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Kazuyuki Ogiso

Stretch Reflex Modulation
during Exercise and Fatigue

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Academic Dissertation

Neuromuscular Research Center,
Department of Biology of Physical Activity,
University of Jyväskylä



UNIVERSITY OF JYVÄSKYLÄ

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ABSTRACT

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Diss

The present series of studies were designed to examine how electromyographic (EMG) and mechanical responses of the stretch reflex were modulated by the background muscle activities and by fatigue induced by a long-lasting low-intensity eccentric exercise in the human ankle plantar flexor muscles. In total six different experiments were performed. Stretch reflex was elicited by a sudden dorsiflexion (SDF) while a given level of effort was being maintained by subjects. The results showed that muscle contraction types and pre-contraction levels before SDF had a considerable influence on stretch reflex behavior. A stretch after an isometric contraction (pre-ISO) elicited a larger stretch-reflex electrical response and generated a larger stretch-reflex mechanical response more efficiently than that after dynamic contractions in both passive and active conditions. A stretch after shortening (pre-SHO) elicited similar average EMG (aEMG) and gentler waveform of the short-latency stretch reflex (SLSR) compared with pre-ISO when the muscle was activated. A stretch after lengthening (pre-LEN) elicited the smallest aEMG of three conditions. These are likely to result from differences in muscle spindle sensitivity induced by a different motor task imposed on subjects and in afferent input from various receptors induced by the preceding muscle activities. This is confirmed by (1) a longer SLSR latency in the relaxed muscle than in the active muscle in pre-SHO, and (2) shorter SLSR latencies than the other conditions in pre-LEN. In case of mechanical response, a close relationship was observed between reflex torque (RT) and torque immediately after SDF. This indicates that the preceding muscle activity modifies the architecture of the muscle-tendon (M-T) complex and subsequently influences its mechanical response. It was shown that fatigue also altered the stretch reflex behavior. In particular, the stretch-reflex EMG response showed a bimodal recovery process comprising an acute and delayed decrease from fatigue irrespective of muscle contraction types before SDF. However, recovery processes of the mechanical response depended on the exercise pattern that induced fatigue. When the stretch reflex was elicited by the same SDF as that used during the exercise, RT did not follow a bimodal trend, but showed a prolonged recovery process. This indicates a movement-specific effect of fatigue. Alterations in M-T complex behavior and in nociceptive afferent activities associated with muscle soreness induced by fatigue are likely to be closely related to the bimodal changes in stretch reflex behavior.

Key words: stretch reflex, isometric, shortening, lengthening, pre-contraction level, motor task, long-lasting low-intensity eccentric exercise, fatigue

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This book is dedicated to my wife and my lovely children.

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ORIGINAL PAPERS

This thesis is based on the following papers, which will be referred to by their Roman numerals.

- I Ogiso K, McBride JM, Finni T, Komi PV. (2002) Short-latency stretch reflex modulation in response to varying soleus muscle activities. *J Electromyogr Kinesiol* 12: 17-26
- II Ogiso K, McBride JM, Finni T, Komi PV. (2002) Stretch-reflex mechanical response to varying types of previous muscle activities. *J Electromyogr Kinesiol* 12: 27-36
- III Ogiso K, McBride JM, Komi PV. (2003) The effects of effort levels and background EMG activities on short-latency stretch reflex modulation to varying types of soleus muscle contraction. Submitted
- IV Ogiso K, Kuitunen S, Avela J and Komi PV (2003) Mechanical response elicited by a mechanical and electrical stimulation after different muscle contractions. Submitted
- V Ogiso K, Kuitunen S, Avela J and Komi PV (2003) Passive stretch reflex behavior and long-lasting eccentric exercise. Submitted
- VI Ogiso K, Kuitunen S, Avela J and Komi PV (2003) Fatigue and effects of background muscle contraction on reflex behavior. Submitted

ABBREVIATIONS AND DEFINITIONS

| | |
|-------------|---|
| aEMG | average amplitude of the rectified surface electromyography |
| AJT | ankle joint torque |
| AL | activation level |
| APF | ankle plantar flexor |
| B-LA | blood lactic acid |
| CC | contractile component of a muscle |
| CK | creatine kinase |
| DT | double twitch |
| EMD | electromechanical delay |
| EME | electromechanical efficiency |
| ES | electrical stimulation |
| FIPA | fascicular insertion point in the aponeurosis |
| I-rate | increasing rate of ankle joint torque with the pre-contraction level |
| LLEE | long-lasting low-intensity eccentric exercise |
| LLSR | long-latency stretch reflex |
| LMT | local minimum torque recorded after non-reflex torque elicited by a stretch |
| MEP | motor evoked potential |
| MF | median frequency |
| MLSR | medium-latency stretch reflex |
| MPF | mean power frequency |
| MS | mechanical stretch |
| M-T complex | muscle-tendon complex |
| MU | motor unit |
| MVC | maximum voluntary isometric plantar flexion contraction |
| NRT | torque recorded immediately after a stretch perturbation |
| PSP | pre-motion silent period |
| RT | reflex torque |
| SDF | sudden dorsiflexion |
| SEC | series elastic component |
| SLSR | short-latency stretch reflex |
| ST | single twitch |
| W-ratio | ratio of absolute work performed in stretch perturbation period to that performed in contraction period |

1 INTRODUCTION

Voluntary movement includes many involuntary mechanisms. A representative example is the stretch reflex, seen in physical activities such as standing, walking, sprinting and jumping, and which represents the activation of α -motoneurons through the discharge of Ia-afferents elicited by stretching a muscle-tendon complex (M-T complex) mechanically.

When we are maintaining our erect postures, the center of pressure trajectory can be modeled as fractional Brownian motion (Collins and De Luca 1993). The stretch reflex plays an important role in control of the static postural sway (Koceja et al. 1995; Nashner 1976). Also during walking that postural control becomes more complicated, it functions to control the posture after being modulated according to postural demands of walking (Grey et al. 2002). These indicate that the stretch reflex is indispensable for our postural and locomotive tasks.

It is known that mechanical energy flows from the foot to the trunk immediately before the foot lands on the ground during sprinting to decrease the energy for the landing (Ae et al. 1988). However, directions of the energy flows are completely reversed by the ankle joint torque (AJT) after landing. During the support phase, the AJT-generated energy flows into the foot to support whole body. Therefore, the stretch reflex elicited immediately after landing might contribute to the change in energy flow direction, although the effects of the stretch reflex is still debatable in counter movements. It has been reported that the stretch reflex increases muscle stiffness and can enhance the following M-T complex performance (Dietz et al. 1979; Horita et al. 1996; Sinkjær et al. 1996; Yang et al. 1991). Great contribution of the stretch reflex to a counter movement jump was also shown (Kilani et al. 1989). Since impulse acting on the foot is closely related to the sprinting speed (Ogiso et al. 1998), it is possible that the stretch reflex behavior influences not only the postural control but also the movement performance.

Reflex depends largely on afferent inputs from the periphery because it is elicited only by the afferent inputs. Therefore, reflex generally shows quick and fixed behavior according to stimulus intensity applied to the M-T complex. The stretch reflex is a mono-synaptic reflex and it is usually regarded as a simple

neuromuscular behavior. However, recent studies have shown that the stretch reflex is modulated according to motor tasks (Doemges and Rack 1992a,b) and phases of movements (Sinkjær et al. 1996). It was also reported that fatigue induced by an exercise could alter the stretch reflex behavior (Avela et al., 1999a,b; Avela and Komi, 1998a,b; Brockett et al., 1997; Nicol et al., 1996b). These indicate that 'gain' of the stretch reflex is obviously modulated according to functional requirements to accomplish a given motor task and to conditions of the M-T complex. Modulating the reflex seems to be useful for efficient maintenance of a given posture and enhancement of movement performance, for example.

This thesis was focused on stretch reflex modulation in response to the background muscle contractions, muscle activity levels and fatigue. To remove uncertain factors relating to the modulation, the stretch reflex and fatigue were elicited from the ankle plantar flexor (APF) muscles only during a single-joint movement. It was thought that this would provide useful information for understanding of the reflex mechanism and for enhancement of physical performance to clarify 1) what modulates the stretch reflex, 2) how it is modulated, and 3) what is induced by the stretch reflex modulated.

2 REVIEW OF THE LITERATURE

2.1 Stretch reflex

2.1.1 Neuromuscular basis of the stretch reflex

M-T complex has some defensive lines against unexpected external perturbations (Latash 1998). Peripheral elasticity of muscles, tendons and the other tissues and preprogrammed reactions against perturbations have important roles to damp the perturbations. The stretch reflex also contributes to the defensive mechanisms against a brief and unexpected increase in muscle length (a mechanical stretch). It increases muscle stiffness represented by the ratio of force change to length change and can enhance the following M-T complex performance (Dietz et al. 1979; Horita et al. 1996; Sinkjær et al. 1996; Yang et al. 1991).

The stretch reflex is indicated as EMG bursts evoked by the activation of α -motoneurons through the asynchronous discharge of Ia-afferents automatically elicited by a mechanical stretch (Burke 1985). The EMG burst generally consists of the following three components: 1) short-latency component, 2) medium-latency component and 3) long-latency component. These components are often referred to as M1, M2 and M3, respectively (Lee and Tatton 1982). The third component (M3) is occasionally observed. Latencies for the three components vary individually and are different for different muscles. Short- and medium-latencies of the soleus muscle (SOL), for example, are about 40 ms and 70 ms, respectively (Nardone and Shieppati 1998; Nicol et al. 1996b). The latencies are slightly shorter in gastrocnemius muscles than in SOL (Nicol et al. 1996). Differences in stretch reflex sensitivity also exist between distal and proximal muscles (Thilmann et al. 1991). In general, lower-limb muscles have larger amplitude of the short-latency component than that of the middle-latency component, while upper-limb muscles shows the opposite trend.

Reflex is based on the existence of short-latency connections between the input (afferent signal) and the output (motor response or efferent output)

(Enoka 2002). The neural circuit underlying the stretch reflex involves the central nervous system (CNS), sensory receptors such as group Ia and II afferents from muscle spindles, group Ib afferents from Golgi tendon organs and group III and IV nociceptive afferents with free nerve endings, and α -motoneurons. The stretch reflex response depends on a sum of the inputs from the receptors. This is confirmed also by the clasp-knife reflex elicited by an ensemble signal from Golgi tendon organs, secondary sensory endings, free nerve endings and the other receptors (Cleland and Rymer 1990).

2.1.2 Afferent inputs from proprioceptors

2.1.2.1 Muscle spindle - group Ia and II afferent nerves, and gamma-motoneurons

Human muscles have about 27500 muscle spindles that are sensitive to a change in muscle length and stretching velocity of muscles, with 7000 in each leg (Prochazka 1996). In one muscle, there is a rough relationship that the number of afferent nerves from muscle spindles corresponds to about 10% of the number of nerves innervating the muscle (Cooper 1966). Banks et al. (1988) have suggested that the number of muscle spindles can be quantified as:

$$\log_{10}N = 1.58 + 0.32 \log_{10}W$$

where N and W are the number of muscle spindles and muscle weight, respectively. This result indicates that the number of muscle spindle depends mainly on the muscle weight. However, it has been also reported that density of muscle spindles is about three times higher in slow-twitch (ST) fibers than in fast-twitch (FT) fibers (Cooper 1961), and that hand and neck muscles have high density of muscle spindles. Thus, although a relationship between muscle functions and density of spindles is still debatable, it has been shown that the density, number of muscle spindles per gram wet weight of the human skeleton muscles, is 18.8 in the lumbricales muscle, 0.4 in gastrocnemius muscle and 0.9 in SOL, for example (von Voss 1971).

Mammalian muscle spindles lie in parallel with the extrafusal fibers and its ends attach to the endomysium or tendon. It varies in length from 5 to 10 mm, which corresponds to about 10 to 20 % of length of the extrafusal fibers (Prochazka 1996). A large difference in length between the muscle spindles and extrafusal fibers indicates that the spindles detect changes in length and stretching speed only around its distribution area (Elek et al. 1990). Therefore, muscle spindles are distributed to appropriate positions for motor control of each muscle.

A muscle spindle is composed of intrafusal fibers, afferent nerves that have endings around equatorial regions of the intrafusal fibers, motoneurons innervating both ends of the intrafusal fibers enclosed in a connective tissue capsule. The intrafusal fibers consist of a type I nuclear bag fiber (bag1), a type II nuclear bag fiber (bag2) and some nuclear chain fibers (Boyd 1980). Nuclear

bag fibers have 12 – 25 μ m in diameter and 7 – 10mm long. Nuclear chain fibers have 12 μ m in diameter and 4mm long. These fibers are smaller than the extrafusal fibers (20 – 100 μ m in diameter and 5 – 30cm long) and hardly contribute to force development. The mechanical properties are similar to those of the slow, intermediate and fast twitch extrafusal fibers (Gladden 1992).

The group Ia afferent nerve has an ending spiraling around equatorial regions of bag1, bag2 and nuclear chain fibers. The group II afferent nerve has a flower spray ending both or either side of the equatorial regions of bag1 and bag2 and has an annulospiral ending both sides of the equatorial region of each nuclear chain fiber. These afferents transmit the action potentials to CNS via the spinal cord when the afferent endings are stretched. Group Ia afferent nerves from extensor muscles make monosynaptic reflex pathways in spinal cord. Primary sensory ending made by the group Ia afferent nerves is more sensitive to stretching velocity than secondary sensory ending made by the group II afferent nerves. The secondary sensory ending is sensitive only to change in muscle length. Muscle spindles have a characteristic that its sensitivity can be altered by CNS because the intrafusal fibers are innervated by γ - and β -motoneurons. This markedly differs from other proprioceptors. γ -motoneurons are smaller in size than α -motoneurons innervating the extrafusal fibers and they innervate the intrafusal fibers only, whereas β -motoneurons are in intermediate size between α - and γ -motoneurons and innervate both the extrafusal and intrafusal fibers. These motoneurons contact myofilament-rich polar regions of the intrafusal fibers. An action potential of γ - or β -motoneurons contracts the polar regions, which results in a stretch of the equatorial region followed by activation of afferent nerves (Matthews 1972; Schmidt 1985). γ -motoneurons are functionally divided into dynamic and static nerves. Since dynamic γ - motoneurons mainly innervate bag1 dominated by the group Ia afferents (Walro et al. 1987), it increases sensitivity of the group Ia afferents. On the other hand, static γ - motoneurons innervate bag2 and nuclear chain fibers and can increase sensitivity of group II afferent nerves (Barker et al. 1986).

2.1.2.2 Golgi tendon organ – group Ib afferent nerve

Golgi tendon organs exist in myotendinous junction of all skeletal muscles of limbs, which have 122 μ m in diameter and 1600 μ m long in humans (Bridgman 1970). Most of them are located around extrafusal fibers as these connect with an aponeurosis of attachment (Botterman et al. 1978). Sixty-three percents of the tendon organs being in series with 10 – 20 extrafusal muscles have spindle shapes covered by a capsule (Barker 1974), and they exist more in slow-twitch fibers than in fast-twitch fibers (Jami 1992). Although these characteristics are similar to those observed in muscle spindles, a mechanism that an Ib afferent nerve and no efferent nerves innervate a tendon organ (Hasan and Stuart 1984) markedly differs from the muscle spindle.

Golgi tendon organs play a role of a strain gauge in vivo because they are monitoring muscle force. This is supported by a result that discharge of a tendon organ parallels electromyographic (EMG) activities that are closely

related to force exerted by muscles (Petit et al. 1997). Golgi tendon organs are sensitive to tension generated within muscle-tendon unit (Schmidt 1985). In particular, the largest response is observed when a motor unit where the organ is arranged contracts. The other motor unit activities do not elicit large response of the tendon organ. Contraction of every motor unit is monitored by at least one tendon organ (Jami 1992; Jami and Petit 1976). When an isokinetic movement is performed, it is known that the discharge rate of a tendon organ is high at the beginning of the movement because muscles have to exert large force to cope with the peripheral weight. Thereafter, it decreases and lasts at higher rate than spontaneous discharge during the movement. This indicates that the tendon organs monitor an alteration in muscle force and contribute to coordination of a given movement.

Group Ib afferent input induces a disynaptic inhibition of the homonymous and synergist α -motoneurons and a disynaptic or trisynaptic excitation of the antagonist α -motoneurons. Simultaneously, it induces a presynaptic inhibition of group Ia afferent nerves through 2 – 6 interneurons (Brink et al. 1984). This reduces the action potential and the subsequent amount of neurotransmitter released at the afferent-motor neuron synapse. Thus, flexible balance between force feedback of group Ib afferent nerves and length feedback of group Ia afferent nerves contribute to maintaining muscle stiffness to attain a given motor task appropriately.

2.1.2.3 Free nerve ending – group III and IV nociceptive nerves

Free nerve endings innervating muscles and fascias account for 75% of the whole nerves innervating skeletal muscles. Nociceptive input from the free nerve endings is transmitted by way of group III and IV nociceptive nerves. These afferents are activated by changes in metabolic environment involving chemical changes induced by an exercise (Garland and Kaufman 1995). Group III nociceptive nerves do not respond to muscle stretch and anemia, but respond to pressure and heat stimulus. Seventy percents of group III nerves are excited by injecting bradykinin, serotonin, histamine, KCL called algescic substance (Mense 1977) and lactic acid (Rotto and Kaufman 1993; Sinoway et al. 1985). Endings of group IV nociceptive nerves are divided into 1) polymodal receptors that respond to both muscle contraction and chemical stimuli, 2) receptors that respond to chemical stimulus only and 3) receptors that respond to muscle contraction only. These nociceptive nerves play a role to warn excessive joint movement.

Group III and IV nociceptive nerves make a powerful input to inhibitory interneurons. Subsequently, they inhibit either Ia terminals (Duchateau and Hainaut 1993) or α -motoneuron pool (Bigland-Ritchie et al. 1986). However, it is known that these nerves may activate also gamma-motoneurons (Jovanovic et al. 1990; Johansson et al. 1993; Djupsjobacka et al. 1995).

2.1.2.4 Fusimotor set

γ -motoneurons are controlled by CNS in a task- or context dependent manner (Loeb 1984). How γ -motoneurons are controlled seems to be closely related to spinal interneuron activities (Pratt et al. 1991).

It is well known that discharge of group Ia afferent nerves decreases temporally at twitch contraction due to decline in tension of equatorial regions of intrafusal fibers (Schmidt 1985). Discharge rate of spindle endings decreased during shortening has been also observed (Burke et al. 1978). As a mechanism to cope with the "unloading effect", α - γ coactivation hypothesis, that is, α -motoneurons innervating extrafusal fibers and γ -motoneurons innervating intrafusal fibers are activated at about same time, was proposed (Granit 1970). This coactivation can be observed during postural control. However, a result that group Ia afferent activities are connected with changes in muscle length rather than α -motoneuron activities (Al-Falahe et al. 1990) does not support it.

Prochazka et al. (1985) have shown that fusimotor action on a given spindle afferent during movements is not rigidly alpha-linked, but set by the CNS to steady levels of gamma activity. This is called "fusimotor set" and is based on independent control between α - and γ - motoneuron activities. This hypothesis is supported by 1) elevated discharge rate of muscle spindles during complicated and high-speed movements, 2) elevated activities of both dynamic and static γ - motoneurons when a precision movement is required and 3) a fact that the midbrain has a part that selectively activates dynamic γ - motoneurons (Prochazka 1996). However, it was also reported that more demanding motor tasks induce not only higher fusimotor activity but also higher EMG activities (Kakuda et al. 1996). This does not support the hypothesis that fusimotor activity is adjusted independently of the skeletomotor activity. In addition, Burke et al. (1980) reported that there was no detectable change in muscle spindle activity when the receptor-bearing muscle did not contract in the interval between warning and perturbation. Dynamic response of spindle endings to the perturbations was not increased in size or altered in latency, even if subjects were warned of the perturbations. A hypothesis "fusimotor set" is also obscure.

2.1.3 Spinal-mediated and transcortical responses

Short-latency stretch reflex (SLSR) is a spinal-mediated monosynaptic reflex via group Ia afferent nerves. This is a common mechanism every muscle has, although SLSR latencies are different among the muscles. On the other hand, medium-latency stretch reflex (MLSR) found by Hammond (1954) is considered to be polysynaptic. MLSR is a transcortical response via group Ia afferent nerves in the hand muscles (Capaday et al. 1991; Day et al. 1991; Goodin et al. 1990; Palmer and Ashby 1992), whereas it is considered to be spinal-mediated reflex via group II afferent nerves in the lower limb muscles (Corna et al. 1996; Dietz et al. 1985; Grey et al. 2001; Nardone et al. 1990; Schieppati et al. 1995; Shieppati and Nardone 1997). Recent studies suggest that long-latency stretch reflex (LLSR) has

a possibility of being a transcortical response (Petersen et al. 1998), although some studies do not regard LLSR as a reflex response because the LLSR may overlap voluntary responses from its long latency (Capaday et al. 1994). Subsequently, wide functional differences exist between a distal and proximal muscle (Thilmann et al. 1991). SLSR is dominantly modulated in the lower limb muscles, whereas MLSR is dominantly modulated in the upper limb muscles.

2.1.4 Mechanical responses

When the muscle-tendon complex is suddenly stretched, a mechanical response is automatically elicited by the intrinsic properties and the stretch reflex (Hoffer and Andreassen 1981, Nichols and Houk 1976, Sinkjær et al. 1988). The response comprises two components: 1) the first component where force rapidly increases immediately after the stretch, and 2) a twitchlike component with a longer latency. The former is dominated by inertia of the perturbed segment and intrinsic properties of the perturbed muscle-tendon complex (Sinkjær et al. 1988) and the latter is mostly due to the stretch-reflex EMG response. It has been suggested that the first component, acute force development immediately after a stretch, is due to increased strain on the attached cross-bridges in combination with a slight increase in the number of attached bridges (Lombardi and Piazzesi 1990; Sugi and Tsuchiya 1988). A temporary fall in force after the first peak also seems to be caused by exceeding short-range elastic limit of intrinsic muscle stiffness and decline in intrinsic muscle viscosity as stretch velocity decreased (Joyce et al. 1969; Rack and Westbury 1974).

There is a time lag between EMG and mechanical responses elicited by an unexpected perturbation. This is called electromechanical delay (EMD). Nicol and Komi (1998, 1999) reported that EMD was 10 - 12 ms in the triceps muscles when the muscles were stretched passively. It was also observed that EMD of the peroneal muscles was 10.54 ± 0.71 ms at bipedal stance and 8.67 ± 0.63 ms at monopodal stance in standing positions (Isabelle et al. 2003).

2.2 Factors that modulate stretch reflex

2.2.1 Stretch condition

Stretch reflex behavior is tightly coupled with the following stretch conditions applied to muscles: joint angle during the stretch (Fellows and Thilmann 1989; Stein and Kearney 1995; Weiss et al. 1986), amplitude (Allum and Mauritz 1984; Stein and Kearney 1995), velocity (Allum and Mauritz 1984), direction and duration of the stretch (Stein and Kearney 1995). Reflex-induced force also depends nonlinearly on position, voluntary activity, vibration, and amplitude, width and velocity of the stretch (Stein and Kearney 1995) as well as on the EMG response.

2.2.2 Motor task

Doemges and Rack (1992a, b) showed that different motor tasks imposed on subjects elicited different LLSR including MLSR in a human wrist flexor muscle. The LLSR was larger during 'maintain position' task than during 'maintain force' task, although the ramp extensions began from a similar finger position, a similar flexing force, and with a similar amount of EMG activity. Since the LLSR modulation was still task-dependent after co-activation of the wrist extensor muscles observed during 'maintain position' task was prevented by local anaesthesia of the radial nerve, they suggested that the modulation is independent of voluntary muscle activities and is task-dependent. Dietz et al. (1994) also observed that amplitude of MLSR was significantly larger during position-control than during torque-control task. They have proposed that the difference in the MLSR behaviour might be achieved by the appropriate central regulation of gamma-motoneurone activity or, alternatively, by selective modulation of different receptor inputs between the two tasks. It is also known that H-reflex is task-dependent, although H-reflex is different from stretch reflex because its stimulus bypasses the fusimotor system. Capaday and Stein (1986) showed that H-reflex amplitude was greater during standing than during walking at the same EMG and stimulus levels.

2.2.3 Phase of movement

It has been recently known that reflex behavior during movement is independent of voluntary muscle activities. A result that human H-reflex amplitude of SOL is not always closely related to the background EMG activity produced during walking confirms it (Capaday and Stein 1986, 1987). Many other studies also shows that H-reflex is modulated during walking and running (Crenna and Frigo 1987; Simonsen and Dyhre-Poulsen 1999). Staines et al. (1996) reported that not only H-reflex amplitude but also tibial nerve somatosensory evoked potential (SEP) amplitude is modulated during passive pedaling and suggested that the movement-induced amplitude modulation of H-reflex and SEP arises partly from phasic discharge of extensor muscle spindles. Stretch reflex also seems to be modulated according to phases of movement. Sinkjær et al. (1996) and Kearney et al. (1999) have observed that SLSR is modulated throughout the gait cycle, although SLSR latency does not depend on the phase in the gait cycle.

2.2.4 Background muscle activity

2.2.4.1 Pre-activation level

Muscle contraction levels prior to a stretch are closely related to the amplitude of the stretch reflex responses (Allum and Mauritz 1984; Stein and Kearney 1995; Toft 1995). However, It has been observed that SLSR and MLSR are independent of the background EMG activity in human SOL (Toft et al. 1991)

and in cat SOL (Hoffer and Andreassen 1981). This observation disagrees with the "automatic gain principle," according to which SLSR and MLSR amplitudes should increase proportionally with the background EMG activity (Marsden et al. 1976; Matthews 1986). On the other hand, SLSR independence observed in SOL was not shown in the tibialis anterior muscle (Toft et al. 1989). The automatic gain compensation, which predicts that the reflex response is an approximately constant proportion of the background activity, has been shown in the thumb and elbow flexors. Therefore, the effects of pre-activation on the SLSR modulation may depend, at least in part, on the differences in the functional requirements made of the various muscles.

2.2.4.2 Background muscle contraction - muscle history

Many human studies have shown that MLSR or LLSR is reduced during non-isometric contractions in the hand (Wallace and Miles 1998), the forearm muscle (Bawa and Sinkjær 1999) and the elbow muscles (Nakazawa et al. 1997, 1998). SLSR behavior is also likely to be influenced by the background muscle contraction. Bawa and Sinkjær (1999) and Nakazawa et al. (1997) observed reduced SLSR during a non-isometric contraction. In particular, smaller SLSR after lengthening than after the other contractions is general agreement among earlier studies (Nakazawa et al. 1997, 1998; Wallace and Miles 1998). Romano and Schieppati (1987) have observed that H-reflex also decreases during lengthening contractions. When SLSR after shortening was compared with that after an isometric contraction, smaller SLSR can be observed in the elbow muscles (Nakazawa et al. 1997, 1998).

Stretch reflex mechanical responses also seem to be influenced by the background muscle activities. It has been reported that joint torque evoked by an electrical stimulation (ES) during lengthening is greater than that during the other contractions under a maximal voluntary (Westing et al. 1990) and relaxed (Gravel et al. 1987) conditions. Higher Ca^{2+} releases have been also observed during lengthening than during isometric actions (Warren et al. 1993, Lowe et al. 1994). These findings indicate that the preceding muscle contraction influences the subsequent performance of the muscle-tendon complex elicited by a stretch. Irregularity of filament overlap seen in tetanized muscle fibers and fibers stretched during tetanus (Brown and Hill 1991; Edman and Tsuchiya 1996) suggests that the preceding muscle contraction may induce changes in the filament overlap. Yanagida et al. (1985, 1993) and Kitamura et al. (1999) clearly showed that the actin is moved a long distance on a myosin head smoothly and efficiently because each ATPase cycle corresponds to multiple power strokes with a moderate load. This molecule-level movement may influence mechanical relations between the preceding muscle contraction and the stretch perturbation.

2.2.5 Neuromuscular fatigue and muscle damage

Fatigue induced by exercises involving eccentric actions, which is described as a loss of force-generating capability (Bigland-Ritchie and Woods 1984) or an inability to maintain further exercise at the required level (Edwards 1981), clearly decreases the stretch reflex peak-to-peak amplitude, resistance force (Nicol et al. 1996b; Avela and Komi 1998a,b; Avela et al. 1999a,b) and receptor sensitivity responsible for position and force sense (Brockett et al. 1997). Amplitude of H-reflex is also decreased by fatigue (Duchateau and Hainaut 1993; Avela et al. 1999a, b, 2001). Both stretch reflex and H-reflex involve the same neural pathways. However, the stretch reflex is evoked through the Ia afferent input from the muscle spindles whose sensitivity gain is mainly controlled by α - γ motoneuron activities, while H-reflex is evoked by an artificial electrical stimulation that bypasses the muscle spindle sensitivity. Therefore, H-reflex is sometimes regarded as an approximate indicator of the excitability of the α motoneuron pool (Hallett et al. 1994). Motor evoked potential (MEP) evoked by transcranial magnetic stimulation, which is an indicator of the efficacy of ascending and descending systems, also decrease during (Ljubisavljevic et al. 1996) and after an exercise (Brasil-Neto et al. 1993; Rollnik and Dengler 2002). This depression can be induced also by a series of electrical stimulation without voluntary muscle activation (Pitcher and Miles 2002).

Yoshimura et al. (1996) showed a significant correlation between recruitment pattern of the bag1 intrafusal fibers and the slow twitch extrafusal fibers, and the largest glycogen depression in the bag1 intrafusal fibers in the initial phase of 8 hours swimming. Since the bag1 intrafusal fibers are mainly dominated by the group Ia afferents, a low-intensity long-lasting exercise imposed on subjects may seriously influence the muscle spindle sensitivity followed by α -motoneuron activity. On the other hand, a maximal intensive short-lasting exercise makes the stretch reflex behavior less influence compared with a low-intensity long-lasting exercise (Strojnik and Komi 1998).

It is known that a low-intensity long-lasting exercise selectively decreases torque evoked by low frequency stimulation (Avela et al. 2001; Edwards et al. 1977). Chin and Allen (1996) suggest that low frequency fatigue results from increases in intracellular free Ca^{2+} concentration, which activates some processes that lead to failure of excitation-contraction (E-C) coupling and Ca^{2+} release. Therefore, force evoked by low frequency stimulation is closely related to E-C coupling. Impairment of E-C coupling is closely related to muscle damage (Jones 1996). Many histological, biomechanical and blood analyses also evidence the muscle damage induced by exercises involving eccentric muscle actions (Clarkson and Newham 1995). Changes in metabolic environment involving chemical changes induced by the exercise activate the group III and IV afferents (Garland and Kaufman 1995), which result in pre- and post-synaptic inhibition of either Ia terminals or α -motoneuron pool. This is supported by a fact that fatigue-induced inhibition of the pre- and post-synaptic waves disappeared when a large number of the group III and IV afferents were

eliminated by injecting capsaicin (Pettorossi et al. 1999). A long-lasting low intensity exercise simultaneously induces decline in the M-wave (e.g. Fuglevand et al. 1993). This indicates an impairment of one or more of the processes involved in converting an axonal action potential into a sarcolemmal action potential, that is, an impairment of neuromuscular propagation. Decline in force can be induced also by the impairment of neuromuscular propagation (Fuglevand et al. 1993).

Subsequently, recovery process of the stretch reflex amplitude takes a long time and follows a bimodal trend that consists of an acute and delayed decrease in the amplitude (Avela et al. 1999b; Komi and Nicol 2000a, b). It has been also reported that the bimodal trend depends on the intensity of exercise imposed on subjects (Nicol et al. 1996a).

3 THE PURPOSE OF THE STUDY

Based on available literature, it is thus possible that stretch reflex elicited by an unexpected mechanical stretch can be modified by the following aspects:

- 1) by various stretch conditions such as amplitude, velocity, direction and duration of the stretch, and joint angle at the stretch.
- 2) during the different phases of movement.
- 3) by motor task imposed on muscle-tendon complex.
- 4) by muscle contraction level prior to the stretch.
- 5) by muscle contraction types prior to the stretch.
- 6) by fatigue induced by an exercise.

Many of these observations are based on MLSR or LLSR obtained from the human upper limb muscles and from animal muscles. Many fatigue studies did not employ an exercise of a specific muscle in which the stretch reflex was elicited, but a voluntary exercise including multi-joint movement. In the present study, stretch reflex and fatigue were elicited from APF muscles only with an ankle ergometer. The most dominant component is SLSR in APF muscles (Thilmann et al. 1991). Although SLSR is monosynaptic and is a simple mechanism, its modulation involves some neural circuits. Therefore, SLSR elicited after different muscle contraction types, different muscle contraction levels and fatigue induced by an exercise was compared to examine the mechanism of SLSR modulation. The detailed aims of the present study were as follows:

- 1) The first aim of this project was to investigate the effects of muscle contraction types and pre-contraction levels before a stretch perturbation on SLSR in SOL. Motor tasks “maintaining an EMG activity level or joint torque level” used in earlier studies is not normally seen in physical activities. Therefore, “maintaining a given effort level” was imposed on subjects. SLSR elicited after different muscle contractions was compared at matched ankle joint torque level at onset of a stretch perturbation (I).

- 2) Most of stretch reflex studies have focused on the EMG responses. Few studies observe the stretch-reflex mechanical response modulated by the muscle activity before a stretch perturbation. The second aim of this study was to examine the effects of muscle contraction types and pre-contraction levels before a stretch perturbation on the stretch-reflex mechanical response. Mechanical response evoked after different muscle contractions was compared at matched ankle joint torque level at onset of a stretch perturbation (II).
- 3) Voluntary force output is controlled by effort levels. Involuntary force output induced by a stretch perturbation may be also influenced by it. Effort levels seem to be proportional to activation levels of the muscle, which is closely related to the mechanical response. Therefore, it is of great interest to investigate relationships between SLSR and the effort levels. The third aim of this study was to examine a relationship between SLSR modulation and background muscle contractions at the same effort levels and at matched EMG activities levels while subjects were maintaining a given effort level. Since maintaining a given effort level is likely to minimize the effects of the CNS on SLR modulation, it may be able to clarify the effects of afferent inputs induced by background muscle contractions before a stretch perturbation on the SLR modulation (III).
- 4) If the preceding muscle activity alters mechanical response elicited by the following stretch perturbation, a question arises what induces its alteration. Therefore, mechanical responses of APF muscles were elicited by a mechanical stretch (MS) and supra-maximal ES immediately after various muscle contractions, and they were compared to examine effects of the muscle contraction on the following M-T complex performance. Compared with ES, MS is characterized as follows: (1) During MS AJT generation involves a neural circuit comprising sensory receptors, afferent nerves, the spinal cord and efferent nerves, and (2) MS is unlikely to activate all motor units of the muscles, whereas supra-maximal ES by-passing the fusimotor system is likely to activate all motor units. Since MS generally makes longer electromechanical delay (EMD) than supra-maximal ES, mechanical responses evoked by supra-maximal ES are likely to be affected by the preceding muscle activity more than that elicited by MS. The fourth aim of this project was to clarify the effects of the preceding muscle contractions on the following M-T complex performance and to examine its mechanism from comparing MS-elicited mechanical responses with ES-evoked ones (IV).
- 5) Fatigue induced by exercises involving eccentric actions is expected to decrease SLSR and its mechanical response. The decreased SLSR should show a bimodal trend of recovery after fatigue. In previous studies, however, fatigue was induced by a voluntary exercise including multi-joint movement such as a running and jumping. In the present study, fatigue was induced only from APF muscles by using a pure long-lasting eccentric exercise (LLEE) precisely controlled with a computer while subjects were relaxing their muscles. In addition, stretch reflex was elicited by the same mechanical

stretch as that using in LLEE. Thus the fifth aim was to examine fatigue effects of LLEE on the stretch reflex behavior (V).

- 6) The final aim of this study was to examine 1) whether fatigue could alter the stretch reflex modulation induced by background muscle contractions, 2) whether recovery processes from fatigue were influenced by differences in background muscle contractions, and 3) what induced the fatigue effects on the stretch reflex modulation (VI).

4 RESEARCH METHODS

4.1 Subjects

A total of 40 volunteers participated in the series studies of this project. They were healthy males, but not active in regular exercises. Subjects were well informed about possible risks associated with each experiment they participated. All studies were approved by the Ethics Committee of the University of Jyväskylä, Finland (I, II, III, IV, V and VI). Physical characteristics of the subjects are presented in TABLE 1.

TABLE 1 Physical characteristics of the subject group (Mean \pm SD)

| Exp. No | Age (yrs) | Body height (m) | Body mass (kg) | Original paper |
|---------|-----------------|-----------------|-----------------|----------------|
| 1 (N=7) | 25.3 \pm 4.9 | 1.80 \pm 0.08 | 72.0 \pm 12.2 | I |
| 2 (N=7) | 25.3 \pm 4.9 | 1.80 \pm 0.08 | 72.0 \pm 12.2 | II |
| 3 (N=7) | 25.3 \pm 4.9 | 1.80 \pm 0.08 | 72.0 \pm 12.2 | III |
| 4 (N=6) | 34.8 \pm 10.4 | 1.75 \pm 0.08 | 77.0 \pm 11.1 | IV |
| 5 (N=4) | 31.3 \pm 8.3 | 1.73 \pm 0.09 | 75.0 \pm 13.5 | V |
| 6 (N=9) | 28.8 \pm 4.6 | 1.80 \pm 0.06 | 82.9 \pm 11.0 | VI |

4.2 Experimental design

4.2.1 Experiment I, II and III

Experiment I, II and III were based on the same experimental design to investigate SLSR behavior in response to various background muscle activities.

A sudden dorsiflexion (SDF) was applied to APF muscles immediately after an isometric (pre-ISO), shortening (pre-SHO) and lengthening contraction (pre-LEN). To begin with, the ankle joint was rotated from 90 deg of the tibio-tarsal joint angle to the initial positions, which were 80 deg in pre-SHO, 90 deg in pre-ISO and 100 deg in pre-LEN, over 3095 ms (preparatory period). Subjects relaxed their muscles fully during this period. After the tibio-tarsal joint angle reached the initial position, subjects were asked to activate their APF muscles and maintain a given ankle joint torque level over 2910 ms (pre-load period). The target torque level and torque being exerted by the subjects were displayed on an oscilloscope as visual feedback. The target torque levels were set to a 0, 10, 20, 30, 40, 50, 60 and 70% level according to maximum voluntary isometric plantar flexion contraction (MVC) at 80 deg in pre-SHO, at 90 deg in pre-ISO and at 100 deg in pre-LEN. The MVCs were randomly measured three times beforehand. Subsequently, subjects performed eight trials for every condition. Thereafter, contraction period lasted for 423 ms. The ankle joint was rotated from 80 deg to 90 deg in pre-SHO and from 100 deg to 90 deg in pre-LEN. In pre-ISO it remained still, although the beginning of contraction period was informed subjects with SDF of 1 deg. For the initial 2.7 deg of this period angular velocity gradually increased to prevent any stretch reflex responses. After 180 ms the angular velocity reached 30 deg/s, which was constantly kept over 243 ms. During this period, subjects were asked not to maintain the target torque levels required during the pre-load period but to maintain the effort level as needed to maintain them. Maintaining the target levels for about 2 s in pre-load period was enough for subjects to grasp the effort levels needed to perform it. SDF of 4 deg over 25 ms was applied when the tibio-tarsal joint angle reached 90 deg (stretch perturbation period) after contraction period. Subjects were asked not to resist SDF but to constantly maintain the same effort level as that made during pre-load and contraction period until the end of the stretch. After SDF the ankle joint movement was stopped at 86 deg for 308 ms (static period) in order to make an equal condition among three conditions. Finally, the ankle joint gradually returned to the position of 90 deg over 1239 ms (recovery period). Subjects fully relaxed their muscles again. A whole ankle joint movement lasted for 8 sec, which was consecutively repeated 10 times (FIGURE 1). The order of each trial was randomized. There were intervals of at least 3 minutes between the trials. Skin temperature on SOL was maintained at 30 °C through the whole experiment.

In experiment I and II, AJT at the onset of SDF was expressed as percentage of MVC at 90 deg to eliminate differences in MVC torque among subjects, which was defined as pre-contraction level. Some trials with equal pre-contraction levels among pre-ISO, pre-SHO and pre-LEN were extracted from eight trials performed by subjects in each condition. Subsequently, AJT was compared at 0%, 35% and 50% MVC pre-contraction level.

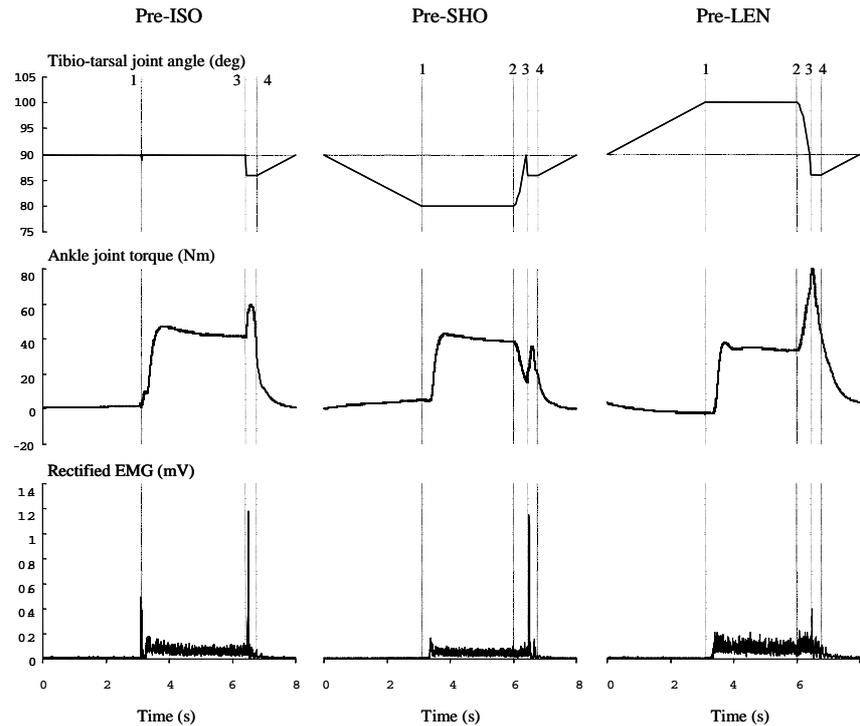


FIGURE 1 A typical example of tibio-tarsal joint angles, ankle joint torque and rectified EMGs for a whole ankle joint movement in one representative subject. The figure shows data at 20% MVC effort level. Dotted lines 1, 2, 3 and 4 represent the onset of pre-load period (-3333 ms relative to SDF onset), contraction period (-423 ms relative to SDF onset), stretch perturbation period (6428 ms) and recovery period (+333ms relative to SDF onset), respectively. One whole ankle joint movement lasted for 8 seconds.

4.2.2 Experiment IV

Mechanical responses elicited by a mechanical stretch (MS) and supra-maximal electrical stimulation (ES) were compared to investigate the effects of the preceding muscle activities on the subsequent muscle-tendon complex behavior. Results of MS-elicited mechanical response were obtained under the same ankle joint movement as that used in experiment I, II and III, which consecutively repeated 5 times. When a supra-maximal ES was applied instead of MS, the tibio-tarsal joint angle was stopped at 90 deg after the ES. The other ankle joint movement was similar to that used in experiment I, II and III (FIGURE 2). Mechanical responses were evoked by a supra-maximal single and double ES separately. Each measurement was consecutively repeated twice. There was an interval of a few minutes between these measurements. Experiment was divided into two parts. In the first part, MVC of APF muscles and the ankle joint torque (AJT) elicited by MS in pre-ISO, pre-SHO and pre-LEN were measured. The second part was performed three weeks later to measure the AJT evoked by a supra-maximal single and double ES. Subjects were asked not to perform any physical exercises for a few days before the measurements.

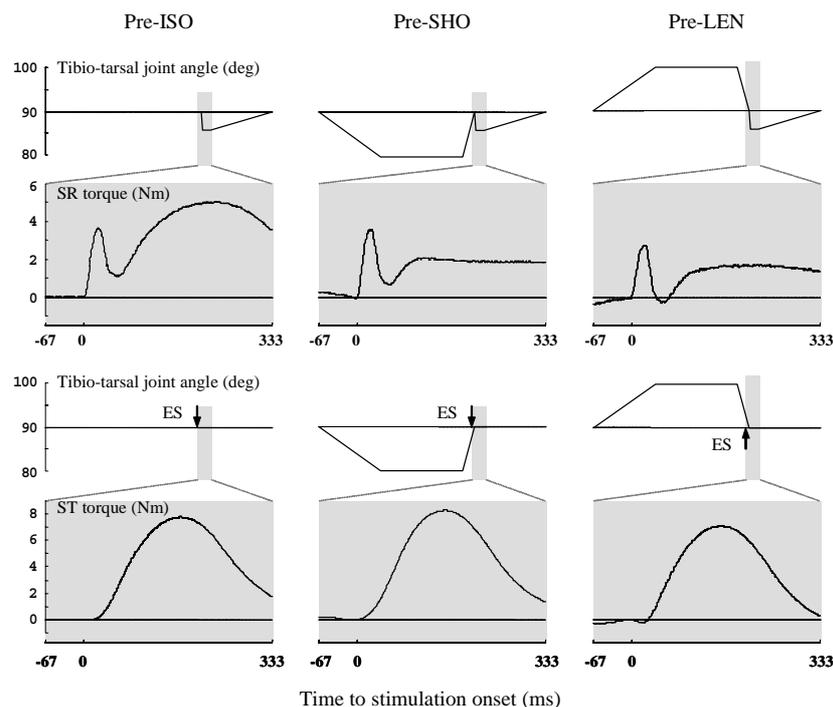


FIGURE 2 Passive ankle joint torque (AJT) elicited by SDF (SR torque) and a supra-maximal single electrical stimulation (ST torque) in a representative subject. AJT is shown in shaded portion (400ms) of a whole ankle joint movement (8 sec). Numerical values "0" on horizontal axes represent the onset of the mechanical stretch or 4 ms after the electrical stimulation was applied, which correspond to instants when the tibio-tarsal joint angle reached 90 deg after shortening and lengthening contractions. ES: electrical stimulation.

4.2.3 Experiment V

The effects of fatigue on reflex behavior were investigated in experiment V. This experiment consisted of two set series of an identical long-lasting low-intensity eccentric exercise (LLEE) separated by three weeks. In the first part, MVC and stretch reflex measurements were performed in the right APF muscles immediately before (Pre), immediately after (Post), 2 hours after (2H), 2 days after (2D) and 7 days after the fatigue task (7D). MVC measurement always preceded stretch reflex measurement at intervals of more than three minutes. Only at Post, the stretch reflex was measured before MVC to avoid recovery from fatigue induced by LLEE, and no intervals were taken between the two measurements (FIGURE 3). Stretch reflex was successively elicited 20 times by SDF of 8 deg over 50 ms. Blood lactate (B-LA) concentration and creatin kinase (CK) activity were also measured simultaneously. In the second part, MVC with a supra-maximal double ES (superimposed MVC), maximum M-wave and H-reflex measurements were performed. To evoke maximum M-wave and H-reflex ES was applied at 70 ms after the onset of SDF, which roughly corresponded to the end of stretch reflex responses. After superimposed MVC measurement, maximum M-wave was measured once, and then H-reflex was successively measured 20 times. AJT evoked by a supra-maximal double ES at

rest (DTr) was also measured to calculate muscle activation level. Except for MVC, subjects were asked to relax their muscles fully throughout the measurement and to avoid any physical exercise for a few days before and throughout the whole experiment. LLEE consisted of SDF and ES (FIGURE 3). SDF was similar to that used in stretch reflex measurements. It was applied at 94 deg of the tibio-tarsal joint angle. ES was directly applied to APF muscles an evoked potential measuring system (MEB-5304K, Nihon Kohden, Japan). The stimulation electrodes (5×5 cm) (StimTrode, Axelgaard Manufacturing, USA) were placed so that two anodes located on the proximal head of the gastrocnemius medialis (GM) and lateralis (GL) and one cathode was located on the distal myotendinous junction over SOL. Impulse duration and frequency of ES were 0.2 ms and 20 Hz, respectively. The ES train lasted for 1 s. Intensity of ES was fixed so that the ES evoked 10% of MVC torque at 90 deg of the tibio-tarsal joint angle. This cycle repeated at 0.5 Hz lasted for 75 min. ES was interrupted for 40 ms after every 14 min 16 s exercise duration to measure SLR during the exercise. Subsequently, number of repeated SDF and ES reached 2250 and 2170 times, respectively, being the entire exercise.

