Effects of Hypodynamia-Hypokinesia on the Muscle Spindle Discharges of Rat Soleus Muscle

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INTRODUCTION

Hypodynamia (absence of weight bearing) and hypokinesia (reduction of motor activity) conditions are present in real microgravity (space flight) or in simulated microgravity when using human or animal models. Hypodynamia-hypokinesia (HH) conditions have been reported to induce changes in many muscular properties mainly in the slow extensor muscles such as the soleus muscle (Edgerton and Roy 1996). On the contrary, no data are available concerning the effects of HH as regards the muscle spindle properties. Two kinds of endings innervate the muscle spindle: the primary and the secondary endings, which arise as the terminations of the Ia and II fibers, respectively (Hulliger 1984; Hunt 1990). The discharge of Ia fibers indicates both the muscular length changes (static sensitivity) and the velocity of length changes (dynamic sensitivity), whereas the discharge of II fibers provides mainly information about the length changes (McCloskey 1978). In a previous study, we have established a classification of rat muscle spindle afferents using ramp-and-hold and sinusoidal stretches (De-Doncker et al. 2003). Our results showed clearly that in the rat, afferent fibers could be clearly divided in two groups: the Ia and II afferents. It appears therefore that the methods that work in cats also work in rats.

In the literature, some data can be found concerning changes in the afferent fiber discharges from muscle spindles when muscles were maintained in a shortened position. In fact, in the gastrocnemius muscle, the muscle spindle structure was preserved after tenotomy, and the rate of muscle spindle discharges was increased (Hnik and Lessler 1973a). After immobilization in plantar flexion of cat peroneus longus muscle, a slight increase in both the static discharge and the dynamic index of Ia fibers in passive spindles has been observed (Gioux and Petit 1993). After a HH period, the discharge of afferent fibers from soleus muscle spindles has never been examined. In HH condition, the soleus was often in a shortened position as after tenotomy and immobilization in a plantar flexion position (Riley et al. 1990), the natural physiological stimulus of muscle spindles being thus removed. Moreover, after a HH period, modifications in elastic properties of soleus muscle and Achilles tendon have been described by several authors. A decrease in the stiffness of isolated soleus muscle (Canon and Goubel 1995) and in Achilles tendon stiffness (Almeida-Silveira et al. 2000) was observed after 3 wk of unloading. The results obtained by Canon and Goubel (1995) were confirmed by Tursel et al. (1999) on isolated skinned fibers of rat soleus muscle. Moreover, the passive tension of in situ rat soleus muscle increased after 7 and 14 days of whole body suspension (Gillette and Fell 1996). A relative increase in the proportion of noncontractile tissue particularly in the soleus and gastrocnemius muscles has also been described (Flynn and Max 1985; Herbert et al. 1988; Templeton et al. 1984). Therefore we suggest that the stretch transmission might be affected after an episode of HH and the electrophysiological afferent discharges of endings consequently modified.

De-Doncker, Laurent, Florence Picquet, Julien Petit, and Maurice Falempin. Effects of hypodynamia-hypokinesia on the muscle spindle discharges of rat soleus muscle. J Neurophysiol 89: 3000–3007, 2003; 10.1152/jn.00875.2002. The aim of this study was to determine whether Ia and II fiber discharges of soleus muscle spindles were modified after a 14-day period of hypodynamia (absence of weight bearing) and hypokinesia (reduction of motor activity). Fifty-one and 38 afferent fibers were studied, respectively, in control and hypodynamia-hypokinesia (HH) groups. Under deep anesthesia (pentobarbital, 30 mg/kg), a L3–L6 laminectomy was performed. Unitary potentials from the L5 dorsal root were recorded in response to ramp-and-hold stretches applied at two stretch amplitudes (3 and 4 mm) and four stretch velocities (6, 10, 15, and 30 mm/s) and to sinusoidal stretches applied at four stretch amplitudes (0.12, 0.25, 0.5, and 1 mm) and six stretch frequencies (0.5, 1, 2, 3, 6, and 10 Hz). In both animal groups, the Ia fibers showed higher dynamic index values, smaller linear range, and higher vibration sensitivity than the II fibers. They also exhibited a pause in their discharges during the stretch release contrary to II fibers, which displayed no pause in their responses. After HH, our results showed that for both fiber types all parameters measured under ramp-and-hold stretches (except the static sensitivity) were significantly increased and under sinusoidal stretches, the vibration sensitivity increased, and the response amplitude only increased at 0.12-mm stretch amplitude. The linear range of Ia afferents was limited to 0.12 mm, whereas it was unchanged for the II fibers. After HH, the stretches could be better transmitted to the muscle spindles, probably resulting from changes in passive mechanical properties of the soleus.

