the length of the muscle fiber to the same joint angular displacement, meaning larger input to muscle spindles. The larger input to the reflex center induces a larger output, even though the gain of the reflex center is unchanged. The higher reflex ratio does not necessarily mean a higher reflex gain.

Modulation of reflex responses due to tasks was more pronounced in brachioradialis than in the other muscles (Fig. 5A, B). If stretch reflex gains of all elbow flexor muscles were modulated in the same manner, the modulations of reflex responses in those muscles would be parallel. However, the fact that the modulation was most pronounced in the brachioradialis suggests there might be some independence in the modulation of stretch reflex gains in elbow flexor muscles according to the muscle contraction mode. This seems to agree with the results of recent studies which have demonstrated task-dependent activation patterns in elbow flexor muscles during voluntary muscle contractions (Buchanan et al. 1986, 1989; Howard et al. 1986; van Zuylen et al. 1988; Schieppati et al. 1991; Nakazawa et al. 1993). The results of this study, therefore, suggest that the coordination of reflex activities in elbow flexor muscles might also be task-dependent. This means that the central nervous system might deal with the elbow flexor muscles as individual units rather than treating them as a single functional unit. However, the organizing principle which determines the coordination of the reflex activities in elbow flexor muscles according to the task is yet to be found.

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