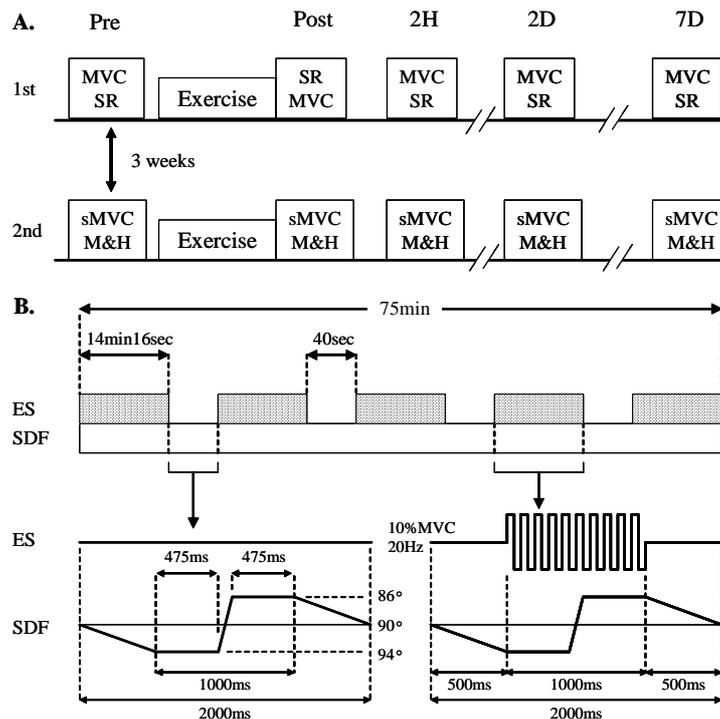


FIGURE 3 Schematic representations of a whole experimental protocol (A) and a stimulation pattern during LLEE (B). SR: stretch reflex, M&H: maximum M-wave and H-reflex, MVC: maximum voluntary isometric plantar flexion, sMVC: superimposed MVC, ES: electrical stimulation, and SDF: sudden dorsiflexion.

4.2.4 Experiment VI

“How does fatigue induced by LLEE influence stretch reflex modulation?” Stretch reflex behavior and AJT evoked by a supra-maximal single ES (ST

torque) were investigated at Pre, Post, 2H, 2D and 6days after LLEE (6D). Patterns of ankle joint movement used in these measurements were similar to those used in experiment I, II, III and IV. SDF pattern and impulse duration of ES used during LLEE were similar to those used in experiment V. However, frequency of ES was set at 20 Hz and its intensity was fixed so that the ES evoked 20% of MVC torque at 90 deg of the tibio-tarsal joint angle. This intensity was higher than that used in experiment V. This LLEE lasted for 60 min without interruption of the ES adopted in experiment V. Stretch reflex was consecutively elicited 5 times in each condition. Intervals of at least 3 minutes were taken among pre-ISO, pre-SHO and pre-LEN. Only in Post, the number of repetition was limited to 3 times and no intervals were taken among the three conditions to avoid recovery from fatigue induced by LLEE.

4.3 Recording procedures and analyses

All measurements of this project were performed with a motor driven isokinetic ankle ergometer controlled by a digital feed-back system (Nicol et al. 1996b), which was similar to that used by Gollhofer and Schmidtbleicher (1989) (FIGURE 4). The maximum torque capacity was 150 Nm (Geisinger, Germany). Torque and angular displacement around the rotational axis of the motor were measured with a piezoelectric crystal transducer (Kistler, Switzerland). While subjects sat in the ergometer chair, their right thigh was clamped with a soft cuff and their right foot was mounted on the rotation platform so that the rotational axis of the ankle joint was aligned with that of the motor torque device. The knee and hip joint angles were also fixed.

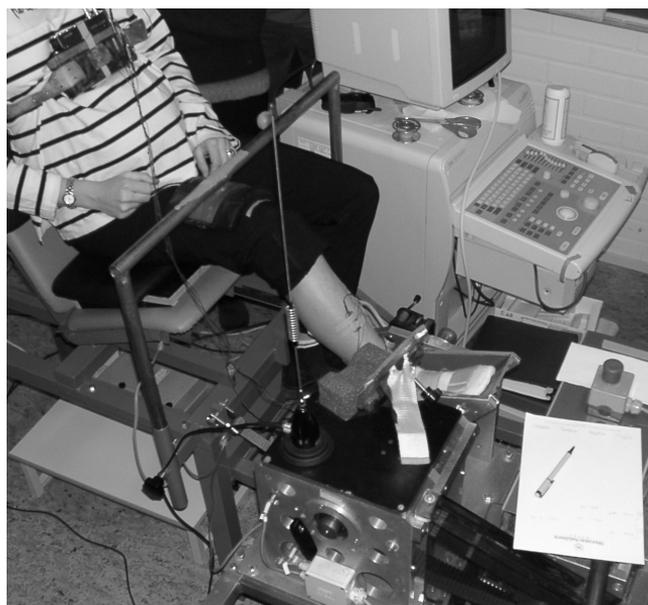


FIGURE 4 Isokinetic ankle ergometer for recording ankle joint torque and angular displacement.

4.3.1 Electromyography (EMG) measurements and analyses

Electromyographic activity (EMG) was obtained telemetrically from SOL, GL, GM and tibialis anterior (TA) muscles of the right leg. Bipolar silver chloride miniature skin electrodes (Beckman 650437, USA) were aligned parallel with the fibers halfway between the estimated center of the innervation zone and the distal end of the muscles. According to the recommendation by SENIAM (1999), a 20 mm inter-electrode distance was employed. The inter-electrode distance was ensured by using a special plastic housing into which an electrode was built. Before electrode application, each site was shaved, abraded and cleansed with alcohol to keep a low interelectrode impedance ($5\text{k}\Omega$). EMG signal was amplified by 200 times with a FM-microvolt amplifier (Glonner Electric GmbH, Germany; bandwidth 3-360Hz, CMRR 90dB, input impedance $>25\text{M}\Omega$).

EMG signals were stored on a computer via a real time data acquisition system (Cudas, Dataq Instruments Inc., USA) which included a 12-bit A/D converter with a sampling frequency of 1 kHz. They were high-pass filtered at cutoff frequency of 10Hz and full-wave rectified. Since each measurement was repeated several times, the rectified EMG signals were averaged respectively. Identification of SLSR and MLSR was modified from that introduced by Lee and Tatton (1978) for upper limbs (FIGURE 5). The onset of SLSR was identified by an onset of consistently steep rise of the rectified EMG activity at about 40 ms after a stretch. The end of SLSR or the onset of MLSR was identified by the lowest rectified EMG activity followed by the second sharp rise at about 60ms after SDF. Latencies of SLSR and MLSR were measured as differences in time between the onset of SDF and onset of their EMG bursts (I). SLSR duration was calculated by subtracting the SLSR latency from MLSR latency. SLSR showed two narrow peaks. Since they represent the positive and negative component of one biphasic potential in the raw EMG signal, a sum of them was defined as peak-to-peak amplitude (I, III, V and VI). The peak-to-peak amplitude and duration of SLSR were regarded as an indicator of the SLSR waveform (I). Average EMGs (aEMG), i.e., area per unit time, of SLSR and from the onset of a stretch to SLSR onset were also calculated (I, II, III, V and VI). They were defined as SLSR and background activity (BGA) area, respectively. After aEMG in contraction period was calculated, ratios of BGA area to it were also calculated (III).

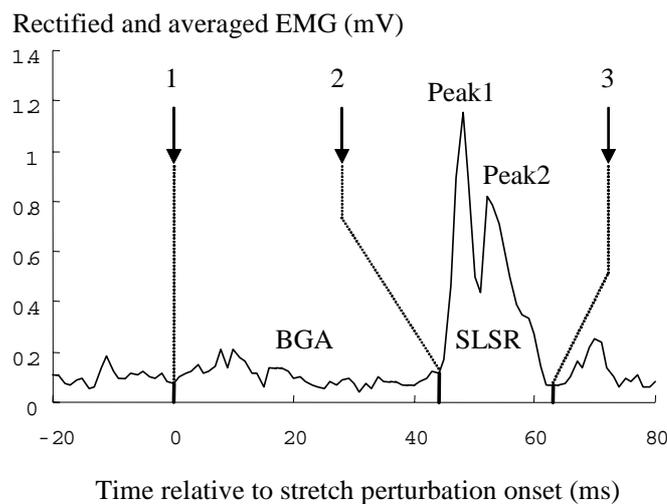


FIGURE 5 A schematic representation of EMG analysis. Arrows 1, 2 and 3 represent the onset of a stretch, SLSR burst and MLSR burst, respectively. Times at arrow 1 and arrow 2 represent latencies of the SLSR and the MLSR, respectively. Time difference between arrow 1 and arrow 2 represents duration of the SLSR. The sum of Peak1 and Peak2 are regarded as peak-to-peak amplitude.

Motor unit (MU) activities are different among varying types of muscle contraction (Nakazawa et al. 1997; Nardone et al. 1989). Therefore, before rectification of EMG signals, EMG power spectrum was calculated in the active muscles for 512 ms before contraction period and for 256 ms before SDF onset by utilizing a fast Fourier transformation (FFT) to obtain median frequency (MF) and mean power frequency (MPF). Ensemble averages were calculated for each trial (I).

4.3.2 Maximal M-wave measurement and analysis

Maximum M-wave were evoked by a supra-maximal ES with a single rectangular pulse over 1 ms. Intensity of the supra-maximal ES was fixed so that the maximum M-wave was evoked at 86 deg of the tibio-tarsal joint angle. A supra-maximal ES was delivered to the tibialis nerve of the right leg with an evoked potential measuring system (MEB-5304K, Nihon Kohden, Japan). Stimulation electrodes (pregelified Ag-AgCl electrode, Niko, Denmark) were placed over the tibialis nerve in the politeal fossa as the cathode (1.5×1.5 cm) and over an upper part of the patella as the anode (5×8 cm). Positions of the stimulation electrodes were found and fixed in the upright stance so that a clear and stable M-wave can be evoked from the SOL beforehand. M-wave represents the positive and negative components of one biphasic potential in the raw signal. A sum of them was defined as M-wave peak-to-peak amplitude (V).

4.3.3 H-reflex measurement and analysis

H-reflex was evoked by the same procedure as that in maximal M-wave measurement. Intensity of the ES was adjusted so that it could elicit 20% of the

maximum M-wave peak-to-peak amplitude. The adjustment was done manually with help of an oscilloscope where the 20% level was displayed (V).

4.3.4 Torque measurements and analyses

Recorded AJT was filtered at 75 Hz with a Butterworth type 4th-order zero-lag low-pass filter to remove the high frequency noise. Since AJT involved an inertial reaction torque induced by the pedal movement, it was subtracted from AJT.

4.3.4.1 Non-reflex and reflex torque

In general, stretching a muscle-tendon complex evokes an immediate increase, a transient drop and a subsequent re-increase in torque (Brown et al. 1982; Carter et al. 1993; Sinkjær et al. 1988). In this study the first and the second increase in the torque were defined as non-reflex torque (NRT) and reflex torque (RT), respectively. Amplitude and duration of the torque were calculated in the following phases: from the stretch onset to the first peak (P1), from the first peak to the subsequent local minimum torque (LMT) (P2), from the LMT to the second peak (P3), and from the stretch onset to the second peak (P4) (see left top figures in FIGURE 12 and 13). P1 and P4 amplitude represent the peak NRT and the peak RT, respectively. Relationships between AJT in each phase and pre-contraction level were investigated with linear regression (I-rate).

4.3.4.2 Electromechanical delay and efficiency

Phase P3 can be considered to be induced mainly by the stretch reflex EMG response. It was impossible to determine a precise start of RT because it was related to two processes, that is, decay in intrinsic muscle stiffness after SDF (Joyce et al. 1969; Rack and Westbury 1974) and the reflex-induced force. However, in this study LMT was defined as the beginning of RT since torque began to re-increase by reflex-induced force at the LMT. A difference in time between SLSR onset and LMT was defined as electromechanical delay (EMD). A ratio of P3 amplitude to SLSR area was also calculated, which was defined as electromechanical efficiency (EME) (II).

4.3.4.3 Mechanical work and increasing rate of the ankle joint torque with the pre-contraction level

Absolute work was calculated in contraction period and in stretch perturbation period. Ratios of the absolute work performed in stretch perturbation period to that performed in contraction period (W-ratio) were calculated at 35% and 50% MVC pre-contraction level. W-ratio was not calculated at 0% MVC pre-contraction level since any work performed at its pre-contraction level was not actively generated by muscles. No work was performed during contraction period in pre-ISO due to the static pedal movement. Therefore, W-ratio could

not be calculated in pre-ISO. Effects of pre-contraction level on each phase of AJT were compared among pre-ISO, pre-SHO and pre-LEN. Amplitudes of AJT were plotted against the pre-contraction levels for each condition in each subject in order to calculate a correlation coefficient and a regression coefficient with a linear regression analysis. Since a regression coefficient is a slope of the regression line, it represents the increasing rate (I-rate) of AJT with the pre-contraction level. Subjects performed eight kinds of trials in each condition. Therefore, its relationships were based on eight data points.

4.3.4.4 Single and double twitch torque

Single (ST) and double twitch (DT) torque was evoked with the same evoked potential measuring system as that used for M-wave and H-reflex measurement. A supra-maximal single and double ES was superimposed to the tibialis nerve at 4 ms before the tibio-tarsal joint angle reached 90 deg after an isometric, shortening and lengthening contraction, because M-wave resulting from direct stimulation of the motor nerves has 4-5 ms latency in APF muscles. A single rectangular pulse of 1 ms duration was used as ES. The stimulus intensity was fixed at about 20% higher level than that at the maximum M-wave. DT torque was evoked by a supra-maximal ES delivered twice at an interval of 10 ms (IV and VI).

4.3.4.5 Voluntary activation measurement

While subjects were performing MVC at 80, 90 and 100 deg of the tibio-tarsal joint angle, a supra-maximal double ES was applied to the tibialis nerve twice at an interval of 10 ms after the MVC torque reached the maximum. DT torque evoked by it was measured once. Pulse form, duration and intensity of ES were similar to those used in single twitch measurement. Similar measurements were performed also in relaxed APF muscles. Activation level (AL) of muscles was calculated as an indicator of central fatigue from these results. AL was quantified as:

$$AL (\%) = 100 - (Tdt - Tb) * (Tb / Tmax) / DTr * 100$$

where Tdt, Tb and Tmax are amplitude of torque evoked by DT immediately after MVC, torque immediately before DT and the maximal MVC torque, respectively (Strojnik and Komi, 2000)(V and VI).

4.3.5 Muscle sonographic measurement and analysis

Two-dimensional geometry characteristics of SOL and GM during LLEE and stretch reflex measurements were estimated from morphometrics of sagittal-plane sonographs by using a real-time ultrasound apparatus with a frequency of 42 Hz (SSD-2000, Aloka, Japan). A 7.5 MHz linear-array probe of 6 cm long was put over GM muscle so that the sharpest image of SOL and GM

fascicles was gotten, and fixed securely with a special support device made of expanded polystyrene. The probe positions were carefully marked on the skin to fix the position surely throughout the whole experiment. Sonographs were recorded on videotape with a light signal to synchronize the images with the angular displacement of the tibio-tarsal joint. For measuring displacement of fascicular insertion points in the aponeurosis (FIPA) of Sol and GM, the FIPA were digitized on muscle sonographs recorded. After the X-Y coordinates digitized were converted into real coordinates, displacement of the FIPA elicited by SDF of 8 deg during LLEE and elicited by shortening and lengthening over 10 deg before SDF in stretch reflex measurements was calculated and averaged. During LLEE analysis was performed from 1st to 10th (initial phase), from 895th to 905th (middle phase) and from 1790th to 1800th (last phase) of repetition (VI).

4.3.6 Blood sampling and analyses

Blood samples were drawn from the ulnar vein at all tests to measure creatine kinase (CK) activity (V and VI). Sampling at Post was performed at 3 min after LLEE. Blood was taken also from fingertip at Pre, Post and 2H to measure blood lactate (B-LA) concentration (V and VI). In Post it was done immediately after (V and VI), 1 min after, 3min after and 5 min after LLEE (VI). CK activity and B-LA were analyzed at 25°C with a CK ultraviolet test kit (Boehringer Mannheim, Germany) and with a commercial kit (Biochemica Boeringer GmbH, Germany).

4.3.7 Statistical methods

A two-way analysis of variance for measurements (ANOVA) was used to test SLSR latency, duration, area and p-to-p amplitude, BGA area, aEMG in each period, ratio of BGA area to aEMG in contraction period, EMG power spectrum (I, III, V and VI), SR, ST and DT torque, W-ratio, EMD, EME, aEMG and torque at MVC, DTr, AL, M-wave and H-reflex amplitude and FIPA displacement (II, IV, V and VI) for significant differences among three conditions against different effort, torque, EMG activity levels or tests. When the result of ANOVA was significant ($p < 0.05$), Fisher's post-hoc test was used to assess the source of difference ($p < 0.05$). A linear regression analysis was also used to clarify relationships between SDF-induced AJT and pre-contraction levels (III), and between RT and SLSR p-to-p amplitude (VI).

5 RESULTS

5.1 SLSR modulation in response to various background muscle activities (I, III)

EMG was obtained not only from SOL but also from GL, GM and TA. However, SLSR p-to-p amplitude of GL, GM and TA was considerably smaller (less than about one-fifth) than that of SOL. It is well known that SLSR is predominantly elicited by SDF in lower limb muscles (Thilmann et al. 1991). Therefore, the present analysis was focused on EMG activity of SOL.

Muscle activities before a stretch perturbation against effort level.

AJT and the EMG activity consistently increased with the effort levels before a stretch in all conditions (FIGURE 6). When the data were compared among three conditions at the same effort level, AJT magnitude was increasing in the order of pre-SHO, pre-ISO and pre-LEN in pre-load period, although there were no significant differences due to the large S.D. However, the magnitude was turned into exactly the opposite order at the stretch because AJT decreased in pre-SHO and increased in pre-LEN during contraction period (FIGURE 1). Subsequently, AJT was significantly larger in pre-LEN than in the other conditions at the stretch. EMG activity was significantly larger in pre-LEN than in the other conditions both in the pre-load and contraction period at the same effort levels. Therefore, levels of AJT and the EMG activity were largely different among three conditions at the stretch.

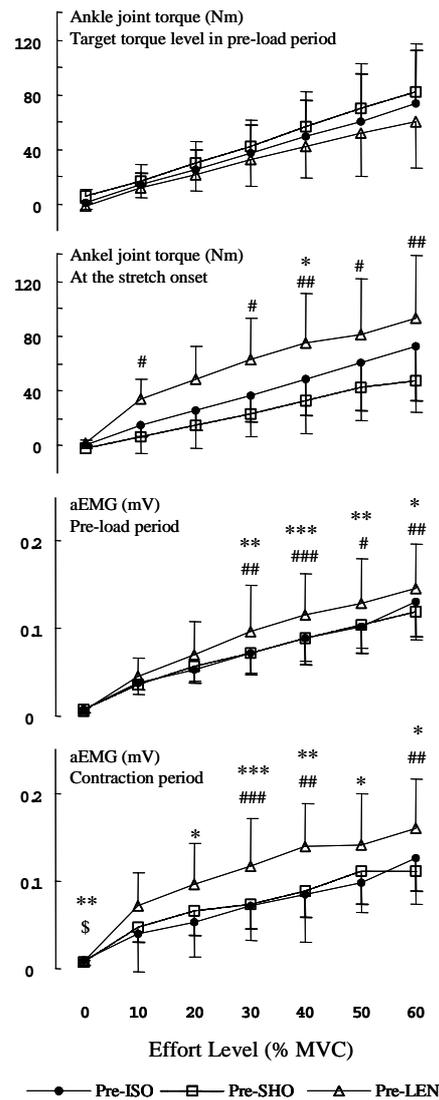


FIGURE 6 Ankle joint torque and average EMGs before a stretch perturbation plotted against effort levels. AJT generated by some subjects exceeded the maximal torque capacity of the ankle ergometer at 70% MVC effort level in pre-LEN. It resulted in inaccurate pedal movements. Therefore, data at 70% MVC effort level in pre-LEN was omitted. *, # And \$ indicate significant differences between pre-ISO and pre-LEN, between pre-SHO and pre-LEN and between pre-ISO and pre-SHO, respectively. *, # And \$ P < 0.05; **, ## and \$\$ P < 0.01; ***, ### and \$\$\$ P < 0.001.

Relationships between SLSR modulations and effort level.

In pre-SHO three of seven subjects did not show SLSR at 0% MVC effort level. This is a unique result shown only in pre-SHO. Therefore, SLSR data at 0% MVC effort level of the three subjects were not included in the following results.

There were two important observations regarding SLSR latency at different effort levels (FIGURE 7): 1) significantly longer latency in pre-SHO than in the other conditions at 0% MVC effort level, and 2) significantly shorter latency in pre-LEN than in the other conditions. Pre-SHO showed a constant SLSR latency of about 43 ms except at 0% MVC effort level, which was similar to that in

pre-ISO. Pre-LEN showed a constant SLSR latency of about 39 ms irrespective of the effort level.

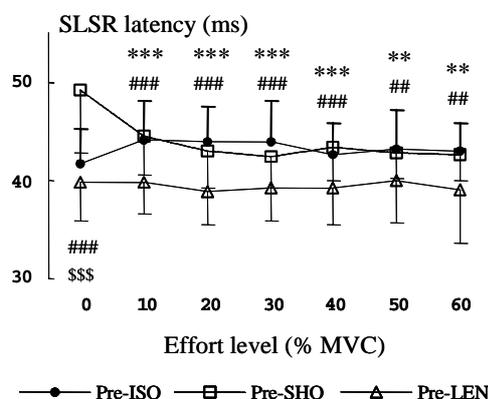


FIGURE 7 SLSR latencies plotted against effort levels. Means \pm S.D. are shown for all subjects. *, # And \$ indicate significant differences between pre-ISO and pre-LEN, between pre-SHO and pre-LEN and between pre-ISO and pre-SHO, respectively. *, # And \$ P < 0.05; **, ## and \$\$\$ P < 0.01; ***, ### and \$\$\$ P < 0.001.

BGA area consistently increased with the effort level in all conditions, whereas SLSR area was constant except at 0% MVC effort level (FIGURE 8). SLSR area increased significantly only from 0% to 10% MVC effort level in all conditions. Pre-LEN showed significantly lower SLSR areas and significantly larger BGA areas than the other conditions. On the other hand, there were no significant differences in the areas between pre-ISO and pre-SHO. These results indicate that SLSR area was independent of the BGA in all conditions and was significantly smaller in pre-LEN than in the other conditions.

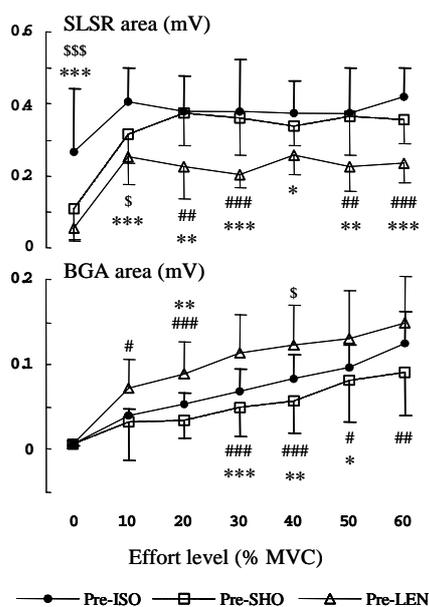


FIGURE 8 SLSR and BGA areas plotted against effort levels. Means \pm S.D. are shown for all subjects. *, # And \$ indicate significant differences between pre-ISO and pre-LEN, between pre-SHO and pre-LEN and between pre-ISO and pre-SHO, respectively. *, # And \$ P < 0.05; **, ## and \$\$\$ P < 0.01; ***, ### and \$\$\$ P < 0.001.

Pre-LEN showed significantly shorter SLR duration and significantly smaller SLSR p-to-p amplitude than the other conditions. Pre-ISO showed slightly shorter SLR duration and slightly larger SLSR p-to-p amplitude than pre-SHO, although there were no significant differences (FIGURE 9). This implies the steeper SLSR waveform in pre-ISO than in pre-SHO. After SLSR duration significantly decreased from 0% to 10% MVC effort level in pre-ISO and pre-SHO, it remained constant being about 22 ms in pre-SHO and about 20 ms in pre-ISO. SLSR p-to-p amplitude remained unchanged irrespective of the effort level in pre-ISO, whereas it significantly increased from at 0% and at 10% MVC effort level in pre-SHO and in pre-LEN.

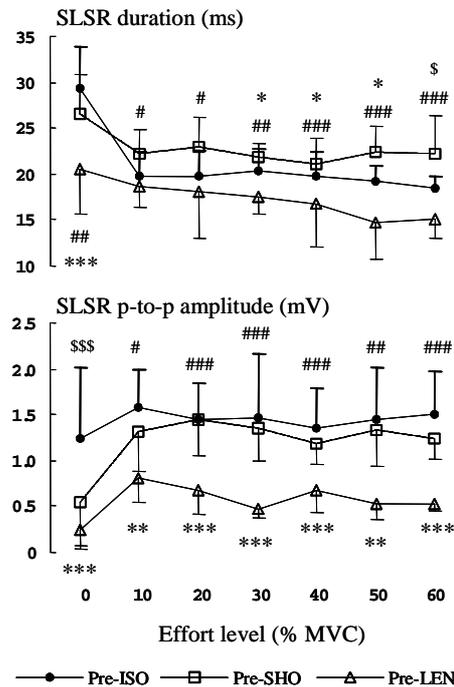


FIGURE 9 SLSR duration and peak-to-peak amplitude plotted against effort levels. Means \pm S.D. are shown for all subjects. *, # And \$ indicate significant differences between pre-ISO and pre-LEN, between pre-SHO and pre-LEN and between pre-ISO and pre-SHO, respectively. *, # And \$ P < 0.05; **, ## and \$\$\$ P < 0.01; ***, ### and \$\$\$ P < 0.001.

FIGURE 10 shows ratios of BGA area to aEMG in the contraction period. The ratios were significantly lower in pre-SHO than in the other conditions except at 0% MVC effort level. There were no differences in the ratio between pre-ISO and pre-LEN except at 0% MVC effort level. The ratio remained unchanged irrespective of the effort levels except pre-SHO. Only in pre-SHO it significantly decreased from 0% to 10% MVC effort level.

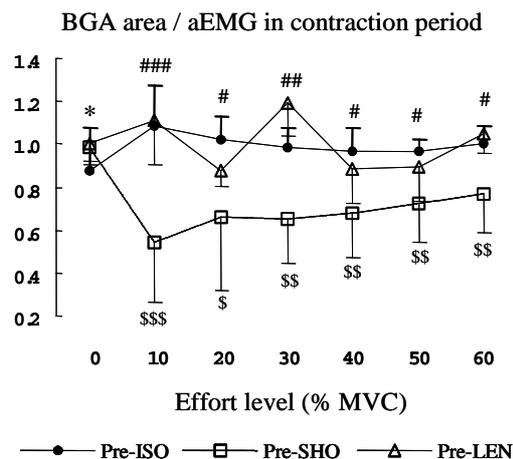


FIGURE 10 Ratios of BGA area to aEMG in contraction period plotted against effort levels. Values below 1.0 indicate that BGA area is lower than aEMG in contraction period. Means \pm S.D. are shown for all subjects. *, # And \$ indicate significant differences between pre-ISO and pre-LEN, between pre-SHO and pre-LEN and between pre-ISO and pre-SHO, respectively. *, # And \$ P < 0.05; **, ## and \$\$ P < 0.01; ***, ### and \$\$\$ P < 0.001.

Comparison of SLRs at matched AJT and EMG activity levels.

SLSR was also compared at the matched levels of AJT (at 0%, 35% and 50% MVC pre-contraction levels) at a stretch and EMG activity before the stretch among pre-ISO, pre-SHO and pre-LEN. To reach 35% and 50% MVC pre-contraction levels at the stretch, pre-SHO needed the largest AJT levels during preparation period, whereas pre-LEN needed the smallest ones. This was due to AJT decreased by 25.8 ± 17.7 Nm at 35% MVC pre-contraction level and 31.0 ± 11.7 Nm at 50% MVC pre-contraction level during contraction period during shortening and increased by 26.4 ± 11.4 Nm at 35% MVC pre-contraction level and 28.5 ± 10.1 Nm at 50% MVC pre-contraction level during contraction period during lengthening, respectively. On the other hand, when SLSR was compared at matched EMG activities, AJT at the stretch was significantly lower in pre-SHO than the other conditions. These are due to rapidly decreased and increased AJT during contraction period in pre-SHO and in pre-LEN, respectively (FIGURE 1). Results of SLSR modulation were similar to those obtained against the effort levels. SLSR latency was significantly shorter in pre-LEN than in the other conditions. On the other hand, there was no significant difference in the SLSR latency between pre-ISO and pre-SHO. Pre-LEN showed a significantly smaller SLSR p-to-p amplitude than the other conditions and shorter SLSR duration than pre-SHO. Pre-SHO showed a slightly longer SLSR duration and slightly smaller SLSR p-to-p amplitude. SLSR area was significantly lower in pre-LEN than in the other conditions. BGA area was significantly lower in pre-SHO than in the other conditions.

5.2 Stretch-reflex mechanical response in response to various background muscle activities (II)

Pattern of the ankle joint torque induced by a stretch perturbation.

A typical variation of AJT showed a sharp increase immediately after a stretch, the first peak (peak NRT), a transient drop, a subsequent increase and the second peak (peak RT)(FIGURE 11). However, two of seven subjects did not show the transient drop in pre-ISO once pre-loads were involved. Their MVCs were 223.4 Nm and 207.2 Nm, respectively, which were more than twice as large as the mean value of the MVC shown by the remaining subjects (85.7 ± 14.1 Nm). Mean values of their peak RT at 0% MVC pre-contraction level were 16.7 ± 3.1 Nm in pre-ISO, 7.7 ± 5.3 Nm in pre-SHO, 4.7 ± 0.5 Nm in pre-LEN, which were about three times as large as the mean values shown by the remaining subjects. Since two of seven subjects did not show the typical variation of the ankle joint torque, their data was not included in the following results.

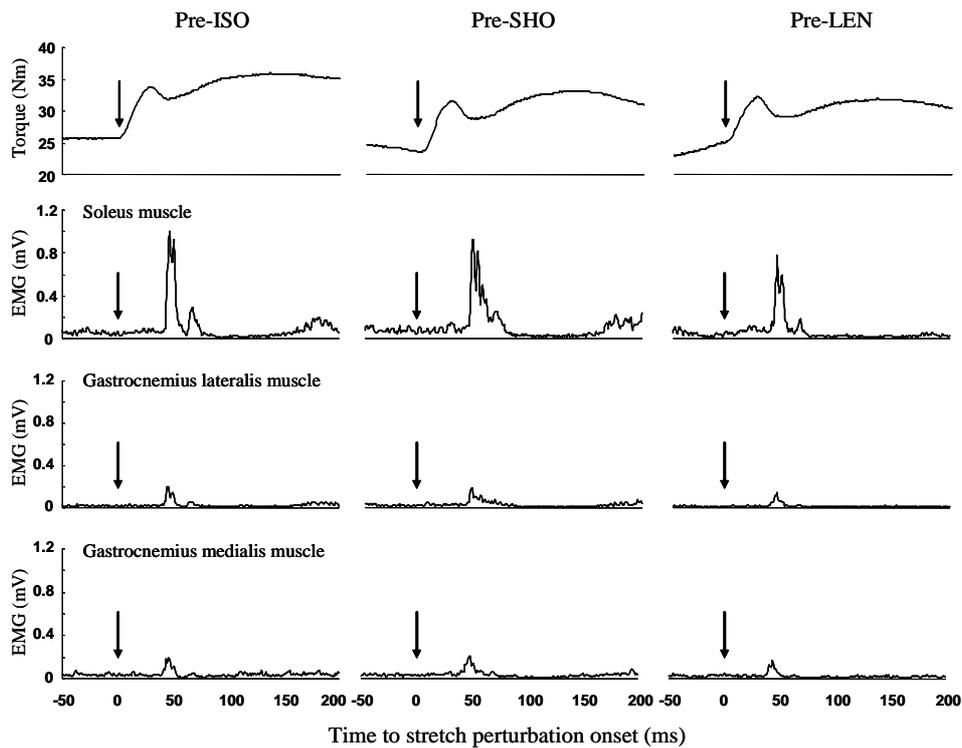


FIGURE 11 Ankle joint torque and rectified EMG activities of soleus, gastrocnemius lateralis and gastrocnemius medialis muscle at 35% MVC pre-contraction level recorded in one representative subject. Arrows represent the onsets of stretch perturbation.

Duration of the ankle joint torque in each phase.

P1 duration was significantly longer at all pre-contraction levels in pre-ISO than the other conditions (left panel in FIGURE 12). Pre-SHO showed significantly longer P1 duration at 0% and 35% MVC level than pre-LEN. However, this difference decreased with increasing pre-contraction level. In all conditions P1 duration significantly lengthened when pre-loads were involved. P2 duration significantly shortened when pre-loads were involved (middle panel in FIGURE 12). In particular, it was dramatic in pre-ISO. Consequently, pre-ISO showed a significantly shorter P2 duration at 35% MVC level than the other conditions, and at 50% MVC level than pre-SHO. P2 duration significantly shortened from 35% to 50% MVC pre-contraction level in pre-ISO and pre-LEN. However, it remained unchanged in pre-SHO. Pre-SHO showed a significantly longer P2 duration than the other conditions at 0% MVC pre-contraction level. P3 duration showed significant differences between pre-ISO and the other conditions at 0% MVC pre-contraction level (right panel in FIGURE 12). Its differences gradually decreased with the pre-contraction level. The P3 duration significantly shortened in all conditions when pre-loads were involved. P4 duration was significantly longer at 0% MVC level in pre-ISO than the other conditions (FIGURE 13). Its significant difference disappeared once pre-loads were involved. The P3 duration significantly shortened with the pre-contraction level in all conditions.

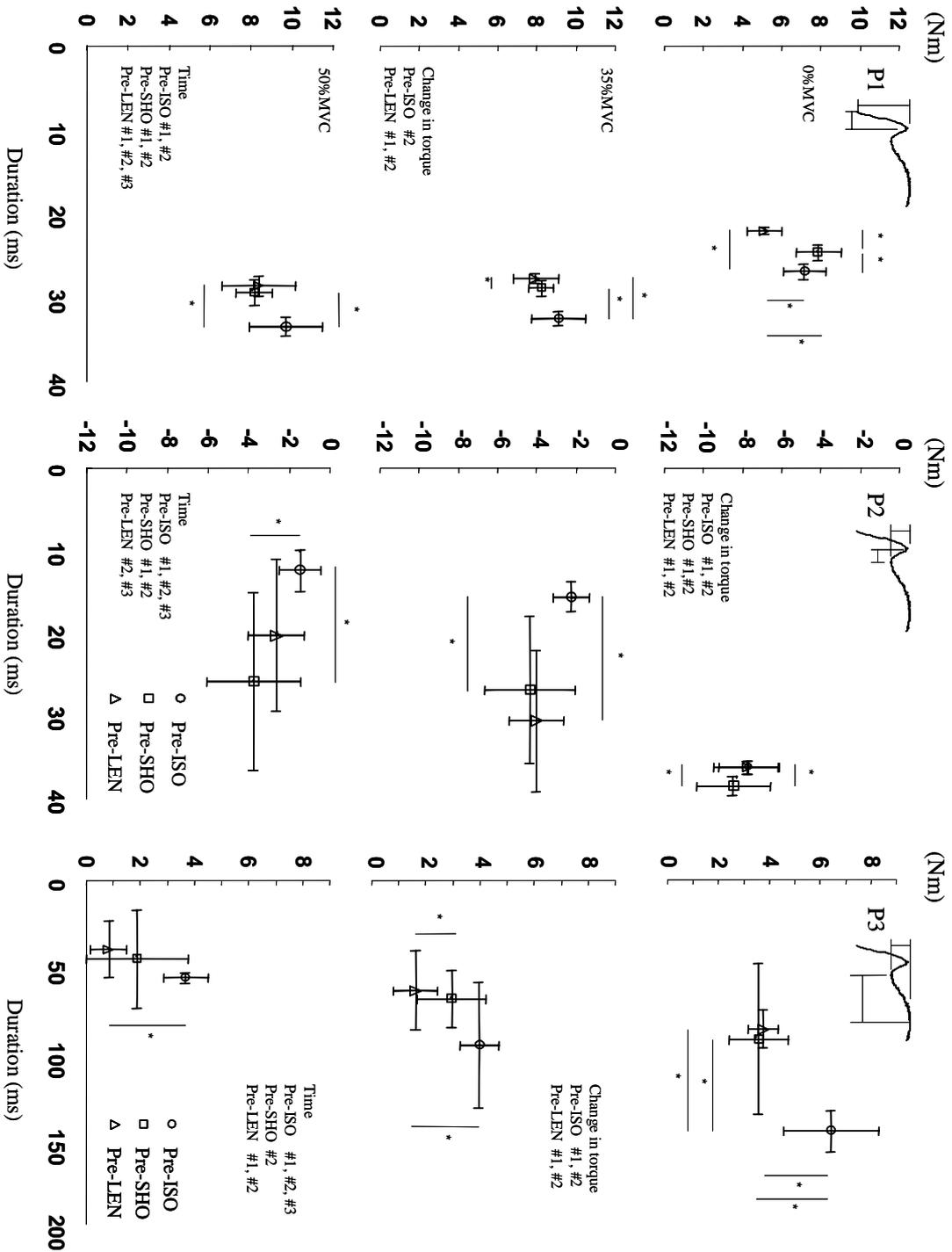


FIGURE 12 Amplitude and duration of ankle joint torque in phase P1, P2 and P3. These data was obtained from 5 subjects who represented the peak non-reflex torque in all conditions. * Indicates a significant difference between the conditions ($p < 0.05$). #1, #2 and #3 Indicate significant differences between 0% and 35%, between 0% and 50%, and between 35% and 50% MVC level, respectively.

Amplitude of the ankle joint torque in each phase.

P1 amplitude was significantly smaller at 0% MVC level in pre-LEN than that in the other conditions (left panel in FIGURE 12). Once pre-load was involved,

pre-ISO showed slightly larger P1 amplitudes than the other conditions (n.s.). There was a significant difference in P2 amplitude only at 50% MVC level between pre-ISO and pre-SHO. Pre-ISO showed slightly smaller P2 amplitudes than the other conditions (n.s.) also at 35% MVC pre-contraction level (middle panel in FIGURE 12). Pre-ISO showed significantly larger P3 amplitude than pre-LEN at all pre-contraction levels, and than pre-SHO at 0% MVC pre-contraction level (right panel in FIGURE 12). There was a significant difference at 35% MVC pre-contraction level between pre-SHO and pre-LEN. P4 amplitude was significantly larger at all pre-contraction level in pre-ISO than that in the other conditions (FIGURE 13). There were no differences between pre-SHO and pre-LEN.

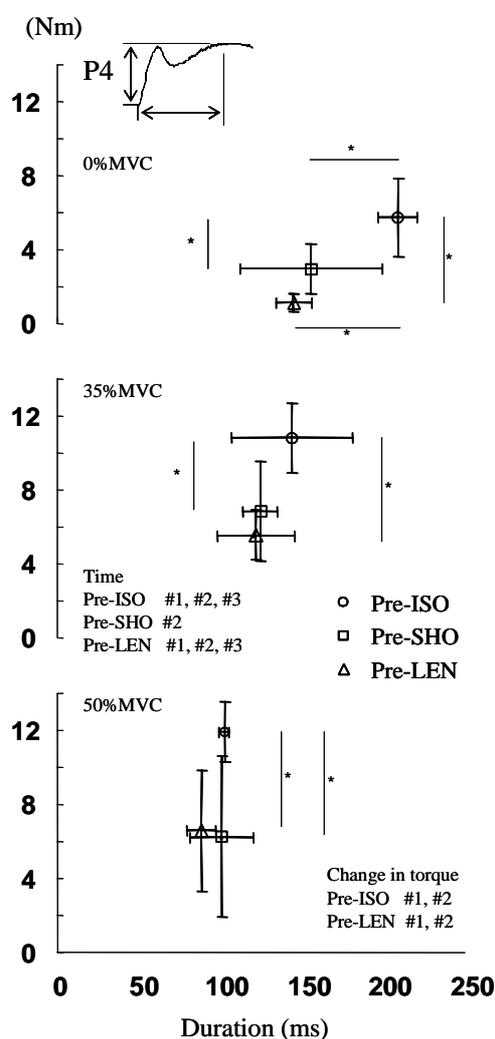


FIGURE 13 Amplitude and duration of ankle joint torque in phase P4. These data were obtained from 5 subjects who represented the peak non-reflex torque in all conditions.

Increasing rate of the ankle joint torque with the pre-contraction level.

FIGURE 14 shows relationships between pre-contraction level and AJT in each phase. P1 amplitude gradually increased with the pre-contraction level in pre-ISO and in pre-LEN. However, the increase was significantly lower in pre-SHO than in the other conditions. I-rates of P2 amplitude were positive in all conditions. Since P2 amplitude was negative, I-rates indicate that the negative values decreased with the pre-contraction level. There were no significant differences in I-rate among three conditions. P3 amplitude decreased with the pre-contraction level in pre-SHO and pre-LEN. However, it was little related with the pre-contraction level in pre-ISO as shown by a low R-square ($R^2=0.19\pm 0.14$). Subsequently, there was a significant difference in I-rate between pre-ISO and pre-SHO. P4 amplitude increased with the pre-contraction level in pre-ISO and in pre-LEN. On the other hand, it remained unchanged in pre-SHO.

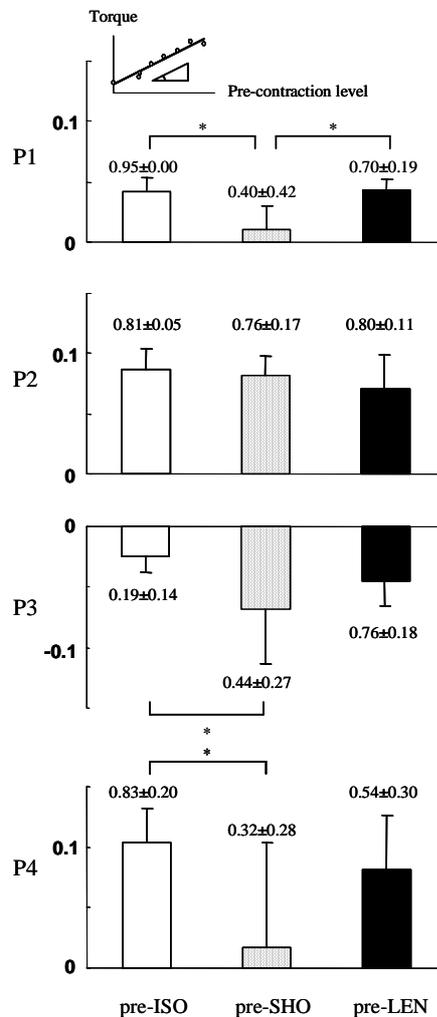


FIGURE 14 Linear regression coefficients between pre-contraction levels and amplitudes of torque in phase P1, P2, P3 and P4. Numerals over bars represent R-squares of the linear regressions (means ± S.D.). * Indicates a significant difference between the conditions ($p < 0.05$).

Absolute work performed during a stretch.

FIGURE 15 shows W-ratio at 35% and 50% MVC pre-contraction level. W-ratios were significantly larger at both pre-contraction levels in pre-LEN than in pre-SHO.

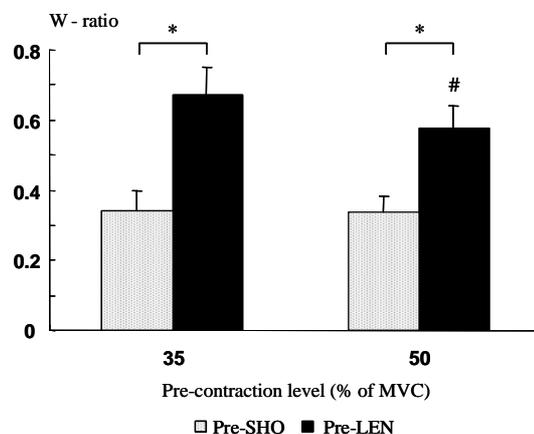


FIGURE 15 Ratios of absolute work performed in stretch perturbation period to that performed in contraction period (W-ratio) in the active muscle. These data was obtained from 5 subjects who represented the peak non-reflex torque in all conditions. * And # indicate significant differences between pre-SHO and pre-LEN, and between 35% and 50% MVC level, respectively ($p < 0.05$).

Electromechanical delay of reflex torque. EMDs were shown in FIGURE 16. There was no difference in EMD at 0% MVC pre-contraction level among three conditions. However, once pre-loads were involved, EMD dramatically decreased in pre-ISO due mainly to shortened P2 duration. Such dramatic decrease in EMD was not shown in the other conditions. Subsequently, pre-ISO showed shorter EMDs than the other conditions, although there were no significant differences due to large SDs in pre-SHO and pre-LEN.

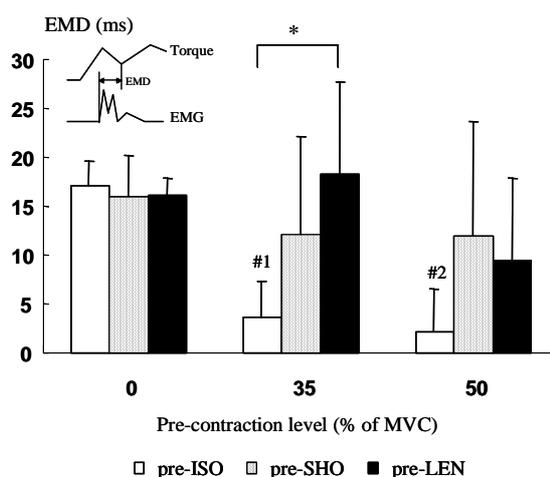


FIGURE 16 Electromechanical delay (EMD) between SLR burst onset and reflex torque onset. These data was obtained from 5 subjects who represented the peak non-reflex torque in all conditions. * Indicates a significant difference between the conditions ($p < 0.05$). #1 And #2 indicate significant differences between 0% and 35%, and between 0% and 50% MVC level, respectively.

Electromechanical efficiency of the reflex torque.

FIGURE 17 shows EME at 35% and 50% MVC pre-contraction level. EME at 0% MVC pre-contraction level was more than 50 Nm/mV due to a considerably small SLSR in every condition. There are no significant differences in EME at 0% MVC pre-contraction level among three conditions. Pre-ISO showed significantly larger EME than the other conditions at 35% and 50% MVC pre-contraction level. There were no differences in EME between pre-contraction levels.

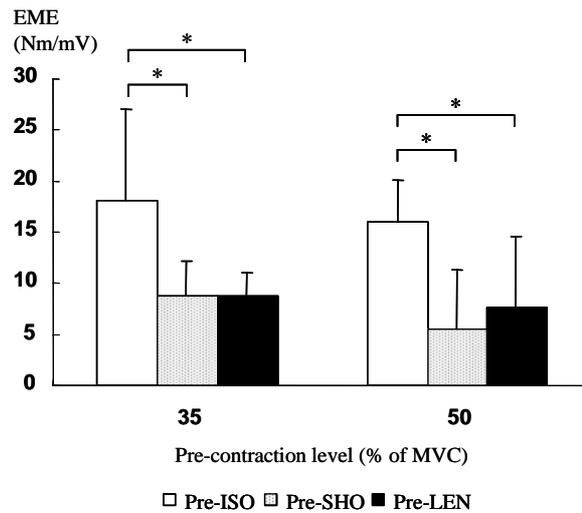


FIGURE 17 Ratios of P3 amplitude to SLR area (EME) in the active muscle. These data was obtained from 5 subjects who represented the peak non-reflex torque in all conditions. * Indicates a significant difference between the conditions ($p < 0.05$).

Relationships between P1, P2, P3 and P4 amplitude.

TABLE 2 shows relationships between P1 and P2 amplitude and between P1 and P4 amplitude. There were no significant relationships between the other amplitudes. P1 amplitude was closely related to P2 and P4 amplitude in all conditions. However, the R-squares were significantly lower in pre SHO than the other conditions.

TABLE 2 Correlation coefficients between amplitudes of torque (Mean \pm SD)

| Amplitude | Pre-ISO | Pre-SHO | Pre-LEN | Difference |
|-----------|--------------------|--------------------|--------------------|----------------|
| P1 - P2 | -0.966 \pm 0.007 | -0.543 \pm 0.353 | -0.934 \pm 0.114 | SHO > ISO, LEN |
| P1 - P4 | 0.916 \pm 0.077 | 0.743 \pm 0.119 | 0.912 \pm 0.113 | ISO, LEN > SHO |

5.3 Effects of the preceding muscle contractions on stretch-reflex mechanical response (IV)

Background ankle joint torque at mechanical and electrical stimulations.

There were significant differences in AJT at the onset of MS or ES among pre-ISO, pre-SHO and pre-LEN ($p < 0.001$) irrespective of whether the muscles were activated (TABLE 3). M-wave peak-to-peak amplitude evoked by a supra-maximal ES did not show significant differences among the three conditions.