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Thus the aim of this study was to determine whether the Ia and II fiber discharges of soleus muscle spindles were modified after a 14-day period of HH.

METHODS

Animal groups

Experiments were performed on 27 male Wistar rats (IFFA CREDO) weighing 280–300 g and randomly divided into two groups: control rats (CONT: n = 15) and hypodynamia-hypokinesia rats (HH: n = 12). To maintain minimal distress, all the rats were housed individually in separate cages and were allowed food and water ad libitum. The rats were acclimatized at a 25°C room temperature with a 12:12-h light-dark cycle for 1 wk before the experiments began. Animals of the HH group were hindlimb unloaded by the tail for 14 days using Morey’s model (Morey et al. 1979). Briefly, the tail of each rat was washed, cleaned, dried, and wrapped in an antiallergic orthopedic tape-adhesive plaster. This cast, covering less than half of the tail, was secured to an overhead swivel, mounted at the top of the cage and permitting free 360° rotation of the animals. The rats were unloaded at 30° head-down angle to mimic fluid shifts characteristic of weightlessness. All the experiments as well as the maintenance conditions of the animals received authorizations from both the Agricultural and Forest Ministry and National Education Ministry (Veterinary Service of Health and Animal Protection: authorization 59-00980).

Surgical technique

Fourteen days after the acclimatization period, each rat of control and HH groups was anesthetized with intraperitoneal injection of pentobarbital sodium (30 mg/kg). Supplementary injections (15 mg/kg) were provided when necessary. At the end of the experiments, the animals were killed with a lethal dose of anesthetic (100 mg/kg). Under deep anesthesia, the right soleus muscle was exposed while care was taken not to damage the main blood supply or the soleus nerve trunk. All the other muscles of the thigh and lower right hindlimb were denervated. Under a stereomicroscope, the soleus nerve was freed and cleaned. In situ, both the minimal [L

min; 3 ± 0.08 (SE) cm] muscle length, measured at full ankle extension, and the maximal [L

max; 4.1 ± 0.02 cm] physiological muscle length, measured at full ankle flexion, were determined.

A laminectomy was performed between L4 and L6. A mineral oil pool was achieved with the dorsal skin of the rat around the incision over the spine. The right L4 and L5 dorsal and ventral roots were transected near their entry into the spinal cord. The right dorsal L5 containing the majority of the soleus afferent fibers was severed from the other roots. It was split into fine filaments until a filament that contained a single fiber innervating the soleus muscle spindles was isolated. A filament was considered to contain a single afferent fiber from the soleus muscle spindle if the stimulation (Grass Instruments S88, Quincy, MA) of the filament evoked an all-or-none action potential in the electroneurogram recorded on the muscle nerve. Isolated afferents from muscle spindles were distinguished from Golgi tendon organs by a pause in their discharge during a twitch or a brief tetanic contraction. Three or four afferent fibers were studied per animal in both CONT and HH groups.

The animal was then placed in a prone position on a heated steel blanket (Harvard), and the dissected right hindlimb was placed in a bath filled with circulating thermostatically controlled (37°C) mineral oil. The tendon of the soleus muscle was connected to a servocontrolled electromagnetic puller coupled with a force transducer (developed in our laboratory), which was used to determine the twitch muscle force and to perform controlled ramp-and-hold and sinusoidal muscle stretches.