TABLE 3 Ankle joint torque at the onset of a mechanical stretch after various muscle contractions (Mean \pm SD)

| | | Relaxed muscle | | | Active muscle | | |
|---------|----|----------------|-----------|-------------------------|---------------|-----------|-------------------------|
| Pre-ISO | Nm | 0.0 | \pm 0.0 |]***]]***]]***] | 18.3 | \pm 3.0 |]***]]***]]***] |
| Pre-SHO | Nm | -0.8 | \pm 0.2 | | 8.3 | \pm 3.8 | |
| Pre-LEN | Nm | 0.9 | \pm 0.4 | | 25.4 | \pm 4.2 | |

Ankle joint torque elicited by a mechanical stretch.

In the relaxed muscles, AJT was significantly greater for pre-ISO than for the other conditions ($p < 0.01$, FIGURE 18). When the muscles were activated, AJT showed increases of 10 - 14 % in pre-ISO (n.s.), 100 - 140 % in pre-SHO ($p < 0.01$) and 220 - 460 % in pre-LEN ($p < 0.01$) over that in the relaxed muscles. Subsequently, differences in AJT among three conditions obviously decreased, although there was still significant difference in AJT between pre-ISO and pre-LEN ($p < 0.05$).

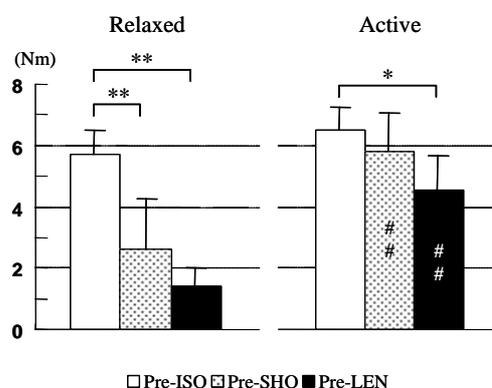


FIGURE 18 Ankle joint torque elicited by a mechanical stretch after an isometric, shortening and lengthening condition. * $P < 0.05$, and ** $p < 0.01$ refer to significant differences between pre-ISO, pre-SHO and pre-LEN conditions. ## $P < 0.01$ refers to a significant difference between the relaxed and active muscles.

Ankle joint torque evoked by an electrical stimulation.

AJT evoked by a single supra-maximal ES is illustrated in FIGURE 19. In the relaxed muscles, no significant differences were observed among three conditions. Once the muscles were activated, AJT significantly decreased in all conditions ($p < 0.01 - 0.001$) and its differences increased among the three conditions. AJT was significantly greater in pre-SHO than in pre-LEN ($p < 0.001$) and in pre-ISO ($p < 0.05$) in the active muscles. The differences observed between pre-ISO and pre-SHO and between the relaxed and active muscles were opposite to those elicited by MS. AJT evoked by a supra-maximal double ES instead of the single one also showed a similar pattern of differences among three conditions. However, compared with a single ES, the differences tended to be smaller when a supra-maximal double ES was applied (FIGURE 20).

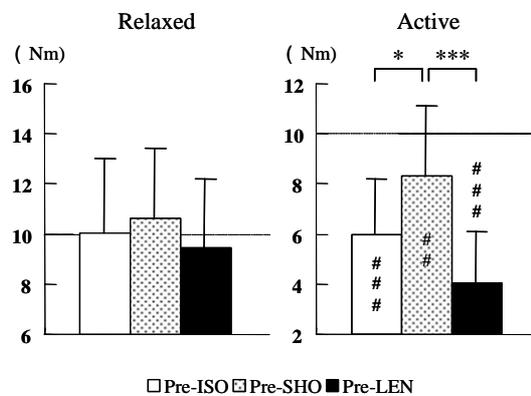


FIGURE 19 Ankle joint torque evoked by a supra-maximal single electrical stimulation after an isometric, shortening and lengthening condition. * $P < 0.05$ and *** $p < 0.001$ refer to significant differences between pre-ISO, pre-SHO and pre-LEN conditions. ## $P < 0.01$ and ### $p < 0.001$ refer to a significant difference between the relaxed and active muscles. Note: scales were different between right and left panels.

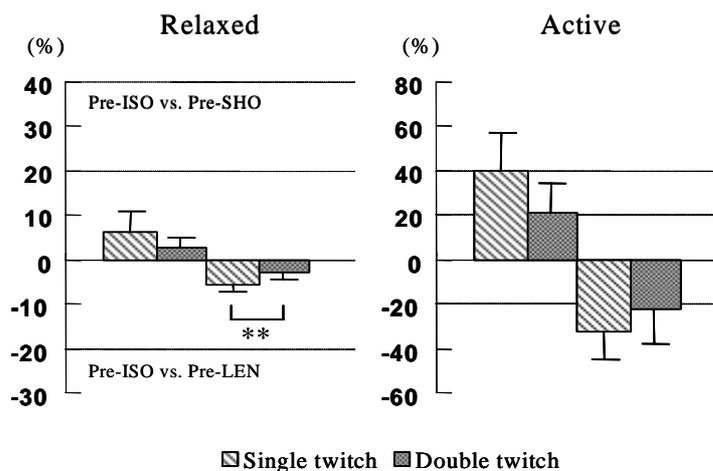


FIGURE 20 Comparison of ankle joint torque elicited by a supra-maximal single and double electrical stimulation between pre-ISO and the other conditions. Values are expressed as percent of those in pre-ISO. ** $P < 0.01$ refers to significant differences between values evoked by the supra-maximal single and double electrical stimulation.

Electromechanical delay.

EMD results in stretch reflex and single twitch measurements are illustrated in FIGURE 21. In the stretch reflex measurement, no significant differences in EMD were observed among three conditions in the relaxed muscle (14.7 ± 1.6 ms in pre-ISO, 13.8 ± 2.0 ms in pre-SHO and 15.7 ± 2.5 ms, in pre-LEN). Once the muscle was activated, EMD became significantly shorter: 4.5 ± 1.6 ms in pre-ISO ($p < 0.001$), 8.5 ± 3.1 ms in pre-SHO ($p < 0.05$) and 8.7 ± 1.6 ms in pre-LEN ($p < 0.01$). In the single twitch measurement when the muscle was relaxed, EMD was 8.3 ± 2.3 ms in pre-ISO, 1.7 ± 1.4 ms in pre-SHO and 14.7 ± 2.0 ms in pre-LEN. Once the muscle was activated, EMDs became longer: 10.8 ± 4.9 ms, 10.8 ± 5.3 ms and 19.6 ± 3.7 ms, respectively. Pre-LEN showed significantly longer EMDs than the other conditions in both relaxed and active muscles ($p < 0.001$). In the relaxed muscle, EMD was significantly shorter for pre-SHO than for pre-ISO ($p < 0.001$). This was not the case in the active muscles. Similar pattern was observed also in the double twitch measurement.

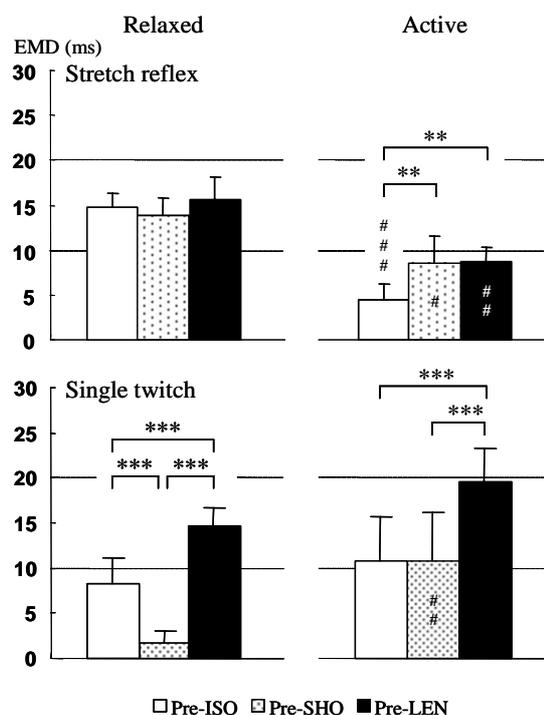


FIGURE 21 Electromechanical delay (EMD) at stretch reflex and single twitch measurement. *** $P < 0.001$ and ** $p < 0.01$ refer to significant differences between pre-ISO, pre-SHO and pre-LEN conditions. # $P < 0.05$, ## $p < 0.01$ and ### $p < 0.001$ refer to a significant difference between the relaxed and active muscles.

EMG power spectrum.

EMG power spectrum was calculated at matched AJT levels in the active muscles among three conditions. MF and MPF during pre-load period and contraction period were shown in FIGURE 22. Pre-SHO showed the lowest MF

and MPF during both periods. There were significant differences in MF and the MPF between pre-SHO and pre-LEN. There were no differences in the MF and the MPF between 35% and 50% MVC pre-contraction levels in all conditions.

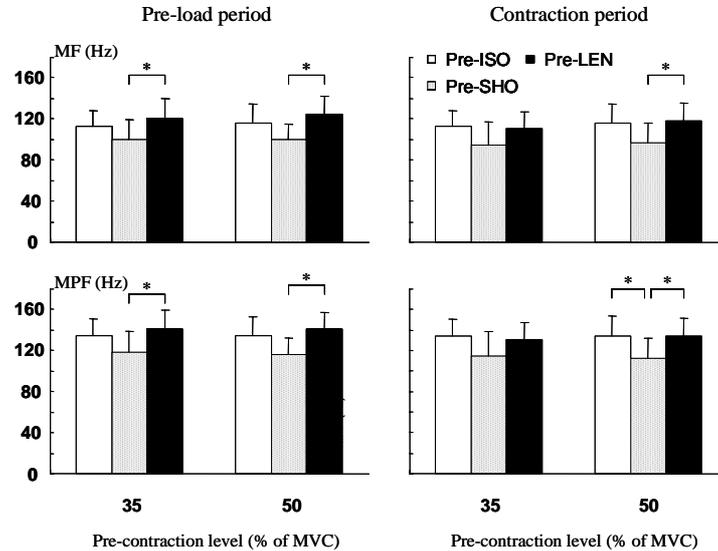


FIGURE 22 Median frequency (MF) and mean power frequency (MPF) during pre-load and contraction period. * Indicates a significant difference between the conditions ($p < 0.05$). # Indicate the significant differences between 35% and 50% MVC pre-contraction levels in each condition ($p < 0.05$).

5.4 Alteration in SLSR behavior induced by fatigue – when SLSR was elicited by the same stretch perturbation as that used during an exercise to induce fatigue - (V)

Maximal voluntary isometric plantar flexion and the activation level.

MVC torque decreased significantly by 19% at Post ($p < 0.01$) and recovered at 2H (FIGURE 23). aEMG at MVC showed a similar change. However, MVC torque remained slightly lower than the initial level at 2H and 2D (6% and 7%, respectively). No significant differences were observed in MVC torque between the 1st and 2nd experiments (85.7±16.0 vs. 76.5±15.2 Nm at Pre, 68.5±9.8 vs. 62.3±9.5 Nm at Post, 80.5±13.7 vs. 74.6±13.9 Nm at 2H, 79.7±17.8 vs. 79.1±13.5 Nm at 2D and 83.0±15.8 vs. 82.9±13.2 Nm at 7D). Change in DTr torque was similar to that in MVC torque. AL also decreased significantly by 11% at Post ($p < 0.01$) and recovered at 2H.

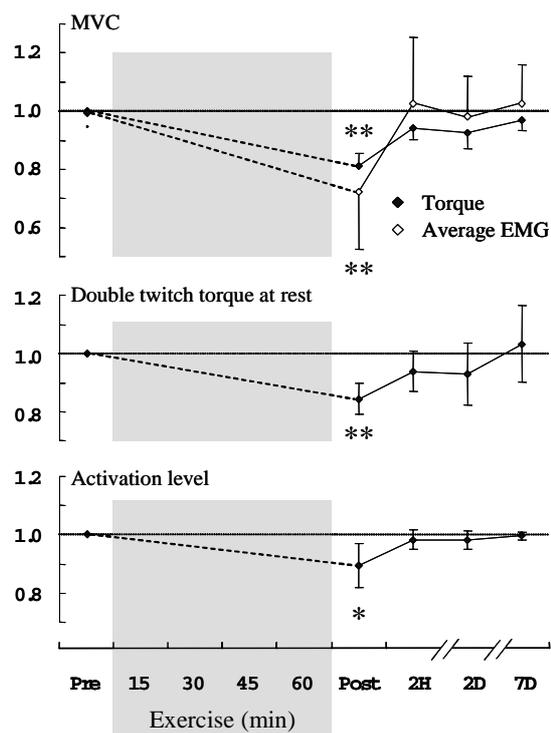


FIGURE 23 Relative changes in MVC torque, average EMG at MVC, double twitch torque at rest and activation level. Changes are expressed as a ratio of pre-exercise value. ** $p < 0.01$ and * $p < 0.05$ compared with pre-test.

Stretch reflex behavior.

SLSR area decreased by 62% during LLEE ($p < 0.05$) and recovered at 2H (FIGURE 24). However, it again decreased by 29% at 2D (n.s.). A change in SLSR p-to-p amplitude was identical to that in the SLSR area. It was not easy to distinguish LLSR from EMG activity due to the small amplitude. Reflex-induced torque (P3 amplitude) decreased by 22% during LLEE ($p < 0.05$). Contrary to SLSR area, it did not recover at 2H. It remained significantly lower until 7D ($p < 0.05$).

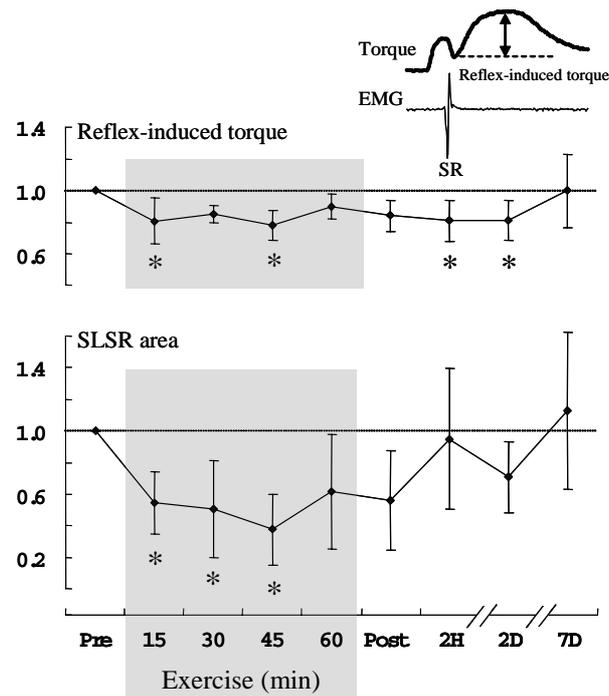


FIGURE 24 Relative changes in reflex-induced torque and SLSR area. Changes are expressed as a ratio of the pre-exercise value. * $P < 0.05$ compared with pre-test.

H-reflex and maximum M-wave.

H-reflex p-to-p amplitude decreased by 32% at Post ($p < 0.05$) and dramatically by 67% at 2D ($p < 0.01$) (FIGURE 25). Maximal M-wave p-to-p amplitude showed no significant changes throughout measurements although it decreased slightly at Post (15%, n.s.) and at 2D (11%, n.s.). Subsequently, changes in H/M ratio depended mainly on H-reflex p-to-p amplitude and showed a bimodal response. H/M ratio recovered once at 2H after decreased by 19% at Post (n.s). Thereafter, it dramatically decreased by 58% at 2D ($p < 0.01$).

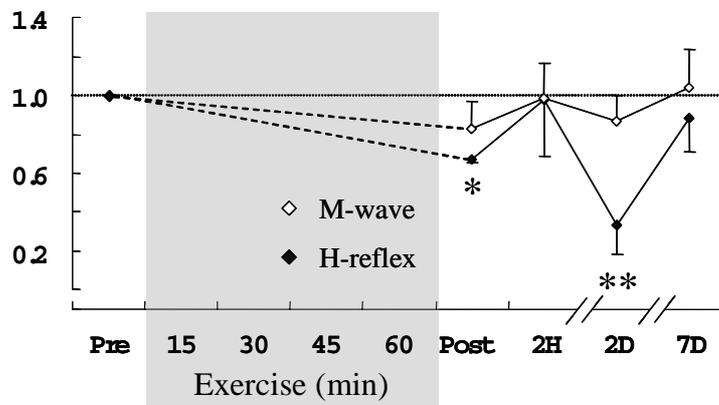


FIGURE 25 Relative changes in M-wave and H-reflex amplitude. Changes are expressed as a ratio of the pre-exercise value. * $p < 0.05$ and ** $p < 0.01$ compared with pre-test.

Lactate acid and creatine kinase activity.

B-LA being $1.5 \pm 0.6 \text{ mmol} \cdot \text{l}^{-1}$ at Pre increased slightly to $2.0 \pm 0.3 \text{ mmol} \cdot \text{l}^{-1}$ at Post (n.s.). No significant differences were observed in CK activity among the tests. CK activity ranged from 60.5 ± 11.2 at Pre to $81.6 \pm 36.6 \text{ U} \cdot \text{l}^{-1}$ at 2D. However, all the subjects felt fatigue in APF muscles at Post and complained of severe muscle soreness at 2D.

5.5 Alteration in SLSR behavior in response to background muscle activities induced by fatigue (VI)

While the tibio-tarsal joint rotated over 10 deg before SDF, AJT decreased by $4.20 \pm 1.61 \text{ Nm}$ in pre-SHO and increased by $3.66 \pm 1.30 \text{ Nm}$ in pre-LEN at Pre. Its decrease and increase altered significantly only at Post compared with at Pre. They increased by $6.92 \pm 2.67 \text{ Nm}$ in pre-SHO ($p < 0.05$) and by $5.38 \pm 1.80 \text{ Nm}$ in pre-LEN ($p < 0.05$) at Post.

SLSR latency.

Pre-SHO showed significantly longer SLSR latencies ($48.3 \pm 4.1 - 49.6 \pm 4.2 \text{ ms}$ in SOL and $46.2 \pm 3.7 - 47.3 \pm 4.0 \text{ ms}$ in GM) than the other conditions at all tests ($p < 0.05 - 0.01$, TABLE 4). The SLSR latency remained unchanged before and after LLEE in all conditions.

TABLE 4 Latencies of short-latency stretch reflex

| | | Unit: ms | | | | | |
|--------|------------|----------------|----------------|----------------|-------------|--------------|--|
| Muscle | Test | Pre-ISO | Pre-SHO | Pre-LEN | Difference | | |
| SOL | Pre | 43.3 ± 4.1 | 48.5 ± 4.1 | 41.9 ± 4.1 | ISO < SHO * | LEN < SHO ** | |
| | Post | 43.5 ± 4.3 | 48.4 ± 4.3 | 44.4 ± 2.6 | ISO < SHO * | LEN < SHO * | |
| | 2H | 43.5 ± 4.0 | 49.6 ± 4.2 | 42.1 ± 5.2 | ISO < SHO * | LEN < SHO ** | |
| | 2D | 42.9 ± 3.9 | 48.9 ± 4.1 | 41.9 ± 4.5 | ISO < SHO * | LEN < SHO ** | |
| | 6D | 42.9 ± 3.7 | 48.3 ± 4.1 | 41.9 ± 4.0 | ISO < SHO * | LEN < SHO ** | |
| | Difference | | n.s. | n.s. | n.s. | | |
| GM | Pre | 41.0 ± 4.0 | 46.5 ± 3.6 | 39.9 ± 3.6 | ISO < SHO * | LEN < SHO ** | |
| | Post | 41.0 ± 4.0 | 46.4 ± 4.0 | 41.8 ± 2.6 | ISO < SHO * | LEN < SHO * | |
| | 2H | 41.1 ± 4.1 | 47.3 ± 4.0 | 40.1 ± 4.3 | ISO < SHO * | LEN < SHO ** | |
| | 2D | 40.6 ± 4.2 | 46.6 ± 4.1 | 40.0 ± 3.9 | ISO < SHO * | LEN < SHO ** | |
| | 6D | 40.6 ± 4.1 | 46.2 ± 3.7 | 40.0 ± 4.1 | ISO < SHO * | LEN < SHO ** | |
| | Difference | | n.s. | n.s. | n.s. | | |

*: $p < 0.05$ and **: $p < 0.01$

SLSR p-to-p amplitude.

SLSR p-to-p amplitude of SOL was significantly larger in pre-ISO than in the other conditions at Pre ($p < 0.05$, FIGURE 26). However, the effects of LLEE on SLSR p-to-p amplitude were similar among three conditions, which showed the following bimodal trend of recovery: an immediate decline after LLEE, temporary recovery at 2H, delayed decline at 2D and final recovery at 6D. Pre-ISO and Pre-SHO showed significant decreases at Post and at 2D compared with at Pre ($p < 0.05 - 0.001$). Although Pre-LEN did not show a significant decrease at 2D, it showed significant changes between at Post and at 2H ($p < 0.001$), between at 2H and at 2D ($p < 0.001$), and between at 2D and at 6D ($p < 0.05$). In particular, Pre-LEN showed a significant increase at 2H compared with at Pre (1.57 ± 0.68 times, $p < 0.05$). Changes in SLSR p-to-p amplitude of GM were similar to those of SOL.

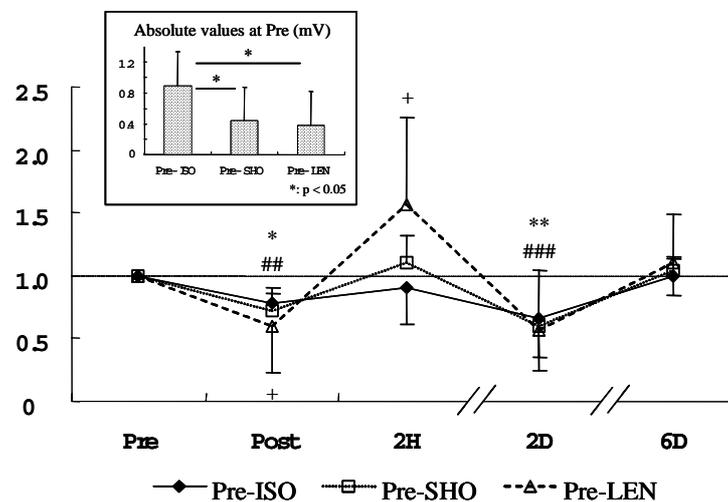


FIGURE 26 Relative changes in SLSR p-to-p amplitudes of SOL. A bar graph in a left top frame shows absolute values of the SLSR p-to-p amplitude at pre-test. *, # and + indicate significant changes ($p < 0.05$, 0.01 and 0.001) compared with pre-test in pre-ISO, pre-SHO and pre-LEN, respectively.

AJT elicited by the stretch reflex.

RT was significantly larger in pre-ISO than in the other conditions at Pre ($p < 0.01 - 0.001$, FIGURE 27). Changes in RT before and after LLEE were smaller than those in SLSR p-to-p amplitude. An obvious change was observed at 2D in pre-LEN as results of significant changes between at 2H and at 2D ($p < 0.05$) and between at 2D and at 6D ($p < 0.05$).

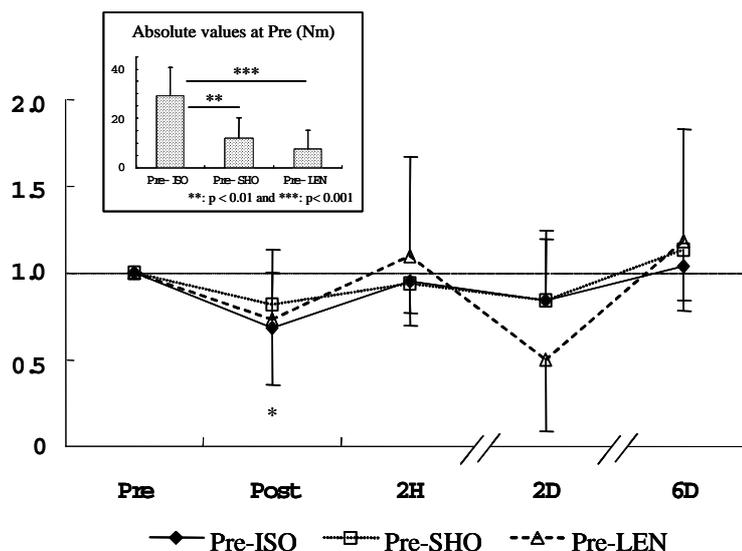


FIGURE 27 Relative changes in reflex torque. A bar graph in a left top frame shows absolute values of the torque at pre-test. * Indicates a significant change ($p < 0.05$) compared with pre-test in pre-ISO.

Relationships between SLSR p-to-p amplitude and reflex torque.

FIGURE 28 shows linear relationships between SLSR p-to-p amplitude divided by aEMG at MVC and RT divided by MVC torque. High correlation coefficients were observed between the two variables (0.721 - 0.921 ($p < 0.001$) in pre-ISO, 0.737 - 0.904 ($p < 0.001$) in pre-SHO and 0.578 - 0.969 ($p < 0.001$) in pre-LEN). Pre-ISO showed the largest reflex torque per SLSR p-to-p amplitude of three conditions in all tests. This result supports a result of EME observed in experiment II (FIGURE 17). Slopes of the linear regression lines ranged from 0.082 to 0.104 Nm/mV in pre-ISO, from 0.061 to 0.075 Nm/mV in pre-SHO, and from 0.04 to 0.071 Nm/mV in pre-LEN throughout this experiment.

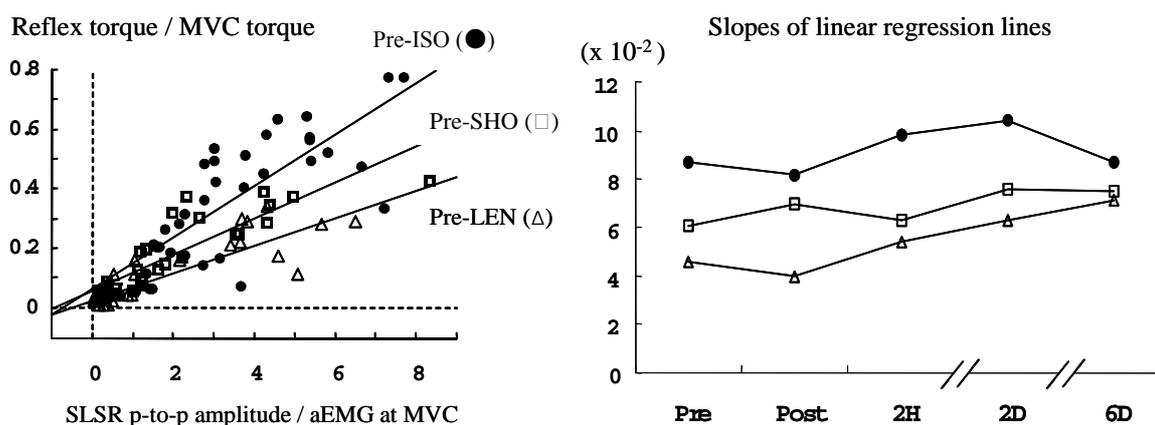


FIGURE 28 Relationships between SLSR p-to-p amplitude and reflex torque (left panel) at Pre. The p-to-p amplitude and torque were divided by aEMG and torque at MVC, respectively. Data of all trials performed by all subjects were plotted. A right panel shows changes in slopes of linear regression line between the two variables before and after LLEE.

AJT evoked by a single twitch.

No significant differences in ST torque were observed among three conditions at Pre (FIGURE 29), which was different from results observed in reflex torque. ST torque indicated significant decreases at Post compared with Pre in all conditions ($p < 0.05 - 0.01$). On the other hand, there were significant differences in EMD of ST torque among three conditions at Pre ($p < 0.001$). An extremely short EMD observed in pre-SHO (2.4 ± 2.1 ms at Pre) increased after LLEE significantly ($p < 0.05$), which was not observed in the other conditions.

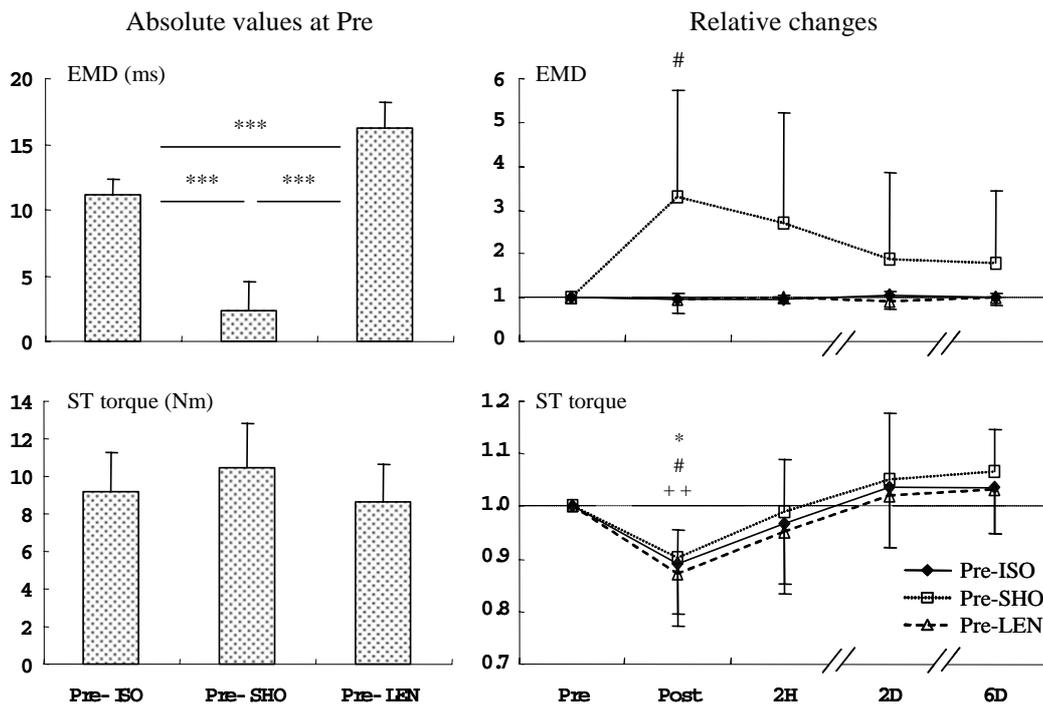


FIGURE 29 EMD and ST torque. Left panels show their absolute values at pre-test. *** indicates a significant difference between three conditions ($p < 0.001$). Right panels show relative changes in EMD and ST torque. *, # and + indicate significant changes ($p < 0.05$ and 0.01) compared with pre-test in pre-ISO, pre-SHO and pre-LEN, respectively.

Activation level and MVC torque.

AL decreased at Post significantly compared with at Pre at all tibio-tarsal joint angles ($p < 0.05 - 0.01$, TABLE 5). MVC torque depending on the tibio-tarsal joint angle also decreased at Post significantly compared with at Pre ($p < 0.05 - 0.001$). These results were similar to results observed in experiment V (FIGURE 23). Although aEMG slightly followed a bimodal trend, significant changes were rarely shown.

TABLE 5 Activation level, ankle plantar flexion torque and average EMG at MVC (Mean±SD)

| Variable | Unit | Angle (deg) | Pre | Post | 2H | 2D | 6D |
|------------|------|-------------|---|--|---------------------------------------|--|--|
| AL | % | 80 | 87,2 ± 16,8 | 75,6 ± 18.4 * | 84,6 ± 14,4 | 85,6 ± 10,4 | 84,0 ± 17,1 |
| | | 90 | 90,0 ± 8,5 | 80,2 ± 15.7 ** | 87,3 ± 11,6 | 90,5 ± 7,1 | 90,9 ± 8,1 |
| | | 100 | 96,4 ± 5,8 | 85,5 ± 11.2 ** | 92,8 ± 7,5 | 88,8 ± 7.9 * | 98,0 ± 4,9 |
| | | Difference | n.s. | n.s. | n.s. | n.s. | 80deg < 100deg # |
| MVC torque | Nm | 80 | 85,9 ± 22,5 | 69,0 ± 16.6 ** | 75,8 ± 21,0 * | 77,0 ± 19,3 | 83,6 ± 23,1 |
| | | 90 | 71,5 ± 18,1 | 63,5 ± 17.7 * | 65,0 ± 18,8 | 67,4 ± 16,7 | 70,1 ± 18,2 |
| | | 100 | 48,1 ± 13,1 | 40,5 ± 13.3 *** | 45,8 ± 12,0 | 43,2 ± 12.1 ** | 46,7 ± 13,7 |
| | | Difference | 100deg < 80deg #### 100deg < 90deg # | 100deg < 80deg ## 100deg < 90deg ## | 100deg < 80deg ## 100deg < 90deg # | 100deg < 80deg #### 100deg < 90deg ## | 100deg < 80deg #### 100deg < 90deg ## |
| aEMG (SOL) | µV | 80 | 226 ± 83 | 181 ± 58 | 217 ± 60 | 193 ± 56 | 222 ± 78 |
| | | 90 | 249 ± 72 | 201 ± 46 * | 237 ± 47 | 219 ± 49 | 248 ± 59 |
| | | 100 | 291 ± 129 | 238 ± 69 | 268 ± 88 | 222 ± 85 ** | 255 ± 96 |
| | | Difference | n.s. | n.s. | n.s. | n.s. | n.s. |
| aEMG (GM) | µV | 80 | 230 ± 47 | 185 ± 67 | 226 ± 74 | 215 ± 49 | 257 ± 69 |
| | | 90 | 239 ± 62 | 214 ± 67 | 233 ± 65 | 237 ± 76 | 254 ± 53 |
| | | 100 | 266 ± 104 | 230 ± 78 | 315 ± 140 | 231 ± 100 | 268 ± 91 |
| | | Difference | n.s. | n.s. | n.s. | n.s. | n.s. |

* and #: p < 0.05, ** and ##: p < 0.01, and *** and ####: p < 0.001

AL: Activation level

Note) * Shows significant differences compared with pre-test at each tibio-tarsal joint angle.

Shows significant differences among 80, 90 and 100 deg of tibio-tarsal joint.

AJT evoked by a double twitch in relaxed muscles.

Significant differences in DT torque were observed among 80, 90 and 100 deg of the tibio-tarsal joint angle (FIGURE 30). Although DT torque decreased significantly after LLEE at all angles ($p < 0.01 - 0.001$), its decrease was the most remarkable at 100 deg.

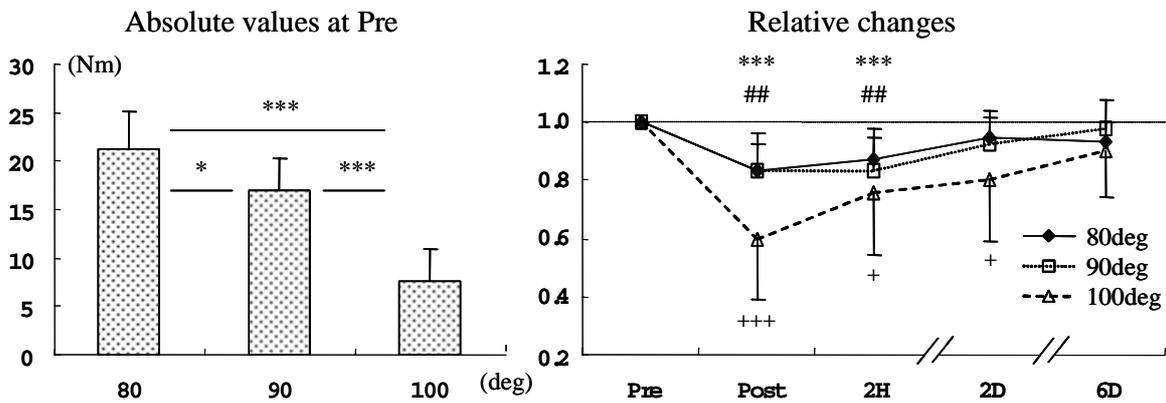


FIGURE 30 DT torque in relaxed muscles. A left panel shows the absolute values at pre-test against the tibio-tarsal joint angle. * And *** indicate significant differences between three conditions ($p < 0.05$ and $p < 0.001$, respectively). A right panel shows relative changes in DT torque. *, # And + indicate significant changes ($p < 0.05$, 0.01 and 0.001) compared with pre-test in pre-ISO, pre-SHO and pre-LEN, respectively.

Sagittal-plane muscle sonographs.

LLEE significantly decreased displacement of FIPA of SOL elicited by a stretch during LLEE. It could be also confirmed visually that movements of fascicles obviously got smaller. The displacement that was 5.0 ± 1.6 mm at the beginning of LLEE decreased by 74.5 ± 23.6 % at the end of LLEE ($p < 0.01$). In stretch reflex measurements, recovery of FIPA displacement elicited by shortening and lengthening before SDF tended to show a bimodal trend. The displacement that was 6.7 ± 1.3 mm at Pre decreased by 69.5 ± 29.5 % at Post ($p < 0.05$) and by 78.5 ± 19.9 % at 2D (n.s.) in pre-SHO. Also in pre-LEN it decreased by 80.1 ± 17.3 % at Post ($p < 0.05$) and by 83.1 ± 29.9 % at 2D (n.s.) from 7.9 ± 1.5 mm at Pre. Similar results were observed also in GM (FIGURE 31).

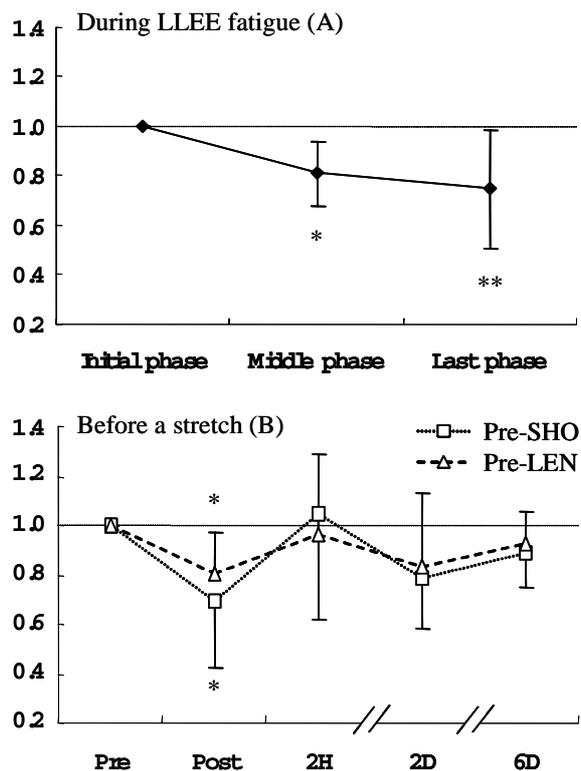


FIGURE 31 Displacement of fascicular insertion in the aponeurosis on sagittal-plane soleus muscle sonograph. Figures show shifts of the fascicular insertion elicited by stretch during LLEE (A), and during shortening (pre-SHO) and lengthening (pre-LEN) of the muscle-tendon complex before a stretch (B) as relative values compared with the initial phase (1th - 10th of the repetition) and with pre-test, respectively. * Over standard deviation bars indicates a significant change compared with pre-test.

Creatine kinase activity and blood lactate concentration.

No significant changes in CK and B-LA were observed before and after LLEE. The CK ranged from 161.4 ± 45.9 U/l at 6D to 205.0 ± 90.4 U/l at 2D. The B-LA ranged from 2.0 ± 0.6 mmol/l at Pre to 2.4 ± 1.0 mmol/l at 5 min after the LLEE. On the other hand, subjects complained of muscle soreness and tired feeling of APF muscles at 2D.

6 DISCUSSION

The main findings in the present study were as follows:

- 1) Muscle contraction types and pre-contraction levels before a stretch perturbation have considerable influence on latency, amplitude, area and waveform of short-latency stretch reflex (SLSR). Specifically, the muscle contraction type had the following effects: (1) Equal SLSR area but different SLSR waveforms between pre-ISO and pre-SHO were observed in the active muscle, (2) The smallest SLSR area was shown in pre-LEN of three conditions in the active muscle, and (3) SLSR latencies were shorter in pre-LEN than in the other conditions in both the active and relaxed muscles. These findings were observed in all cases including the same effort levels, matched ankle joint torque (AJT) levels and matched EMG activity levels. Pre-contraction levels, on the other hand, affected SLSR as follows: (1) Pre-SHO showed a longer SLSR latency in the relaxed muscle than in the active muscle, and (2) The active muscle had larger SLSR area than the relaxed muscle. Although large differences in SLSR behavior were observed between the relaxed and active muscles, the SLSR behavior was almost steady in each condition irrespective of the activation levels once the muscle was activated.
- 2) Muscle contraction types before a stretch perturbation influenced the stretch-reflex mechanical response. Pre-ISO generated a larger stretch-reflex mechanical response more efficiently than that generated after the dynamic contractions. Pre-contraction levels altered also the mechanical response, which depended on the muscle contraction types before the stretch. When the stretch-reflex mechanical response was divided between non-reflex torque (NRT) and reflex torque (RT), the RT was closely related to the NRT in all conditions.
- 3) There were large differences among AJT elicited by a mechanical stretch (MS) and electrical stimulation (ES). MS-elicited AJT was larger in pre-ISO than in pre-SHO, whereas ES-evoked one showed the opposite trend. Differences in MS-elicited AJT among three conditions decreased once the muscles were activated, whereas results observed in ES-evoked one was

opposite to it. MS-elicited AJT increased when the muscles were activated, whereas ES-evoked one decreased. These findings indicate that AJT behavior depends on whether length of the muscle-tendon (M-T) complex is changed by an external force after the preceding muscle contraction. Differences in AJT among three conditions decreased when a supra-maximal double ES was applied as ES instead of a supra-maximal single ES. This finding shows a strong influence of the preceding muscle contraction types on the following M-T complex performance.

- 4) EMD was greatly influenced by the preceding muscle contraction types, pre-contraction levels and stimulation types. Activating the muscle shortened EMD induced by MS in all conditions. In particular, it resulted in an extremely short EMD in pre-ISO. On the other hand, EMD induced by ES tended to increase once the muscles were activated. Above all, the following interesting findings were observed in pre-SHO: (1) an extremely short EMD in the relaxed muscle, and (2) a significant increase in EMD when the muscles were activated.
- 5) Effects of fatigue on the stretch reflex behavior depended on the fatigue protocol. When the stretch reflex was elicited by the same sudden dorsiflexion (SDF) as that used during a long-lasting low-intensity eccentric exercise (LLEE) to induce fatigue, its recovery processes were different between SLSR and RT. SLSR showed a bimodal recovery process comprising an acute and delayed declines, whereas RT did not follow the same process and needed a prolonged recovery time. H-reflex also showed a similar bimodal recovery process. M-wave remained unchanged before and after LLEE. When the stretch reflex was elicited by different SDF as that used during LLEE, fatigue induced by the LLEE elicited a bimodal recovery process in both SLSR and RT, which was not influenced by the background muscle contraction types before the SDF.

The following discussion will focus on attempts to find some mechanisms to clarify these observations.

6.1 Methodological considerations

The present results demonstrated that SLSR was regularly modulated according to the background muscle contractions while a given effort level was being maintained. For this finding to be valid, some artificial possibilities of modulating SLSR need to be ruled out. One possibility is a difference in backlash effects induced by different pedal movements among pre-ISO, pre-SHO and pre-LEN. In a series of experiments, the right foot of subjects was tightly mounted on a rotation platform of the ankle ergometer. Although part of a stretch perturbation might be absorbed by the inertia of the foot generated by the platform movements and the tissue around the ankle joint, a tight mounting

made between the foot and the platform was likely to minimize the backlash effects induced by the platform movements. Significant backlash effects would result in longer SLR latency in pre-SHO than in pre-ISO also in the active muscles. However, this was never observed. Another consideration is whether the sampling frequency of 1 kHz is enough for SLSR analysis. This is relevant to the issue of backlash effects and strongly influences SLSR modulation, especially its latency. However, similar SLSR latencies between pre-ISO and pre-SHO were observed in every trial and every repetition. This suggests that there would be little possibility that the present observations resulted from artificial effects.

A recent study showed that EMG could be affected by cancellation of the positive and negative phases of motor unit action potentials (Day and Hulliger, 2001). This does not support that the similar EMG activity among different modalities of muscle contraction does not always imply the similar activation level. Therefore, it must be noted that the present result of EMG activity is not always regarded as the effect of activation level on SLR modulation.

6.2 SLSR modulation and background muscle activities

SLR modulation depends on the types of muscle contractions before a stretch.

Significantly smaller SLSR area after lengthening than after the other contractions (see FIGURE 8) was in accordance with observation in earlier studies (Bawa and Sinkjær 1999; Nakazawa et al. 1997, 1998; Wallace and Miles 1998). However, two large differences in methodology existed between the present and earlier studies: (1) subjects were asked to maintain a given effort level while contracting the muscles before SDF in the present study, but to track target joint angles (Nakazawa et al. 1997, 1998; Bawa and Sinkjær 1999) and to maintain a given EMG activity level (Wallace and Miles 1998) in the earlier studies, and (2) analyses of the present study were focused on SLSR in SOL, whereas those of the earlier ones were focused on MLSR or LLSR in the elbow muscles (Nakazawa et al. 1997, 1998) and in the hand muscle (Wallace and Miles 1998). Therefore, smaller SLSR area after lengthening depends not on descending commands to attain the motor task but mainly on afferent inputs such as Ib afferents from Golgi tendon organs (Houk et al. 1980), group II afferents (Robinson et al. 1982), afferent inputs from joint receptors (Schieppati and Crenna 1984) and presynaptic inhibition (Abbruzzese et al. 1994) elicited by lengthening before SDF. In addition, muscle thixotropic effects induced by the preceding contraction are likely to be partly related to the alteration in SLSR (Hagbarth et al., 1985; 1995).

An observation that SLSR area after shortening was similar to that after an isometric contraction in the active muscle (see FIGURE 8) obviously differs from that in earlier studies (Nakazawa et al. 1997, 1998; Bawa and Sinkjær 1999). It is possible to consider a few mechanisms about the similar SLSR area

between pre-ISO and pre-SHO when a given effort level is maintained. The first possibility is an effect of different motor unit recruitment on SLSR area. However, it cannot reasonably be assumed due to the following aspects: (1) SOL is dominated mostly by slow twitch fibers (Johnson et al. 1973), (2) higher frequency values of EMG power spectrum have been observed during the isometric contraction than the shortening contraction (see FIGURE 22), and (3) there were no differences in SLSR latency between the conditions in the active muscle (see FIGURE 7).

The second possibility is an effect of afferent inputs on SLSR area. A compliant tendon is stretched by muscle tension during an isometric contraction (Fukashiro et al. 1995), which may increase the discharge rate of group Ib afferents since Golgi tendon organ is sensitive to tension generated within muscle-tendon unit (Schmidt, 1985). However, a result of SLSR p-to-p amplitude in the active muscle is likely to deny this possibility. If SLSR area was influenced by group Ib afferents during an isometric contraction, SLSR p-to-p amplitude would be smaller in pre-ISO than in pre-SHO because the discharge rate of the Ib afferents could be lower during shortening than during the isometric contraction.

The third possibility is an effect of muscle spindle sensitivity on SLSR area. Prochazka et al. (1985) have shown that fusimotor action on a given spindle afferent during movements is not rigidly alpha-linked, but set by the CNS to steady levels of gamma activity. Wilson et al. (1995) have reported that the discharge rate of muscle spindle afferents remains elevated in complete relaxation after an isometric contraction for approximately 5 seconds. Therefore, it is likely that the present motor task, maintenance of the effort level as needed to maintain a given pre-load torque level, resulted in high sensitivity of muscle spindles also during shortening. This is confirmed by the following observations in the relaxed muscle because unloading of muscle spindles is maximal: (1) no SLSR was shown in some subjects, (2) smaller SLSR p-to-p amplitude and longer SLSR duration than in the active muscle (see FIGURE 9) and (3) longer SLSR latency than in the active muscle (see FIGURE 7). Burke et al. (1978) have observed that the discharge rate of spindle endings decreases during shortening, but it always remained higher than before the onset of contraction. Smaller and blunter SLSR waveform in pre-SHO than in pre-ISO in the active muscle may indicate resistance of fusimotor drive to the muscle spindle unloading (slacking) induced by contraction of extrafusal fibers and external action of the pedal movement during shortening (FIGURE 32). This would be supported by shorter SLSR latency after lengthening in which the muscle spindles are also stretched by the external action of the pedal movement (see FIGURE 7). A recent study in which H-reflex was evoked (Kallio et al. 2003) also confirmed involvement of the muscle spindle slacking in the SLSR waveform.

| Muscle | Condition | Spindle | Equatorial region | Ia activity | Characteristics of SLSR | Ib activity | Collagen in GTO | Goldi tendon organ (GTO) |
|---------|-----------|---------|-------------------|---------------|---|---|------------------|--------------------------|
| Relaxed | Pre-ISO | | Normal | Spontaneous | Largest amplitude | Spontaneous | normal | |
| | Pre-SHO | | Slack | Low | Small amplitude Longest latency | Low | Slack | |
| | Pre-LEN | | Stretch | High | Small amplitude Shortest duration Shortest latency | High | Stretch | |
| Active | Pre-ISO | | Stretch | High (Static) | Largest amplitude | High (Particularly, at the beginning of contraction) | Stretch | |
| | Pre-SHO | | Stretch vs slack | Instable | Smaller amplitude & longer duration than pre-ISO | Instable | Stretch vs slack | |
| | Pre-LEN | | Stretch | Very high | Smallest amplitude Shortest duration Shortest latency | Very high | Stretch | |

: force generated by contraction of polar regions of intrafusal fibers
 : force generated by extrafusal fibers or by pedal movement of the ankle ergometer

FIGURE 32 A hypothesis of mechanical force acting on the muscle spindles and on Golgi tendon organs and the expected neural behavior during passive and active muscle contractions before a stretch perturbation. This hypothesis can be considered only when a given effort level is being maintained and does not include any length changes in the muscle spindles. It should be noted that discharge rate of group Ia and Ib afferents is not constant during a given muscle contraction.