Data recordings

The twitch tension of the soleus muscle was obtained by stimulation of the soleus nerve using a monopolar electrode located under the soleus nerve. For the CONT group, the twitch tension was 0.301 ± 0.01 (SE) N and was decreased after a HH period (0.121 ± 0.005 N) according to results obtained in the literature (Edgerton and Roy 1996; Falempin and In-Albon 1999). The muscle length for maximal twitch response was measured. The soleus muscle length was then set to L

min (3 ± 0.08 cm). To record the electroneurogram, a monopolar platinum electrode was positioned under the soleus nerve and a reference electrode was inserted into the neighboring denervated muscle mass. A monopolar platinum electrode placed under the dorsal root filament was used to record the afferent responses. The afferent fibers were stimulated to measure their conduction velocities. The antidromic potential was recorded on the soleus nerve electromyogram. The axonal conduction velocities were calculated as the ratio of the nerve conduction distance to the antidromic spike delay. The conduction distance was measured after postmortem dissection. Muscle spindle afferent spikes were recorded using a digital tape recorder (DTR 1404, Biologic Science Instruments) and a CED 1401 interface with Spike 2 processing package (Cambridge Electronic Design) that converted the analogic discharge to an instantaneous discharge frequency.

Parameters used to identify the muscle spindle afferents

RAMP-AND-HOLD STRETCH. Ramp-and-hold stretches were applied at three different initial muscle lengths: L

min +10% + 15%, L

min +20% (110, 115, and 120% of L

min respectively). These lengths were set using a micrometer and were included in the physiological range comprised between L

min and L

max muscle lengths. For each length, after a prestretch of 1 mm maintained during all the experiments, ramp-and-hold stretches were applied with amplitude ranges of 3 mm (S1) and 4 mm (S2) at 6, 10, 15, 30 mm/s velocities. The plateau phase was held for 5 s. Two stretches were separated by 25 s. Each series of stretches was repeated five times with the same parameters.

Several parameters were measured to characterize primary and secondary responses: 1) the value of the resting discharge (RD) during the 0.5 s before the start of the stretch, 2) the dynamic peak discharge (DP), which was the value of the discharge frequency at the end of the ramp phase, 3) the final static value (FST), which was the mean value of the discharge frequency at the end of the 5-s plateau phase, 4) the dynamic index (DI), which was the difference between the dynamic peak (DP) and the frequency at 0.5 s after completion of the stretch (Matthews 1963), 5) the presence or the absence of a discharge during the stretch release (Hunt et al. 1978; Hunt 1990), and 6) the static sensitivity, which was the difference between the static response (FST – RD) divided by the amplitude of the stretch: (FST – RD amplitude of the stretch) (Boyd 1981). The significance of RD, DP, DI, and FST parameters is illustrated in Fig. 1.

SINUSOIDAL STRETCH. Sinusoidal stretches (0.5, 1, 2, 3, 6, 10 Hz frequencies) and vibrations (50- and 100-Hz frequencies) of 0.12, 0.25, 0.5, and 1 mm amplitudes were applied at L

min +20% muscle length.

Several parameters were used: 1) the amplitude of the afferent response equal to half the peak-to-peak response, 2) the sensitivity to a sinusoidal stretch that was the ratio of the afferent response by the stretch amplitude (Matthews and Stein 1969), 3) the modalities of the discharge of the afferent (continuous or discontinuous). For a given frequency, the range of amplitude in which the afferent discharge did not fall silent at any time during sinusoidal stretching and with slight distortion was called “linear range” (Matthews and Stein 1969). The response was considered as linear when the discharge was sinusoidally modulated. 4) The vibration responses to 50- and 100-Hz stretch frequencies applied at the four stretch amplitudes were also studied.
Statistical analysis

The linear regression slopes of DI as a function of the stretch velocities were determined for each afferent fiber from muscle spindles. From these slope values, a distribution histogram was achieved using GraphPad Prism 3 software to determine the presence of two fiber populations. The significant differences of results expressed as means ± SE were established using a nonpaired Student t-test (P < 0.05). The significances between the linear regression straight lines (slopes, correlation coefficients, interception values with the y axis) were determined by GraphPad Prism 3 (P < 0.0001).

Asterisks (*) indicated a significant difference with the CONT group, and daggers (†) with the Ia fibers in the same animal group. Double daggers (‡) indicated a significant difference between linear regression straight lines of Ia and II fibers with paired fibers of the CONT group (P < 0.0001).

RESULTS

Fifty-one and 38 afferent fibers were respectively studied in the CONT and HH groups. The data obtained after a 14-day period of HH were compared with results of the CONT group.

Muscle length

Our results showed no significant difference between CONT (3 ± 0.08 cm, n = 15) and HH (2.8 ± 0.06 cm, n = 12) muscle lengths measured at full extension of the ankle.

Comparison of Ia and II fiber responses in CONT versus HH groups

RAMP-AND-HOLD STRETCH. Under ramp-and-hold stretch of 3 mm amplitude applied at \( L_{\text{min}} + 20\% \) and at 3 mm/s stretch velocity, two types of responses were observed in muscle spindles of the HH group similarly to the CONT group (De-Doncker et al. 2003). These fiber responses are illustrated in Fig. 1 (A and B). However, the mean DP values of Ia (n = 18, 168 ± 4.9 Hz) and II (n = 20, 77 ± 4.2 Hz) fiber responses were significantly different from Ia (n = 26, 125 ± 6.7 Hz) and II (n = 25, 63 ± 3.5 Hz) fibers of the CONT group.

The changes in RD, DI, and FST parameters of Ia and II fibers observed after HH were illustrated in Fig. 2. This figure shows the Ia and II fiber responses of CONT (A and C) and HH (B and D) groups under 3 mm amplitude and 30 mm/s stretch velocity of a ramp-and-hold stretch.

Whatever the stretch amplitude, the muscle length, and the stretch velocities, the static sensitivities of Ia and II fibers did not change after HH.

Resting discharge. After a period of HH, the RD of both Ia and II fibers significantly increased (P < 0.05). This was illustrated in Fig. 3.

Dynamic index. Figure 4A illustrates the DI linear regression of Ia and II fibers for CONT and HH groups at \( L_{\text{min}} + 10\% \) and 3-mm amplitude. Similar figures were obtained for 3-
4-mm amplitudes at \( L_{\text{min}} + 15\% \) and \( L_{\text{min}} + 20\% \) (data not shown). DI increased with the stretch velocity for Ia and II fibers of CONT and HH groups. However, in both groups, whatever the stretch amplitude and the muscle length, the correlation coefficient and the linear regression slopes between DI and stretch velocities of Ia fibers were significantly higher than those of the II fibers. Therefore for Ia fibers, the increase in DI parameter was better correlated with the stretch velocity than for II fibers.

After HH, whatever the stretch amplitude and the muscle length, the DI linear regression straight lines were shifted toward higher values for both Ia and II fibers (\( P < 0.0001 \)). However, the slopes and correlation coefficients of the linear regression straight lines were unchanged for both fiber types.

**Final static value.** Figure 4B illustrates the FST linear regression of Ia and II fibers for CONT and HH groups at 3-mm amplitude and \( L_{\text{min}} + 10\% \) muscle length. Similar variations were observed for 3- and 4-mm amplitudes at \( L_{\text{min}} + 15\% \) and \( L_{\text{min}} + 20\% \). In both animal groups, the FST values of Ia and II fibers did not increase with the stretch velocity. For both CONT and HH groups, whatever the initial muscle length and the stretch amplitude, the FST values of Ia fibers were slightly higher than those of the II afferents.

In HH group, whatever the stretch amplitude and the muscle length, the FST linear regression straight lines between FST and stretch velocities were shifted toward higher values both for Ia and II fibers (\( P < 0.0001 \)).

**SINUSOIDAL STRETCH. Linear range.** Experiments were performed at \( L_{\text{min}} + 20\% \) under sinusoidal stretches and vibration stimuli on 33 and 38 endings for CONT and HH groups, respectively. Figure 5 shows the Ia and II responses of CONT and HH groups to 0.5-Hz stretches with amplitudes ranging from 0.12 to 1 mm.

For the CONT group, the linear range of Ia afferents (\( n = 15 \)) extended from 0.12 (between 0.5 and 3 Hz) to 0.25 (between 0.5 and 3 Hz), and from 0.12 to 1 mm (between 0.5 and 3 Hz) for II fibers (\( n = 18 \)).