The fourth possibility is an effect of BGA. Pre-SHO showed considerably lower ratios of BGA area to aEMG before SDF than in pre-ISO (see FIGURE 10). This result reminds us of premotion silent period (PSP) when a ballistic movement is performed on a low level of contraction. It has been considered that PSP increases susceptibility of motor units (Tsukahara et al. 1995), which is related to speed (Yabe 1976) and dynamic force (Aoki et al. 1989) in the first part of the movement. SDF-induced AJT is lower after shortening than after an isometric contraction (see FIGURE 12). Therefore, smaller BGA area after shortening might lead to large SLSR area, which might subsequently function to compensate a disadvantage of the mechanical output induced by SDF after shortening. It has been shown that muscle filament overlap becomes irregular in muscle fibers stretched during tetanus (Brown and Hill 1991; Edman and Tsuchiya 1996). SDF after shortening may induce larger irregularity of the filament overlap. Smaller EME in pre-SHO than in pre-ISO support it (see FIGURE 17 and 28). Slightly longer SLSR duration and smaller SLSR p-to-p amplitude in pre-SHO compared with pre-ISO may partly result from the irregularity. However, This possibility is no better than speculation. It remains an unsettled question why BGA markedly decreases after SDF following a shortening contraction compared with the other contraction types.

SLSR modulation is independent of background torque and EMG activity.

Differences in SLSR modulation among pre-ISO, pre-SHO and pre-LEN observed at matched AJT and EMG activity levels were similar to those observed at similar effort levels. This implies that SLSR modulated by the preceding muscle contraction is independent of the background AJT and EMG activity. In addition, although SLSR was larger and sharper in the active muscle than in the relaxed muscle, it remained unchanged irrespective of the effort level once the muscle was activated (see FIGURE 9). SLSR area was also independent of the effort levels in the active muscle. These are a complete contrast to EMG activity before a stretch being proportional to the effort level (see FIGURE 6). A similar SLSR independence was observed in human SOL (Toft et al. 1991) and in cat SOL (Hoffer and Andreassen 1981), which is not agreement with the automatic gain compensation (Marsden et al. 1976; Matthews 1986). Toft et al. (1991) suggested that absence of scaling of SLSR increment might be attributed to “saturation” of the motor neuron pool excitability. If this suggestion is correct, SLSR may not be sensitive to a change in the effort level once the muscle was activated. However, SLSR independence was not shown in TA (Toft et al. 1989). The automatic gain compensation, which predicts that the reflex response is an approximately constant proportion of the background activity, has been shown also in the thumb and elbow flexors. Therefore, the effects of background AJT and EMG activity on SLSR modulation may depend, at least in part, on differences in functions required by each muscle.

6.3 Alteration in stretch-reflex mechanical response in response to background muscle activities

A stretch after an isometric contraction generated larger NRT with longer duration and larger RT more quickly and more efficiently than those after dynamic contractions in the active muscle, which increased with the pre-contraction level (see FIGURES 12, 14, 16 and 17). These may be related to MU activity before SDF. Higher frequency components of EMG power spectrum have been observed during the isometric contraction and during lengthening than during shortening (see FIGURE 22). However, shorter EMDs and higher EMEs in pre-ISO than in pre-LEN (see FIGURES 16 and 17) cannot be explained by the different MU activities. Therefore, these phenomena are likely to be influenced considerably by conditions of M-T complex induced by muscle activities before SDF.

It has been suggested that force development immediately after a stretch extended during tetanic activity is due to increased strain on the attached cross-bridges in combination with a slight increase in the number of attached bridges (Lombardi and Piazzesi 1990; Sugi and Tsuchiya 1988). This force development corresponds to NRT in this study. Therefore, NRT behavior in

pre-ISO may indicate a better condition of the cross-bridges to generate the force after the isometric contraction than after the dynamic contractions in the active muscle. This would be supported by NRT behavior in the relaxed muscle, because the NRT was larger after shortening and smaller after lengthening than that after an isometric contraction in the relaxed muscle in which the activation level of the muscle is minimum (Suzuki et al. 1993) (see FIGURE 12). Similarly, condition of the cross-bridges may be closely related to similar I-rates but different NRT behavior between pre-ISO and pre-LEN (see FIGURE 14). Since elasticity of the cross-bridges utilized during lengthening (Moritani et al. 1988; Piazzesi et al. 1992) contributes to generate force efficiently, it might lead to increased NRM with the pre-contraction level in pre-LEN. On the other hand, a severe strain imposed on the cross-bridges by a stretch following lengthening might exceed the elastic limits, which might result in lower peak and shorter duration of NRT in pre-LEN than in pre-ISO (see FIGURE 12).

Before SDF, AJT was consistently decreasing during shortening and increasing during lengthening (see FIGURE 1). Because of a constant angular velocity, this indicates decreasing and increasing ankle joint stiffness during shortening and lengthening respectively, which is closely related to the Achilles tendon stiffness. Also during an isometric contraction compliant tendon stiffness is increased by the muscle contraction (Fukashiro et al. 1995). Since high Achilles tendon force is generated during a stretch (Nicol and Komi 1999), the Achilles tendon condition induced by the muscle activities before the stretch may influence the NRT behavior. Positive I-rates in pre-ISO and in pre-LEN would confirm it (see FIGURE 14) because the Achilles tendon stiffness also increases with the pre-contraction level. Fellows and Thilmann (1989) have observed longer stretch-reflex latencies at more plantar flexed positions in relaxed ankle extensors and suggested that it results from properties of a compliant tendon through which the joint movement is transmitted to a muscle. However, there were no differences in SLSR latency between pre-ISO and pre-SHO in the active muscle (see FIGURE 7). This observation indicates that a stretch was transmitted to the muscle in pre-SHO as well as in pre-ISO, which appears to contradict the lower Achilles tendon stiffness at the stretch in pre-SHO. Thus, the extent to which the tendon condition influences NRT behavior is less clear.

RT, which is represented as P3 and P4 amplitude, showed larger differences between pre-ISO and the other conditions than NRT (see FIGURES 12 and 13). NRT is directly related to M-T complex condition before SDF and inertia of the perturbed segment because it appears during the SDF and before SLSR burst. On the other hand, RT is likely to depend on the muscle condition after SDF and the reflex amplitude since there are no kinematic differences among three conditions during static period. It has been reported that irregularity of filament overlap is seen in tetanized muscle fibers and fibers stretched during tetanus (Brown and Hill 1991; Edman and Tsuchiya 1996). A relationship between its irregularity and force generated is less clear, especially in vivo. However, it is likely that greater filament overlaps generate larger force and higher regularity of the filament overlap generates force more efficiently. If

a stretch following a shortening contraction induces less regularity of the filament overlap, it may be able to explain longer EMDs and lower EMEs in pre-SHO and in pre-LEN than in pre-ISO (see FIGURES 16, 17 and 28). AJT results not only from SOL but also from all muscle activities at the ankle. However, it has been reported that SOL generates above two thirds of MVC in a sitting position (Toft et al. 1991). In addition, GL, GM and TA activity were substantially smaller than SOL activity. MLSR in SOL was also substantially smaller than SLSR (see FIGURE 11). Therefore, it may be safely assumed that RT depends mainly on SLSR in SOL. Positive relationships between peak NRT and peak RT (see TABLE 2) suggests that the RT is influenced not only by stretch-reflex EMG response but also by muscle condition immediately after SDF. Muscle condition such as higher regularity of the filament overlap at the onset of SDF seems to result in larger NRT. At the same time, it would have a good effect on reflex-induced torque because it is related to muscle condition after SDF.

Similar I-rates but lower amplitude of P2 in pre-ISO than in the other conditions (see FIGURES 12 and 14) may confirm that a stretch following a dynamic contraction induces less regularity of the filament overlap. Higher regularity would result in quicker and more efficient mechanical response induced by the stretch reflex as shown by shorter EMD and higher EME (see FIGURE 16, 17 and 28). A fall in tension that corresponds to P2 amplitude is induced by the end of pedal movement of the ankle ergometer. However, it would be related also to exceeding short-range elastic limit of intrinsic muscle stiffness and decline in intrinsic muscle viscosity as stretch velocity decreased (Joyce et al. 1969; Rack and Westbury 1974). No P2 amplitudes in the active muscle in pre-ISO shown by two subjects who developed large MVC indicate that the P2 represents decay in passive force of the visco-elastic components. It is likely that their strong passive and reflex-induced force did not allow the transient drop of AJT. It is supported also by a strongly negative relationship between peak NRT and P2 amplitude in every condition (see TABLE 2).

Pre-ISO showed steeper SLR waveforms, i.e., large amplitude and short duration, in the active muscle than the other conditions (see FIGURE 9). This may indicate higher excitability of α -motoneurons and higher rate of MU synchronization. Therefore, different SLSR waveform can partly explain why pre-SHO showed smaller RTs and lower EMEs than pre-ISO in the active muscle in spite of similar SLSR size.

Pre-SHO needed larger pre-load torque levels and effort levels for a stretch to be applied at the same torque levels as those in the other conditions. As a result, RT did not exceed the pre-load torque levels only in pre-SHO (see FIGURE 1). When an electrical stimulus is delivered to a muscle in a voluntary contraction, size of the superimposed twitch falls off linearly with increasing tension (Merton 1954). This is unlikely to be directly applicable to the present results because the present stimulus is a mechanical stretch. However, negative I-rates of P3 amplitude may be in line with this observation (see FIGURE 14). Therefore, it is possible that larger pre-load torque level leads to lower W-ratio,

lower EME and lower RT. This may explain why peak RT remained unchanged only in pre-SHO irrespective of the pre-contraction level.

6.4 Effects of the preceding muscle contractions on stretch-reflex mechanical response

It may be likely that differences in AJT elicited by MS and ES was affected by significant differences in AJT at the onset of MS or ES induced by the preceding muscle contractions. However, this difference is unlikely to explain the opposite results of AJT observed between pre-ISO and pre-SHO when ES was applied instead of MS (see FIGURES 18 and 19). Only pre-LEN tended to show lower AJT than the other conditions irrespective of stimulation types. This has not been observed when ES was applied during passive lengthening and shortening (Gravel et al. 1987) and during maximal voluntary eccentric and concentric contractions (Westing et al. 1990). These discrepancies are likely to result from a difference in the stimulation protocol (immediately after vs. during dynamic contractions) or muscle contraction level (20% vs. 100% MVC level). It is possible that ES-evoked AJT during dynamic contractions includes an effect of the force-length relationship (Rassier et al. 1999), and that a difference in the muscle contraction level induces variation in the neural input to the alpha-motoneurons from various receptors.

Duchateau and Hainaut (1986a, b) had shown that potentiation of force produced by the second stimulus of a double ES increases with reducing twitch-to-tetanus ratio, which is associated with a potentiation of intracellular Ca^{2+} movements. It is also known that higher Ca^{2+} is released during lengthening (Warren et al. 1993, Lowe et al. 1994). These may partly explain AJT behavior evoked by supra-maximal ES because the ES seems to activate all motor units as shown by the constant M-wave amplitude. Differences in ES-evoked AJT among three conditions decreased when a double ES was applied instead of a single ES (see FIGURE 20). Since the second stimulus of the double ES was applied at 10ms after the first one under the same M-T complex condition, this result would result from smaller effects of the preceding muscle contraction on intracellular Ca^{2+} movements when the second stimulus was applied.

An important finding of the present study is that EMD was greatly influenced by the preceding muscle contraction types, pre-activation levels and stimulation types. EMD observed in stretch reflex measurement was similar to that observed in earlier studies (Nicol and Komi 1998). However, the following results of EMD observed in pre-SHO are very new ones: (1) an extremely short EMD in the relaxed muscle, and (2) a significant increase in EMD when the muscles were activated (see FIGURE 21). It is a challenge to explain these findings, especially when literature lacks these particular aspects.

Directions in which the muscle is sliding before and after ES are similar in pre-SHO and opposite in pre-LEN. Differences in the sliding direction may result in significantly longer EMD in pre-LEN and shorter EMD in pre-SHO in the relaxed muscles (see FIGURE 21). It is known that the actin is moved a long distance on a myosin head smoothly and efficiently because each ATPase cycle corresponds to multiple power strokes with a moderate load (Yanagida et al. 1985; 1993, Kitamura et al. 1999). This behavior may explain significantly larger ES-evoked AJT in pre-SHO than in the other conditions in the active muscles. However, it is unlikely to explain why EMD increased significantly when the muscles were activated in pre-SHO. Other factors such as Ca^{2+} release in the active muscles and a low proportion of the attached cross-bridges in the relaxed muscles (Suzuki et al. 1993) may play a role in this mechanism.

It is known that function of the tendon changes according to the joint angle (Fellows and Thilmann 1989, Fukunaga et al. 1997). Fukunaga et al. (1997) observed that movement of the tendinous tissue occurs in parallel with the joint displacement in an un-loaded condition. Although Ikegawa et al. (1999) also observed the similar synchronization during active lengthening, they showed also that the tendinous tissue was lengthened earlier than the muscle at the beginning of eccentric contraction. ES contracts the muscles first, which induces a stretch of the tendon. On the other hand, MS stretches the tendon first, followed by a stretch of the muscle and muscle contraction elicited by the stretch reflex. Therefore, this difference in transmission of the stimulation results in different muscle-tendon complex behavior among three conditions, which is likely to influence AJT behavior and plays an important role to transmit force generated by the muscles to the skeleton.

6.5 SLSR modulation and fatigue

Exercise-induced fatigue is described as a loss of force-generating capability (Bigland-Ritchie and Woods 1984) or an inability to maintain further exercise at the required level (Edwards 1981). Since LLEE decreased MVC, DTr and RT significantly, it is reasonable to suppose that the LLEE induced peripheral fatigue. Although B-LA did not show significant changes between at Pre and at Post, the increment rate of B-LA seemed to be considerably high when mass of the shank including APF muscles was taken into consideration. The mass of the shank was only 4.3 ± 0.3 % of the whole body mass (Zatsiorsky et al. 1990). Therefore, no significant change in B-LA may be attributed to small APF muscles where LLEE was imposed. In fact, a repeated exhaustive stretch-shortening cycle exercise performed by larger muscles increased B-LA significantly (Horita et al. 2003). At the same time, LLEE was likely to recruit faster-contracting MUs because ES used in the present study is known to result in completely reversed MU recruitment orders to the "Size Principle" proposed by Henneman (1957) (Fang and Mortimer 1991; Feiereisen et al. 1997; Trimble and Enoka 1991). Rapid decrease in reflex-induced torque after the onset of

LLEE supports it (see FIGURE 24). The recruitment of the faster-contracting MUs may be also one reason of no significant increase in B-LA. However, the slower-contracting MUs seem to be also recruited finally because of LLEE duration. This might result in higher increment rate of B-LA compared with size of the APF muscles.

In the present study, LLEE induced a bimodal change in SLSR p-to-p amplitude composing of an acute and delayed decrease in all conditions (see FIGURE 26). This is in line with results in earlier studies (Avela and Komi 1998b; Avela et al. 1999b; Horita et al. 1996; Komi and Nicol 2000a,b; Nicol et al. 1996a). RT also showed the similar bimodal recovery process from fatigue although it was modest (see FIGURE 27). Close relationships between SLSR p-to-p amplitude and RT shown in FIGURE 28 confirm similarity of the change between SLSR p-to-p amplitude and RT. However, a discrepancy of the recovery processes between SLSR area and RT was observed when the stretch reflex was elicited by the same SDF pattern as that repeated during LLEE (see FIGURE 24). SLSR area showed a bimodal trend, whereas RT did not recover until 7days after LLEE. This seems to indicate that fatigue has a movement-specific effect.

Muscle fatigue induced by an exercise is attributed to decline in discharge rate of α -motoneurons (Bigland-Ritchie et al. 1986). The decreased discharge rate is considered to be influenced by CNS (Brasil-Neto et al. 1994; Gandevia et al. 1996) and by afferent feedback from peripheral receptors (Macefield et al. 1993). When motor evoked potential (MEP) is evoked by transcranial magnetic stimulation, it is known that it decreases during (Ljubisavljevic et al. 1996) and after an exercise (Brasil-Neto et al. 1993; Rollnik and Dengler 2002), and even after a series of ES without voluntary muscle activation (Pitcher and Miles 2002). Post-exercise MEP depression is associated with central fatigue, afferent input from exercising muscles and synaptic transmission. Also in the present study AL, regarded as an indirect indicator of central fatigue, decreased significantly at Post (see FIGURE 23). These results indicate that an acute decrease in reflex behavior is, at least partly, related to central fatigue. On the other hand, quick recovery of AL implies that the depression of reflex amplitude at Post differs from that at 2D on the underlying mechanism.

M-T complex is generally represented as a model comprising of contractile components (CC) surrounded by parallel elastic components and series elastic components (SEC). If the simplest model of M-T complex is adopted, CC and SEC can be roughly regarded as the muscle and tendinous tissue. In this case, decrease observed in FIPA displacement during and after LLEE in spite of a constant displacement of the tibio-tarsal joint (see FIGURE 31) implies the following: 1) changes in sarcomere length at SDF and 2) increases in SEC displacement. These represent decreased stiffness of the SEC, that is, a decreased spring constant. Differences in sarcomere length at SDF can contribute to differences in RT on the force-length relationship (Rassier DE et al., 1999). On the other hand, DT torque in relaxed muscles showed the largest decrease at 100 deg of the tibio-tarsal joint where SEC seems to be slacked most strongly after LLEE (see FIGURE 29). EMD of ST torque significantly increased

at Post only in pre-SHO in which SEC is shortening before SDF. These results support decreased stiffness of SEC after LLEE since only SEC transmits CC behavior to externals after the slack was stretched out of the SEC (Kawakami and Lieber 2000). Therefore, it is likely that alteration in muscle-tendon complex behavior induced by fatigue contributed to an acute decrease in SLSR p-to-p amplitude and RT.

However, results such as no delayed decrease in ST torque, smaller alteration in DT torque and in EMD of ST torque at 2D than at Post (see FIGURE 29 and 30) indicate that an acute and delayed decreases in reflex behavior were induced by different mechanisms. Effects of CC on the delayed decrease in RT are likely to be less compared with that at the acute decrease.

It seems reasonable to suppose that acute decreases at Post were influenced also by central fatigue and by slack of SEC. On the other hand, delayed decreases at 2D might be more closely related with peripheral inhibition via small muscle afferent group III and IV (Komi 2000). It has been demonstrated in decerebrate cats (Hayward et al. 1988) and in spinalized rats (Pettorossi et al. 1999) that the group III and IV activities elicited by electrically induced-fatigue inhibit monosynaptic reflex. The present results showed no changes in metabolic environment involving the chemical changes after LLEE. However, severe muscle soreness at 2D subjects complained of may suggest participation of nociceptive afferents in the delayed decreases because nociceptive signals are transmitted by the afferents. A dramatic decrease in H-reflex p-to-p amplitude at 2D supports it (see FIGURE 25).

H-reflex p-to-p amplitude evoked by ES that by-passed the muscle spindles showed much larger decrease at 2D than that of SLSR (see FIGURE 24 and 25). A difference in amplitude between H-reflex and SLSR observed at Post would be due to an effect of superimposed MVC measurement on the H-reflex amplitude. However, the difference observed at 2D seems to result from the following mechanisms: 1) although H-reflex mainly involves activation of low-threshold MUs, SLSR might be related to different MUs, 2) while inhibiting α -motoneurons, group III and IV afferents activate also gamma-motoneurons (Jovanovic et al. 1990; Johansson et al. 1993; Djupsjobacka et al. 1995). If the nociceptive afferents increased fusimotor activity, it may explain a different decline in amplitude between H-reflex and SLSR, and 3) swelling and stiffer muscles observed at 2D (see FIGURE 31) may result in higher sensitivity of the muscle spindles, which might compensate decreased α -motoneuron activity.

LLEE did not change differences in SLSR latency, SLSR p-to-p amplitude and reflex torque among three conditions. A result that pre-ISO always showed the largest RT per SLSR EMG activity of three conditions (see FIGURE 28) indicates pre-ISO has an advantage over the other conditions on force generated by the stretch reflex. On the other hand, facilitation of SLSR p-to-p amplitude at 2H shown in pre-LEN was not observed in pre-ISO (see FIGURE 26). Moreover, RT per SLSR EMG activity tended to increase after LLEE only in pre-LEN. Since APF muscles were stretched while being contracted by ES during LLEE, pre-LEN has the closest resemblance to LLEE on M-T complex behavior. If fatigue has a movement-specific effect, pre-LEN might be more

strongly influenced by the following mechanism that can be considered. Fatigue induced by LLEE activated type III and IV afferent nerves (Kaufman and Rybicki 1987; Decherchi et al. 1998), which might activate gamma-motoneurons followed by increases in muscle spindle sensitivity and alpha-motoneuron activity (Jovanovic et al. 1990; Johansson et al. 1993; Djupsjobacka et al. 1995; Travell et al. 1942). No difference in displacement of FIPA between at Pre and at 2H (see FIGURE 31) may support that their increases played an important role on facilitation of SLSR p-to-p amplitude at 2H. Large increases in B-LA and CK activity were not observed at 2H compared with at Pre, although metabolic changes can activate group III and IV afferent nerves (Garland and Kaufman 1995). Since it is also known that group III and IV afferent nerves make a powerful input to inhibitory interneurons, 'facilitation or inhibition' seems to depend on balance between metabolic changes induced by an exercise and afferent nerve activities. However, a question why SLSR p-to-p amplitude was facilitated at 2H in pre-LEN remains unclear.

It is known that a low-intensity long-lasting exercise selectively decreases torque evoked by low frequency stimulation (Avela et al. 2001; Edwards et al. 1977). Chin and Allen (1996) suggest that low frequency fatigue results from increases in intracellular free Ca^{2+} concentration, which activates some processes that leads to failure of excitation-contraction (E-C) coupling and Ca^{2+} release. These indicate that a prolonged recovery of RT might be attributed to impairment of processes associated with E-C coupling and Ca^{2+} release. Impairment of E-C coupling is closely related also to muscle damage (Jones 1996). As Duchateau and Hainaut (1985) suggest that intracellular processes pay a major role in contractile failure, a slight difference in recovery processes between AL and MVC or DTr torque (see FIGURE 23) may indicate impairment of the contractile tissue itself. Incomplete recovery of torque in contrast to complete recovery of aEMG observed at MVC supports it. Although no significant changes in CK activity were observed, it increased by about 30 % at 2D. This is considerably higher compared with mass of the shank including APF muscles (about 4 % of the whole body mass). In addition, fatigue APF muscles at Post and severe muscle soreness at 2D of which complained by all subjects seems to indicate muscle damage and the following inflammation.

7 PRIMARY FINDINGS AND CONCLUSION

The main findings and conclusion of the present study can be summarized as follows:

- 1) Muscle contraction types before a stretch perturbation had considerable influence on SLSR behavior. When subjects were maintaining a given effort level, a stretch perturbation after an isometric and shortening contractions showed an equal SLSR area but a different SLR waveform in the active muscle. Similar findings were not observed when the subjects were required to maintain a given torque level or EMG activity level, or track a moving target joint angle. On the other hand, small SLSR area elicited by a stretch perturbation after lengthening was observed also in the earlier studies. These findings are likely to result from differences in muscle spindle sensitivity induced by a given motor task imposed on subjects and in afferent input from various receptors induced by the preceding muscle activities. This is confirmed by (1) a longer SLSR latency in the relaxed muscle than in the active muscle in pre-SHO, and by (2) shorter SLSR latencies in pre-LEN than in the other conditions.
- 2) Pre-contraction levels before a stretch perturbation also had considerable influence on SLSR behavior. SLSR area was larger and SLSR waveform was steeper in the active muscle than in the relaxed muscle in all conditions. However, the SLSR behavior was independent of the effort level, background torque level and background EMG activity level once the muscles were activated. This differed markedly from the background torque and EMG activity in proportion to the effort level. Pattern of SLSR modulation in each condition remained unchanged in the active muscles. These findings may indicate that the stretch reflex in SOL is not sensitive to changes in muscle activation once the muscle is activated.
- 3) Stretch-reflex mechanical response was also influenced by muscle contraction types and pre-contraction levels before a stretch perturbation.

A stretch perturbation after an isometric contraction generated a larger stretch-reflex mechanical response more efficiently than that after dynamic contractions. In addition, a close relationship between the reflex-elicited torque and the torque recorded immediately after a stretch indicates that M-T complex condition induced by the preceding muscle activity strongly influences the mechanical response.

- 4) Effects of the preceding muscle activity on the following mechanical response depended on the stimulation type that elicited the response. When a mechanical stretch was applied, AJT elicited by it was characterized as follows: (1) Larger AJT after an isometric contraction than after shortening, and (2) smaller differences in AJT among three conditions in the active muscle than in the relaxed one. However, when a supra-maximal single electrical stimulation was applied, it evoked the opposite characteristics of AJT to those elicited by a mechanical stretch. Obvious differences between a mechanical stretch and a supra-maximal single electrical stimulation were based on (1) motor unit recruitment, (2) involvement of a neural circuit, (3) timing when the tendon tissue is stretched, and (4) changes in length of the whole muscle-tendon complex. Therefore, the mechanical response seems to be modulated by interaction between the preceding muscle activity and the following stimulation type. This is confirmed by decreased differences in AJT among three conditions when a supra-maximal double electrical stimulation was applied instead of a supra-maximal single electrical stimulation.
- 5) The preceding muscle contraction types, pre-contraction levels and stimulation types influenced EMD. EMD elicited by a mechanical stretch shortened in all conditions once the muscle was activated. In particular, EMD after an isometric contraction shortened dramatically. On the other hand, EMD evoked by a supra-maximal single electrical stimulation tended to increase when the muscle was activated. A supra-maximal single electrical stimulation after shortening induced very short EMD in the relaxed muscle, which significantly increased when the muscle was activated. It is likely that these findings are closely related to muscle and tendon conditions induced by the preceding muscle activity, and to differences in muscle sliding direction before and after stimulation.
- 6) When the stretch reflex was elicited by the same stretch perturbation as that used during LLEE to induce fatigue, its recovery processes were different between reflex EMG activity and reflex-induced torque. Reflex EMG activity showed a bimodal recovery process comprising acute and delayed decreases, whereas the reflex-induced torque needed a prolonged recovery time. This indicates structural changes in M-T complex. When the stretch reflex was elicited by a different stretch perturbation from that used during LLEE, fatigue induced by the LLEE elicited a bimodal recovery process in both reflex EMG activity and reflex-induced torque. No effects of the background muscle contraction types before a stretch perturbation were observed during the recovery process. These findings may indicate a movement-specific effect of fatigue. It was likely that alteration in

muscle-tendon complex behavior and nociceptive afferent activities associated with muscle soreness induced by fatigue contributed to the bimodal changes in reflex EMG activity and reflex-induced torque.

YHTEENVETO

Venytyksrefleksin muutokset liikkeessä ja väsymyksessä

Tutkimussarjan tarkoituksena oli selvittää sähköisen ja mekaanisen refleksivasteen muutoksia eri aktivaatiotasolla sekä silloin, kun plantaarifleksorit on väsytetty pitkäkestoisessa, intensiteetiltään kevyessä, eksentrisessä harjoitteessa. Projekti koostui kuudesta mittaussarjasta. Venytysrefleksi aiheutettiin venyttämällä eri intensiteetillä aktivoituja plantaarifleksoreita nopealla dorsifleksioilla. Tulokset osoittavat, että sekä venytystä edeltävällä lihassupistustavalla että aktivaatiotasolla on merkittävä vaikutus refleksivasteeseen.

Passiivisessa lihaksessa havaittiin suurempi sähköinen refleksivaste sekä suurempi ja tehokkaampi mekaaninen refleksivaste silloin, kun lihas ei pidentynyt (pre-LEN) tai lyhentynyt (pre-SHO) vaan kun pituus pysyi muuttumattomana (pre-ISO) ennen venytystä. Aktiivisessa lihaksessa venytystä edeltävä lyheneminen (pre-SHO) ei muuttanut lyhytlatenssin refleksin (SLSR) keskimääräistä EMG:tä (aEMG) verrattuna isometriseen esiaktivaatioon, vaikka vasteen muoto olikin loivempi. Pienin refleksivasteen aEMG havaittiin silloin kun venytys aiheutettiin lihaksen pitenemisen jälkeen (pre-LEN). Yllä mainitut tulokset ovat todennäköisesti seurausta venytystä edeltävän liikkeen aiheuttamista muutoksista lihassukkulan herkkyudessa ja eri sensorien tuottamassa palautteessa. Tätä oletusta tukevat seuraavat löydökset: (1) Lihaksen lyheneminen ennen venytystä (pre-SHO) johti pidempään SLSR latenssiin passiivisessa kuin aktiivisessa tilanteessa, ja (2) SLSR latenssi oli lyhyempi pre-LEN:issä verrattuna muihin tilanteisiin. Mekaanisen vasteen osalta havaittiin merkittävä riippuvuus refleksin aiheuttaman momentin (RT) ja pedaalin liikkeen aiheuttaman momentin välillä, mikä viittaisi siihen että edeltävä lihasaktiivisuus muokkaa lihas-jänne kompleksin rakennetta ja vaikuttaa siten tämän mekaaniseen vasteeseen.

Myös väsymys vaikutti refleksivasteisiin. Erityisesti venytysrefleksin sähköinen vaste palautui kaksivaiheisesti: refleksivasteessa havaittiin akuutti ja viivästynyt heikentyminen riippumatta edeltävästä aktivaatiotavasta. Palautumisprosessi sen sijaan oli riippuvainen väsymyksen aiheuttaneen harjoitteen tyypistä. Kun venytysrefleksi aiheutettiin väsytyksessä käytetyllä liikkeellä, RT:n palautuminen ei ollut kaksivaiheinen vaan tasainen, mikä viittaisi liikkeestä riippuvaiseen väsymykseen. Väsymyksen aiheuttama refleksin kaksivaiheinen palautuminen lienee yhteydessä muutoksiin lihas-jännekompleksin käyttäytymisessä sekä kipua aistivien hermoratojen aktiivisuudessa.

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ORIGINAL PAPERS

I

**Short-latency stretch reflex modulation
in response to varying soleus muscle activities**

By

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Short-latency stretch reflex modulation in response to varying soleus muscle activities

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Abstract

The current investigation examined the effect of various types of background muscle contractions on the short-latency stretch reflex (SLR) elicited from the soleus muscle while subjects were in a sitting position. A stretch was applied to the calf muscles while they performed an isometric (pre-ISO), shortening (pre-SHO) and lengthening contraction (pre-LEN) with several pre-contraction levels. The ankle was at a 90° tibio-tarsal joint angle when the perturbation was applied. Subjects developed and maintained a given pre-load level, which was maintained at various percentages of the maximum voluntary isometric plantar flexion torque. This was performed at 80° in pre-SHO, 90° in pre-ISO and 100° in pre-LEN for about 2 s before the contractions. The SLRs in trials with 0, 35 and 50% of the maximum voluntary contraction torque level were compared among the three conditions. The main results were as follows. (1) Pre-ISO and pre-SHO showed an equal SLR area and a different SLR waveform in the active muscle. (2) Pre-LEN showed the smallest SLR area of three conditions in the active muscle. (3) Pre-LEN showed shorter SLR latencies than the other conditions. (4) Pre-SHO showed a longer SLR latency in the relaxed muscle than in the active muscle. (5) The SLR area was larger in the active muscle than in the relaxed muscle. These findings demonstrate that the muscle contraction type and the pre-contraction level before a stretch perturbation have a considerable influence on the latency, the area and the waveform of the SLR. In particular, the equal area and the different waveforms of the SLR between pre-ISO and pre-SHO were a unique finding in the present study. They might result from differences in muscle spindle sensitivity and afferent input from various receptors induced by the present motor task. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Motor control; Short-latency stretch reflex; Human soleus muscle; Degree of effort; Type of muscle contraction; Pre-contraction level

1. Introduction

Voluntary movement includes many involuntary mechanisms. An example is the stretch reflex that is automatically elicited by a mechanical stretch of muscle during movements. The reflex is influenced by the following conditions: joint angle during the stretch [7,26,32], amplitude [1,26], velocity [1], direction [26], and duration of the stretch [26]. However, it has been observed that the amplitude of the short-latency stretch reflex (SLR) response in the human soleus muscle (SOL) depends not on background EMG activity but on the phase of the gait cycle during walking [25]. It has also been reported that in the

sitting position the SLR in the human SOL is not proportional to the background torque level [29]. This indicates that the 'gain' of the SLR depends on the specific conditions of the neuromuscular system, which are controlled according to a functional requirement to accomplish a given motor task. Doemges and Rack [5,6] showed different long-latency reflex responses (LLR) in a human hand muscle during different motor tasks. Wallace and Miles [31] showed that the amplitude of the LLR was sharply reduced during non-isometric contractions in a human hand muscle. There is no doubt that the LLR is modulated by the motor task imposed on subjects, i.e. what the subjects are requested to perform, and the muscle contraction type before a stretch. With regard to the SLR, Bawa and Sinkjær [4] observed a reduced SLR during a non-isometric contraction in a human forearm muscle. Nakazawa et al. [16] also showed that the SLR was

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reduced during non-isometric contractions in human elbow muscles. It is likely that the SLR is also modulated by the muscle contraction type before a stretch.

It has been shown that a large and clear SLR is elicited in the SOL by stretching the calf muscles when the subject is in a sitting position [29] and during walking [25]. It has also been shown that the contraction level prior to a stretch is closely related to the amplitude of the reflex responses [1,26,28]. However, it is unclear whether the SLR in the SOL is modulated by various types of muscle activities prior to a stretch. Therefore, this study was designed to investigate the effects of muscle contraction types and pre-contraction levels before a stretch perturbation on the SLR in the SOL under a given effort.

2. Materials and methods

2.1. Subjects

Seven healthy male subjects (age, 25.3 ± 4.9 years; body height, 1.80 ± 0.08 m; body mass, 72.0 ± 12.2 kg) volunteered in this study. They gave informed consent to participate in the present experimental procedure that was approved by the University Ethics Committee.

2.2. Apparatus and position

Stretch reflex responses in the calf muscle were elicited by a mechanical stretch perturbation using a motor driven ankle ergometer controlled by a digital feedback system [18], which was similar to that used by Gollhofer and Schmidtbleicher [9]. The maximum torque capacity was 150 N·m (Geisinger, Germany). The torque and angular displacement around the rotational axis of the motor were measured with a piezoelectric crystal transducer (Kistler, Switzerland). After a warm-up the subjects sat in the ergometer chair. Their right thigh was clamped with a soft cuff. Their right foot was mounted on the rotation platform so that the rotational axis of the ankle joint coincided with that of the motor torque device. The tibio-tarsal joint was rotated from 80 to 100°. The knee and hip joint angles were fixed (131 ± 7 and 111 ± 7 °, respectively) so that the stretch reflex responses were elicited as consistently as possible at 90° of the tibio-tarsal joint.

2.3. Experimental procedure and motor tasks

Three movement tasks, which comprised an isometric (pre-ISO), shortening (pre-SHO) and lengthening contraction (pre-LEN) before a stretch perturbation, were performed at intervals of at least 30 min. To begin with, the platform rotated from 90° of the tibio-tarsal joint angle to the initial positions, which were 80° in pre-SHO, 90° in pre-ISO and 100° in pre-LEN, over

3095 ms (top panel of Fig. 1). The subjects were instructed to relax their muscles fully during this period (preparatory period). The platform moved over a time period of 2910 ms (pre-load period). In the case of pre-ISO, in order to keep the subjects informed, the beginning of this period was marked by a small triangular stretch of 1° over 40 ms. The subjects were asked to activate their calf muscles and maintain a given ankle joint torque level during this period with the help of visual feedback shown on an oscilloscope. The pre-load levels were set to 0, 10, 20, 30, 40, 50, 60 and 70% torque level according to maximum voluntary isometric plantar flexion contractions (MVC) at 80° in pre-SHO, at 90° in pre-ISO and at 100° in pre-LEN. Therefore, the subjects performed eight trials for every condition. The pre-load level relative to the MVC torque level was defined as the 'degree of effort'. The MVCs at 80, 90 and 100° were randomly measured three times beforehand. These trials were performed in order to select some trials with an equal torque level among three conditions at the onset of the stretch. In fact the subjects maintained the pre-load torque level for about 2 s because it took some time to match it to its target level (bottom panel of Fig. 1). Thereafter, the contraction period lasted for 423 ms. The platform rotated from 80 to 90° in pre-SHO and from 100 to 90° in pre-LEN. In pre-ISO it remained still. For the initial 2.7° of this period the angular velocity gradually increased to prevent any stretch reflex responses. After 180 ms the angular velocity reached 30°/s, which was constantly kept over 243 ms. During this period, the subjects were asked to maintain an effort level as needed to maintain the target torque level during the pre-load period (second panel from the top in Fig. 1). Therefore, the ankle joint torque consistently decreased in pre-SHO and increased in pre-LEN (bottom panel in Fig. 1). A stretch perturbation of 4° over 25 ms was applied at 90° of the tibio-tarsal joint angle (stretch perturbation period). The subjects were asked not to resist the stretch but to constantly maintain the same effort as that made during the pre-load and contraction period. After the stretch the platform was stopped at 86° for 308 ms (static period) in order to make an equal condition among three conditions because the stretch reflex responses generally appear in this period. The subjects tried to maintain constant effort until the end of this period. Finally, the platform gradually returned to the position of 90° over 1239 ms (recovery period). The subjects fully relaxed their muscles again. A whole platform movement lasted for 8 s and was repeated 10 times. The order of each trial was randomized. There were intervals of at least 3 min between the trials.

Skin temperature on the SOL muscle was maintained at 30°C through the whole experiment with a lamp, and it was checked with a thermometer (Line Seiki, Japan).

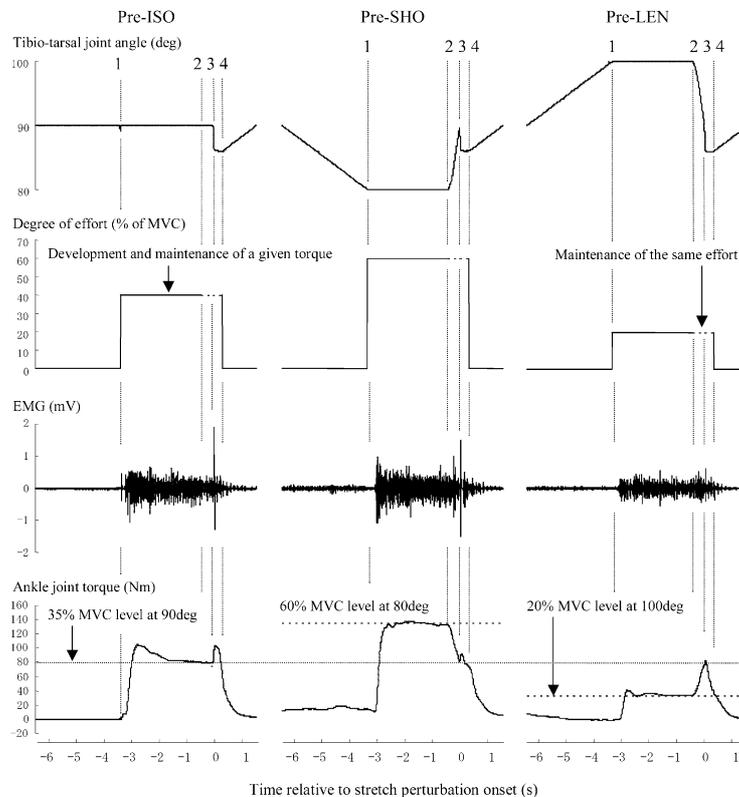


Fig. 1. Experimental protocol. This figure shows a typical example of the tibio-tarsal joint angles, degrees of effort performed by the subject, raw electromyograms and the ankle joint torque for a whole trial at 35% MVC pre-contraction level. Dotted lines 1–4 represent the onset of pre-load period (–3333 ms relative to the stretch onset), contraction period (–423 ms), stretch perturbation and recovery period (333 ms), respectively. One whole trial lasts for 8 s. The torque sometimes increased larger than the target torque level at the beginning of the pre-load period as shown in the bottom left panel.

2.4. Electromyography

Electromyographic activity (EMG) was obtained telemetrically from the SOL, gastrocnemius lateralis (GL), gastrocnemius medialis (GM) and tibialis anterior (TA) muscles of the right leg. Bipolar silver chloride miniature skin electrodes (Beckman 650437, USA; 20 mm interelectrode distance) were aligned parallel with the fibers halfway between the estimated center of the innervation zone and the distal end of the muscles. Before electrode application, each site was shaved, abraded and cleansed with alcohol to keep a low interelectrode impedance (5 k Ω). EMG signal was amplified by 200 times with a FM-microvolt amplifier (Glonner Electric GmbH, Germany; bandwidth 3–360 Hz, CMRR 90 dB, input impedance >25 M Ω).

2.5. Data analysis

EMG signals were stored on a computer via a real time data acquisition system (Cudas, Dataq Instruments Inc.,

USA) which included a 12-bit A/D converter with a sampling frequency of 1 kHz. They were high-pass filtered at cutoff frequency of 10 Hz and full-wave rectified. The rectified EMG signals were averaged over a period of 2000 ms before and 350 ms after an onset of stretch perturbation in each condition (10 repetitions). Identification of the SLR and LLR was modified from that introduced by Lee and Tatton [14] for upper limbs (Fig. 2). The onset of SLR was identified by an onset of consistently steep rise of the rectified EMG activity at about 40 ms after the stretch. The end of SLR or the onset of LLR was identified by the lowest rectified EMG activity followed by the second sharp rise at about 60 ms after the stretch. Latency and duration of the SLR were measured. The SLR duration was calculated by subtracting the SLR latency from the LLR latency. The SLR showed two narrow peaks. Since they represent the positive and negative component of one biphasic potential in the raw EMG signal, a sum of them was defined as peak-to-peak amplitude. The peak-to-peak amplitude and the duration of the SLR were regarded as an indicator of the SLR waveform. Average

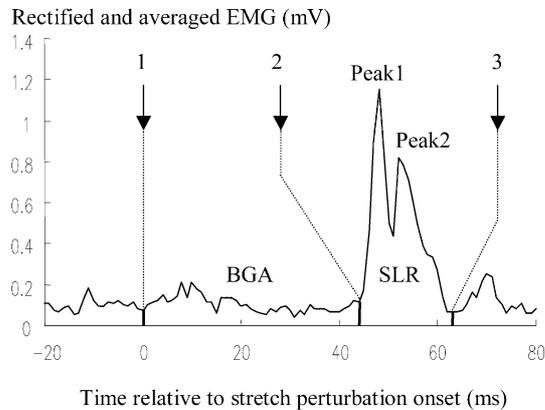


Fig. 2. A schematic representation of EMG analysis. The figure shows a result at 35% MVC pre-contraction level in pre-ISO in a representative subject. Arrows 1–3 represent the onset of stretch, SLR burst and LLR burst, respectively. Times at arrow 1 and 2 represent latencies of the SLR and the LLR, respectively. Time difference between arrow 1 and 2 represents duration of the SLR. The sum of Peak1 and Peak2 is regarded as peak-to-peak amplitude.

EMG (aEMG) of the SLR, i.e. area per unit time, was calculated for 1000 ms before contraction period, for the contraction period, from the stretch onset to the SLR onset as background activity (BGA) and for the SLR. It was defined as SLR area.

It has been shown that motor unit (MU) activities are different among varying types of muscle contraction [16,19]. Therefore, before rectification of the EMG signals, the EMG power spectrum was also calculated for the active muscles utilizing a fast Fourier transformation (FFT) for 512 ms before the contraction period and for 256 ms before the stretch onset for each platform movement to obtain median frequency (MF) and mean power frequency (MPF). Ensemble averages were calculated for each trial.

The ankle joint torque and the angular displacement were simultaneously recorded with the EMG activity. An inertial reaction torque induced by the movement of the rotating platform was subtracted from the recorded torque in each condition. The torque was filtered at 75 Hz with a Butterworth type 4th-order zero-lag low-pass filter to remove the high frequency noise. External work performed in the contraction period was calculated from these data. In the case of pre-ISO, the external work was zero due to a constant angle at 90°. Absolute external work was also calculated since the ankle joint performed the positive work in pre-SHO and the negative work in pre-LEN.

In the MVC measurement the aEMG, MF and MPF were also calculated for 512 ms after the torque visually reached its plateau about the maximum for each trial. Ensemble averages were calculated for each tibio-tarsal joint angle.

The ankle joint torque at the stretch onset was nor-

malized to the MVC torque level at 90° for every trial to eliminate a difference in the MVC among the subjects. It was defined as pre-contraction level. Some trials with equal pre-contraction levels among pre-ISO, pre-SHO and pre-LEN were individually selected from eight trials performed in each condition (bottom panel of Fig. 1). They were compared among the conditions to investigate effects of the muscle contraction type before the stretch on the SLR. Consequently, the SLRs at about 0, 35 and 50% MVC pre-contraction levels were compared for all subjects. Its precise mean values were 0.0 ± 0.0 , 34.0 ± 3.1 and $51.6 \pm 2.7\%$ MVC level in pre-ISO, -1.3 ± 0.3 , 34.0 ± 2.2 and $50.4 \pm 4.3\%$ MVC level in pre-SHO and 1.9 ± 0.6 , 35.8 ± 3.1 and $52.3 \pm 2.2\%$ MVC level in pre-LEN.

2.6. Statistical analysis

A two-way analysis of variance (ANOVA) was used to test all variables for significant differences among three pre-contraction levels and three muscle contraction types. When the result of the ANOVA was significant ($p < 0.05$), Fisher's post hoc test was used to assess the source of difference ($p < 0.05$)

3. Results

3.1. Maximum voluntary isometric plantar flexion contraction

The ankle joint torque, aEMG, MF and MPF at MVC are shown in Table 1. The torque decreased with increase in the tibio-tarsal joint angle. On the other hand, the MF and the MPF were significantly larger at 100° than at 80°. The aEMG remained unchanged irrespective of the tibio-tarsal joint angle.

3.2. Muscle activity before a stretch perturbation onset

In this study the SLRs at 0, 35 and 50% MVC pre-contraction levels were compared among three conditions. Therefore, events prior to the onset of a stretch differed among pre-ISO, pre-SHO and pre-LEN as shown in Table 2. Pre-SHO needed the largest pre-load torque levels for the ankle joint torque to reach their pre-contraction levels because the torque rapidly decreased during the contraction period. On the other hand, pre-LEN needed the smallest pre-load torque levels because the torque rapidly increased during the contraction period. Therefore, there were large differences in the pre-load torque level required to reach 35 and 50% MVC pre-contraction level between the conditions. Significant differences in degree of effort were also present. The required efforts in pre-SHO, pre-ISO and pre-LEN were 48.6 ± 6.9 , 34.3 ± 5.3 and $15.7 \pm 5.3\%$ at the 35% MVC pre-

Table 1
Ankle joint torque, aEMG, MF and MPF at MVC (numerical values show means \pm standard deviations)

| Variables | Unit | Tibio-tarsal joint angle ($^{\circ}$) | | | Difference |
|--------------------|------|---|-------------------|-------------------|-------------------------------|
| | | 80 | 90 | 100 | |
| Ankle joint torque | N m | 145.9 \pm 76.4 | 120.0 \pm 66.0 | 98.7 \pm 54.4 | n.s. |
| aEMG | mV | 0.229 \pm 0.072 | 0.242 \pm 0.089 | 0.237 \pm 0.071 | n.s. |
| MF | Hz | 107.0 \pm 18.1 | 115.2 \pm 16.8 | 126.5 \pm 15.0 | 80 $^{\circ}$ <100 $^{\circ}$ |
| MPF | Hz | 120.1 \pm 17.4 | 128.4 \pm 16.4 | 138.5 \pm 14.5 | 80 $^{\circ}$ <100 $^{\circ}$ |

Table 2
Soleus muscle activities and torque before a stretch perturbation (Numerical values show means \pm standard deviations. Work is that performed about the ankle joint during the contraction period.)

| Pre-contraction level (%) | Condition | Pre-load period | | Contraction period | | At a stretch |
|---------------------------|-----------|-----------------|------------------|--------------------|------------------|-----------------|
| | | Torque (N m) | aEMG (μ V) | Work (J) | aEMG (μ V) | Torque (N m) |
| 0 | Pre-ISO | 0.0 \pm 0.0 | 9.1 \pm 5.1 | 0.0 \pm 0.0 | 9.0 \pm 4.9 | 0.0 \pm 0.0 |
| | Pre-SHO | 2.8 \pm 1.1 | 8.0 \pm 4.0 | 0.1 \pm 0.1 | 7.6 \pm 3.6 | -1.5 \pm 0.5 |
| | Pre-LEN | -2.4 \pm 1.5 | 6.4 \pm 2.1 | -0.1 \pm 0.1 | 7.1 \pm 2.8 | 2.2 \pm 1.5 |
| 35 | Pre-ISO | 41.8 \pm 22.7 | 79.9 \pm 26.1 | 0.0 \pm 0.0 | 78.0 \pm 24.5 | 41.8 \pm 22.6 |
| | Pre-SHO | 68.0 \pm 32.6 | 103.6 \pm 20.3 | 9.1 \pm 4.6 | 103.6 \pm 36.6 | 42.4 \pm 24.3 |
| | Pre-LEN | 18.9 \pm 14.9 | 58.0 \pm 27.1 | -5.6 \pm 3.6 | 77.6 \pm 34.6 | 44.8 \pm 26.2 |
| 50 | Pre-ISO | 64.5 \pm 36.9 | 110.0 \pm 28.9 | 0.0 \pm 0.0 | 105.0 \pm 26.4 | 64.3 \pm 36.7 |
| | Pre-SHO | 94.1 \pm 42.4 | 141.3 \pm 32.6 | 12.9 \pm 6.4 | 137.6 \pm 35.8 | 63.3 \pm 37.2 |
| | Pre-LEN | 35.3 \pm 22.3 | 101.7 \pm 56.1 | -8.9 \pm 4.9 | 114.4 \pm 54.2 | 63.3 \pm 31.0 |

contraction level, and 68.6 \pm 3.8, 52.9 \pm 4.9 and 32.9 \pm 9.5% at the 50% MVC pre-contraction level, respectively. The EMG activity during the pre-load and contraction period was larger in pre-SHO than in the other conditions. The absolute external work performed in the contraction period was larger in pre-SHO than in pre-LEN. The ratios of Pre-LEN to pre-SHO were 59.4 \pm 12.5% at the 35% MVC pre-contraction level and 68.0 \pm 10.0% at the 50% MVC pre-contraction level.