After HH, the linear range of II fibers (\( n = 20 \)) was unchanged. On the contrary, for Ia fibers (\( n = 18 \)), the linear range was limited to 0.12 mm.

**Response amplitude and sensitivity.** The response amplitude linear regression straight lines of Ia and II fibers were obtained under 0.12-mm sinusoidal stretch for both animal groups (not illustrated).

For the CONT group, within the linear range of Ia afferents, II fibers had a significantly smaller response amplitude and sensitivity than Ia afferents at all stretching frequencies (Table 1). Moreover, the response amplitude of Ia and II afferents increased significantly with the stretch amplitude.

The same evolution in the response amplitude and sensitivity was observed for Ia and II fibers of the HH group except at 0.25 mm for Ia fibers when the response became nonlinear.
After HH, the response amplitude and sensitivity of both fiber groups were significantly ($P < 0.0001$) increased at 0.12-mm stretch amplitude (Table 1). Indeed, the linear regression straight lines of Ia and II fibers were shifted toward a higher level and the slopes increased. The slopes of linear regression straight line of Ia fibers were, respectively, 0.44 and 0.85 for CONT and HH groups, and, respectively, 0.52 and 0.67 for II fibers of CONT and HH groups. More than 0.12-mm stretch amplitude, no significant difference was seen in the amplitude and sensitivity of Ia and II fibers between the two animal groups.

Vibration sensitivity. Vibrations were only applied at $L_{\text{min}} + 20\%$ to the distal tendon of the soleus muscle.

For the CONT group, at 50 Hz and with an 0.12-mm stretch amplitude, the discharges of Ia fibers were 1:1 driven (1 imp/sinusoidal cycle) by vibration. At 100 Hz and for the same stretch amplitude, 12 Ia fiber responses have a 1:1 driving and 3 Ia afferent responses show a 1:2 driving. When the amplitude of the vibrations was increased to 0.25 mm, the responses of Ia fibers were all driven by the 100-Hz vibrations. For the 18 II afferents, driving was rarely observed with vibrations whose amplitude exceeded 0.25 mm. The discharge of every second-ary ending was 1:1 driven by a 50-Hz vibration with a 1-mm amplitude. At 1-mm amplitude, almost all the secondary endings were 1:1 driven by a 100-Hz vibration.

After HH, all the Ia fibers were 1:1 driven by 50- and 100-Hz vibrations with 0.12-mm stretch amplitude. The vibration sensitivity of II fibers was increased. Indeed, the II afferents chiefly discharged to 1 imp/sinusoidal cycle with 0.5-mm vibrations applied at 50 and 100 Hz.

Conduction velocities. The mean conduction velocities of Ia fibers were significantly higher than those of II fibers for both animal groups. The mean conduction velocities of Ia fibers were $43.3 \pm 0.8$ and $45 \pm 0.9$ m/s for CONT and HH groups ($P > 0.05$), respectively. For the II fibers, the mean in CONT group was $33.9 \pm 0.9$ and $35.8 \pm 1.3$ m/s in HH group ($P > 0.05$).

Discussion

The aim of this study was to determine whether the discharges of the Ia and II fibers were modified after HH. Our results showed that under a ramp-and-hold stretch, RD, DI, and FST parameters of Ia and II fibers were significantly increased. On the contrary, the static sensitivity was unchanged. Under a sinusoidal stretch, the response amplitude and sensitivity of both fiber types were only increased at 0.12-mm stretch amplitude, the smallest value of the range used. Moreover, the vibration thresholds of II fibers were decreased. From our experiments, we can suggest that the stretch was better detected by muscle spindles after HH.

This effect could be due to a change in muscle spindle structure. Indeed, Maier et al. (1972) showed an intrafusal fiber atrophy after an immobilization of cat’s medial gastrocnemius muscle in a shortened position. However, in studies of Soukup et al. (1990) and De-Doncker et al. (2002), it has been demonstrated that the muscle spindle and intrafusal fiber numbers and the cross sectional area (CSA) of intrafusal fibers were not modified after a 14-day period of HH. Therefore the previous hypothesis can be discarded. Modifications observed in Ia and II fiber discharges after a HH period could be also due to a shorter soleus muscle. However, our results showed no significant difference between CONT (3 ± 0.08 cm) and HH (2.8 ± 0.06 cm) muscle lengths measured at full extension of the ankle. Our results were in accordance with the data obtained by Gillette and Fell (1996), Edgerton and Roy (1996), and Brown et al. (1999) after 2 wk in HH. In our experiments, the effects of a possible shortening of the soleus muscle on the spindle discharges could therefore be discarded. Moreover, the muscle lengths on which stretches were applied were always expressed as a percentage of the minimum physiological muscle length (i.e., $L_{\text{min}} + 10\%$, $L_{\text{min}} + 15\%$, $L_{\text{min}} + 20\%$) to prevent the possible effect of muscle shortening.

The effects observed on afferent responses from soleus muscle spindles after HH, could be explained by changes in muscle elasticity described in the literature. According to the model of Shorten (1987), the elastic properties of a muscle depend on several structures: the series elastic component (SEC) divided into an active part (cross bridges of fiber types) and a passive part (tendons) and the parallel elastic component (PEC: sarcolemma, titin, connective tissue). The SEC was only developed by the contractile component to the joints. On the contrary, in passive conditions, only the PEC was implied. Titin, sarcolemma and connective tissue (endomysium, perimysium, epimysium) participated in the passive resistance to stretch (Gajdosik 2001).

After HH, modifications in stiffness of soleus muscle and...
Achilles tendon have been observed. However, the results were contradictory. A decrease in the stiffness of isolated soleus muscle (Canon and Goubel 1995) and in Achilles tendon stiffness (Almeida-Silveira et al. 2000) was observed after 3 wk of unloading. These changes in elastic properties were interpreted in terms of modifications occurring in the active part and the passive part of the SEC (Canon and Goubel 1995). According to these authors, an increase in SEC compliance as a consequence of HH had probably two origins: a relative increase in fast-twitch fibers (adaptation of the active part of the SEC) and alterations in tendinous structures (adaptation of the passive part of the SEC). Indeed, hindlimb unweighting has been found to result in a higher proportion of type II fibers in the soleus muscle (Edgerton and Roy 1996). These fibers are less stiff than the slow type I fibers (Petit et al. 1990). After HH, in rat soleus muscle, Tourse et al. (1999) also reported an
TABLE 1. Stretch frequencies at 0.12-mm amplitude

<table>
<thead>
<tr>
<th>Fiber types (groups)</th>
<th>0.5 Hz</th>
<th>1 Hz</th>
<th>2 Hz</th>
<th>3 Hz</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ia (CONT)</td>
<td>4.9 ± 0.2</td>
<td>5.5 ± 0.2</td>
<td>6.2 ± 0.2</td>
<td>6.9 ± 0.3</td>
</tr>
<tr>
<td>Ia (HH)</td>
<td>6.3 ± 0.3*</td>
<td>7.1 ± 0.4*</td>
<td>7.8 ± 0.4*</td>
<td>8.5 ± 0.4*</td>
</tr>
<tr>
<td>II (CONT)</td>
<td>3.3 ± 0.1†</td>
<td>3.9 ± 0.2†</td>
<td>4.3 ± 0.2†</td>
<td>4.7 ± 0.2†</td>
</tr>
<tr>
<td>II (HH)</td>
<td>4.8 ± 0.2††</td>
<td>5.2 ± 0.2††</td>
<td>5.8 ± 0.2††</td>
<td>6.5 ± 0.2††</td>
</tr>
</tbody>
</table>

* Significant difference with the CONT group. †† Significant difference with the Ia fibers in the same animal group.