3.3. Difference in stretch reflex among subjects

There were two obvious differences in the SLR among the subjects. Firstly, three of seven subjects showed no SLR at the 0% MVC pre-contraction level in pre-SHO. Although the remaining subjects showed the SLRs at the 0% MVC pre-contraction level, the SLR latencies were longer than at the other levels. Secondly, three of seven subjects showed slightly larger SLR peak-to-peak amplitudes and longer SLR duration at the 0% MVC pre-contraction level than at the other pre-contraction levels in pre-ISO, whereas the remaining subjects showed smaller SLR peak-to-peak amplitudes. These results led to large

differences in aEMG (Fig. 3), peak-to-peak amplitude and duration (Fig. 4) of the SLR at the 0% MVC pre-contraction level among the three conditions.

3.4. Average EMG of SLR and BGA

Fig. 3 shows aEMGs of the SLR and the BGA. There were no differences in the aEMG of the SLR at 35 and 50% MVC pre-contraction level between pre-ISO and pre-SHO. However, pre-LEN showed significantly smaller aEMGs at these pre-contraction levels than the other conditions. There were no differences in the aEMG of the BGA at all pre-contraction levels among three conditions.

The aEMG of the SLR significantly increased in pre-SHO and pre-LEN when pre-loads were involved, whereas pre-ISO did not significantly increase due to the large aEMGs at the 0% pre-contraction level recorded by three subjects. There were no differences in the aEMG of the SLR between 35 and 50% MVC pre-contraction levels in all conditions. The aEMG of the BGA significantly increased in all conditions when the pre-loads were involved. It consistently increased with the pre-contraction level, although its significant difference between 35 and 50% MVC pre-contraction levels was present in pre-ISO only.

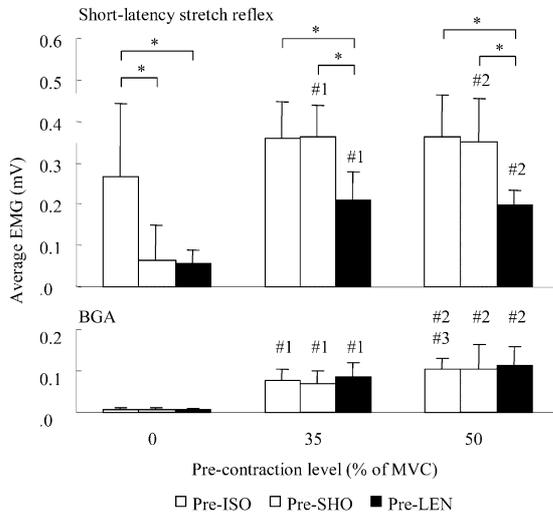


Fig. 3. Effect of the previous muscle activities on average EMGs of SLR and BGA. * Indicates a significant difference between the conditions ($p < 0.05$); #1–3 indicate the significant differences between 0 and 35%, between 0 and 50%, and between 35 and 50% MVC pre-contraction levels in each condition, respectively ($p < 0.05$).

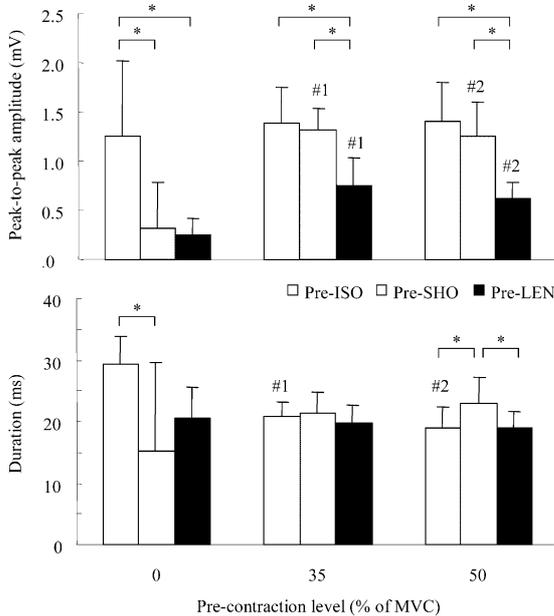


Fig. 4. Effect of the previous muscle activities on SLR peak-to-peak amplitudes and SLR duration. * Indicates a significant difference between the conditions ($p < 0.05$). #1–3 indicate the significant differences between 0 and 35%, between 0 and 50%, and between 35 and 50% MVC pre-contraction levels in each condition, respectively ($p < 0.05$).

3.5. SLR latency

Table 3 shows latencies of the SLR. The SLR latencies were shorter at all pre-contraction levels in pre-LEN compared with the other conditions. Pre-ISO and pre-LEN exhibited constant latencies irrespective of the pre-contraction level. However, pre-SHO displayed a significantly longer latency at 0% MVC pre-contraction level than the other pre-contraction levels, which was significantly longer than that at 0% MVC pre-contraction level in the other conditions.

3.6. SLR peak-to-peak amplitude and SLR duration

Fig. 4 shows peak-to-peak amplitudes and duration of the SLR. The peak-to-peak amplitudes were significantly smaller at 35 and 50% MVC level in pre-LEN than in the other conditions. Pre-ISO showed slightly larger peak-to-peak amplitudes at the 50% MVC level than pre-SHO. The duration was significantly longer at 50% MVC level in pre-SHO than in the other conditions. There were no differences in the duration between pre-ISO and pre-LEN.

The peak-to-peak amplitudes significantly increased when the pre-loads were involved. There were no significant differences in the duration among the pre-contraction levels in pre-SHO and pre-LEN. Pre-ISO displayed the significantly longer duration at the 0% MVC pre-contraction level due to slightly smaller peak-to-peak amplitude and longer duration recorded by three of seven subjects.

3.7. EMG power spectrum

Fig. 5 shows the MF and the MPF during the pre-load period and the contraction period. Pre-SHO showed the lowest MF and MPF during both periods. There were significant differences in the MF and the MPF between pre-SHO and pre-LEN.

There were no differences in the MF and the MPF between 35 and 50% MVC pre-contraction levels in all conditions.

Table 3

SLR latencies (Numerical values show means \pm standard deviations. Since three of seven subjects showed no SLR at 0% MVC level in pre-SHO, their data were not included.)

| Pre-contraction level (% of MVC) | Condition (ms) | | | Difference |
|----------------------------------|----------------|----------------|----------------|---------------|
| | Pre-ISO | Pre-SHO | Pre-LEN | |
| 0 | 41.6 \pm 3.6 | 49.3 \pm 6.5 | 39.7 \pm 3.9 | SHO>ISO, LENO |
| 35 | 42.7 \pm 3.6 | 40.9 \pm 3.5 | 38.3 \pm 3.3 | ISO>LEN |
| 50 | 42.1 \pm 3.7 | 41.7 \pm 3.5 | 38.3 \pm 3.7 | |
| Difference | | 0%>35%, 50% | | |

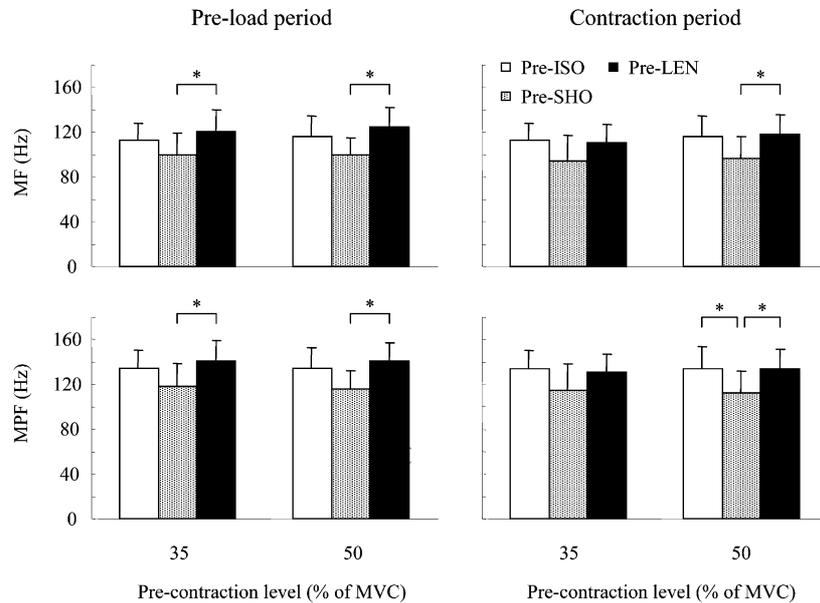


Fig. 5. MF and MPF during pre-load and contraction period. * Indicates a significant difference between the conditions ($p < 0.05$).

4. Discussion

The present study demonstrates that muscle contraction type and the pre-contraction level before a stretch perturbation have considerable influence on the latency, the size and the waveform of the SLR. The results show that: (1) pre-ISO and pre-SHO show an equal SLR area and a different SLR waveform in the active muscle, (2) pre-LEN shows the smallest SLR area of three conditions in the active muscle, (3) pre-LEN shows shorter SLR latencies than the other conditions, (4) pre-SHO shows a longer SLR latency in the relaxed muscle than in the active muscle, and (5) the SLR area is larger in the active muscle than in the relaxed muscle. These observations may be explained by the following mechanisms.

4.1. Differences in MU activity

We observed different frequency components (MF and MPF) of the EMG power spectrum during the pre-load and the contraction period among the three conditions. In particular, there were significant differences between pre-LEN and pre-SHO. It is known that the frequency components are closely related to the muscle fiber conduction velocity [3], which is higher for fast twitch fibers than for slow ones [2]. Consequently, a high number of active fast twitch fibers result in high frequency values of the EMG power spectrum [8,15]. These results may indicate different MU activities during the different contractions before the stretch. A result

shown by Nardone et al. [19] is likely to be in line with the present result of the EMG power spectrum. They have shown preferential recruitment of high threshold fast twitch MUs in eccentric actions and low threshold slow twitch MUs in concentric actions. Therefore, it is possible that the different MU activity before the stretch results in some differences in the SLR among the three conditions.

An interesting finding is that the frequency of the EMG power spectrum during the pre-load period was similar to that during the contraction period. It was higher at a smaller tibio-tarsal joint angle than at a larger one during the pre-load period. A similar phenomenon was observed at the MVC. It has been known that the increase in muscle fiber diameter with decreasing muscle length potentially increases the conduction velocity [13,20,30]. It is possible that the muscle fiber conduction velocity changes with joint angles. Therefore, these results indicate that the MU activity before the stretch may depend on the initial angle of movement, which may affect the SLR modulation.

However, the different MU activity cannot explain the following results: (1) the similar SLR latencies in the active muscle between pre-ISO and pre-SHO, (2) the similar SLR area in the contracting muscle between pre-ISO and pre-SHO, and (3) the smaller SLR area in pre-LEN than in the other conditions. A physiological property of the SOL muscle, i.e. a considerably higher quantity of slow twitch fibers than that of fast twitch fibers, also makes the effect of the MU activity on the SLR dubious. It may indicate that the different fre-

quency components resulted from the methodological effect. It is not to be denied that in phasic contractions its movement may affect the EMG power spectrum [23] because it may change the locations of the electrodes in relation to the innervation zone. Between pre-SHO and pre-LEN there were differences in the tibio-tarsal joint angle of 20° at its maximum and in the direction of muscle contraction. Thus, to what extent the MU activity pattern before the stretch influences the SLR is less clear.

4.2. Differences in muscle spindle sensitivity and α -motor neuron excitability

The most interesting finding in the present study was the similar SLR area between pre-ISO and pre-SHO in the active muscle. This markedly differs from observations in some earlier studies [16,17]. They observed a smaller SLR area after shortening than after isometric contraction in the elbow muscles. It has been known that wide functional differences exist between a distal and proximal muscle [27]. Therefore, the different observation might be partly caused by differences in the muscles on which a stretch was imposed. However, the most obvious difference between the present study and the earlier studies [16,17] is the motor task imposed on the subjects. In the earlier studies, the subjects were requested to track a moving target joint angle during phasic contraction before a stretch. This may imply that the central nervous system (CNS) always has to control its descending command according to afferent inputs from various receptors during the contractions. Since the SLR prevents the CNS from controlling it appropriately, the large SLR seems to be undesirable. On the other hand, no physical targets were set during the contraction period in the present study. During this period, the subjects attempted to maintain an effort needed to maintain a given pre-load torque level during the pre-load period. This motor task might lead to steadier descending commands, which seem to be supported by consistent decreases in the ankle joint torque during shortening and consistent increases during lengthening.

It has been known from the early 1950s that the CNS activates γ -motoneurons during contraction to maintain tension of intrafusal fibers of muscle spindles [12]. In a later experiment Granit [10] has found that not only γ -motoneurons but also α -motoneurons are simultaneously activated by electrical stimulation of the motor cortex and other higher centers (α - γ coactivation). Therefore, the similar SLR area between pre-ISO and pre-SHO may be induced by increased sensitivity of muscle spindles through γ -motoneurons activated by performing the present motor task, which might increase the excitability of the reflex arc at the stretch.

As a part of the present motor task, a given pre-load torque level was maintained for at least 2 s during the

pre-load period. Wilson et al. [33] reported that the discharge rate of muscle spindle afferents increased during an isometric contraction for approximately 5 s and remained elevated after a complete relaxation. In addition, pre-SHO necessitated larger pre-load torque levels than pre-ISO to reach 35 and 50% MVC pre-contraction levels, which simultaneously necessitated larger degrees of effort. Therefore, the events during the pre-load period in pre-SHO might have facilitated the excitability of the α -motoneurons and elevated muscle spindle sensitivity until after the shortening, which might have led to the large SLR areas in pre-SHO.

Although there were no differences in the SLR areas between pre-ISO and pre-SHO in the active muscle, the SLR waveform was different at the 50% MVC pre-contraction level. Pre-SHO showed slightly lower peak-to-peak amplitude and significantly longer duration than pre-ISO at 50% MVC pre-contraction level. During shortening in the active muscle the muscle spindles may be slackened by shortening of the extrafusal fibers. This is closely related to no SLR shown by a half of the subjects and longer SLR latency shown by the remaining ones in the relaxed muscle in pre-SHO. In the relaxed muscle, the muscle spindles seem to be unloaded by shortening of the extrafusal fibers induced by the pedal movement because the activation of the γ -motoneurons is minimal. It is likely that this markedly differs from the muscle spindle condition in pre-ISO. The decreased muscle spindle sensitivity may influence the SLR behavior induced by the stretch after shortening. In fact, Hunt and Kuffler [12] observed a pause in firing of the Ia afferents during shortening when the γ -motoneurons were not stimulated. Slacking of the muscle spindles in pre-SHO is likely to be supported by shorter SLR latencies in pre-LEN than in the other conditions, because the muscle spindles are further stretched by the pedal movement during lengthening. Therefore, the similar area but the different waveform of the SLR between pre-ISO and pre-SHO may be due to a reciprocal effect induced by gamma-motoneuron activity and shortening of the muscle on the muscle spindle sensitivity.

The SLR area was larger in the active muscle than in the relaxed one, whereas it remained unchanged irrespective of the pre-contraction level once the muscle contracted. Toft et al. [29] mentioned that this might be explained by 'saturation' of the motor neuron pool. It may be supported by considerably larger SLR peak-to-peak amplitude than the amplitude recorded during the MVC in the present study. However, the different SLR waveforms between pre-ISO and pre-SHO at the 50% MVC pre-contraction level may suggest that the optimal pre-contraction level exists to efficiently induce the SLR, that is, the large peak-to-peak amplitude and the short duration.

4.3. Differences in afferent inputs from various receptors

Pre-LEN showed significantly smaller SLR area than the other conditions. This is in line with the earlier studies [16,17,31]. In the case of pre-LEN, it is likely that the high threshold fast twitch MUs were recruited and the muscle spindle sensitivity was high due to the pedal movement as shown by shorter SLR latencies and SLR duration. Therefore, the smaller SLR area in pre-LEN may result from smaller pre-load torque levels and degrees of effort than those in the other conditions, because larger ones were unnecessary in pre-LEN for the ankle joint torque to reach 35 and 50% MVC pre-contraction level at the stretch. Another possibility is the inhibitory effects of peripheral inputs on the α -motor neuron excitability. It is possible that the lengthening contraction before the stretch induced the following inhibitory influences: (1) Ib afferents from golgi tendon organs [11], (2) group II afferents from the muscle spindles [21], (3) afferent inputs from joint receptors [24]. Romano and Schieppati [22] observed that H-reflex decreased during lengthening contractions. Therefore, these may lead to a decrease in the α -motoneuron excitability during lengthening, which may result in a decrease in the SLR area in pre-LEN. On the other hand, in pre-SHO the muscle-tendon unit is slacking during shortening more than in pre-LEN due to the pedal movement even if the muscle is contracting. This may provide little inhibitory effect on the α -motoneuron excitability, which is favorable in inducing a large SLR area.

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ORIGINAL PAPERS

II

**Stretch-reflex mechanical response
to varying types of previous muscle activities**

By

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Stretch-reflex mechanical response to varying types of previous muscle activities

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Abstract

This study was designed to examine the effects of varying types of background muscle activity on the stretch-reflex mechanical response. A rapid stretch was applied to the calf muscles after an isometric (pre-ISO), shortening (pre-SHO) and lengthening contraction (pre-LEN) with several pre-contraction levels, respectively. The stretch perturbation was applied with the tibio-tarsal joint angle at 90°. The ankle joint torque elicited by the stretch showed a first peak (non-reflex torque: NRT), a transient drop and a second peak (reflex torque: RT). The muscle activities before the stretch clearly influenced the stretch-reflex mechanical response. The NRT reached the largest peak with the longest duration in pre-ISO. The peak NRT increased with the pre-contraction level in pre-ISO and pre-LEN, whereas it remained unchanged in pre-SHO. The RT responded to the stretch-reflex EMG response most quickly and reached the largest peak in pre-ISO. Pre-ISO generated the mechanical response most efficiently against the size of the stretch-reflex EMG response. Pre-SHO showed lower peak RT than pre-ISO in spite of the similar size of stretch-reflex EMG response. The peak RT was closely related to the peak NRT in all conditions. Consequently, the peak RT also increased with the pre-contraction level in pre-ISO and pre-LEN, whereas it remained unchanged in pre-SHO. In conclusion, a stretch after an isometric contraction evoked a larger stretch-reflex mechanical response more efficiently than that after phasic contractions when a given effort was being maintained. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Human ankle joint; Non-reflex torque; Reflex torque; Degree of effort; Muscle contraction type; Pre-contraction level

1. Introduction

The stretch reflex is a phenomenon normally seen in physical activities such as walking, sprinting and jumping. It represents the activation of α -motoneurons through the discharge of Ia-afferents elicited by a mechanical stretch. Therefore, the stretch reflex may be regarded as a simple neuromuscular behavior. However, it has been shown that the stretch-reflex EMG responses are clearly modulated by muscle contraction types, pre-contraction levels [16,25–27] and imposed motor tasks on a muscle–tendon complex [4,5] before the stretch perturbation.

The stretched muscle–tendon complex typically generates a mechanical response through one or two joints.

It comprises two components: an initial component where force increases immediately after the stretch and a twitchlike component with a longer latency. It has been considered that the former is dominated by inertia of the perturbed segment and intrinsic properties of the perturbed muscle–tendon complex [19] and the latter is mostly due to the stretch-reflex EMG response. Sinkjær et al. [20] have reported that the initial component produced by the ankle extensors changes throughout the gait cycle. Stein and Kearney [21] have shown that the reflex-induced force depends non-linearly on position, voluntary activity, vibration, and amplitude, width and velocity of the stretch. Their findings suggest that the stretch-reflex mechanical response depends on functional requirements to perform a given motor task and the muscle–tendon complex conditions at or during the stretch, which may be influenced by muscle activities before the stretch. However, little is known about influences of muscle contraction types, pre-contraction levels and

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motor tasks before the stretch on the mechanical response.

As voluntary force output is controlled by the degree of effort, so involuntary force output induced by the stretch may also be influenced by it. The degree of effort would be proportional to the activation level of the muscle, which is closely related to the mechanical response. Therefore, it is of great interest to investigate the stretch-reflex mechanical response on the basis of the degree of effort.

This study was designed to examine the effects of contraction types and pre-contraction levels before a stretch perturbation on the stretch-reflex mechanical response under a given degree of effort.

2. Methods

2.1. Subjects

Seven healthy male subjects volunteered in this study. They gave informed consent to the present experimental procedure that had been approved by the University Ethics Commission. Their mean age, height and body weight were 25 years (20–34 years), 1.80 m (1.66–1.91 m) and 76 kg (48–88 kg), respectively.

2.2. Experimental procedure

Details of the experimental method have been described in an earlier paper [16]. Stretch-reflex responses in the right calf muscles of sitting subjects were elicited by a mechanical stretch perturbation using a motor driven ankle ergometer controlled by a digital feedback system [15]. After their right foot was mounted on the rotation pedal, the rotational axis of the ankle joint was aligned with that of the motor torque device. The tibio-tarsal joint was rotated from 80 to 100°. The knee and hip joint angles were, respectively, fixed at $131 \pm 7^\circ$ and $111 \pm 7^\circ$ so that the reflex responses might be elicited consistently at 90° of the tibio-tarsal joint in each subject.

Three movement tasks, which comprised an isometric (pre-ISO), shortening (pre-SHO) and lengthening contraction (pre-LEN) before a stretch perturbation were performed. Each condition consisted of eight trials with different pre-load levels: 0, 10, 20, 30, 40, 50, 60 and 70% torque level of maximum voluntary isometric plantar flexion contraction (MVC). The pre-load torque levels used in pre-SHO, pre-ISO and pre-LEN were normalized to torque levels at the MVC measured at 80, 90 and 100° of the tibio-tarsal joint angle, respectively. The level was defined as 'degree of effort'. A pedal movement consisted of six cycles: preparatory, pre-load, contraction, stretch perturbation, static and recovery period. Subjects were requested to activate their calf muscles

and maintain a given pre-load torque level during the pre-load period (2910 ms) with the help of visual feedback shown on an oscilloscope. The pre-load torque level was maintained for about 2 s at 80° in pre-SHO, at 90° in pre-ISO and at 100° in pre-LEN. After the pre-load period, the contraction period commenced. The pedal rotated from 80 to 90° in pre-SHO and from 100 to 90° in pre-LEN over 423 ms. In pre-ISO it remained still. This period included a gradual increase in angular velocity over 180 ms at its beginning and a constant angular velocity of 30°/s over 243 ms. The gradual increase in angular velocity was used to prevent the stretch-reflex responses at the beginning of the contraction period. A stretch perturbation was applied when the tibio-tarsal joint angle reached 90°. The stretch was 4° over 25 ms. After the stretch the pedal was stopped for 308 ms (static period). The subjects were requested to maintain a given effort needed to maintain the pre-load torque level during the pre-load period from the contraction period to the static period. After the static period, the pedal gradually returned to the initial position for 4334 ms. The subjects relaxed their muscles fully during this period.

2.3. Electromyography

Electromyographic activity (EMG) was obtained telemetrically from the right soleus (SOL), gastrocnemius lateralis (GL), gastrocnemius medialis (GM) and tibialis anterior (TA) muscle. Bipolar silver chloride miniature skin electrodes (Beckman 650437, USA; 20 mm inter-electrode distance) were aligned parallel with the fibers halfway between the estimated center of the innervation zone and the distal end of muscles. In the case of SOL, they were placed approximately 6 cm above the superior aspect of calcaneus. Before electrode application, each site was shaved, abraded and cleansed with alcohol to reduce interelectrode impedance (5 k Ω). EMG signals were amplified by 200 times with a FM-microvolt amplifier (Glonner Electric GmbH, Germany; bandwidth 10–360 Hz, –3 dB).

2.4. Data analysis

EMG signals, the ankle joint torque and the angular displacement sampled at 1 kHz (Coda, Dataq Instruments Inc., USA) were simultaneously recorded. The EMG signals were high-pass filtered at cutoff frequency of 10 Hz and full-wave rectified. Thereafter, they were averaged over a period of 2000 ms before and 350 ms after the onset of stretch perturbation in each condition (10 repetitions). Short-latency stretch reflex (SLR) and long-latency stretch reflex (LLR) were identified. Average EMG (aEMG) of the SLR and from the stretch onset to the SLR onset as background activity (BGA) was cal-

culated. The aEMG of the BGA was subtracted from that of the SLR, which was defined as SLR area.

The recorded ankle joint torque was filtered at 75 Hz with a Butterworth type 4th-order zero-lag low-pass filter to remove the high frequency noise. Since the ankle joint torque involved an inertial reaction torque induced by the pedal movement, it was subtracted from the ankle joint torque. In general, an imposed stretch on a muscle evokes an immediate increase in the torque, a transient drop in the torque and a subsequent re-increase in the torque [2,3,19]. In the present study the first and the second increases in the torque were defined as non-reflex torque (NRT) and reflex torque (RT), respectively. Amplitude and duration of the torque were calculated in the following phases: from the stretch onset to the first peak (P1), from the first peak to the subsequent local minimum torque (LMT) (P2), from the LMT to the second peak (P3), and from the stretch onset to the second peak (P4). Each phase is illustrated in the top left trace of Figs. 2 and 3. The P1 and P4 amplitude represent the peak NRT and the peak RT, respectively. When an isolated single muscle fiber is stretched during tetanus, it generates no RT, although force enhancement may be induced after the stretch [6,7]. Therefore, it can be considered that the phase P3 was induced by the stretch-reflex EMG response. It was impossible to determine a precise start of the RT because it was related to two processes, that is, decay in intrinsic muscle stiffness after the stretch [10,18] and the reflex-induced force. However, in the present study the LMT was defined as the beginning of RT since the torque began to re-increase by the reflex-induced force at the LMT. The difference in time between the SLR onset and the LMT was defined as electromechanical delay (EMD). This definition is illustrated in the top left figure in Fig. 6. A ratio of the P3 amplitude to the SLR area was also calculated as electromechanical efficiency (EME). Relationships between the P1, P2, P3 and P4 amplitude were analyzed with a linear regression for each condition in each subject.

The ankle joint torque at the stretch was expressed as percentage of MVC at 90° to eliminate the difference in the MVC among the subjects, which was defined as pre-contraction level. Some trials with equal pre-contraction levels among pre-ISO, pre-SHO and pre-LEN were extracted from eight trials performed by the subjects in each condition. This was to compare phase P1, P2, P3 and P4 with the equal torque levels at the stretch among three conditions. Consequently, they were compared at 0, 35 and 50% MVC pre-contraction level.

Absolute work was calculated in the contraction period and in the stretch perturbation period. Ratios of the absolute work performed in the stretch perturbation period to that performed in the contraction period (W_{abs} -ratio) were calculated at 35 and 50% MVC pre-contraction level. The W_{abs} -ratio was not calculated at 0% MVC

pre-contraction level since any work performed at its pre-contraction level was not actively generated by muscles. No work was performed during the contraction period in pre-ISO due to the static pedal movement. Therefore, the W_{abs} -ratio could not be calculated in pre-ISO.

Effects of the pre-contraction level on each phase of the torque were compared among pre-ISO, pre-SHO and pre-LEN. The amplitudes of the torque were plotted against the pre-contraction levels for each condition in each subject in order to calculate a correlation coefficient and a regression coefficient with a linear regression analysis. Since the regression coefficient is the slope of the regression line, it represents the increasing rate (*I*-rate) of the torque with the pre-contraction level. The subjects performed eight kinds of trials in each condition. Therefore, its relationships were based on eight data points.

2.5. Statistical analysis

A two-way analysis of variance (ANOVA) was used to test all variables for the significant differences among three pre-contraction levels and three conditions. When the result of the ANOVA was significant ($p < 0.05$), Fisher's post hoc test was used to assess the source of difference ($p < 0.05$).

3. Results

3.1. The ankle joint torque before a stretch perturbation

The ankle joint torque prior to a stretch differed among three conditions. Pre-SHO was characterized by the largest pre-load torque level and degree of effort of the three conditions in the pre-load period, and a rapid decrease in the torque in the contraction period. The torque decreased by 25.8 ± 17.7 N m at 35% MVC pre-contraction level and 31.0 ± 11.7 N m at 50% MVC pre-contraction level during the contraction period. On the other hand, pre-LEN showed the smallest pre-load torque level and degree of effort in the pre-load period, and a sharp increase in the torque in the contraction period. The torque increased by 26.4 ± 11.4 N m at 35% MVC pre-contraction level and 28.5 ± 10.1 N m at 50% MVC pre-contraction level during the contraction period. The degrees of effort required in pre-SHO, pre-ISO and pre-LEN were 48.6 ± 6.9 , 34.3 ± 5.3 and $15.7 \pm 5.3\%$ at 35% MVC pre-contraction level, and 68.6 ± 3.8 , 52.9 ± 4.9 and $32.9 \pm 9.5\%$ at 50% MVC pre-contraction level, respectively. The absolute external work performed in the contraction period was smaller in pre-LEN than pre-SHO (5.6 ± 3.6 vs. 9.1 ± 4.6 J at 35% MVC pre-contraction

level and 8.9 ± 4.9 vs. 12.9 ± 6.4 J at 50% MVC pre-contraction level).

3.2. Pattern of the ankle joint torque induced by a stretch perturbation

Fig. 1 shows the stretch-reflex EMG responses and the corresponding ankle joint torque patterns at 35% MVC pre-contraction level. A typical variation of the torque showed a sharp increase immediately after a stretch, the first peak (the peak NRT), a transient drop, a subsequent increase and the second peak (the peak RT). However, two of seven subjects did not show the transient drop in pre-ISO once pre-loads were involved. Their MVCs were 223.4 and 207.2 N m, respectively, which were more than twice as large as the mean value of the MVC shown by the remaining subjects (85.7 ± 14.1 N m). Mean values of their peak RT at 0% MVC pre-contraction level were 16.7 ± 3.1 N m in pre-ISO, 7.7 ± 5.3 N m

in pre-SHO, 4.7 ± 0.5 N m in pre-LEN, which were about three times as large as the mean values shown by the remaining subjects.

Since two of seven subjects did not show the typical variation of the ankle joint torque, their data was not included in the following results.

3.3. Duration of the ankle joint torque in each phase

3.3.1. Phase P1

The P1 duration was significantly longer at all pre-contraction levels in pre-ISO than the other conditions (left panel in Fig. 2). Pre-SHO showed significantly longer P1 duration at 0 and 35% MVC level than pre-LEN. However, its difference decreased with the pre-contraction level. In all conditions the P1 duration significantly lengthened when pre-loads were involved.

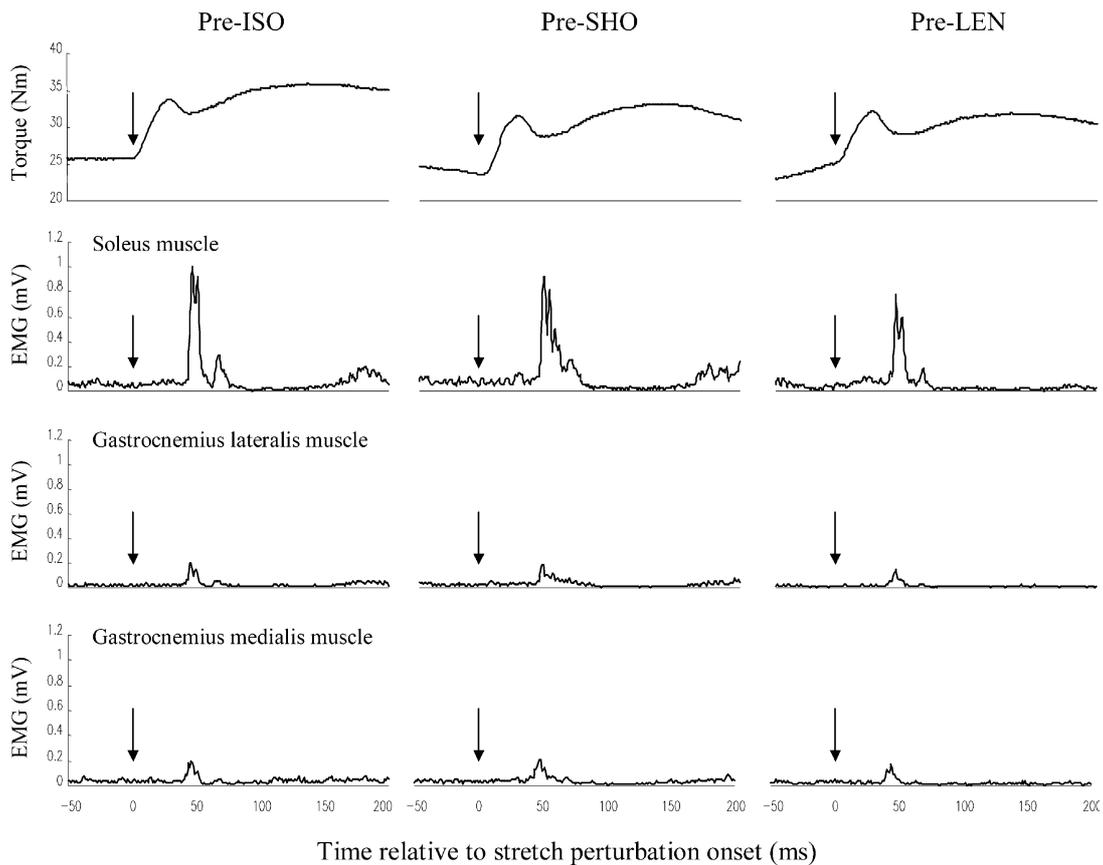


Fig. 1. Ankle joint torque and rectified EMG activities of soleus, gastrocnemius lateralis and gastrocnemius medialis muscle at 35% MVC pre-contraction level recorded in one representative subject. Arrows represent onsets of a stretch perturbation.

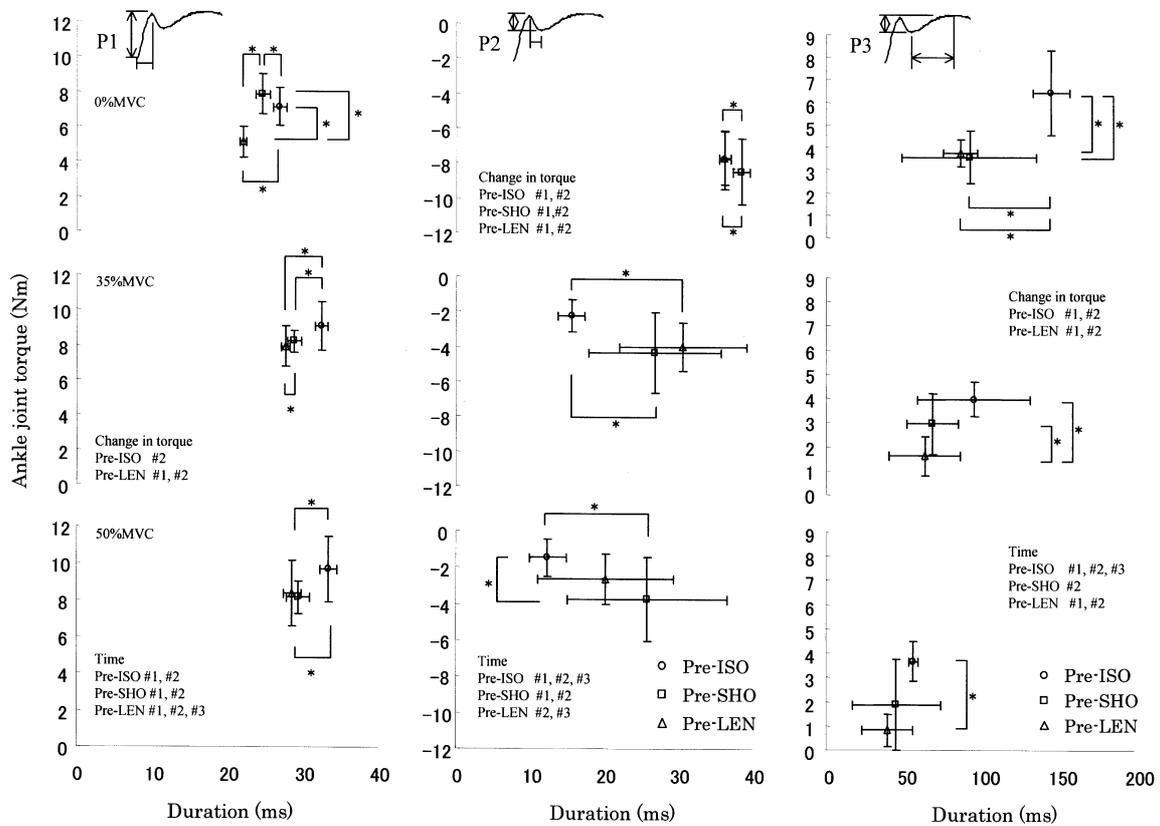


Fig. 2. Amplitudes and duration of ankle joint torque in phase P1, P2 and P3. These data were obtained from 5 subjects who represented the peak non-reflex torque in all conditions. * Indicates a significant difference between the conditions ($p < 0.05$); #1, #2 and #3 indicate significant differences between 0 and 35%, between 0 and 50%, and between 35 and 50% MVC level, respectively ($p < 0.05$).

3.3.2. Phase P2

The P2 duration significantly shortened when pre-loads were involved (middle panel in Fig. 2). In particular, it was dramatic in pre-ISO. Consequently, pre-ISO showed a significantly shorter P2 duration at 35% MVC level than the other conditions, and at 50% MVC level than pre-SHO. The P2 duration significantly shortened from 35 to 50% MVC pre-contraction level in pre-ISO and pre-LEN. However, it remained unchanged in pre-SHO. Pre-SHO showed a significantly longer P2 duration than the other conditions at 0% MVC pre-contraction level.

3.3.3. Phase P3

The P3 duration showed significant differences between pre-ISO and the other conditions at 0% MVC pre-contraction level (right panel in Fig. 2). Its differences gradually decreased with the pre-contraction level. The P3 duration significantly shortened in all conditions when pre-loads were involved.

3.3.4. Phase P4

The P4 duration was significantly longer at 0% MVC level in pre-ISO than the other conditions (Fig. 3). Its significant difference disappeared once pre-loads were involved. The P3 duration significantly shortened with the pre-contraction level in all conditions.

3.4. Amplitude of the ankle joint torque in each phase

3.4.1. Phase P1

The P1 amplitude was significantly smaller at 0% MVC level in pre-LEN than that in the other conditions (left panel in Fig. 2). Its significant differences disappeared once pre-loads were involved, although pre-ISO showed slightly larger amplitudes than the other conditions.

3.4.2. Phase P2

There was a significant difference in the P2 amplitude only at 50% MVC level between pre-ISO and pre-SHO

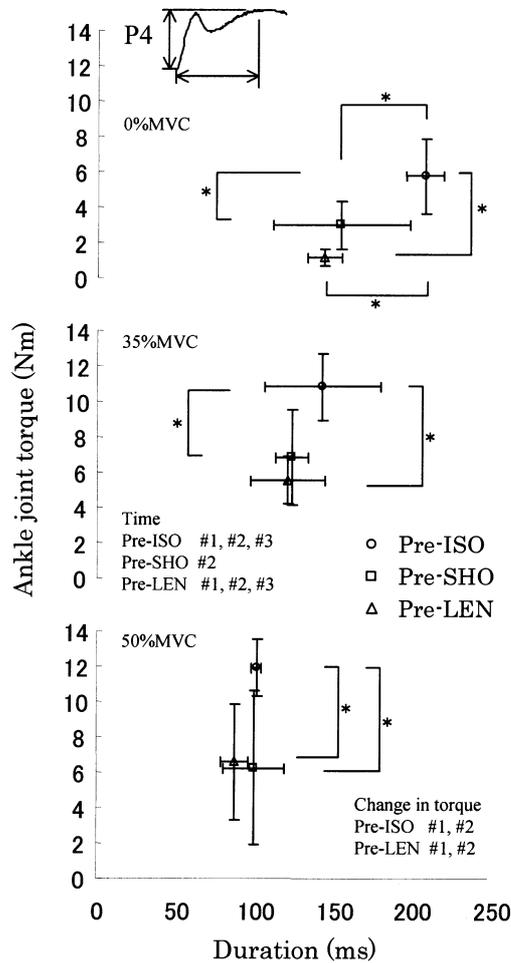


Fig. 3. Amplitudes and duration of ankle joint torque in phase P4. These data were obtained from 5 subjects who represented the peak non-reflex torque in all conditions.

although pre-ISO showed slightly smaller amplitudes at 35 and 50% MVC pre-contraction level than the other conditions (middle panel in Fig. 2).

3.4.3. Phase P3

Pre-ISO showed significantly larger P3 amplitude at all pre-contraction levels than pre-LEN, and at 0% MVC pre-contraction level than pre-SHO (right panel in Fig. 2). There was a significant difference at 35% MVC pre-contraction level between pre-SHO and pre-LEN.

3.4.4. Phase P4

The P4 amplitude was significantly larger at all pre-contraction level in pre-ISO than that in the other conditions (Fig. 3). There were no differences between pre-SHO and pre-LEN.

3.5. Increasing rate of the ankle joint torque with the pre-contraction level

3.5.1. Phase P1

The P1 amplitude gradually increased with the pre-contraction level in pre-ISO and in pre-LEN (top panel in Fig. 4). However, its increase was significantly lower in pre-SHO than in the other conditions.

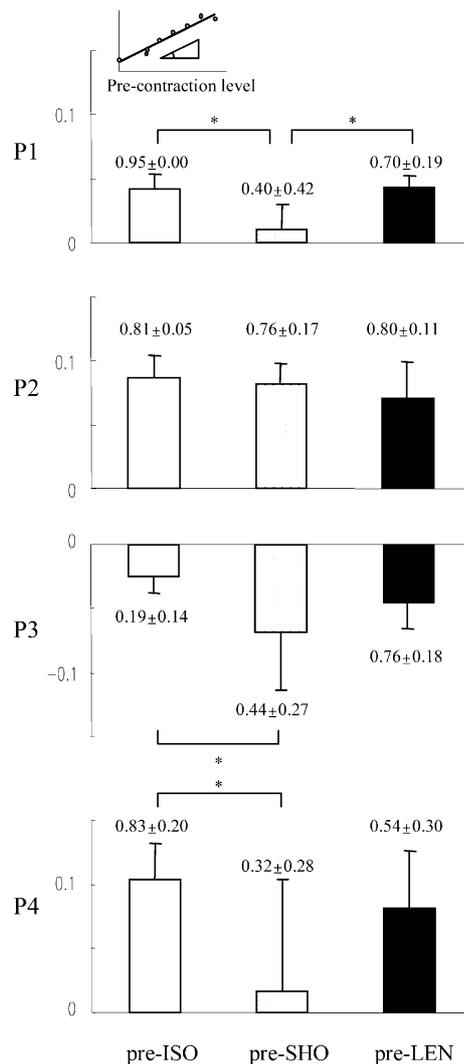


Fig. 4. Linear regression coefficients between all pre-contraction levels measured and amplitudes of torque (A), and increment rate (B) in phases P1–P4. Numerals over bars represent R-squares of the linear regressions (means ± SD). * Indicates a significant difference between the conditions ($p < 0.05$).

3.5.2. Phase P2

The *I*-rates of the P2 amplitude were positive in all conditions (second panel from the top in Fig. 4). Since the P2 amplitudes were negative, the *I*-rates indicate that the negative values decreased with the pre-contraction level. There were no significant differences in the *I*-rate among three conditions.

3.5.3. Phase P3

The P3 amplitude decreased with the pre-contraction level in pre-SHO and pre-LEN (third panel from the top in Fig. 4). However, it was little related with the pre-contraction level in pre-ISO as shown by a low *R*-square ($R^2=0.19\pm 0.14$). Consequently, there was a significant difference in the *I*-rate between pre-ISO and pre-SHO.

3.5.4. Phase P4

The P4 amplitude increased with the pre-contraction level in pre-ISO and in pre-LEN (bottom panel in Fig. 4). On the other hand, it remained unchanged in pre-SHO.

3.6. Absolute work performed during a stretch

Fig. 5 shows the W_{abs} -ratio at 35 and 50% MVC pre-contraction level. The W_{abs} -ratios were significantly larger at both pre-contraction levels in pre-LEN than in pre-SHO.

3.7. EMD of the RT

The EMDs were shown in Fig. 6. There was no difference in the EMD at 0% MVC pre-contraction level among three conditions. Once pre-loads were, however,

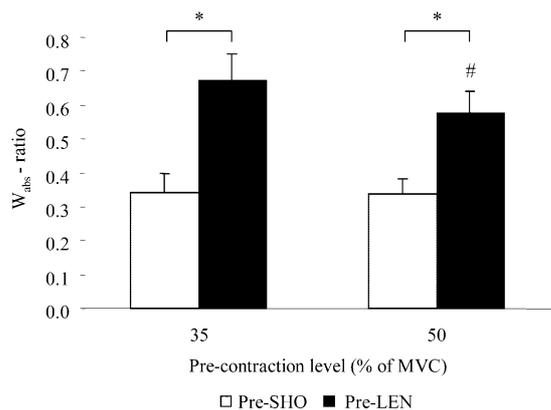


Fig. 5. Ratios of absolute work performed in stretch perturbation period to that performed in contraction period (W_{abs} -ratio) in the active muscle. These data were obtained from 5 subjects who represented the peak non-reflex torque in all conditions. * Indicates a significant difference between the conditions ($p<0.05$); # indicate significant differences between 35% and 50% MVC level ($p<0.05$).

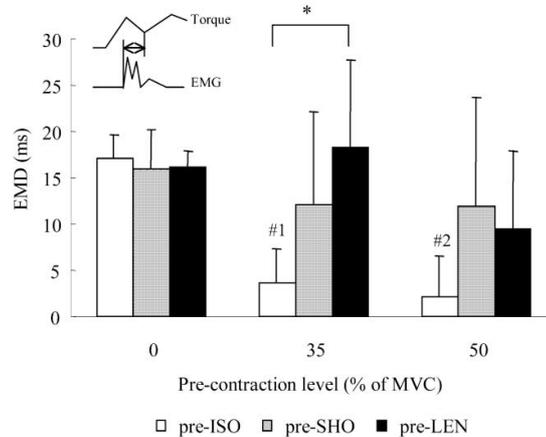


Fig. 6. Electromechanical delay (EMD) between SLR burst onset and reflex torque onset. These data were obtained from 5 subjects who represented the peak non-reflex torque in all conditions. * Indicates a significant difference between the conditions ($p<0.05$); #1 and #2 indicate significant differences between 0% and 35% and between 0% and 50%, respectively.

involved, the EMD dramatically decreased in pre-ISO mainly due to shortened P2 duration. Such dramatic decrease in the EMD was not shown in the other conditions. Consequently, pre-ISO showed shorter EMDs than the other conditions, although there were no significant differences due to large SDs in pre-SHO and pre-LEN.