Response amplitude values (means ± SE) of Ia and II fibers in control (CONT; Ia: n = 15; II: n = 18) and hypodynamia-hypokinesia (HH; Ia: n = 18; II: n = 20) groups under a 0.12-mm sinusoidal stretch applied at 18±6 Hz and at different stretch frequencies. * Significant difference with the CONT group; †† significant difference with the Ia fibers in the same animal group.

increase in the compliance on a population of hybrid fast fibers, which coexpressed the MHC IIA and MHC I isoforms (MHC IIA > MHC I). Moreover, Miller et al. (2001) have demonstrated that HH induced a shift in the relative proportion of collagen isoform (type I to III) in the soleus muscle in relation to the fiber type transition (slow to fast). Thus because HH induces fiber type transitions, it can be a factor for stiffness modifications (Canon and Goubel 1995). These changes could affect the muscle passive tension as previously suggested by McHugh et al. (1999). However, it has been demonstrated recently by Kubo et al. (2001) that the passive stiffness was independent of the elasticity of tendon structures (SEC), which had no effect on the muscle performance during stretch shortening cycle exercise. Although an immobilization in a shortened position led to an increase in the tendinous structure extensibility, it has been observed that prolonged immobilization in this position produced an increase in stiffness of the whole muscle tendon complex (Woo 1986).

Moreover, Gillette and Fell (1996) have demonstrated that passive tension of the soleus muscle significantly increased in rat hindlimbs after 7 and 14 days of whole body suspension. The increased passive tension in hindlimb muscle was not attributed to a shorter muscle but was supposed to be due to changes in muscle architecture, visco-elastic properties of the muscle or its connective tissue elements, or cytoskeletal protein alterations (Gillette and Fell 1996). The major factor contributing to the passive tension in a muscle was the extensibility of the connective tissue in parallel with the muscle fibers. Indeed, Gajdosik (2001) showed that passive stiffness was influenced by lengthening deformation of the connective tissues of the endomysium, perimysium, and epimysium (PEC) of the muscle belly with a large contribution of the perimysium due to its large amount in a muscle. After HH, a decrease in the concentration of myofibrillar proteins and a relative increase in the proportion of noncontractile tissue (Flynn and Max 1985; Herbert et al. 1988; Templeton et al. 1984) in the rat soleus muscles have been observed. More recently, Brown and Hasser (1996) have also described an increase in connective tissue. Miller et al. (2001) reported an increase in collagen concentration when expressed as a function of soleus cross-sectional area. Brown et al. (1999) have shown that after 2 wk in HH, the soleus muscle stiffness remained unchanged, whereas the muscle mass decreased. In these conditions, the stiffness normalized to the muscle mass appeared increased after HH. These authors concluded that after HH, the remaining muscle tissue became stiffer. Moreover, when a muscle is stretched, the viscosity and/or stiffness of the muscle-tendon unit is reduced, which could be a factor to increase the joint range of motion (Kubo et al. 2001). However, after a period of hindlimb unloading, the range of motion of the rat soleus muscle was reduced and could thus suggest an increase in soleus muscle stiffness (Brown et al. 1999).

To conclude, the muscle spindle discharges were increased after HH. This could be in relation with an increase in the connective tissue that could contribute to a better transmission of the passive muscle stretch as previously advanced by authors in tenotomized (Hnik and Lessler 1973a) and shortened immobilized muscles (Gioux and Petit 1993; Jozsa et al. 1990; Maier et al. 1972; Tardieu et al. 1982). Maier et al. (1972) suggested that the increased of muscle spindle discharge, observed after immobilization in a plantar flexion, was due to great atrophy of extrafusal fibers. In this condition, the proportion of total tension borne by intrafusal fibers should be greater. However, modifications in mechanical properties of intrafusal fibers could not be discounted after HH. In fact, it has been demonstrated that after a chronic de-efferentation of the rat gastrocnemius, there was an increase inafferent responsiveness of muscle spindles to stretch (Hnik and Lessler 1973b). Arutiuonian (1976) attributed these increases to changes in the visco-elastic properties of the intrafusal fibers. From the functional point of view, it has been demonstrated that the threshold of the tendon stretch reflex was reduced after short- and long-term space flights. This reflex occurred in response to a lower tendon tap (for review, see Edgerton and Roy 1996). Our results could explain this previous data because for a given stretch amplitude, the discharges of Ia and II fibers were increased after a HH period comparatively to those of the CONT group.

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