3.8. EME of the RT

Fig. 7 shows the EME at 35 and 50% MVC pre-contraction level. The EME at 0% MVC pre-contraction

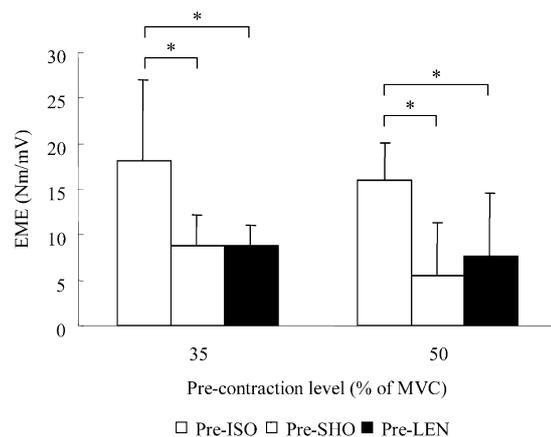


Fig. 7. Ratios of P3 amplitude to SLR area (EME) in the active muscle. These data were obtained from 5 subjects who represented the peak non-reflex torque in all conditions. * Indicates a significant difference between the conditions ($p<0.05$).

level was more than 50 N m/mV due to a fairly small SLR in every condition. There are no significant differences in the EME at 0% MVC pre-contraction level among three conditions. Pre-ISO showed significantly larger EME than the other conditions at 35 and 50% MVC pre-contraction level. There were no differences in the EME at both pre-contraction levels between pre-SHO and pre-LEN.

3.9. Relationships between P1, P2, P3 and P4 amplitude

Table 1 shows relationships between the P1 and the P2 amplitude and between the P1 and the P4 amplitude. There were no significant relationships between the other amplitudes. The P1 amplitude was closely related to the P2 and P4 amplitude in all conditions. However, the *R*-squares were significantly lower in pre-SHO than the other conditions.

4. Discussion

The results in the present study show that: (1) the different types of muscle contractions before a stretch alter the stretch-reflex mechanical response, (2) the different pre-contraction levels alter the mechanical response, which depends on the types of the muscle contractions before the stretch, and (3) the RT is closely related to the NRT in all conditions.

A stretch after an isometric contraction generated larger NRT with longer duration and larger RT more quickly and more efficiently after the SLR burst than that after phasic contractions in the active muscle, which increased with the pre-contraction level. These may be related to the motor unit (MU) activity before the stretch. Higher frequency components of EMG power spectrum have been observed during the isometric contraction and during lengthening than during shortening [16]. However, shorter EMDs and higher EMEs in pre-ISO than in pre-LEN cannot be explained by the different MU activities. Therefore, these phenomena are likely to be influenced considerably by conditions of the muscle–tendon complex induced by muscle activities before the stretch.

It has been suggested that force development immedi-

ately after a stretch extended during tetanic activity is due to increased strain on the attached cross-bridges in combination with a slight increase in the number of attached bridges [11,22]. This force development corresponds to the NRT in the present study. Therefore, the NRT behavior in pre-ISO may indicate a better condition of the cross-bridges to generate the force after the isometric contraction than after the phasic contractions in the active muscle. This would be supported by the NRT behavior in the relaxed muscle, because the NRT was larger after shortening and smaller after lengthening than that after an isometric contraction in the relaxed muscle in which the activation level of the muscle is minimum [23]. Similarly, the condition of the cross-bridges may be closely related to the similar *I*-rates but the different NRT behavior between pre-ISO and pre-LEN. Since elasticity of the cross-bridges utilized during lengthening [13,17] contributes to generate force efficiently, it might lead to the increased NRM with the pre-contraction level in pre-LEN. On the other hand, a severe strain imposed on the cross-bridges by the stretch following lengthening might exceed the elastic limits, which might result in the lower peak and the shorter duration of the NRT in pre-LEN than in pre-ISO.

Before the stretch, the ankle joint torque was consistently decreasing during shortening and increasing during lengthening. Because of a constant angular velocity, this indicates decreasing and increasing ankle joint stiffness during shortening and lengthening, respectively, which is closely related to the Achilles tendon stiffness. Also during an isometric contraction compliant tendon stiffness is increased by the muscle contraction [9]. Since huge Achilles tendon force is generated during a stretch [14], the Achilles tendon condition induced by the muscle activities before the stretch may influence the NRT behavior. The positive *I*-rates in pre-ISO and in pre-LEN would corroborate it because the Achilles tendon stiffness also increases with the pre-contraction level. Fellows and Thilmann [8] have observed longer stretch-reflex latencies at more plantar flexed positions in relaxed ankle extensors and suggested that it results from properties of a compliant tendon through which the joint movement is transmitted to a muscle. However, there were no differences in SLR latency between pre-ISO and pre-SHO in the active muscle [16]. This observation indicates that the stretch was transmitted to the muscle in pre-SHO as well as in pre-ISO. It appears to contradict the lower Achilles tendon stiffness at the stretch in pre-SHO. Thus, the extent to which the tendon condition influences the NRT behavior is less clear. Further studies are necessary to elucidate it.

The RT, which is represented as the P3 and P4 amplitude, showed larger differences between pre-ISO and the other conditions than the NRT. The NRT is directly related to the muscle–tendon complex condition before the stretch and inertia of the perturbed

Table 1
Correlation coefficients between amplitudes of torque

| Amplitude | Pre-ISO | Pre-SHO | Pre-LEN | Difference |
|-----------|--------------|--------------|--------------|-----------------|
| P1–P2 | –0.966±0.007 | –0.543±0.353 | –0.934±0.114 | SHO>ISO, LEN |
| P1–P4 | 0.916±0.077 | 0.743±0.119 | 0.912±0.113 | ISO, LEN>SHO |

segment because it appears immediately after the stretch and before the SLR burst. On the other hand, the RT is likely to depend on the muscle condition after the stretch and the reflex gain since there are no kinematic differences among three conditions during the static period. It has been reported that irregularity of filament overlap is seen in tetanized muscle fibers and fibers stretched during tetanus [1,7]. A relationship between its irregularity and force generated is less clear, especially *in vivo*. However, it is likely that greater filament overlaps generate larger force and higher regularity of the filament overlap generates the force more efficiently. If the stretch following the phasic contractions induces less regularity of the filament overlap, it may be able to explain the longer EMDs and the lower EMEs in pre-SHO and in pre-LEN than in pre-ISO. The ankle joint torque results not only from the SOL but also from all muscle activities at the ankle. However, it has been reported that the SOL generates above two-thirds of the MVC in sitting position [24]. In addition, the GL, GM and TA activity were substantially smaller than the SOL activity. The LLR in the soleus muscle was also substantially smaller than the SLR. Therefore, it may be safely assumed that the RT depends mainly on the SLR in the SOL. The strongly positive relationship between the peak NRT and the peak RT suggests that the mechanical response to the stretch-reflex EMG response depends mainly on the muscle–tendon complex condition immediately after the stretch.

The similar *I*-rates but the lower amplitudes of P2 in pre-ISO than in the other conditions may corroborate that the stretch following the phasic contractions induces less regularity of the filament overlap. It has been assumed that a fall in tension that corresponds to the P2 amplitude is caused by exceeding short-range elastic limit of intrinsic muscle stiffness and decline in intrinsic muscle viscosity as stretch velocity decreased [10,18]. No P2 amplitudes in the active muscle in pre-ISO shown by two subjects who developed the large MVC indicate that the P2 represents the decay in passive force of the visco-elastic components. It is likely that their strong passive and reflex-induced force did not allow the transient drop in the torque. It is also supported by a strongly negative relationship between the peak NRT and the P2 amplitude in every condition. On the other hand, the condition of the filament overlap is likely to be closely related to the P2 amplitude. The higher regularity would result in the quicker and more efficient mechanical response to neural inputs to the muscle as shown by the shorter EMD and the higher EME.

Pre-ISO showed steeper SLR waveforms, i.e. the large amplitudes and short duration, in the active muscle [16] than the other conditions. This may indicate higher excitability of α -motoneurons and higher rate of MU synchronization. Therefore, the different SLR waveform can

partly explain why pre-SHO showed smaller RTs and lower EMEs than pre-ISO in the active muscle in spite of the similar SLR size.

Pre-SHO needed larger pre-load torque levels and degrees of effort for the stretch to be applied at the same torque levels as those in the other conditions. As a result, the RT did not exceed the pre-load torque levels only in pre-SHO. When an electrical stimulus is delivered to a muscle in a voluntary contraction, the size of the superimposed twitch falls off linearly with increasing tension [12]. This is unlikely to be directly applicable to the present results because the present stimulus is a mechanical stretch. However, the negative *I*-rates of the P3 amplitude may be in line with this observation. Therefore, it is possible that the larger pre-load torque level leads to the lower W_{abs} -ratio, lower EME and lower RT. This may explain why the peak RT remained unchanged only in pre-SHO irrespective of the pre-contraction level.

In conclusion, a stretch after an isometric contraction generated a larger stretch-reflex mechanical response more efficiently than that after phasic contractions when a given effort was being maintained. It is likely that it is closely related to the muscle–tendon complex condition induced by muscle activities before the stretch as well as neural inputs to the muscle.

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ORIGINAL PAPERS

III

The effects of effort levels and background EMG activities on short-latency stretch reflex modulation to varying types of soleus muscle contraction

By

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Submitted for publication

The effects of effort levels and background EMG activities on short-latency stretch reflex modulation to varying types of soleus muscle contraction

Short title: Short-latency stretch reflex modulation

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ABSTRACT

This study was designed to examine the effect of various types of muscle contractions before a stretch perturbation on the short-latency stretch reflex (SLR) in the soleus muscle (SOL) at the same levels of effort and at matched electromyographic (EMG) activity levels. A mechanical stretch perturbation was applied at a ninety degree tibio-tarsal joint angle after the calf muscles performed an isometric (pre-ISO), shortening (pre-SHO) and lengthening contraction (pre-LEN) in a sitting position. The subjects seated on an ankle ergometer chair developed and maintained a given ankle joint torque, which consisted of 0, 10, 20, 30, 40, 50, 60 and 70 % torque levels of maximum voluntary isometric plantar flexion contraction, at 80° in pre-SHO, 90° in pre-ISO and 100° in pre-LEN for about 2 s before the isometric or phasic contractions started. After the contractions started, they were asked to maintain levels of effort as needed to maintain the target torque levels until the end of the stretch. The subjects relaxed their muscles fully after the stretch. This chain of processes was consecutively repeated 10 times. Electromyographic signals obtained from the SOL were averaged after they were high-pass filtered and full-wave rectified. Three major findings on the background muscle contractions resulted: 1) there were no differences in the SLR area in the active muscle between pre-ISO and pre-SHO. This differed markedly from observations in the earlier studies where tracking movement was used as a motor task. 2) The SLR waveform was steeper in pre-ISO than in pre-SHO in the active muscle. 3) The SLR area was significantly smaller in pre-LEN than in the other conditions at the same levels of effort in the active muscle. These findings were observed also at matched EMG activity levels. Two major findings on the levels of effort resulted: 1) the SLR area was larger and the SLR waveform was steeper in the active muscle than in the relaxed muscle in all conditions. 2) The SLR area and waveform were independent of the level of effort once the muscles were activated. This differed markedly from the background EMG activity in proportion to the level of effort. These findings suggest that 1) the SLR is modulated by the type of muscle contraction before a stretch, 2) the SLR modulation is influenced by the motor task imposed on subjects, and 3) the pattern of the SLR modulation is similar once the muscles are activated.

Key words: Stretch reflex; Human soleus muscle; Level of effort; Type of muscle contraction; Electromyography

INTRODUCTION

It has been demonstrated that the stretch reflex is modulated by the muscle activities before a stretch. Many human studies have shown that long-latency reflex (LLR) is reduced during non-isometric contractions in the hand (Wallace and Miles 1998), the forearm muscle (Bawa and Sinkjær 1999) and the elbow muscles (Nakazawa et al. 1997, 1998) when subjects tracked a given EMG activity or movement. Since the LLR are mediated through cerebral, possibly cortical, pathways in the upper limbs (Goodin et al. 1990; Matthews et al. 1990; Capaday et al. 1991), it seems reasonable to assume that the LLR was controlled by the central nervous system (CNS) (Stein and Capaday, 1988) to proceed with the muscle contractions being performed before the stretch appropriately. In fact, Doemges and Rack (1992a, 1992b) have observed that modulation of the LLR depends on the motor task imposed on subjects using the hand muscle.

The short-latency reflex (SLR) agreed to reflect the Ia mediated monosynaptic reflex is also modulated by the background muscle activities. Sinkjær et al. (1996) and Kearney et al. (1999) have shown that the SLR in the SOL is modulated throughout the gait cycle during walking. H-reflex studies have also shown that the H-reflex is modulated during walking (Capaday and Stein 1986; Crenna and Frigo 1987; Simonsen and Dyhre-Poulsen 1999), running (Capaday and Stein 1987). It is difficult to interpret the SLR behavior from the H-reflex behavior strictly because the electrical stimulation applied in the H-reflex measurement bypasses the fusimotor system and mechanical stretch on the muscle spindles by which the SLR can be modified. However, these findings suggest that the SLR is modulated in a phase-dependent manner so that it is utilized effectively during a given movement since the H-reflex can provide information on the excitability of the neural pathway related to the SLR.

Some studies have shown that the SLR is reduced during non-isometric contractions in the elbow (Nakazawa et al. 1997, 1998) and forearm muscles (Bawa and Sinkjær 1999) when a given movement is tracked. The background muscle contractions also seem to modulate the SLR. When subjects were not, however, tracking a given movement but maintaining a given level of effort, the SLR elicited after shortening was similar to that elicited after an isometric contraction in the soleus muscle (SOL) (Ogiso et al. 2001). This finding differs markedly from the other findings (Nakazawa et al. 1997, 1998; Bawa and Sinkjær 1999). It might be partly related to a difference in the examined muscles

to which the stretch was applied as shown by Thilmann and Schwarz (1991). However, the difference is likely to depend mainly on the motor task imposed on the subjects. Precisely tracking a given movement, joint torque or EMG activity during phasic contractions needs to make the CNS control the descending commands on the afferent information without a break. On the other hand, maintaining the levels of effort would make the CNS control steadier since it does not need to track the physical targets. The CNS is likely to be modulating the SLR in a task-dependent manner. A finding that the H-reflex modulation during walking differs from that during running (Capaday and Stein 1987; Simonsen and Dyhre-Poulsen 1999) would also support it.

We have already compared the SLR elicited by a stretch at matched ankle joint torque after an isometric, shortening and lengthening contractions while the subjects were maintaining a given level of effort (Ogiso et al. 2002). However, matching the ankle joint torque led to the different levels of effort and background electromyographic (EMG) activities at the onset of stretch. Therefore, the present study was designed to examine a relation between the SLR modulation and the background muscle contractions at the same levels of effort and at matched EMG activity levels while the subjects were maintaining a given level of effort. Since maintaining a given effort level is likely to minimize the effects of the CNS on the SLR modulation, it may be able to clarify the effects of the afferent inputs induced by the background muscle contractions before the stretch on the SLR modulation.

MATERIAL AND METHODS

Subjects

Seven healthy male subjects (age, 25.3 ± 4.9 years; body height, 1.80 ± 0.08 m; body mass, 72.0 ± 12.2 kg) volunteered for this study. They gave informed consent to the present experimental procedure that had been approved by the University Ethics Committee.

Apparatus and position

Stretch reflex responses in the calf muscle were elicited by a mechanical stretch perturbation using a motor driven ankle ergometer controlled by a digital feed-back system (Nicol et al., 1996), which was similar to that used by

Gollhofer & Schmidtbleicher (1989). The torque and angular displacement around the rotational axis of the motor were measured with a piezoelectric crystal transducer (Kistler, Switzerland). After the subjects sat in the ergometer chair, their right thigh was clamped with a soft cuff and their right foot was tightly mounted on the rotation platform so that the rotational axis of the ankle joint was aligned with that of the motor torque device. The knee and hip joint angles were fixed (131 ± 7 deg and 111 ± 7 deg, respectively) so that the stretch reflex responses were elicited as consistently as possible at 90 deg of the tibio-tarsal joint angle.

Experimental procedure and motor tasks

A mechanical stretch perturbation was applied to the calf muscle immediately after the muscle performed an isometric (pre-ISO), shortening (pre-SHO) and lengthening contraction (pre-LEN)(top panel in Fig.1). To begin with, the platform rotated from 90 deg of the tibio-tarsal joint angle to the initial positions, which were 80 deg in pre-SHO, 90 deg in pre-ISO and 100 deg in pre-LEN, over 3095 ms (preparatory period). The subjects relaxed their muscles fully during this period. After the platform reached the position, the subjects were asked to activate their calf muscles and maintain a given ankle joint torque level over 2910 ms (pre-load period). The target torque level and torque being exerted by the subjects were displayed on an oscilloscope as visual feedback. On average, the subjects maintained the target torque level for about 2000 ms of 2910 ms because it took some time to reach the target levels. The target torque levels were set to a 0, 10, 20, 30, 40, 50, 60 and 70% level according to maximum voluntary isometric plantar flexion contraction (MVC) at 80 deg in pre-SHO, at 90 deg in pre-ISO and at 100 deg in pre-LEN. The MVCs were randomly measured three times beforehand (Table 1). Consequently, the subjects performed eight trials for every condition. Thereafter, the contraction period lasted for 423 ms. The platform rotated from 80 deg to 90 deg in pre-SHO and from 100 deg to 90 deg in pre-LEN. In pre-ISO it remained still. For the initial 2.7 deg of this period the angular velocity gradually increased to prevent any stretch reflex responses. After 180 ms the angular velocity reached 30 deg/s, which was constantly kept over 243 ms. During this period, the subjects were asked not to maintain the target torque levels required during the pre-load period but to maintain the levels of effort (effort level) as needed to maintain them. The effort level was represented as the percentage of the MVC torque level (%MVC) because it corresponds with the target torque level set according

to the MVC. Maintaining the target levels for about 2 s in pre-load period was enough for the subjects to grasp the effort levels needed to perform it. Therefore, the ankle joint torque consistently decreased in pre-SHO and increased in pre-LEN (second panel from top in Fig.1). The stretch perturbation of 4 deg over 25 ms was applied when the tibio-tarsal joint angle reached 90 deg (stretch perturbation period). The subjects were asked not to resist the stretch but to constantly maintain the same effort level as that made during the pre-load and contraction period until the end of the stretch. After the stretch the platform was stopped at 86 deg for 308 ms (static period) in order to make an equal condition among three conditions. Finally, the platform gradually returned to the position of 90 deg over 1239 ms (recovery period). The subjects fully relaxed their muscles again. A whole platform movement lasted for 8 sec, which was consecutively repeated 10 times. The order of each trial was randomized. There were intervals of at least 3 minutes between the trials. Skin temperature on the soleus muscle was maintained at 30°C through the whole experiment with a lamp, and it was checked with a thermometer (Line Seiki, Japan).

Table 1. Ankle joint torque and average EMG at MVC

| Variables | unit | Tibio-tarsal joint angle (deg) | | | Difference |
|--------------------|------|--------------------------------|---------------|---------------|------------|
| | | 80 | 90 | 100 | |
| Ankle joint torque | Nm | 145.9 ± 76.4 | 120.0 ± 66.0 | 98.7 ± 54.4 | n.s. |
| aEMG | mV | 0.229 ± 0.072 | 0.242 ± 0.089 | 0.237 ± 0.071 | n.s. |

Numerical values show means ± S.D.

Electromyography

Electromyographic activity (EMG) was obtained telemetrically from the SOL, gastrocnemius lateralis (GL), gastrocnemius medialis (GM) and tibialis anterior (TA) muscles of the right leg. Bipolar silver chloride miniature skin electrodes (Beckman 650437, USA; 20 mm interelectrode distance) were aligned parallel with the fibers halfway between the estimated center of the innervation zone and the distal end of muscles. Before electrode application, each site was shaved, abraded and cleansed with alcohol to reduce interelectrode impedance (5kΩ). The EMG signal was amplified by 200 times with a FM-microvolt amplifier

(Glonner Electric GmbH, Germany; bandwidth 3-360Hz).

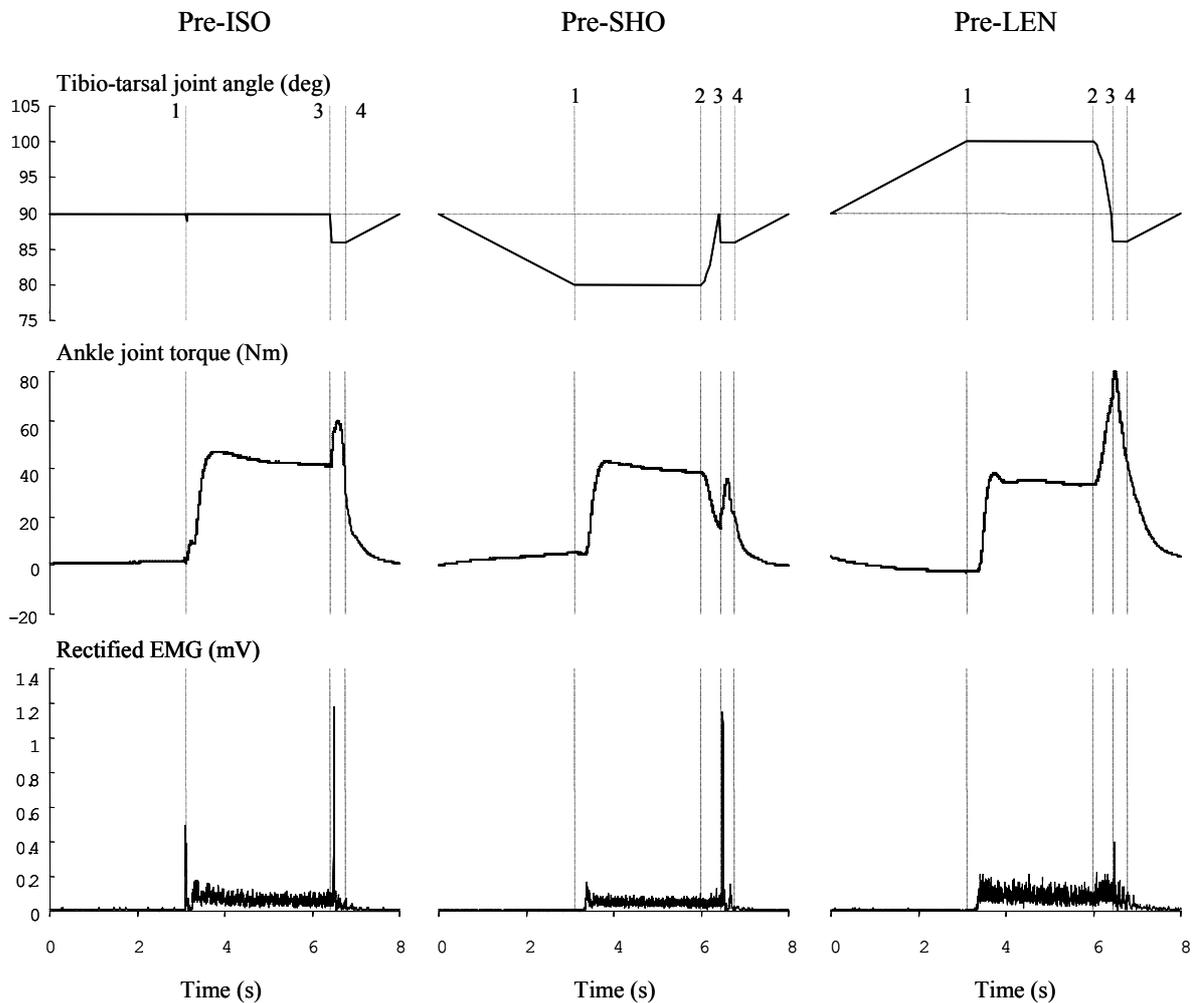


Fig.1 A typical example of tibio-tarsal joint angles, ankle joint torque and rectified EMGs for a whole platform movement in one representative subject. The figure shows the data at the 20% MVC effort level. Dotted lines 1, 2, 3 and 4 represent the onset of pre-load period (-3333 ms to the stretch onset), contraction period (-423 ms to the stretch onset), stretch perturbation period (6428 ms) and recovery period (+333ms to the stretch onset), respectively. One whole platform movement lasted for 8 seconds.

Data analysis

EMG signals were stored on a computer via a real time data acquisition system (Cudas, Dataq Instruments Inc., USA) that included a 12-bit A/D converter with a sampling frequency of 1 kHz. They were high-pass filtered at cutoff frequency of 10Hz and full-wave rectified. The rectified EMG signals were

averaged over a period of 2000 ms before and 350 ms after an onset of stretch perturbation for each trial (10 repetitions) in each condition. Identification of the SLR and the LLR was modified from that introduced by Lee and Tatton (1978) for upper limbs. The onset of SLR was identified by the onset of a consistently steep rise in the rectified EMG activity at about 40 ms after the stretch. The end of SLR or the onset of LLR was identified by the lowest rectified EMG activity followed by the second sharp rise at about 60ms after the stretch. Latency and duration of the SLR were measured. The SLR duration was calculated by subtracting the SLR latency from the LLR latency. Average EMG (aEMG), i.e., area per unit time, was calculated for 1000 ms before contraction period, for the contraction period, from the stretch onset to the SLR onset as BGA (BGA area) and for the SLR (SLR area). The SLR area where the BGA area was subtracted was normalized to the SLR area, which was defined as SLR ratio. The SLR showed two narrow peaks. Since they represent the positive and negative component of one biphasic potential in the raw EMG signal, a sum of them was defined as peak-to-peak amplitude. Since the peak-to-peak amplitude includes amplitude of the BGA, its amplitude where the aEMG of the BGA was subtracted was defined as SLR peak-to-peak amplitude (SLR p-to-p amplitude). The SLR p-to-p amplitude and the duration of the SLR (SLR duration) were regarded as an indicator of the SLR waveform.

In the present study, the EMG activity levels before the stretch were different among pre-ISO, pre-SHO and pre-LEN when the subjects were maintaining the same effort levels. Therefore, some SLR data with the similar integrated EMG levels for 243 ms before the stretch among the three conditions were selected in each condition irrespective of the effort levels and compared among the three conditions. Since one or two sets of SLR data could be compared per subject, the SLR data compared totaled 12 sets. The SLR data selected in pre-SHO and pre-LEN were normalized to those in pre-ISO to make the comparison among the three conditions easier.

The ankle joint torque and the angular displacement were recorded simultaneously with the EMG activity. An inertial reaction torque induced by the movement of the rotating platform was subtracted from the recorded torques in each condition. The torque was filtered at 75 Hz with Butterworth type 4th-order zero-lag low-pass filter to remove the high frequency noise.

Statistical analysis

A two-way analysis of variance for measurements (ANOVA) was used to test all variables, which were the ankle joint torque, aEMG before the stretch, SLR latency, SLR duration, SLR area, SLR SLR p-to-p amplitude, BGA area and the ratio of BGA area to aEMG in the contraction period, for the significant differences among three muscle contraction types against seven effort levels. When the result of the ANOVA was significant ($p < 0.05$), Fisher's post-hoc test was used to assess the source of difference ($p < 0.05$).

RESULTS

The ankle joint torque generated by some subjects exceeded the maximal torque capacity of the ankle ergometer at 70% MVC effort level in pre-LEN. It resulted in inaccurate pedal movements. Therefore, the data at 70% MVC effort level in pre-LEN was omitted.

The EMG was obtained not only from the SOL but also from the GL, GM and TA in the present study. However, the SLR p-to-p amplitude of the GL, GM and TA was considerably smaller (less than about one-fifth) than that of the SOL. Therefore, the present analysis was focused on the EMG activity of the SOL only.

Muscle activities before a stretch perturbation

The ankle joint torque and the EMG activity consistently increased with the level of effort before the stretch in all conditions (Fig.2). When these data were compared among three conditions at the same levels of effort, the torque magnitude was increasing in the order of pre-SHO, pre-ISO and pre-LEN in the pre-load period, although there were no significant differences due to the large S.D. However, the magnitude was turned into exactly the opposite order at the stretch because the torque decreased in pre-SHO and increased in pre-LEN during the contraction period (Fig.1). Subsequently, the torque was significantly larger in pre-LEN than in the other conditions at the stretch. The EMG activity was significantly larger in pre-LEN than in the other conditions both in the pre-load and contraction period at the same effort levels. Therefore, the levels of the ankle joint torque and the EMG activity were largely different among three conditions at the stretch.

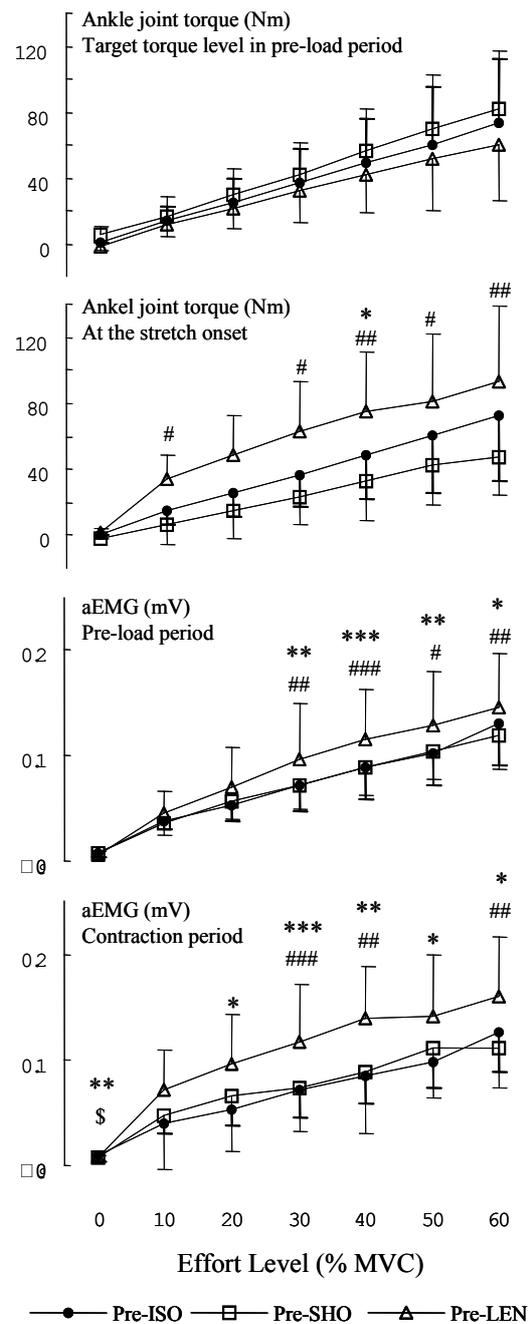


Fig.2 Ankle joint torque and average EMGs before a stretch perturbation plotted against effort levels. *, # And \$ indicate significant differences between pre-ISO and pre-LEN, between pre-SHO and pre-LEN and between pre-ISO and pre-SHO, respectively. *, # And \$ $P < 0.05$; **, ## and \$\$ $P < 0.01$; ***, ### and \$\$\$ $P < 0.001$.

Relationships between SLR modulations and level of effort

In pre-SHO three of seven subjects did not show the SLR at 0% MVC effort level. This is a unique result shown only in pre-SHO. Therefore, the data at 0% MVC effort level about the SLR were not included in the following results.

Fig.3 shows SLR latencies against the level of effort. There are two important observations about the SLR latency: first, there was significantly longer latency in pre-SHO than in the other conditions at 0% MVC effort level; secondly, significantly shorter latency in pre-LEN than in the other conditions was shown in every effort level. Pre-SHO showed a constant SLR latency of about 43 ms except at 0% MVC effort level, which was similar to that in pre-ISO. Pre-LEN showed a constant SLR latency of about 39 ms irrespective of the effort level.

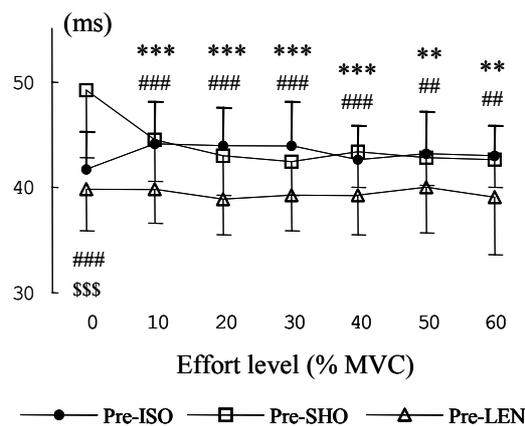


Fig.3 SLR latencies plotted against effort levels. Means \pm S.D. are shown for all subjects. *, # And \$ indicate significant differences between pre-ISO and pre-LEN, between pre-SHO and pre-LEN and between pre-ISO and pre-SHO, respectively. *, # And \$ $P < 0.05$; **, ## and \$\$ $P < 0.01$; ***, ### and \$\$\$ $P < 0.001$.

Fig.4 shows data related to the SLR area. The BGA area consistently increased with the effort level in all conditions, whereas the SLR area was constant except at 0% MVC effort level. The SLR area increased significantly only from 0% to 10% MVC effort level in all conditions. Pre-LEN showed significantly lower SLR areas and significantly larger BGA areas than the other conditions. On the other hand, there were no significant differences in their areas between pre-ISO and pre-SHO. This indicates that the SLR area was independent of the BGA in all conditions, and that the SLR area was significantly smaller in pre-LEN than in the other conditions.

Fig.5 shows data related to the SLR waveform. Pre-LEN showed significantly shorter SLR duration and significantly smaller SLR p-to-p amplitude than the other conditions. Pre-ISO showed slightly shorter SLR duration and slightly larger SLR p-to-p amplitude than pre-SHO, although there were no significant differences. This implies the steeper SLR waveform in pre-ISO than in pre-SHO.

After the SLR duration significantly decreased from 0% to 10% MVC effort level in pre-ISO and pre-SHO, it remained constant being about 22 ms in pre-SHO and about 20 ms in pre-ISO. The SLR p-to-p amplitude remained unchanged irrespective of the effort level in pre-ISO, whereas it significantly increased from 0% and at 10% MVC effort level in pre-SHO and in pre-LEN.

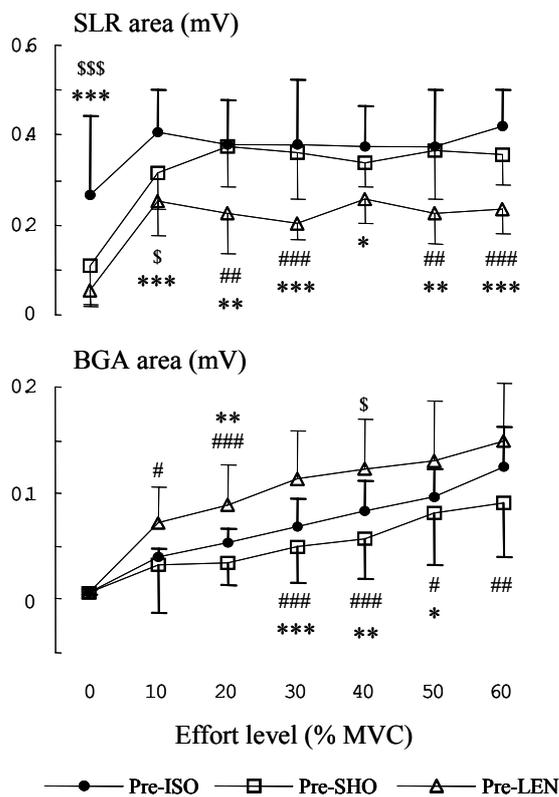


Fig.4 SLR and BGA areas plotted against effort levels. Means \pm S.D. are shown for all subjects. *, # And \$ indicate significant differences between pre-ISO and pre-LEN, between pre-SHO and pre-LEN and between pre-ISO and pre-SHO, respectively. *, # And \$ $P < 0.05$; **, ***, ### and \$\$\$ $P < 0.01$; ***, ### and \$\$\$ $P < 0.001$.

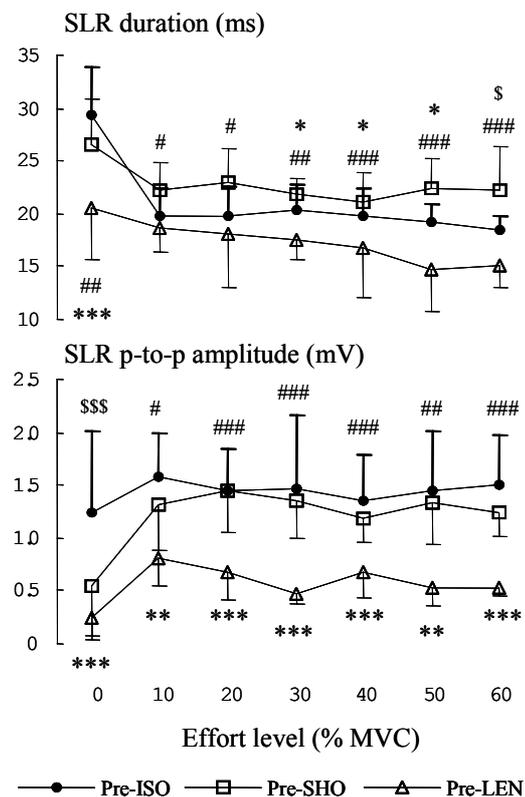


Fig.5 SLR duration and SLR peak-to-peak amplitude plotted against effort levels. Means \pm S.D. are shown for all subjects. *, # And \$ indicate significant differences between pre-ISO and pre-LEN, between pre-SHO and pre-LEN and between pre-ISO and pre-SHO, respectively. *, # And \$ $P < 0.05$; **, ***, ### and \$\$\$ $P < 0.01$; ***, ### and \$\$\$ $P < 0.001$.

Fig.6 shows ratios of the BGA area to the aEMG in the contraction period. The ratios were significantly lower in pre-SHO than in the other conditions except at 0% MVC effort level. There were no differences in the ratio between pre-ISO

and pre-LEN except at 0% MVC effort level. The ratio remained unchanged irrespective of the level of effort except pre-SHO. Only in pre-SHO it significantly decreased from 0% to 10% MVC effort level.

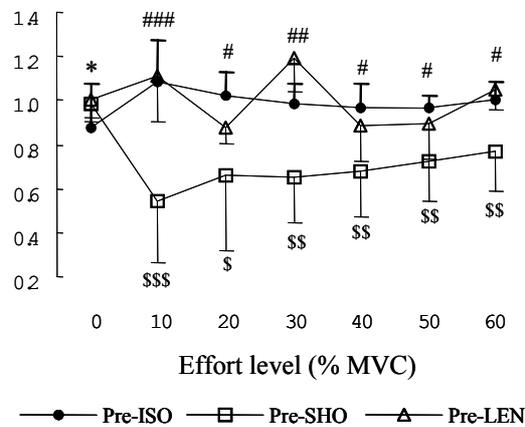


Fig.6 Ratios of BGA area to aEMG in the contraction period plotted against effort levels. Values below 1.0 indicate that the BGA area is lower than aEMG in the contraction period. Means \pm S.D. are shown for all subjects. *, # And \$ indicate significant differences between pre-ISO and pre-LEN, between pre-SHO and pre-LEN and between pre-ISO and pre-SHO, respectively. *, # And \$ $P < 0.05$; **, ## and \$\$ $P < 0.01$; ***, ### and \$\$\$ $P < 0.001$.

Comparison of SLRs at matched EMG activity levels

To compare the SLR at the matched levels of the EMG activity among three conditions, data were normalized for each subject with respect to those in pre-ISO. There were no significant differences in the aEMG before the stretch among three conditions (0.98 ± 0.09 in both pre-SHO and pre-LEN). Therefore, it may safely be assumed that the stretch was applied at the similar EMG activity level. The ankle joint torque at the stretch was significantly lower in pre-SHO (0.73 ± 0.19) than the other conditions (1.08 ± 0.57 in pre-LEN). The SLR latency was significantly shorter in pre-LEN (0.92 ± 0.03) than in the other conditions. On the other hand, there was no significant difference in the SLR latency between pre-ISO and pre-SHO (0.99 ± 0.04).

Fig.7 shows differences in the SLR waveform, SLR and BGA area among three conditions. Pre-LEN showed a significantly smaller SLR p-to-p amplitude than the other conditions and shorter SLR duration than pre-SHO. Pre-SHO showed a slightly longer SLR duration (1.13 ± 0.22) and slightly smaller SLR p-to-p

amplitude (0.92 ± 0.32). The SLR area was significantly lower in pre-LEN than in the other conditions. The BGA area was significantly lower in pre-SHO than in the other conditions.

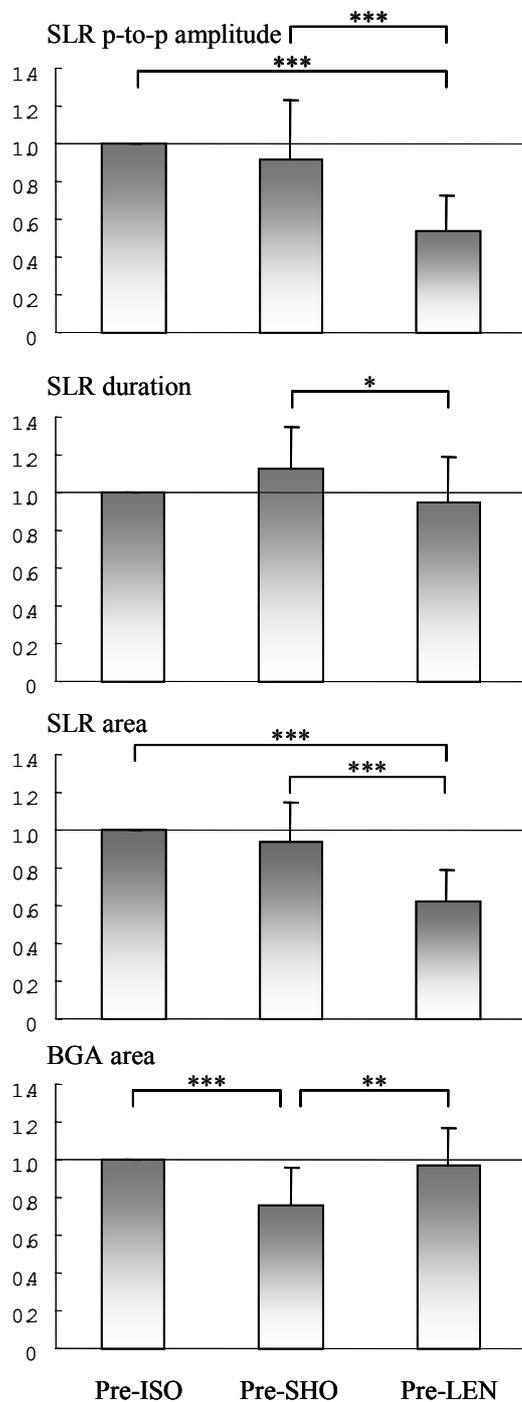


Fig.7 Comparison of SLR p-to-p amplitude, SLR duration, SLR area and BGA area among three conditions at matched EMG activity levels. Means \pm S.D. of value normalized with respect to that in pre-ISO are shown for all subjects. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

DISCUSSION

Methodological considerations

The present results demonstrated that the SLR was modulated according to the background muscle contractions while a given effort level was being maintained. The SLR modulation was almost similar to that observed at matched ankle joint torque (Ogiso et al. 2002a). This was due to the constant SLR modulation in the activated muscle. For this finding to be valid, some artificial possibilities of modulating the SLR need to be ruled out. One possibility is the difference in backlash effects induced by the different pedal movements among the three conditions. In the present study, the right foot of the subjects was tightly mounted on the rotation platform of the ankle ergometer. Although part of the stretch might be absorbed by the inertia of the foot generated by the pedal movements and the tissue around the ankle joint, the tight mounting made between the foot and the platform was likely to minimize the backlash effects induced by the pedal movements on the stretch. Significant backlash effects would result in longer SLR latency in pre-SHO than in pre-ISO also in the active muscle, for example. However, it was never observed in the present study. Another one is whether the sampling frequency of 1 kHz is enough for the SLR analysis. This is relevant to the issue of the backlash effects and strongly influences the SLR modulation, especially the latency. However, the results of the SLR latency, such as the similar SLR latency between pre-ISO and pre-SHO, observed in every trial and repeated 10 times, suggest that there would be little possibility that the observations resulted from artificial effects.

A recent study showing that EMG can be affected by cancellation of the positive and negative phases of motor unit action potentials (Day and Hulliger, 2001) does not support that the similar EMG activity among the different modalities of contraction invariably signify the similar level of activation. Therefore, it must be noted that the present result of the EMG activity does not always show the effect of the activation level on the SLR modulation.

SLR modulation depends on the types of muscle contractions before a stretch

In the present study the subjects were asked to perform three kinds of muscle contractions while maintaining a given effort level. This motor task differs

markedly from that, such as a moving joint angle (Nakazawa et al. 1997, 1998; Bawa and Sinkjær 1999) and an EMG activity level (Wallace and Miles 1998), imposed on the subjects in earlier studies where the similar methodology was adopted. The muscle where the stretch was applied and the stretch reflex component analyzed was also different between the studies. In the present study where the stretch reflex was elicited by a short stretch from the SOL, the early part of LLR (M2, in the terminology of Lee and Tatton, 1975) probably mediated by the group II afferents (Schieppati and Nardone, 1997; Grey et al. 2001) was very small compared with the SLR analyzed and the late part of the LLR (M3) was hardly observed. On the other hand, in the previous studies the SLR and the LLR in elbow muscles (Nakazawa et al. 1997, 1998) and the LLR in the hand muscle (Wallace and Miles 1998) were examined. This may be due to functional differences between the SOL and the upper limb muscles (Thilman et al, 1991) and differences in the condition of the background muscle contractions and the stretch. However, one result that the SLR area was significantly smaller after lengthening than after the other contractions was in accordance with that in the earlier studies. This suggests that the small SLR area after lengthening depends not on the descending commands on the motor task but mainly on afferent inputs, such as Ib afferents from Golgi tendon organs (Houk et al. 1980), group II afferents from the muscle spindles (Robinson et al. 1982), afferent inputs from joint receptors (Schieppati and Crenna 1984) and presynaptic inhibition (Abbruzzese et al. 1994) elicited by lengthening before the stretch. In addition, muscle thixotropic effects induced by the preceding contraction is likely to be partly related to the alteration in the SLR (Hagbarth et al., 1985; 1995).

An observation that the SLR area after shortening was similar to that after an isometric contraction in the active muscle obviously differs from that in the earlier studies (Nakazawa et al. 1997, 1998; Bawa and Sinkjær 1999). It is possible to consider a few mechanisms about the similar SLR area between the conditions when a given effort level is maintained. The first possibility is an effect of different motor unit recruitment on the SLR area. However, it can not reasonably be assumed due to the followings: (1) the SOL is dominated mostly by slow twitch fibers (Johnson et al. 1973), (2) higher frequency values of the EMG power spectrum have been observed during the isometric contraction than the shortening contraction (Ogiso et al. 2002a), and (3) there were no differences in the SLR latency between the conditions in the active muscle.

The second possibility is an effect of the afferent inputs on the SLR area. It has been observed that a compliant tendon is stretched by muscle tension during an isometric contraction (Fukashiro et al. 1995). It may increase the discharge rate of Ib afferents since the Golgi tendon organ is sensitive to tension generated within muscle-tendon unit (Schmidt, 1978). However, the result of the SLR p-to-p amplitude in the active muscle is likely to deny this possibility. If the SLR area was influenced by the Ib afferents during the isometric contraction, the SLR p-to-p amplitude would be smaller in pre-ISO than in pre-SHO because the discharge rate of the Ib afferents could be lower during shortening than during the isometric contraction.

The third possibility is an effect of the muscle spindle sensitivity on the SLR area. Prochazka et al. (1985) have shown that fusimotor action on a given spindle afferent during movements is not rigidly alpha-linked, but set by the CNS to steady levels of gamma activity. Wilson et al. (1995) have reported that the discharge rate of muscle spindle afferents remains elevated in a complete relaxation after an isometric contraction for approximately 5 seconds. Therefore, it is likely that the present motor task, maintenance of the effort level as needed to maintain a given pre-load torque level, resulted in high sensitivity of muscle spindles also during shortening. This is corroborated by the following observations in the relaxed muscle because unloading of the muscle spindles is maximal: (1) No SLR was shown in three subjects, (2) Smaller SLR p-to-p amplitude and longer SLR duration than in the active muscle and (3) longer SLR latency than in the active muscle. Burke et al. (1978) have observed that the discharge rate of spindle endings decreases during shortening, but it always remained higher than before the onset of contraction. Smaller and blunter SLR waveform in pre-SHO than in pre-ISO in the active muscle may indicate resistance of fusimotor drive to the muscle spindle unloading induced by contraction of extrafusal fibers and external action of the pedal movement during shortening. This would be supported by the shorter SLR latency after lengthening in which the muscle spindles are also stretched by the external action of the pedal movement.

The fourth possibility is an effect of the BGA. Pre-SHO showed considerably lower ratios of the BGA to the EMG activity before the stretch than in pre-ISO. This reminds us of premotion silent period (PSP) when a ballistic movement is performed on a low level of contraction. It has been considered that the PSP increases the susceptibility of motor units (Tsukahara et al. 1995), which is

related to speed (Yabe, 1976) and dynamic force (Aoki et al. 1989) in the first part of the movement. We have reported that ankle joint torque induced by a stretch is lower after shortening than after an isometric contraction (Ogiso et al. 2002b). Therefore, the behavior of the EMG activity like the PSP may be one of the neural mechanism to compensate a disadvantage of the mechanical output induced by the stretch after shortening. However, it remains an unsettled question why the BGA markedly decreases after a stretch that follows a shortening contraction compared with the other contraction types.

SLR modulation is independent of background torque and EMG activity

The differences in the SLR modulation among three conditions observed at matched EMG activity levels were similar to those at the similar effort levels, which has been observed also in an earlier study in which a stretch was applied at matched torque levels (Ogiso et al. 2002a). This implies that the SLR modulated by the preceding muscle contraction is independent of the background EMG activity and torque. In addition, although the SLR was larger and sharper in the active muscle than in the relaxed muscle, it remained unchanged irrespective of the effort level once the muscle was activated. The SLR area was also independent of the effort levels in the active muscle. These are a complete contrast to the EMG activity before the stretch being proportional to the effort level. A similar SLR independence was observed in human SOL (Toft et al. 1991) and in cat SOL (Hoffer and Andreassen 1981), which is not agreement with the automatic gain compensation (Marsden et al. 1976; Matthews 1986). Toft et al. (1991) suggested that the absence of scaling of the SLR increment might be attributed to “saturation” of the motor neuron pool excitability. Larger SLR p-to-p amplitude than the EMG amplitude recorded at MVC observed in the present study may support it. If this suggestion is correct, the SLR may not be sensitive to a change in the effort level once the muscle was activated. However, the SLR independence was not shown in the TA (Toft et al. 1989). The automatic gain compensation, which predicts that the reflex response is an approximately constant proportion of the background activity, has been also shown in the thumb and elbow flexors. Therefore, effects of the background EMG activity and torque on the SLR modulation may depend, at least in part, on the differences in the functional requirements made of the various muscles.

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ORIGINAL PAPERS

IV

**Mechanical response elicited by a mechanical and electrical stimulation
after different muscle contractions**

By

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Submitted for publication

Mechanical response elicited by a mechanical and electrical stimulation after different muscle contractions

Short title: Joint torque elicited by a mechanical and electrical stimulation

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ABSTRACT

The present study was designed to examine the effects of the preceding muscle activities on the following muscle performance by comparing the mechanical responses of the ankle plantar flexor muscles (APF) elicited by either a mechanical stretch (MS) or an electrical stimulation (ES). Six healthy male subjects volunteered in this study. The MS was set as a sudden dorsiflexion of 4 deg at 160 deg/s. Intensity of the ES was fixed at about 20% higher level than that at the maximum M-wave. They were applied at 90 deg of the tibio-tarsal joint after an isometric (pre-ISO), shortening (pre-SHO) and lengthening contraction (pre-LEN). Ankle joint torque (AJT) elicited by MS and ES was respectively measured with an interval of three weeks. The main findings were as follows: (1) pre-LEN showed lower AJT than the other conditions irrespective of stimulation types, (2) AJT elicited by MS was larger in pre-ISO than in pre-SHO, which is opposite to that evoked by ES, (3) differences in AJT elicited by MS among three conditions were smaller in the active muscles than in the relaxed ones, which is opposite to those evoked by ES, (4) in the relaxed muscles the electromechanical delay (EMD) was extremely shorter in pre-SHO and longer in pre-LEN compared with pre-ISO and (5) a difference in EMD between pre-ISO and pre-SHO disappeared once the muscles were activated. These results show that the preceding muscle activity influences the following muscle-tendon complex performance, which greatly depends on the muscle-tendon complex behavior induced by stimulation, on a difference in the muscle sliding direction before and after stimulation, and on muscle pre-activation level.

Key words: background muscle activity; stretch reflex; twitch superimpositions; ankle joint torque; electromechanical delay

INTRODUCTION

When the muscle-tendon complex is suddenly stretched, a mechanical response is automatically elicited by the intrinsic properties and the stretch reflex (Hoffer and Andreassen 1981, Nichols and Houk 1976, Sinkjær et al. 1988). However, the mechanical response is likely to be influenced by the stretch conditions and functional requirements of the movement. Stein and Kearney (1995) reported that stretch-induced force depended non-linearly on position, voluntary activity, vibration, and amplitude, width and velocity of the mechanical stretch (MS). Sinkjær et al. (1996) showed that the initial increase in torque elicited by MS was changing throughout the gait cycle. The effects of the muscle activities before MS on the mechanical response were clarified by Ogiso et al. (2002b). They showed that the MS after an isometric contraction evoked a larger stretch-reflex mechanical response more efficiently and quickly than that after phasic contractions. A mechanical response evoked by an electrical stimulation (ES) also seems to be influenced by the muscle activities before the stimulation. It has been reported that the joint torque evoked by ES during lengthening was

greater than that during the other contractions under a maximal voluntary condition (Westing et al., 1990) and a relaxed condition (Gravel et al., 1987). These earlier studies obviously show that the preceding muscle activity influences the subsequent performance of the muscle-tendon complex.

In the present study, we compared mechanical responses of the ankle plantar flexor muscles (APF) elicited by MS and ES immediately after various muscle contractions. Compared with ES, MS is characterized as follows: (1) MS makes a process of AJT generation involve a neural circuit comprising the sensory receptors, afferent nerves, the spinal cord and efferent nerves, and (2) MS is unlikely to activate all motor units of the muscles. ES by-passes the fusimotor system and is likely to activate all motor units if it has intensity that can evoke maximal M-wave. Since MS has a delayed influence on the muscle-tendon complex compared to ES situation, mechanical responses evoked by ES is likely to be affected by the preceding muscle activity more than that elicited by MS. Therefore, comparing MS-elicited mechanical responses with ES-evoked ones would be able to clarify the effects of the preceding muscle contractions on the following muscle-tendon complex performance and its mechanism, which was the purpose of the present study.

MATERIALS AND METHODS

Subjects. Six healthy male subjects (age, 34.8 ± 10.4 years; body height, 1.75 ± 0.08 m; body mass, 77.0 ± 11.1 kg) volunteered in this study. The subjects were not active in regular exercises. They gave informed consent to the present experimental procedure that had been approved by the ethics committee of the University of Jyväskylä.

Experimental protocol. The measurements started with recording of isometric maximum voluntary contractions (MVC) of the APF. This was followed by the ankle joint torque (AJT) elicited by MS (stretch reflex measurement) immediately after an isometric (pre-ISO), shortening (pre-SHO) and lengthening contraction (pre-LEN). The same protocol was repeated three weeks later to measure the AJT evoked by a supra-maximal single and double ES (single and double twitch measurements). Subjects were asked not to perform any physical exercises for a few days before the measurements.

The stretch reflexes of the relaxed and active APF were elicited by a sudden dorsiflexion of 4 deg over 25 ms (160 deg/s) in pre-ISO, pre-SHO and pre-LEN (top of Fig.1). To begin with, the tibio-tarsal joint angle was altered from 90 deg to 80 deg in pre-SHO, 90 deg in pre-ISO and 100 deg in pre-LEN over 3095 ms (preparatory period). The subjects relaxed their muscles fully during the preparatory period. After the tibio-tarsal joint reached the initial angles, it had been stopped for 2910 ms (pre-load period). In the active condition, subjects were asked to develop and maintain AJT of 20% MVC level at 80 deg in

pre-SHO, at 90 deg in pre-ISO and at 100 deg in pre-LEN during the pre-load period. The MVC torque at 80, 90 and 100 deg had been measured twice beforehand in a random order. Target torque corresponding to 20% MVC level and AJT being actually exerted by the subjects were displayed on an oscilloscope as visual feedback. On average, the subjects maintained the required torque level for about 2000 ms of 2910 ms because it took some time to reach the level. Thereafter, the tibio-tarsal joint was rotated at 30 deg/s over 423 ms from 80 deg to 90 deg in pre-SHO and from 100 deg to 90 deg in pre-LEN (contraction period). In pre-ISO it remained still. In the active condition, subjects were asked not to exert the 20% MVC torque level required during the pre-load period but to maintain a given level of effort (effort level) as needed to maintain it. Maintaining the 20% MVC torque for about 2 s in the pre-load period was enough for the subjects to grasp the effort levels needed. Subsequently AJT consistently decreased in pre-SHO and increased in pre-LEN during the contraction period. MS was applied when the tibio-tarsal joint angle reached 90 deg (stretch perturbation period). The subjects were asked not to resist the MS but to constantly maintain the same effort level as that during the pre-load and contraction period until the end of the MS in the active condition. After the MS the tibio-tarsal joint angle remained unchanged at 86 deg for 308 ms (static period) in order to make an equal condition among three conditions. Finally, the tibio-tarsal joint was gradually returned to the position of 90 deg over 1239 ms (recovery period). Subjects fully relaxed their muscles during the recovery period. A sequence of the tibio-tarsal joint movement lasted 8 sec, which was consecutively repeated 10 times. There was an interval of a few minutes between the MVC and the stretch reflex measurements.

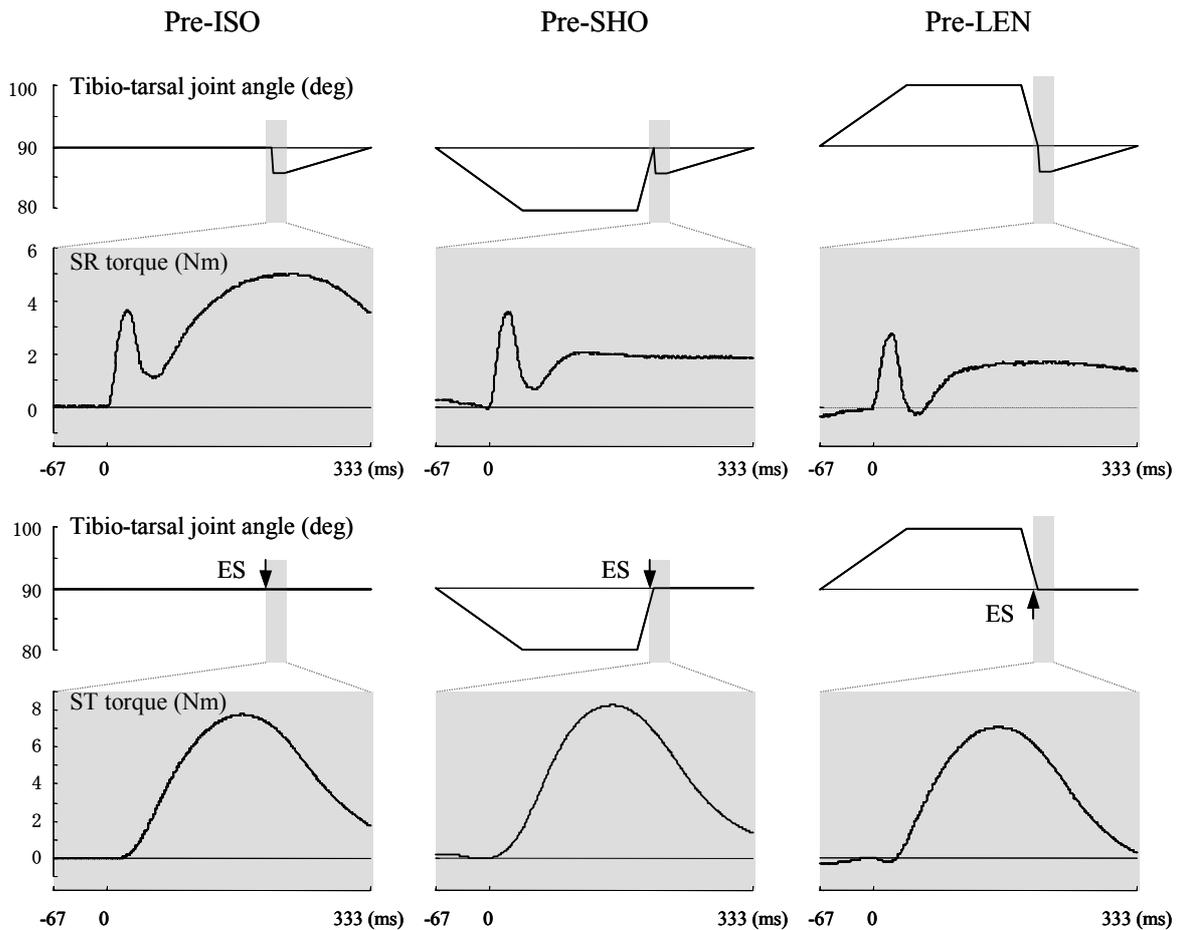


Fig.1 Passive ankle joint torque (AJT) elicited by a mechanical stretch (SR torque) and a supra-maximal single electrical stimulation (ST torque) in a representative subject. AJT is shown in shaded portion (400ms) of a whole platform movement (8 sec). Numerical values "0" on horizontal axes represent the onset of mechanical stretch or 4 ms after the electrical stimulation was applied, which correspond to instants when the tibio-tarsal joint angle reaches 90 deg after shortening and lengthening contractions. In SR torque, the second peak of AJT elicited by the mechanical stretch was measured as the peak AJT. ES: electrical stimulation.

A procedure for the single and double twitch measurements was similar to that for the stretch reflex measurement except that 1) a supra-maximal ES was applied instead of MS, and 2) the tibio-tarsal joint angle was stopped at 90 deg after ES. ES was superimposed to the tibialis nerve at 4 ms before the tibio-tarsal joint angle reached 90 deg, because the M-wave resulting from direct stimulation of the motor nerves has 4-5 ms latency in APF muscles. A single rectangular pulse of 1 ms duration was used as ES. The stimulus intensity was fixed at about 20% higher level than that at the maximum M-wave. In the double twitch measurement, ES was delivered twice at an interval of 10 ms. The measurements were consecutively repeated twice, respectively. There was an interval of a few minutes between the first and second measurements.

Ergometric apparatus and position. All measurements were performed with a motor driven ankle ergometer controlled by a digital feed-back system (Nicol et al., 1996) which was similar to that used by Gollhofer & Schmidtbleicher (1989). The torque and angular displacement around the rotational axis of the motor were measured with a piezoelectric crystal transducer (Kistler, Switzerland). While subjects were sitting in the ergometer chair, their right thigh was clamped with a soft cuff. Their right foot was mounted on the rotation platform so that the rotational axis of the ankle joint was aligned with that of the motor torque device. The knee and hip joint angles were fixed (133.3 ± 6.1 deg and 107.5 ± 2.7 deg, respectively).

Electrical stimulation device. ES was delivered to the tibialis nerve of the right leg with an evoked potential measuring system (MEB-5304K, Nihon Kohden, Japan) to elicit the mechanical twitch. Stimulation electrodes (pregelified AG/AGCL electrode, Niko, Denmark) were placed over the tibialis nerve in the popliteal fossa as the cathode (1.5×1.5 cm) and over an upper part of the patella as the anode (5×8 cm). Positions of the stimulation electrodes were found and fixed in the upright stance so that a clear and stable M-wave can be evoked from the soleus muscle (SOL) beforehand.

Electromyography. Electromyographic activity (EMG) was obtained telemetrically from the SOL, gastrocnemius medialis and lateralis muscles of the right leg. Bipolar silver chloride miniature skin electrodes (Beckman 650437, USA; 20 mm interelectrode distance) were aligned parallel with the fibers halfway between the estimated center of the innervation zone and the distal end of muscles. Before the electrode application, each site was shaved, abraded and cleansed with alcohol to reduce interelectrode impedance ($5\text{k}\Omega$). EMG signal was amplified by 200 times with a FM-microvolt amplifier (Glonner Electric GmbH, Germany; bandwidth 3-360Hz).

Data analysis. AJT, angular displacement and EMG signals sampled at 1kHz (Coda, Dataq Instruments Inc., USA) were simultaneously recorded. AJT was filtered at 75 Hz with a Butterworth type 4th-order zero-lag low-pass filter to remove the high frequency noise. Since AJT involved an inertial reaction torque induced by the pedal movement, it was subtracted from the torque. The peak AJT was measured every repetition and averaged in each condition. In single twitch measurement, a difference in time between the onsets of ES and a steep rise of AJT after the stimulation was defined as electromechanical delay (EMD). In case of stretch reflex measurement, EMD was defined as a difference in time between the onsets of short-latency stretch reflex (SLSR) and a steep rise of AJT elicited by the SLSR.

Statistics. A two-way analysis of variance for measurements (ANOVA) was used to test all variables. When the result of the ANOVA was significant ($p < 0.05$), Fisher's post-hoc test was used to assess the source of difference ($p < 0.05$).

RESULTS

Background ankle joint torque at mechanical and electrical stimulations. There were significant differences in AJT at the onset of MS or ES among three conditions ($p < 0.001$) irrespective of whether the muscles were activated or not (Table 1). The M-wave peak-to-peak amplitude evoked by a supra-maximal ES did not show significant differences among the three conditions (Table 2).

Table 1. Ankle joint torque at the onset of mechanical stretch after muscle contractions

| | | Relaxed muscle | | Active muscle | |
|---------|----|----------------|-------------------------|----------------|-------------------------|
| Pre-ISO | Nm | 0.0 ± 0.0 |]***]]***]]***] | 18.3 ± 3.0 |]***]]***]]***] |
| Pre-SHO | Nm | -0.8 ± 0.2 | | 8.3 ± 3.8 | |
| Pre-LEN | Nm | 0.9 ± 0.4 | | 25.4 ± 4.2 | |

*** $p < 0.001$

Table 2. M-wave p-to-p amplitude evoked by a supra-maximal electrical stimulation

| | | Relaxed muscle | | Active muscle | |
|---------|----|-----------------|--|-----------------|--|
| Pre-ISO | mV | 7.45 ± 2.78 | | 8.27 ± 3.24 | |
| Pre-SHO | mV | 7.25 ± 2.96 | | 7.45 ± 3.04 | |
| Pre-LEN | mV | 7.58 ± 2.62 | | 8.47 ± 2.78 | |

Ankle joint torque elicited by a mechanical stretch. In the relaxed muscles, AJT was significantly greater for pre-ISO than for the other conditions ($p < 0.01$, Fig.2). When the muscles were activated, AJT showed increases of 10 - 14 % in pre-ISO (n.s.), 100 - 140 % in pre-SHO ($p < 0.01$) and 220 - 460 % in pre-LEN ($p < 0.01$) over that in the relaxed muscles. Consequently, differences in AJT among three conditions obviously decreased, although there was still significant difference in AJT between pre-ISO and pre-LEN ($p < 0.05$).

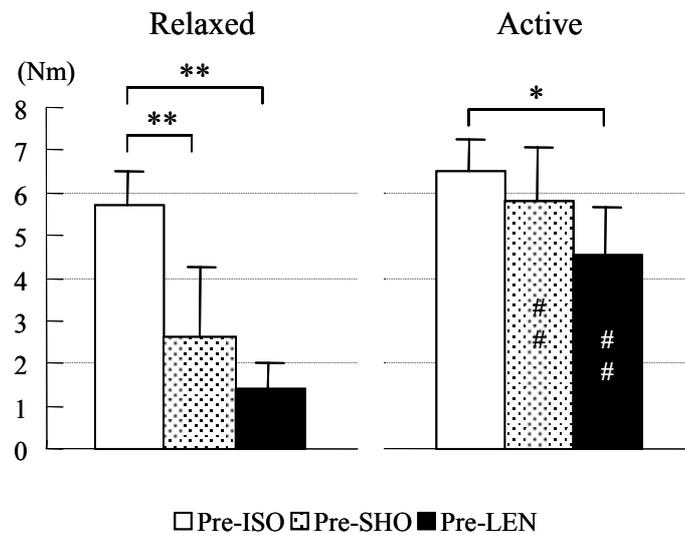


Fig.2 Ankle joint torque elicited by a mechanical stretch after an isometric, shortening and lengthening condition. * $P < 0.05$, and ** $p < 0.01$ refer to significant differences between pre-ISO, pre-SHO and pre-LEN conditions. ## $p < 0.01$ refers to a significant difference between the relaxed and active muscles.

Ankle joint torque evoked by an electrical stimulation. AJT evoked by a single supra-maximal ES is illustrated in Fig.3. In the relaxed muscles, no significant differences were observed among three conditions. Once the muscles were activated, AJT significantly decreased in all conditions ($p < 0.01 - 0.001$) and its differences increased among the three conditions. AJT was significantly greater for pre-SHO than for pre-LEN ($p < 0.001$) and for pre-ISO ($p < 0.05$). The differences observed between pre-ISO and pre-SHO and between the relaxed and active muscles were opposite to those elicited by MS. AJT evoked by a supra-maximal double ES instead of the single one also showed a similar pattern of the differences among the three conditions. However, compared with the single ES, the differences tended to be smaller when the supra-maximal double ES was applied (Fig.4).

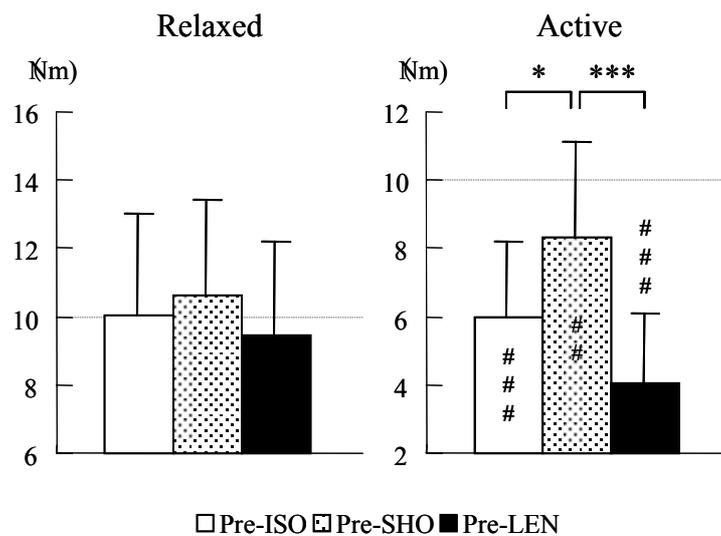


Fig.3 Ankle joint torque evoked by a supra-maximal single electrical stimulation after an isometric, shortening and lengthening condition. * $P < 0.05$ and *** $p < 0.001$ refer to significant differences between pre-ISO, pre-SHO and pre-LEN conditions. ## $p < 0.01$ and ### $p < 0.001$ refer to a significant difference between the relaxed and active muscles.

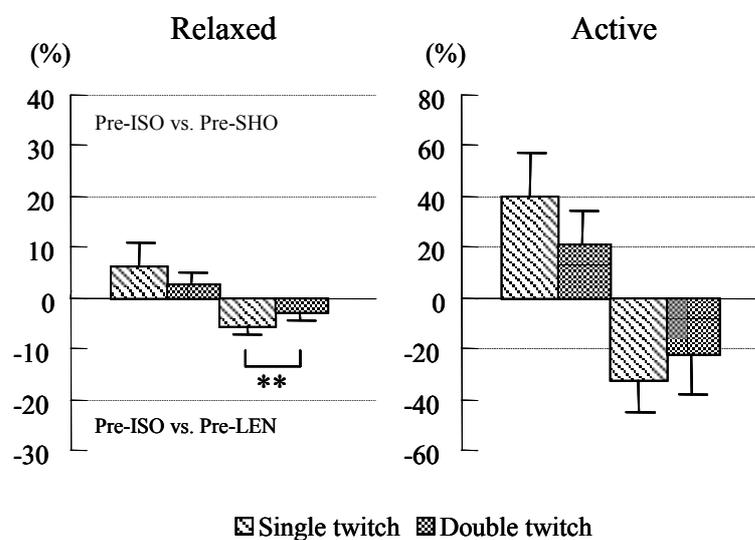


Fig.4 Comparison of ankle joint torque elicited by a supra-maximal single and double electrical stimulation between pre-ISO and the other conditions. Values are expressed as percent of those in pre-ISO. ** $p < 0.01$ refers to significant differences between values evoked by the supra-maximal single and double electrical stimulation.

Electromechanical delay. EMD results in stretch reflex and single twitch measurements are illustrated in Fig.5. In the stretch reflex measurement, no significant differences in the EMD were observed among three conditions in the relaxed muscle (14.7 ± 1.6 ms in pre-ISO, 13.8 ± 2.0 ms in pre-SHO and 15.7 ± 2.5

ms, in pre-LEN). Once the muscle was activated, EMD became significantly shorter: 4.5 ± 1.6 ms in pre-ISO ($p < 0.001$), 8.5 ± 3.1 ms in pre-SHO ($p < 0.05$) and 8.7 ± 1.6 ms in pre-LEN ($p < 0.01$). In the single twitch measurement when the muscle was relaxed, EMD was 8.3 ± 2.3 ms in pre-ISO, 1.7 ± 1.4 ms in pre-SHO and 14.7 ± 2.0 ms in pre-LEN. Once the muscle was activated EMDs became longer: 10.8 ± 4.9 ms, 10.8 ± 5.3 ms and 19.6 ± 3.7 ms, respectively. Pre-LEN showed significantly longer EMDs than the other conditions in both relaxed and active muscles ($p < 0.001$). In the relaxed muscle, EMD was significantly shorter for pre-SHO than for pre-ISO ($p < 0.001$). This was not the case in the active muscles. The similar pattern was observed also in the double twitch measurement.

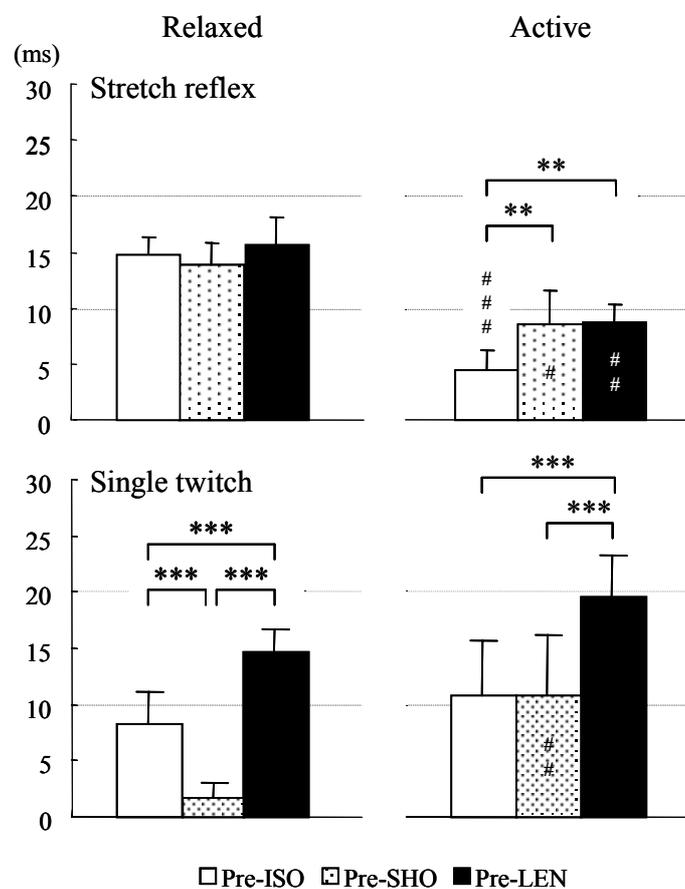


Fig.5 Electromechanical delay at stretch reflex and single twitch measurement. *** $p < 0.001$ and ** $p < 0.01$ refers to significant differences between pre-ISO, pre-SHO and pre-LEN conditions. # $p < 0.05$, ## $p < 0.01$ and ### $p < 0.001$ refer to a significant difference between the relaxed and active muscles.

DISCUSSION

The findings were characterized by two major types, the first of which deal with AJT. Depending on the type of preceding muscle contraction AJT was influenced also by stimulation type that elicited AJT: (1) MS-elicited AJT was larger in pre-ISO than pre-SHO, which was opposite to the ES-evoked one, (2) differences in MS-elicited AJT among three conditions decreased once the muscles were activated, which was opposite to those in the ES-evoked one, and (3) MS-elicited AJT increased when the muscles were activated, which was opposite to the ES-evoked one.

It must be admitted that it is not an easy task to find objective explanations for these findings. For this reason the following discussion includes aspects which are also partly speculative. One may suppose that AJT behavior was affected by significant differences in AJT at the onset of MS or ES induced by the preceding muscle contractions. However, this difference is unlikely to explain the opposite results of AJT observed between pre-ISO and pre-SHO when ES was applied instead of MS. Only pre-LEN tended to show lower AJT than the other conditions irrespective of stimulation types. This has not been observed when ES was applied during passive lengthening and shortening (Gravel et al. 1987) and during maximal voluntary eccentric and concentric contractions (Westing et al. 1990). These discrepancies are likely to result from a difference in the stimulation protocol (immediately after vs. during phasic contractions) or muscle contraction level (20% vs. 100% MVC level). It is possible that ES-evoked AJT during phasic contractions includes an effect of the force-length relationship (Rassier et al., 1999), and that the difference in the muscle contraction level induces variation in the neural input to the alpha-motoneurons from various receptors.

Duchateau and Hainaut (1986a, b) has shown that potentiation of force produced by the second stimulus of a double ES increases with reducing twitch-to-tetanus ratio, which is associated with a potentiation of intracellular Ca^{2+} movements. It is also known that higher Ca^{2+} releases during lengthening (Warren et al. 1993, Lowe et al. 1994). These may partly explain AJT behavior evoked by ES because the ES seems to activate all motor units as shown by the constant M-wave amplitude. This would be supported by decreased differences in AJT among three conditions when a double ES was applied instead of a single ES because the second stimulus of the double ES was applied at the same condition.

Another important finding of the present study is that EMD was greatly influenced by the preceding muscle contraction types, pre-activation levels of the muscles and stimulation types. EMD observed in stretch reflex measurement was nearly identical with that observed in earlier studies (Nicol & Komi 1998; Ogiso et al. 2002). However, the following results of EMD observed in pre-SHO are very new ones: (1) an extremely short EMD in the relaxed

muscle, and (2) a significant increase in EMD when the muscles were activated.

Directions in which the muscle is sliding before and after ES are similar in pre-SHO and opposite in pre-LEN. Differences in the sliding direction may result in significantly longer EMD in pre-LEN and shorter EMD in pre-SHO in the relaxed muscles. This is supported also by smaller differences in AJT among the three conditions evoked by a double ES. On the other hand, it is known that the actin is moved a long distance on a myosin head smoothly and efficiently because each ATPase cycle corresponds to multiple power strokes with a moderate load (Yanagida et al. 1985; 1993, Kitamura et al. 1999). This behavior may explain the significantly larger AJT in pre-SHO than in the other conditions in the active muscles. However, it is unlikely to explain why EMD increased significantly when the muscles were activated in pre-SHO. Other factors such as Ca^{2+} release in the active muscles and a low proportion of the attached cross-bridges in the relaxed muscles (Suzuki et al. 1993) may play a role in this mechanism.

It is known that function of the tendon changes according to the joint angle (Fellows and Thilmann 1989, Fukunaga et al. 1997). Fukunaga et al. (1997) observed that movement of the tendinous tissue occurs in parallel with the joint displacement in an un-loaded condition. Although Ikegawa et al. (1999) also observed the similar synchronization during active lengthening, they showed also that the tendinous tissue was lengthened earlier than the muscle at the beginning of isometric contraction. ES contracts the muscles first, which induces a stretch of the tendon. On the other hand, MS stretches the tendon first, followed by a stretch of the muscle and muscle contraction elicited by the stretch reflex. Therefore, this difference in transmission of the stimulation results in different muscle-tendon complex behavior among three conditions, which is likely to influence AJT behavior and plays an important role to transmit force generated by the muscles to the skeleton.

In conclusion, the present study clearly showed that the preceding muscle activity influences the muscle-tendon complex performance immediately after stimulation was applied. In addition, its influences greatly depended on the muscle-tendon complex behavior induced by stimulation and on muscle activation level.

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ORIGINAL PAPERS

V

Passive stretch reflex behavior and long-lasting eccentric exercise

By

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Passive stretch reflex behavior and long-lasting eccentric exercise

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ABSTRACT

This study was designed to examine fatigue effects of a long-lasting eccentric exercise (LLEE) on the stretch reflex EMG and mechanical responses. Four healthy male subjects volunteered in this study. The short-latency stretch reflex (SLSR) of the soleus muscle (SOL) in a passive condition and maximal voluntary isometric plantar flexion (MVC) torque were measured before (Pre), immediately after (Post), 2 hours after (2H), 2 days after (2D) and 7 days after LLEE (7D). The same protocol was repeated three weeks later to measure MVC torque with a double twitch (DT), passive DT torque, maximum M-wave and H-reflex. LLEE was applied to the ankle plantar flexor (APF) muscles and it consisted of a sudden dorsi-flexion (SDF) of 160 deg/s combined with an electrical stimulation that evoked 10% MVC torque. This cycle was repeated at 0.5 Hz, which lasted for 75 min. MVC torque and the corresponding average EMG (aEMG) decreased significantly after LLEE and recovered at 2H. H/M ratio showed a bimodal recovery process consisting of depression at Post, recovery at 2H, dramatic re-depression at 2D and final recovery at 7D. aEMG of SLSR also showed a bimodal trend, whereas its re-depression at 2D was less dramatic than that observed in the H/M ratio. Ankle joint torque elicited by the stretch reflex (RT) did not recover until 7D. Blood lactate and CK activity showed no significant changes throughout the experiment. However, their increment rate after LLEE was much higher than the ratio of APF muscle volume to the whole muscular one. All the subjects complained of severe muscle soreness at 2D. In conclusion, LLEE decreased both the stretch reflex electrical and mechanical responses, but its recovery processes were different between the two responses. Reflex EMG activity showed a bimodal response, which seemed to be largely influenced by nociceptive afferents associated with muscle soreness. On the other hand, prolonged recovery of RT may be attributed to impairment of processes associated with the excitation-contraction coupling induced by muscle damage.

Key word: stretch reflex; H-reflex; M-wave; reflex torque; fatigue

INTRODUCTION

Fatigue induced by exercise involving eccentric actions is expected to decrease the stretch reflex EMG activity and force (Nicol et al., 1996b; Avela and Komi, 1998a,b; Avela et al., 1999a,b), and stretch-shortening cycle performance (Horita et al., 2003). It has been also reported that the recovery process of electromyographic (EMG) response shows a bimodal trend (Avela et al., 1999b; Komi and Nicol 2000a, b), which depends on intensity of the exercise imposed on subjects (Nicol et al., 1996a). In most of these previous studies, fatigue was induced by voluntary exercise including multi-joint movement such as running and jumping. The present study examined the fatigue effects of a more isolated eccentric exercise by minimizing the central control. Fatigue was induced only for the ankle plantar flexor (APF) muscles by a computer-controlled

long-lasting eccentric exercise (LLEE) while the subjects were relaxing their muscles fully. In addition, the stretch reflex was elicited by the same sudden dorsiflexion (SDF) as that using in LLEE

MATERIALS and METHODS

Four male subjects aged 23 - 43 volunteered in this study. All measurements and LLEE were performed with a motor driven ankle ergometer controlled by a digital feed-back system (Nicol et al., 1996; Ogiso et al., 2002) and with an evoked potential measuring system (MEB-5304K, Nihon Kohden, Japan).

The present experiment consisted of two set series of an identical fatigue LLEE separated by three weeks (Fig.1A). In the first fatigue experiment, stretch reflex and maximal voluntary isometric plantar flexion (MVC) measurements were performed in the right APF muscles immediately before (Pre), immediately after (Post), 2 hours after (2H), 2 days after (2D) and 7days after LLEE (7D). The stretch reflex was measured more than three minutes after MVC measurement. Only at Post it was done immediately after the exercise as terminated. The stretch reflex was successively elicited 20 times by SDF of 8 deg (from 94 deg to 86 deg of the tibio-tarsal joint angle) over 50 ms. Blood lactate (B-LA) concentration and creatine kinase (CK) activity were also measured simultaneously. In the second fatigue protocol, the following parameters were measured: MVC with a supra-maximal double electrical shock (E_{shock}) (superimposed MVC), maximum M-wave and H-reflex. Maximum M-wave and H-reflex were evoked by E_{shock} with a single rectangular pulse over 1 ms. E_{shock} was applied at 70 ms after the onset of SDF when the stretch reflex response had roughly finished. In M-wave measurement, the intensity of E_{shock} was fixed so that the maximum M-wave was evoked at 86 deg of the tibio-tarsal joint angle. H-reflex was evoked by E_{shock} with intensity that could elicit 20% of the maximum M-wave peak-to-peak amplitude. After superimposed MVC measurement, the maximum M-wave was measured once, and then H-reflex was successively measured 20 times. Ankle joint torque (AJT) evoked by a supra-maximal double E_{shock} at rest (DTr) was also measured. Electromyographic (EMG) activity was obtained telemetrically from the right soleus (SOL) and tibialis anterior muscles. Except for the MVC, subjects were asked to relax their muscles fully throughout the measurement and to avoid any physical exercise for 7 days before and throughout the experiment.

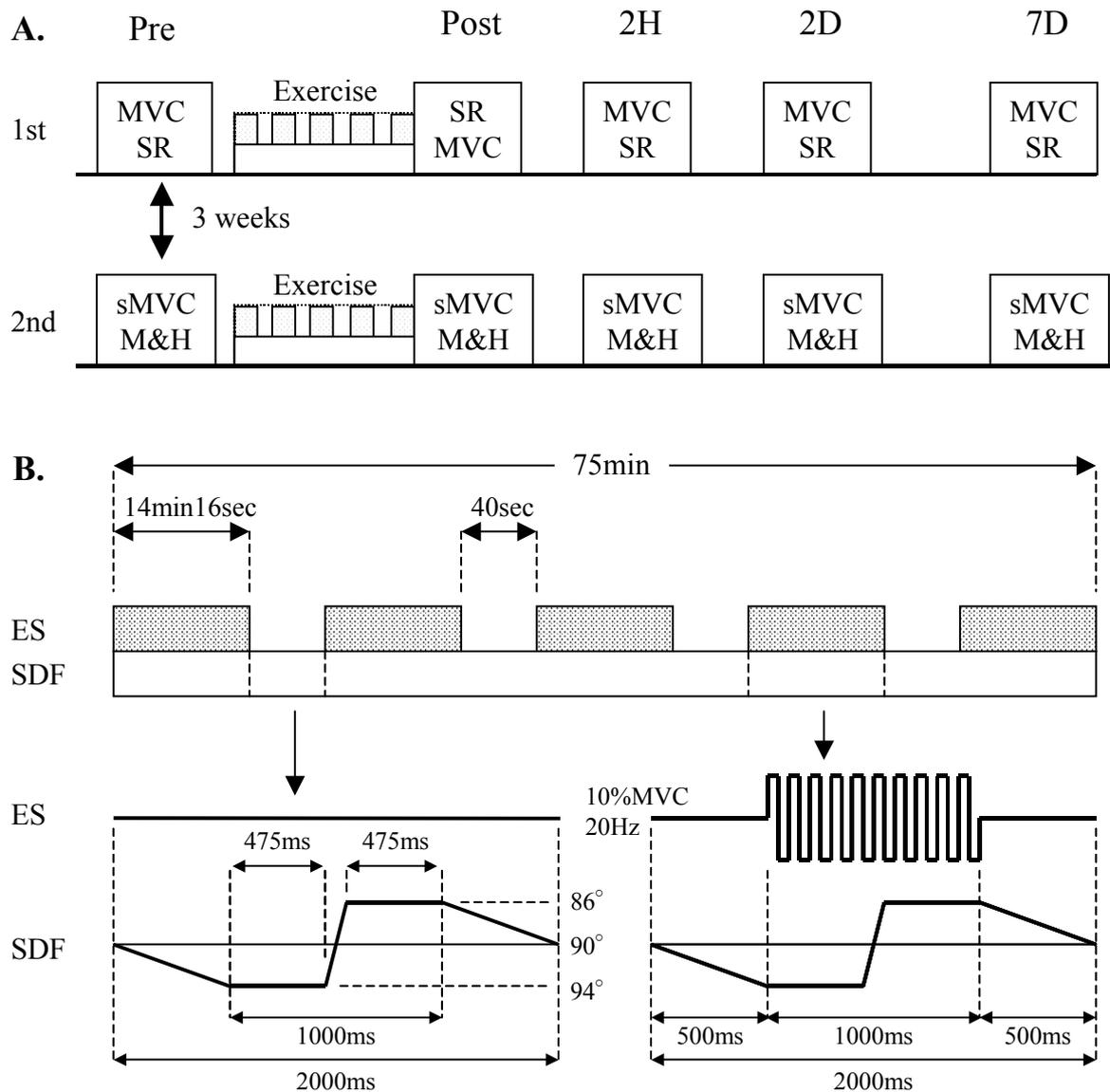


Fig.1 Schematic representations of experimental protocol (A) and a stimulation pattern during LLEE (B). MVC: maximum voluntary isometric plantar flexion, sMVC: superimposed MVC, SR: stretch reflex, M&H: maximal M-wave and H-reflex, ES: electrical stimulation, and SDF: sudden dorsiflexion.

LLEE consisted of the same SDF as that used in the stretch reflex measurement combined with an electrical stimulation (ES) (Fig.1B). SDF was applied at 94 deg of the tibio-tarsal joint angle. Impulse duration and frequency of ES were 0.2 ms and 20 Hz, respectively. The ES train lasted for 1 s. Intensity of ES was fixed so that ES evoked 10% of MVC torque at 90 deg of the tibio-tarsal joint angle. This cycle was repeated at 0.5 Hz and lasted for 75 min. ES was interrupted for 40 ms after every 14 min 16 s exercise duration to measure the stretch reflex response during LLEE. Subsequently, the number of repeated SDF and ES reached 2250 and 2170 times, respectively, during the entire exercise.

AJT, angular displacement and EMG signals sampled at 1kHz (Cudas, Dataq Instruments Inc., USA) were simultaneously recorded. AJT was filtered at 75 Hz. An inertial reaction torque induced by pedal movement of the ankle ergometer was subtracted from AJT. AJT elicited by SDF comprises two components: an initial component where the force increases immediately after SDF, and a twitchlike component with a longer latency. The latter is mostly generated by the stretch reflex response. Therefore, the latter component was defined as reflex-induced torque (RT) (see top right of Fig.3) and was measured every repetition and averaged.

EMG signals were high-pass filtered at a cutoff frequency of 10 Hz and full-wave rectified. Short-latency (SLSR) and long-latency stretch reflex (LLSR) were identified according to Lee and Tatton (1978). A sum of two narrow peaks shown by SLSR was defined as peak-to-peak (p-to-p) amplitude. Average EMG (aEMG) of SLSR was also calculated, which was defined as SLSR area. P-to-p amplitude of H-reflex and M-wave was used to calculate the H/M ratio, an indicator of excitability of the alpha-motoneurons and the synaptic transmission. In the MVC measurement, aEMG was calculated for 100 ms after the torque reached the maximum.

Statistics. A one-way analysis of variance (ANOVA) was used to test all variables for significant differences among the tests. When the result of the ANOVA was significant ($p < 0.05$), Fisher's post-hoc test was used to assess the source of difference ($p < 0.05$).

RESULTS

Maximal voluntary isometric plantar flexion and activation level. MVC torque decreased significantly by 19% on the average at Post ($p < 0.01$) and recovered already at 2H (Fig.2). aEMG at MVC showed a similar change. No significant differences were observed in the MVC torque between the 1st and 2nd experiments (85.7 ± 16.0 vs. 76.5 ± 15.2 Nm at Pre, 68.5 ± 9.8 vs. 62.3 ± 9.5 Nm at Post, 80.5 ± 13.7 vs. 74.6 ± 13.9 Nm at 2H, 79.7 ± 17.8 vs. 79.1 ± 13.5 Nm at 2D and 83.0 ± 15.8 vs. 82.9 ± 13.2 Nm at 7D). Change in DTr torque was similar to that in MVC torque (Fig.2).

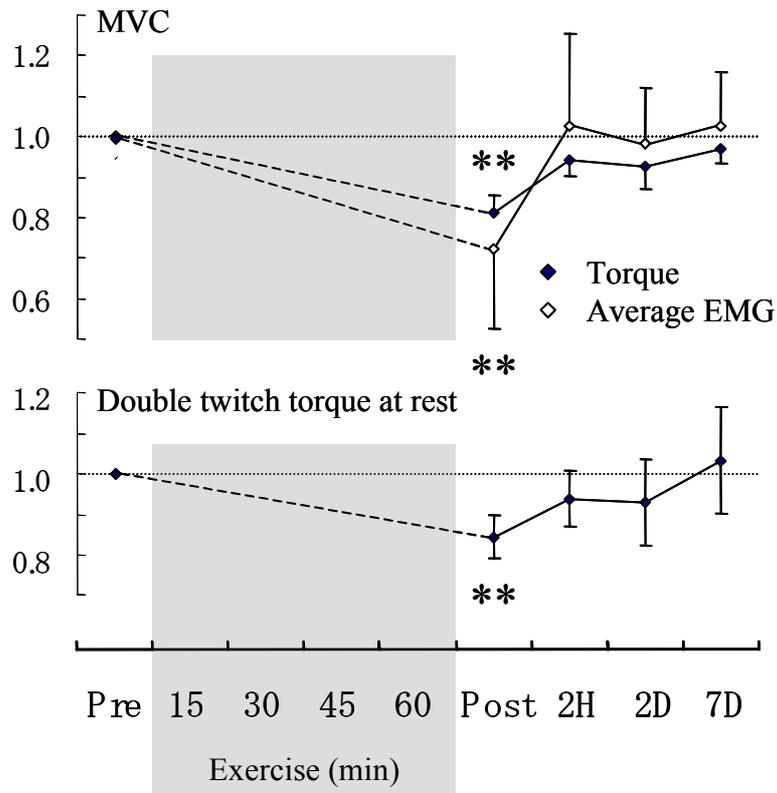


Fig.2 Relative changes in MVC torque, average EMG at MVC and double twitch torque at rest. Changes are expressed as a ratio of pre-exercise value. ** $p < 0.01$ and * $p < 0.05$ compared with pre-test.

Stretch reflex behavior. SLSR area decreased by 62% on the average during LLEE ($p < 0.05$) and recovered at 2H (Fig.3). However, it again decreased by 29% at 2D (n.s.). A change in SLSR p-to-p amplitude was almost similar to that in the SLSR area. LLSR was so small that it could not be easily distinguished from the gross EMG activity. RT decreased by 22% on the average during LLEE ($p < 0.05$, Fig.3) Contrary to SLSR area, it did not recover at 2H. It remained significantly lower until 7D ($p < 0.05$).

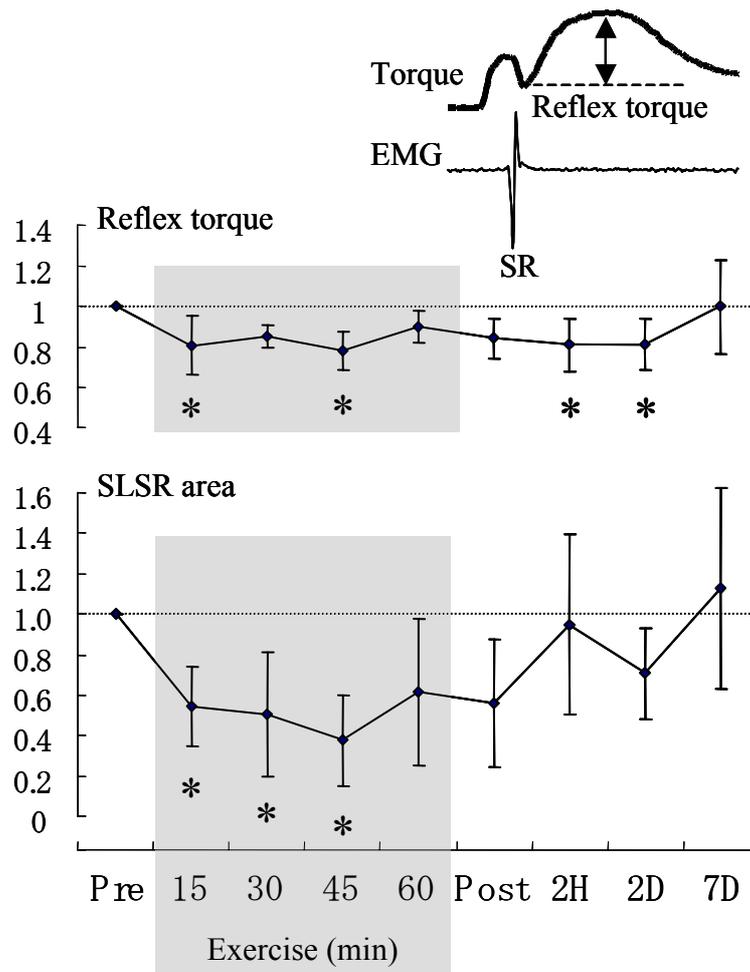


Fig.3 Relative changes in reflex torque and SLSR area. Change in SLSR p-to-p amplitude was similar to that in the SLSR area. Changes are expressed as a ratio of the pre-exercise value. * $p < 0.05$ compared with pre-test.

H-reflex and M-wave. H-reflex p-to-p amplitude decreased by 32% at Post ($p < 0.05$) and dramatically by 67% at 2D ($p < 0.01$) (Fig.4). Maximal M-wave p-to-p amplitude showed no significant changes throughout measurements although it decreased slightly at Post (15%, n.s.) and at 2D (11%, n.s.). Subsequently, changes in H/M ratio depended mainly on H-reflex p-to-p amplitude and showed a bimodal response. H/M ratio recovered once at 2H after decreased by 19% at Post (n.s). Thereafter, it dramatically decreased by 58% at 2D ($p < 0.01$).

Lactate acid and creatine kinase activity. B-LA being $1.5 \pm 0.6 \text{ mmol} \cdot \text{l}^{-1}$ at Pre increased slightly to $2.0 \pm 0.3 \text{ mmol} \cdot \text{l}^{-1}$ at Post (n.s.). No significant differences were observed in CK activity among the tests. CK activity ranged from 60.5 ± 11.2 at Pre to $81.6 \pm 36.6 \text{ U} \cdot \text{l}^{-1}$ at 2D. However, all the subjects felt fatigue in APF muscles at Post and complained of severe muscle soreness at 2D.

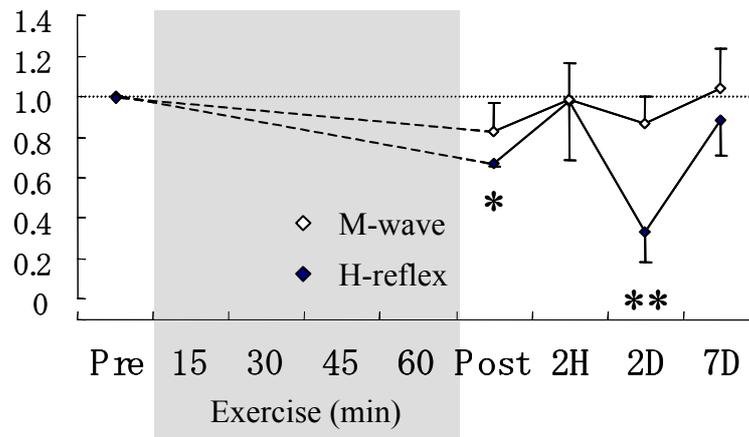


Fig.4 Relative changes in M-wave and H-reflex amplitude. Changes are expressed as a ratio of the pre-exercise value. * $p < 0.05$ and ** $p < 0.01$ compared with pre-test.

DISCUSSION

Exercise-induced fatigue is described as a loss of force-generating capability (Bigland-Ritchie and Woods, 1984) or an inability to maintain further exercise at the required level (Edwards 1981). Since LLEE decreased MVC, DTr and RT significantly, it is reasonable to suppose that the LLEE induced peripheral fatigue. Although B-LA did not show significant changes between at Pre and at Post, the increment rate of B-LA (about 33%) seemed to be considerably high when mass of the shank including APF muscles was taken into consideration. The mass of the shank is only 4.3 ± 0.3 % of the whole body mass (Zatsiorsky et al. 1990). Therefore, no significant change in B-LA may be attributed to small APF muscles where LLEE was imposed. In fact, a repeated exhaustive stretch-shortening cycle exercise performed by larger muscles increased B-LA significantly (Horita et al. 2003). At the same time, LLEE was likely to recruit faster-contracting motor units (MU) because ES used in the present study is known to result in completely reversed MU recruitment orders to the "Size Principle" (Trimble and Enoka 1991). Rapid decrease in RT after the onset of LLEE supports this notion.

Recovery processes between SLSR and RT had different patterns in the present study. A bimodal response including an acute and delayed declines shown by SLSR area was in line with observations in earlier studies (Avela et al., 1999b; Komi and Nicol 2000a, b), while un-recovered RT until 7D has not been observed previously. This difference may depend on difference in protocols between the present and earlier studies. In contrast to earlier studies, the stretch reflex was elicited by the same SDF as that used during LLEE in the present study. Therefore, a prolonged recovery of RT may indicate existence of movement-specific mechanical fatigue effects. It is known that a long-lasting low-intensity exercise selectively decreases torque evoked by low frequency

(LF) stimulation (Avela et al. 2001; Edwards et al. 1977). Chin and Allen (1996) suggest that LF fatigue results from increases in intracellular free Ca^{2+} concentration, which activates some processes that lead to failure of excitation-contraction (E-C) coupling and Ca^{2+} release. This implies that a prolonged recovery of RT might be attributed to impairment of processes associated with E-C coupling and Ca^{2+} release. Impairment of E-C coupling is closely related also to muscle damage (Jones 1996). As Duchateau and Hainaut (1985) suggest, the intracellular processes play a major role in contractile failure. Thus, a slight difference in recovery processes between AL and MVC or DTr torque may indicate impairment of the contractile tissue itself. Incomplete recovery of torque in contrast to complete recovery of aEMG observed at MVC is in line with this notion. Although no significant changes in CK activity were observed, it increased by about 35 % at 2D. This is considerably higher compared with mass of the shank including APF muscles (about 4 % of the whole body mass). As all the subjects complained of severe muscle soreness at 2D, it is possible that muscle damage and associated inflammation may have taken place after the present exercise protocol.

Motor evoked potential (MEP) induced by transcranial magnetic stimulation decreases during (Ljubisavljevic et al. 1996) and after an exercise (Rollnik & Dengler 2002), and even after a series of ES without voluntary muscle activation (Pitcher & Miles 2002). Post-exercise MEP depression includes central fatigue, afferent input failure from exercising muscles and synaptic transmission failure. Strojnik and Komi (2000) proposed activation level (AL) as one indirect indicator of central fatigue. When AL was calculated from superimposed MVC torque and DTr according to their formula, it decreased significantly at Post and recovered already at 2H in the present study. Therefore, central fatigue might be also related to depression of SLSR area at Post, which may indicate that the underlying mechanism of the acute depression differs from that at 2D.

All the subjects complained of severe muscle soreness at 2D. It is known that the nociceptive signals are transmitted by small muscle afferent group III and IV nerves. Pettorossi et al. (1999) observed that fatigue-induced inhibition of the pre- and post-synaptic waves disappeared when a large number of the group III and IV afferents were eliminated by injecting capsaicin. Since aEMG at MVC has already recovered at 2D, the second decline in SLSR area can be attributed mainly to activity of the peripheral afferents. In line with this, significant decrease in H-reflex p-to-p amplitude was observed at 2D.

H-reflex p-to-p amplitude evoked by ES that by-passed the muscle spindles showed much larger decrease at 2D than that of SLSR. A difference in amplitude between H-reflex and SLSR observed at Post would be due to an effect of superimposed MVC measurement on the H-reflex amplitude. However, the difference observed at 2D seems to result from the following mechanisms: 1) although H-reflex mainly involves activation of low-threshold MUs, SLSR

might be related to different MUs; 2) while inhibiting α -motoneurons, group III and IV afferents can activate also gamma-motoneurons (Jovanovic et al. 1990; Johansson et al. 1993; Djupsjöbacka et al. 1995). If the nociceptive afferents increased fusimotor activity, it may explain a different decline in amplitude between H-reflex and SLSR; and 3) swelling and stiffer muscles observed at 2D (unpublished our data) may result in higher sensitivity of the muscle spindles, which might compensate for decreased α -motoneuron activity.

Finally, we may argue that the number of subjects (n=4) in the present study is too small to allow general conclusions. While this is true, it was surprising to see that all the subjects showed similar response. Thus, with this limitation in my mind we may conclude that LLEE decreased both the stretch reflex EMG and mechanical responses, but its recovery processes were different between the two responses when the reflex was elicited by the same SDF as that used during LLEE. A bimodal recovery response shown by SLSR is likely to be largely influenced by nociceptive afferents associated with muscle soreness. On the other hand, prolonged recovery of RT may be attributed to impairment of processes associated with E-C coupling induced by muscle damage.

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ORIGINAL PAPERS

VI

Fatigue and effects of background muscle contraction on reflex behavior

By

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Fatigue and effects of background muscle contraction on reflex behavior

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ABSTRACT

The present study was designed to examine 1) whether fatigue can alter the stretch reflex modulation induced by the background muscle contractions and 2) whether differences in the background muscle contractions alters recovery processes of the stretch reflex from fatigue. Nine healthy males volunteered in the present study. The stretch reflex was elicited by a sudden dorsi-flexion (SDF) from the relaxed ankle plantar flexion (APF) muscles immediately after an isometric (pre-ISO), shortening (pre-SHO) and lengthening contraction (pre-LEN). At the same time, APF torque (ST torque) was also evoked by supra-maximal single electrical stimulation (ES) in the same way. Double twitch torque (DT torque) was measured at 80, 90 and 100 deg of the tibio-tarsal joint angle. These were measured before (Pre), immediately after (Post), 2 hours after (2H), 2 days after (2D) and 6days (6D) after a long-lasting low-intensity eccentric exercise (LLEE) comprising SDF and ES. Latency of Short-latency stretch reflex (SLSR) remained unchanged before and after LLEE in all conditions. SLSR p-to-p amplitude showed the following bimodal trend of recovery in all conditions: an immediate decline after LLEE, temporary recovery at 2H, delayed decline at 2D and final recovery at 6D. Reflex torque (RT) also showed a similar bimodal trend, but it was slight. High correlation coefficients were observed between SLSR p-to-p amplitude and RT throughout experiments. Pre-ISO showed the largest RT per SLSR p-to-p amplitude of three conditions in all tests. These results indicate that fatigue influences stretch reflex amplitude, whereas it does not influence modulation of SLSR induced by the background muscle contraction. ST torque decreased at Post and recovered at 2H in all conditions, which was similar to MVC torque. An extremely short EMD observed in pre-SHO significantly increased after LLEE, which was not observed in the other conditions. Although DT torque decreased significantly after LLEE at all angles, its decrease was remarkable at 100 deg. LLEE significantly decreased displacement of fascicular insertion points in the aponeurosis (FIPA) elicited by SDF used during LLEE. Recovery of FIPA displacement elicited by shortening and lengthening before SDF tended to follow a bimodal trend slightly. These results suggest that alteration in muscle-tendon complex behavior and nociceptive afferent activities induced by fatigue contributed to bimodal changes in reflex behavior.

Key words: stretch reflex; single twitch; background muscle contraction

INTRODUCTION

It is well known that the stretch reflex elicited to react to stretching muscle-tendon complexes unexpectedly is modified by the stretching conditions: amplitude (1, 23), velocity (1), direction (23), and duration of the stretch (23), joint angle during the stretch (9, 23, 29) and muscle contraction level prior to the stretch (1, 17, 23, 26). Not only stretch conditions but also movement and motor task imposed on muscles is closely associated with the

reflex behavior, which is, in particular, obvious in the long-latency stretch reflex of the upper limb muscles involving the motor cortex (7, 8, 28). However, it has been observed that the short-latency stretch reflex (SLSR), which is a monosynaptic reflex mediated by the spinal cord only, seen more clearly in the lower limb muscles (25) is also modified by phases of the gait cycle during walking (22) and by background muscle contraction types (17).

Stretch reflex behavior is altered also by fatigue induced by an exercise (2, 3, 4, 5, 16, 19), which is likely to depend on exercise types that induce fatigue. Compared with a low-intensity long-lasting exercise, a maximal intensive short-lasting exercise makes the stretch reflex behavior less influence (24). It has been also reported that recovery processes from fatigue have intensity-specific (15) and movement-specific effects (19).

The present study was designed to examine 1) whether fatigue alter the stretch reflex modulation induced by background muscle contractions, 2) whether recovery processes from fatigue are influenced by differences in background muscle contractions, and 3) what are mechanisms that induce the fatigue effects on the stretch reflex modulation. In the present study, fatigue was induced by a low-intensity long-lasting eccentric exercise (LLEE) so that the stretch reflex behavior is altered obviously.

MATERIALS and METHODS

Subjects. The present study was conducted on the soleus (SOL) and gastrocnemius medialis muscles (GM) of nine healthy males who were not active in regular exercise (age 28.8 ± 4.6 years; height 180.2 ± 6.3 cm; body mass 82.9 ± 11.0 kg; lower leg length 43.4 ± 2.3 cm). They gave informed consent to the present experimental procedure that had been approved by the ethics committee of the University of Jyväskylä. Subjects were instructed to relax their muscles fully throughout measurements and LLEE, and to avoid any physical exercise from a few days before the present experiment to the end of the experiment.

Long-lasting low-intensity eccentric exercise. LLEE consisted of a sudden dorsiflexion (SDF) of 8 deg over 50 ms (160 deg/s) combined with an electrical stimulation (ES) of the right ankle plantar flexor (APF) muscles. SDF was applied at 94 deg of the tibio-tarsal joint angle with the same ankle ergometer as that used in stretch reflex measurements. Impulse duration and frequency of ES were 0.2 ms and 30 Hz, respectively. The ES train lasted for 1 s. Intensity of ES was fixed so that the ES evoked 20% of MVC torque at 90 deg of the tibio-tarsal joint angle. This cycle repeated at 0.5 Hz lasted for 60 min. Subsequently, the number of SDF and ES reached 1800 times.

ES was directly applied to APF muscles an evoked potential measuring system

(MEB-5304K, Nihon Kohden, Japan). The stimulation electrodes (5×5 cm) (StimTrode, Axelgaard Manufacturing, USA) were placed so that two anodes located on the proximal head of GM and the lateral gastrocnemius muscle and one cathode was located on the distal myotendinous junction over SOL.

Stretch reflex measurement. The stretch reflex was elicited from the right SOL and GM with an isokinetic ankle ergometer that has been used in earlier studies (15, 16, 17, 18, for example) before (Pre), immediately after (Post), 2 hours after (2H), 2 days after (2D) and 6 days after LLEE (6D). The right thigh of subjects sitting in the ergometer chair was clamped with a soft cuff, and their right foot was mounted on the footplate so that the rotational axis of the ankle joint was aligned with that of the motor torque device. Knee and hip joint angles were individually fixed at positions where the stretch reflex can be elicited stably and clearly (123 ± 4 deg and 102 ± 4 deg, respectively). SDF of 4 deg over 25 ms (160 deg/s) was applied to APF muscles at 90 deg of the tibio-tarsal joint angle after an isometric (pre-ISO), shortening (pre-SHO) and lengthening contraction (pre-LEN). The contractions lasted for 423 ms (30deg/s) from 80 deg to 90 deg in pre-SHO, from 100 deg to 90 deg in pre-LEN and at 90 deg in pre-ISO. After SDF the tibio-tarsal joint was fixed at 86 deg for 308 ms to make the angle where the stretch reflex response appears equal among three conditions. Such angular displacement patterns of the tibio-tarsal joint were similar to those in earlier studies reported by Ogiso et al. (17, 18). The stretch reflex was consecutively elicited 5 times in each condition. Intervals of at least 3 minutes were taken among three conditions. Only in Post, the number of repetition was limited to 3 times and no intervals were taken among the three conditions to avoid recovery from fatigue induced by LLEE.

Electromyographic (EMG) activity was obtained telemetrically from the right SOL, GM and tibialis anterior muscle. Bipolar silver chloride miniature skin electrodes (Beckman 650437, USA) were aligned parallel with muscle fibers halfway between the estimated center of the innervation zone and the distal end of the muscles. According to the recommendation by SENIAM (1999), a 20 mm inter-electrode distance was employed. The electrode positions were carefully marked on the skin to fix the position surely throughout the present experiment. Before electrode application, each site was shaved, abraded and cleansed with alcohol to keep lower interelectrode impedance ($5k \Omega$). APF torque and angular displacement during stretch reflex measurement were measured with a piezoelectric crystal transducer (Kistler, Switzerland) attached on the ankle ergometer.

Single and double twitch measurement. APF torque evoked by a single twitch (ST torque) was measured to examine effects of the preceding muscle contraction on the following muscle-tendon (M-T) complex performance. The procedure was similar to that for measuring the stretch reflex except that 1) a supra-maximal single electrical shock (E_{shock}) was applied instead of SDF, and 2)

the tibio-tarsal joint angle was fixed at 90 deg after E_{shock} . The supra-maximal single E_{shock} was applied to the tibialis nerve at 4 ms before the tibio-tarsal joint angle reached 90 deg, because M-wave that stimulates the motor nerves directly has 4-5 ms latency in APF muscles. Single rectangular pulse of 1 ms duration was used as the supra-maximal single E_{shock} . The stimulus intensity was fixed at about 20% higher level than that at the maximum M-wave.

APF torque evoked by a double twitch was measured at 80, 90 and 100 deg of the tibio-tarsal joint angle while subjects were relaxing their muscles (DTr torque) and were performing the maximum isometric voluntary plantar flexion (MVC). A supra-maximal E_{shock} was applied to the tibialis nerve twice at an interval of 10 ms during the relaxation or after the MVC torque reached the maximum. Pulse form, duration and intensity of E_{shock} were similar to those used in single twitch measurement. This was done once after the stretch reflex measurements.

A supra-maximum single and double E_{shock} was generated with the same evoked potential measuring system as that used to generate ES during LLEE. Patterns of the electrical stimulation could be changed with a switch. The stimulation electrodes (pregelified AG/AGCL electrode, Niko, Denmark) were placed over the tibialis nerve in the politeal fossa as the cathode (1.5×1.5 cm) and over an upper part of the patella as the anode (5×8 cm). A position of the cathode was searched in the upright stance before Pre so that a clear and stable M-wave can be elicited from SOL.

Sagittal-plane muscle sonograph. To examine M-T complex behavior induced by LLEE, two-dimensional geometry characteristics of SOL and GM during LLEE and stretch reflex measurements were estimated from morphometrics of sagittal-plane sonographs by using a real-time ultrasound apparatus with a frequency of 42 Hz (SSD-2000, Aloka, Japan). A 7.5 MHz linear-array probe of 6 cm long was put over GM muscle so that the sharpest image of SOL and GM fascicles was gotten, and fixed securely with a special support device made of expanded polystyrene. The probe positions were carefully marked on the skin to fix the position surely throughout the present experiment. Sonographs were recorded on videotape with a light signal to synchronize the images with the angular displacement of the tibio-tarsal joint.

Blood sampling. Blood sample was drawn from the ulnar vein at all tests to measure creatine kinase (CK) activity. Sampling at Post was performed at 3 min after LLEE. Blood was taken also from fingertip at Pre, Post and 2H to measure blood lactate (B-LA) concentration. In Post it was done immediately after, 1 min after, 3min after and 5 min after LLEE. CK activity and B-LA were analyzed at 25°C with a CK ultraviolet test kit (Boehringer Mannheim, Germany) and with a commercial kit (Biochemica Boeringer GmbH, Germany).

Data analysis. APF torque, angular displacement and EMG signals sampled at 1kHz (Cudas, Dataq Instruments Inc., USA) were simultaneously recorded. APF torque was filtered at 75 Hz with a Butterworth type 4th-order zero-lag low-pass filter to remove the high frequency noise. Since APF torque elicited by SDF involved an inertial reaction torque induced by the pedal movement, it was subtracted from the APF torque. SDF-elicited APF torque normally comprises two components: an initial component where force increases immediately after the SDF and a twitchlike component with a longer latency. The latter is mostly generated by the stretch reflex EMG response. Therefore, the latter components was defined as reflex torque (RT) and was measured every repetition and averaged.

EMG signals were high-pass filtered at cutoff frequency of 10 Hz and full-wave rectified. In stretch reflex measurements, the short-latency stretch reflex (SLSR) and long-latency stretch reflex (LLSR) were identified on a definition introduced by Lee and Tatton [14]. The onset of SLSR was identified by an onset of consistently steep rise of the rectified EMG activity at about 40 ms after SDF. The end of SLSR or the onset of LLSR was identified by the lowest rectified EMG activity followed by the second sharp rise at about 60ms after SDF. SLSR showed two narrow peaks. Since they represent positive and negative components of one biphasic potential in the raw EMG signal, a sum of them was defined as peak-to-peak (p-to-p) amplitude. In MVC measurements, average EMG (aEMG) was calculated for 100 ms after the MVC torque reached the maximum.

SLSR p-to-p amplitude and RT were divided by aEMG and APF torque at MVC respectively to remove individual differences in EMG activity and APF torque. These data obtained in all trials performed by all subjects were plotted to analyze its relationships with a linear regression.

For measuring displacement of fascicular insertion points in the aponeurosis (FIPA) of Sol and GM, X-Y coordinates of the FIPA were digitized on muscle sonographs recorded and were convert into real coordinates. Displacement of the FIPA durin SDF of 8 deg in LLEE and during shortening and lengthening over 10 deg before SDF in stretch reflex measurements was calculated and averaged. During LLEE the analysis was performed from 1st to 10th (initial phase), from 895th to 905th (middle phase) and from 1790th to 1800th (last phase) of repetition.

Statistics. A one-way analysis of variance (ANOVA) was used to test all variables for significant differences among the tests. When the result of the ANOVA was significant ($p < 0.05$), Fisher's post-hoc test was used to assess the source of difference ($p < 0.05$)

RESULTS

In the present study, only SLSR was analyzed because LLSR was too small to confirm its p-to-p amplitude. While the tibio-tarsal joint rotates over 10 deg before SDF, APF torque decreased by 4.20 ± 1.61 Nm in pre-SHO and increased by 3.66 ± 1.30 Nm in pre-LEN at Pre. Its decrease and increase altered significantly only at Post compared with at Pre. They increased by 6.92 ± 2.67 Nm in pre-SHO ($p < 0.05$) and by 5.38 ± 1.80 Nm in pre-LEN ($p < 0.05$) at Post.

SLSR latency. Pre-SHO showed significantly longer SLSR latencies ($48.3 \pm 4.1 - 49.6 \pm 4.2$ ms in SOL and $46.2 \pm 3.7 - 47.3 \pm 4.0$ ms in GM) than the other conditions at all tests ($p < 0.05 - 0.01$, Table 1). The SLSR latency remained unchanged before and after LLEE in all conditions.

Table 1 Latencies of short-latency stretch reflex

| | | | | | | Unit: ms | |
|--------|------------|----------------|----------------|----------------|-------------|--------------|--|
| Muscle | Test | Pre-ISO | Pre-SHO | Pre-LEN | Difference | | |
| SOL | Pre | 43.3 ± 4.1 | 48.5 ± 4.1 | 41.9 ± 4.1 | ISO < SHO * | LEN < SHO ** | |
| | Post | 43.5 ± 4.3 | 48.4 ± 4.3 | 44.4 ± 2.6 | ISO < SHO * | LEN < SHO * | |
| | 2H | 43.5 ± 4.0 | 49.6 ± 4.2 | 42.1 ± 5.2 | ISO < SHO * | LEN < SHO ** | |
| | 2D | 42.9 ± 3.9 | 48.9 ± 4.1 | 41.9 ± 4.5 | ISO < SHO * | LEN < SHO ** | |
| | 6D | 42.9 ± 3.7 | 48.3 ± 4.1 | 41.9 ± 4.0 | ISO < SHO * | LEN < SHO ** | |
| | Difference | n.s. | n.s. | n.s. | | | |
| GM | Pre | 41.0 ± 4.0 | 46.5 ± 3.6 | 39.9 ± 3.6 | ISO < SHO * | LEN < SHO ** | |
| | Post | 41.0 ± 4.0 | 46.4 ± 4.0 | 41.8 ± 2.6 | ISO < SHO * | LEN < SHO * | |
| | 2H | 41.1 ± 4.1 | 47.3 ± 4.0 | 40.1 ± 4.3 | ISO < SHO * | LEN < SHO ** | |
| | 2D | 40.6 ± 4.2 | 46.6 ± 4.1 | 40.0 ± 3.9 | ISO < SHO * | LEN < SHO ** | |
| | 6D | 40.6 ± 4.1 | 46.2 ± 3.7 | 40.0 ± 4.1 | ISO < SHO * | LEN < SHO ** | |
| | Difference | n.s. | n.s. | n.s. | | | |

*: $p < 0.05$ and **: $p < 0.01$

SLSR p-to-p amplitude. SLSR p-to-p amplitude of SOL was significantly larger in pre-ISO than in the other conditions at Pre ($p < 0.05$, Fig.1). However, the effects of LLEE on the SLSR p-to-p amplitude were similar among three conditions, which showed the following bimodal trend of recovery: an immediate decline after the LLEE, temporary recovery at 2H, delayed decline at 2D and final recovery at 6D. Pre-ISO and Pre-SHO showed significant decreases at Post and at 2D compared with at Pre ($p < 0.05 - 0.001$). Although Pre-LEN did not show a significant decrease at 2D, it showed significant changes between at Post and at 2H ($p < 0.001$), between at 2H and at 2D ($p < 0.001$), and between at 2D and at 6D ($p < 0.05$). In particular, Pre-LEN showed a significant increase at 2H compared with at Pre (1.57 ± 0.68 times, $p < 0.05$). Changes in SLSR p-to-p amplitude of GM were similar to those of SOL.

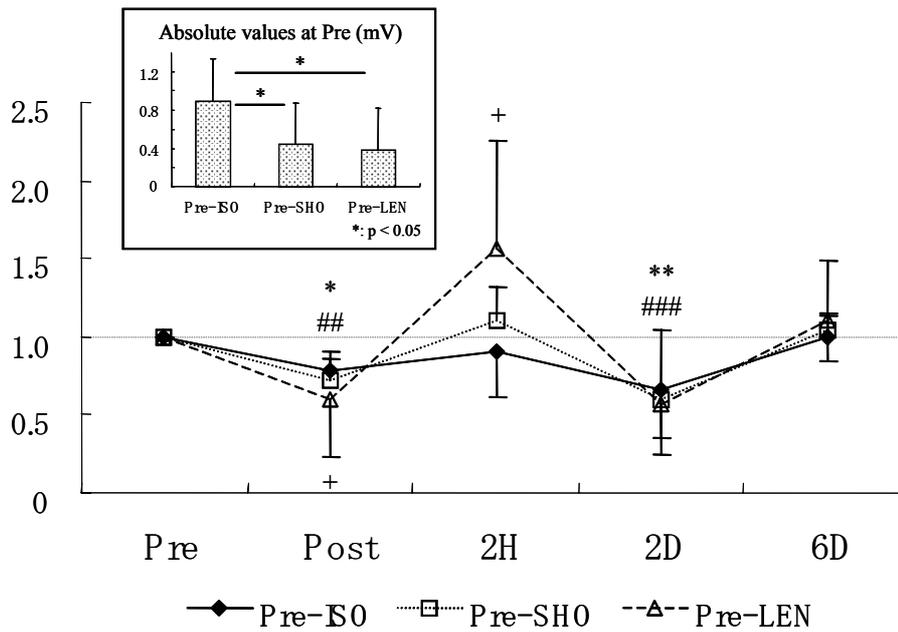


Fig.1 Relative changes in SLSR p-to-p amplitudes of SOL. A bar graph in a left top frame shows absolute values of the SLSR p-to-p amplitude at pre-test. *, # and + indicate significant changes ($p < 0.05$, 0.01 and 0.001) compared with pre-test in pre-ISO, pre-SHO and pre-LEN, respectively.

APF torque elicited by the stretch reflex. RT was significantly larger in pre-ISO than in the other conditions at Pre ($p < 0.01 - 0.001$, Fig.2). Changes in RT before and after LLEE were smaller than those in the SLSR p-to-p amplitude. An obvious change was observed at 2D in pre-LEN as results of significant changes between at 2H and at 2D ($p < 0.05$) and between at 2D and at 6D ($p < 0.05$).

Relationships between SLSR p-to-p amplitude and reflex torque. Fig.3 shows linear relationships between SLSR p-to-p amplitude divided by aEMG at MVC and RT divided by MVC torque. High correlation coefficients were observed between the two variables ($0.721 - 0.921$ ($p < 0.001$) in pre-ISO, $0.737 - 0.904$ ($p < 0.001$) in pre-SHO and $0.578 - 0.969$ ($p < 0.001$) in pre-LEN). Pre-ISO showed the largest RT per SLSR p-to-p amplitude of three conditions in all tests. Slopes of the linear regression lines ranged from 0.082 to 0.104 Nm/mV in pre-ISO, from 0.061 to 0.075 Nm/mV in pre-SHO, and from 0.04 to 0.071 Nm/mV in pre-LEN.

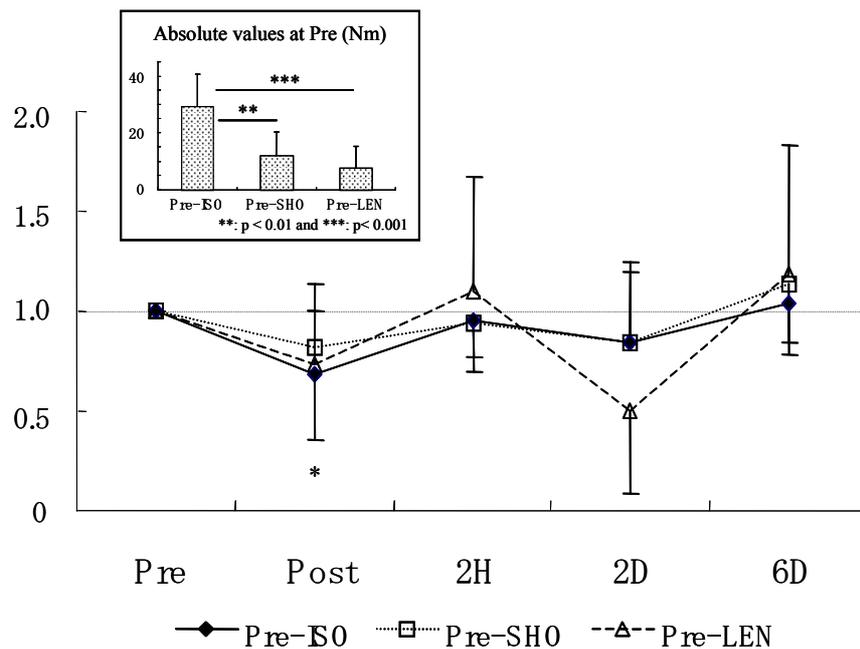


Fig.2 Relative changes in reflex torque. A bar graph in a left top frame shows absolute values of the torque at pre-test. * indicates a significant change ($p < 0.05$) compared with pre-test in pre-ISO.

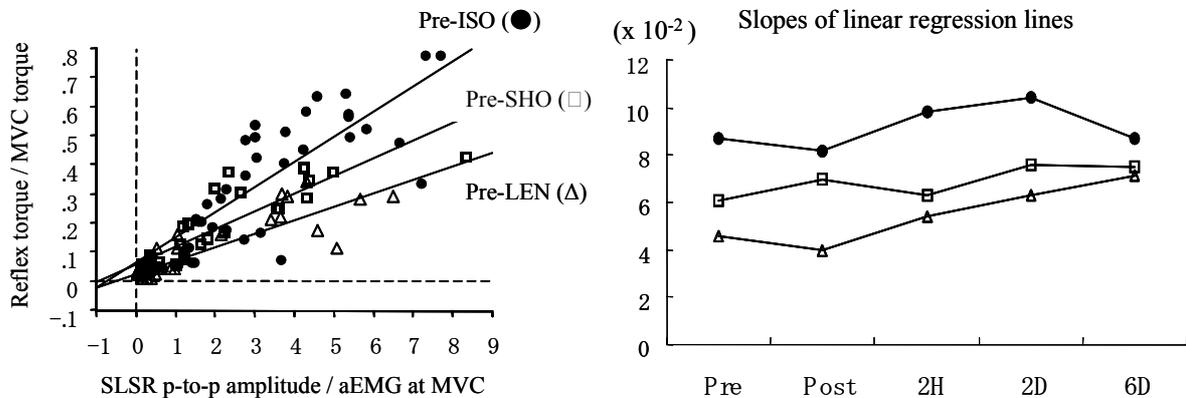


Fig.3 Relationships between SLSR p -to- p amplitude and reflex torque (left panel). The p -to- p amplitude and torque were divided by aEMG and torque at MVC, respectively. Data of all trials performed by all subjects were plotted. A right panel shows changes in slopes of linear regression line between the two variables.

APF torque evoked by a single twitch. No significant differences in ST torque were observed among three conditions at Pre (Fig.4), which was different from results observed in RT. ST torque indicated significant decreases at Post compared with Pre in all conditions ($p < 0.05 - 0.01$). On the other hand, there were significant differences in EMD of ST torque among three conditions at Pre ($p < 0.001$). An extremely short EMD observed in pre-SHO (2.4 ± 2.1 ms at Pre) increased after LLEE significantly ($p < 0.05$), which was not observed in the other conditions.

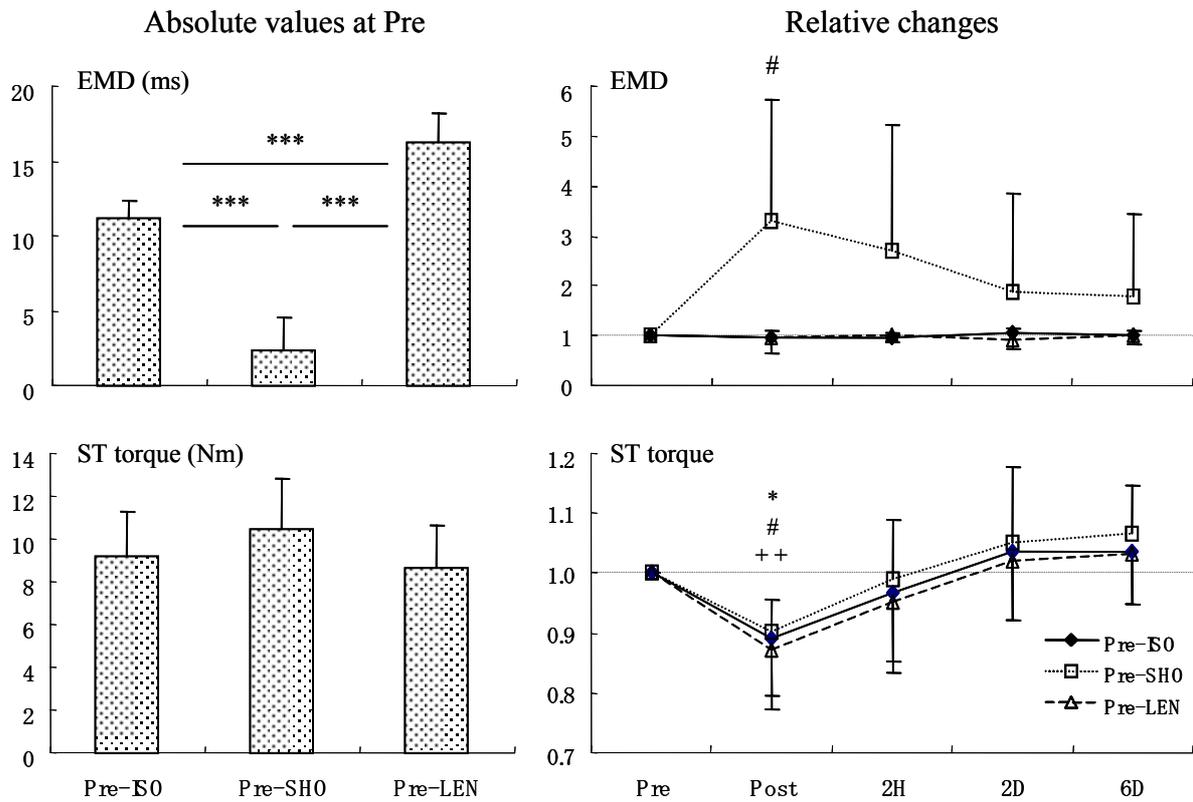


Fig.4 Electromechanical delay (EMD) and single twitch (ST) torque. Left panels show their absolute values at pre-test. *** indicates a significant difference between three conditions ($p < 0.001$). Right panels show relative changes in EMD and ST torque. *, # and + indicate significant changes ($p < 0.05$ and 0.01) compared with pre-test in pre-ISO, pre-SHO and pre-LEN, respectively.

Torque and aEMG at MVC. MVC torque depending on the tibio-tarsal joint angle decreased at Post significantly compared with at Pre ($p < 0.05 - 0.001$, Table 2). Although aEMG slightly showed bimodal trends, significant changes were rarely shown.

Table 2 Ankle plantar flexion torque and average EMG at MVC

| Variable | Unit | Angle (deg) | Pre | Post | 2H | 2D | 6D |
|------------|------|-------------|--------------------|-------------------|-------------------|--------------------|--------------------|
| MVC torque | Nm | 80 | 85.9 ± 22.5 | 69.0 ± 16.6 ** | 75.8 ± 21.0* | 77.0 ± 19.3 | 83.6 ± 23.1 |
| | | 90 | 71.5 ± 18.1 | 63.5 ± 17.7 * | 65.0 ± 18.8 | 67.4 ± 16.7 | 70.1 ± 18.2 |
| | | 100 | 48.1 ± 13.1 | 40.5 ± 13.3 ** | 45.8 ± 12.0 | 43.2 ± 12.1 ** | 46.7 ± 13.7 |
| | | Difference | 100deg < 80deg ### | 100deg < 80deg ## | 100deg < 80deg ## | 100deg < 80deg ### | 100deg < 80deg ### |
| | | | 100deg < 90deg # | 100deg < 90deg ## | 100deg < 90deg # | 100deg < 90deg ## | 100deg < 90deg # |
| aEMG (SOL) | µV | 80 | 226 ± 83 | 181 ± 58 | 217 ± 60 | 193 ± 56 | 222 ± 78 |
| | | 90 | 249 ± 72 | 201 ± 46 * | 237 ± 47 | 219 ± 49 | 248 ± 59 |
| | | 100 | 291 ± 129 | 238 ± 69 | 268 ± 88 | 222 ± 85 ** | 255 ± 96 |
| | | Difference | n.s. | n.s. | n.s. | n.s. | n.s. |
| | | | | | | | |
| aEMG (GM) | µV | 80 | 230 ± 47 | 185 ± 67 | 226 ± 74 | 215 ± 49 | 257 ± 69 |
| | | 90 | 239 ± 62 | 214 ± 67 | 233 ± 65 | 237 ± 76 | 254 ± 53 |
| | | 100 | 266 ± 104 | 230 ± 78 | 315 ± 140 | 231 ± 100 | 268 ± 91 |
| | | Difference | n.s. | n.s. | n.s. | n.s. | n.s. |
| | | | | | | | |

* and #: p < 0.05, ** and ##: p < 0.01, and *** and ###: p < 0.001

AL: Activation level

Note) * Shows significant differences compared with pre-test at each tibio-tarsal joint angle.

Shows significant differences among 80, 90 and 100 deg of tibio-tarsal joint

APF torque evoked by a double twitch in relaxed muscles. Significant differences in DTr torque were observed among 80, 90 and 100 deg of the tibio-tarsal joint angle (Fig.5). Although DTr torque decreased significantly after LLEE at all angles ($p < 0.01 - 0.001$), its decrease was remarkable at 100 deg.

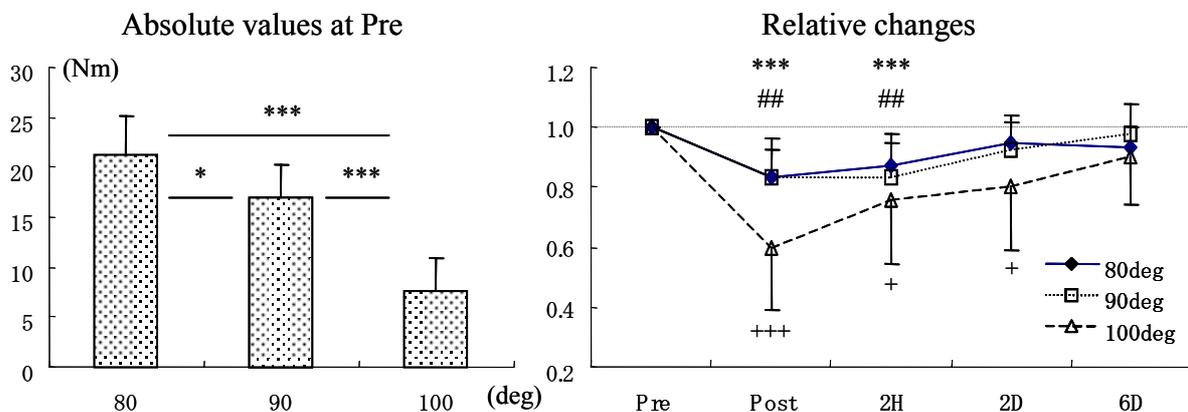


Fig.5 Double twitch torque in relaxed muscles (DTr). A left panel shows the absolute values at pre-test against the tibio-tarsal joint angle. * and *** indicate significant differences between three conditions ($p < 0.05$ and $p < 0.001$, respectively). A right panel shows relative changes in DTr. *, # and + indicate significant changes ($p < 0.05$, 0.01 and 0.001) compared with pre-test in pre-ISO, pre-SHO and pre-LEN, respectively.

Sagittal-plane muscle sonographs. LLEE significantly decreased displacement of FIPA of SOL elicited by SDF during LLEE (Fig.6). It could be also confirmed visually that movements of fascicles obviously got smaller. The displacement that was 5.0 ± 1.6 mm at the beginning of LLEE decreased by 74.5 ± 23.6 % at the end of LLEE ($p < 0.01$). In stretch reflex measurements, recovery of FIPA

displacement elicited by shortening and lengthening before SDF tended to show a bimodal trend. The displacement that was 6.7 ± 1.3 mm at Pre decreased by 69.5 ± 29.5 % at Post ($p < 0.05$) and by 78.5 ± 19.9 % at 2D (n.s.) in pre-SHO. Also in pre-LEN it decreased by 80.1 ± 17.3 % at Post ($p < 0.05$) and by 83.1 ± 29.9 % at 2D (n.s.) from 7.9 ± 1.5 mm at Pre. Similar results were observed also in GM.

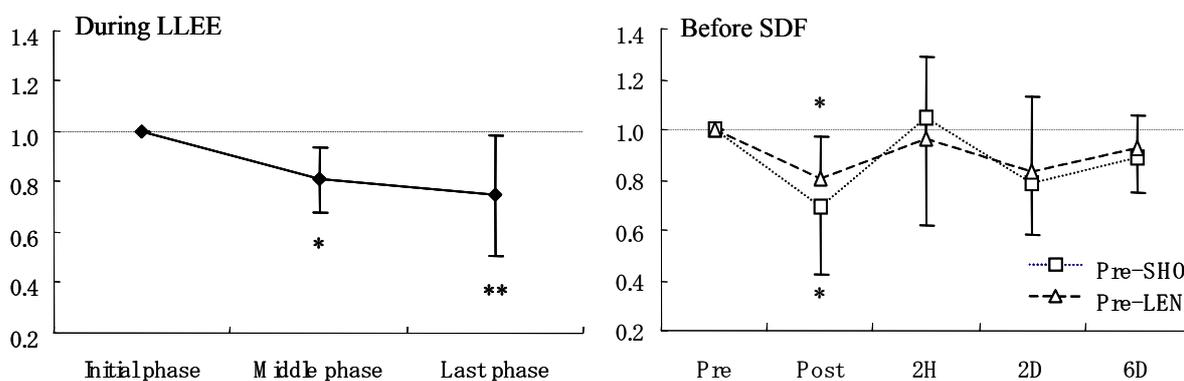


Fig.6 Displacement of fascicular insertion in the aponeurosis on sagittal-plane soleus muscle sonograph. Figures shows shifts of the fascicular insertion elicited by SDF during LLEE (A), and during shortening (pre-SHO) and lengthening (pre-LEN) of the muscle-tendon complex before SDF (B) as relative values compared with the initial phase (1th - 10th of the repetition) and with pre-test, respectively. * over standard deviation bars indicates a significant change compared with pre-test.

Creatine kinase activity and blood lactate concentration. No significant changes in CK and B-LA were observed before and after LLEE. The CK ranged from 161.4 ± 45.9 U/l at 6D to 205.0 ± 90.4 U/l at 2D. The B-LA ranged from 2.0 ± 0.6 mmol/l at Pre to 2.4 ± 1.0 mmol/l at 5 min after the LLEE. On the other hand, subjects complained of muscle soreness and tired feeling of APF muscles at 2D.

DISCUSSION

Results of the present study indicated that LLEE used in the present study induced primarily peripheral fatigue. The LLEE induced a bimodal change in SLSR p-to-p amplitude composing of an acute and delayed decrease in all conditions. This was in line with results observed in earlier studies (3, 15, 19). RT also followed the similar bimodal trend. Close relationships between SLSR p-to-p amplitude and RT shown in Fig.3 corroborate the similarity between SLSR p-to-p amplitude and RT. However, no delayed decrease in ST torque evoked by a supra-maximal single E_{shock} instead of SDF suggests less influence of contractile components (CC) on the delayed decrease in RT compared with that at the acute decrease.

In an earlier study (19), we observed disagreement on recovery patterns between SLSR p-to-p amplitude and RT, SLSR p-to-p amplitude followed a bimodal trend while RT did not recover until 7days after a long-lasting low-intensity exercise, when the stretch reflex was elicited by the same SDF pattern as that repeated during LLEE. The difference in recovery process between the present and earlier studies strongly supports that fatigue has a movement-specific effect.

LLEE did not change differences in SLSR latency, SLSR p-to-p amplitude and RT among three conditions. The differences among the three conditions are in agreement with results in earlier studies (17, 18). A result that pre-ISO always showed the largest RT per SLSR EMG activity of three conditions indicates pre-ISO has an advantage over the other conditions on force generated by the stretch reflex. On the other hand, facilitation of SLSR p-to-p amplitude at 2H shown in pre-LEN was not observed in pre-ISO. Moreover, RT per SLSR EMG activity tended to increase after LLEE only in pre-LEN. Since APF muscles were stretched over 8 degrees while being contracted by ES during LLEE, pre-LEN has the closest resemblance to LLEE on the muscle-tendon (M-T) complex behavior. If fatigue has a movement-specific effect, pre-LEN might be more strongly influenced by the following mechanism that can be considered. Fatigue induced by LLEE activated group III and IV afferent nerves (6, 12), which might activate gamma-motoneurons followed by increases in muscle spindle sensitivity and alpha-motoneuron activity (27). No difference in displacement of FIPA between at Pre and at 2H may support that their increases played an important role on facilitation of SLSR p-to-p amplitude at 2H. Large increases in B-LA and CK activity were not observed at 2H compared with at Pre, although metabolic changes can activate group III and IV afferent nerves (10). Since it is also known that group III and IV afferent nerves make a powerful input to inhibitory interneurons, 'facilitation or inhibition' seems to depend on balance between metabolic changes induced by an exercise and afferent nerve activities. However, a question why SLSR p-to-p amplitude was facilitated at 2H in pre-LEN remains unclear.

M-T complex is generally represented as a model comprising of CC surrounded by parallel elastic components and series elastic components (SEC). If the simplest model of M-T complex is adopted, CC and SEC can be roughly regarded as the muscle and tendinous tissue. In this case, decreases in FIPA displacement during and after LLEE in spite of a constant displacement of the tibio-tarsal joint imply the followings: 1) a decrease in sarcomere length stretched during SDF and 2) an increase in SEC displacement. These represent decreased stiffness of the SEC, that is, a decreased spring constant. Differences in sarcomere length at SDF can contribute to differences in RT on the force-length relationship (21). On the other hand, DT torque in relaxed muscles showed the largest decrease at 100 deg of the tibio-tarsal joint where SEC seems to be slacked most strongly after LLEE. EMD of ST torque significantly increased at Post only in pre-SHO in which SEC is shortening before SDF. These

results support the decreased stiffness of SEC after LLEE since only SEC can transmit CC behavior to externals after the slack was stretched out of the SEC (13). Therefore, it is likely that alteration in M-T complex behavior induced by fatigue contributed to bimodal changes in SLSR p-to-p amplitude and RT. However, smaller alteration in DT torque and EMD of ST torque observed at 2D than at Post indicate that its contribution may differ between at Post and at 2D. It seems reasonable to suppose that the acute decrease at Post was, at least partly, related to slack of SEC, whereas the delayed decrease at 2D might be mainly influenced by peripheral inhibition via small muscle afferent group III and IV (14). It has been demonstrated in decerebrate cats (11) and in spinalized rats (20) that the group III and IV activities elicited by electrically induced fatigue inhibit monosynaptic reflex. The present results did not show significant changes of B-LA and CK activity after LLEE. This may be related to size of APF muscles where LLEE was imposed. However, the increment rate of B-LA and CK activity seemed to be considerably high when mass of the shank including APF muscles was taken into consideration. The mass of the shank was only 4.3 ± 0.3 % of the whole body mass (30). In addition, muscle soreness and tired feeling of APF muscles at 2D subjects complained of suggest participation of nociceptive afferents in the delayed decreases because nociceptive signals are transmitted by the afferents. A significant decrease in H-reflex p-to-p amplitude at 2D shown by Ogiso et al. (19) confirms it.

In conclusion, fatigue induced by LLEE elicited bimodal changes in reflex amplitude comprising an acute and delayed decrease, which was independent of background muscle contraction types before SDF. When the SDF pattern used during LLEE was not similar to that used to elicit the stretch reflex, RT also followed the similar bimodal trend. It was likely that alteration in M-T complex behavior and nociceptive afferent activities induced by LLEE contributed to the bimodal changes in SLSR p-to-p amplitude and RT.

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