Electromyographic Activity of Rat Ankle Extensors During Treadmill Locomotion after Hindlimb Unloading

Cécile Langlet, Marie-Hélène Canu, and Maurice Falempin

Laboratoire de Plasticité Neuromusculaire, Université des Sciences et Technologies de Lille, Villeneuve d'Ascq, France

Abstract

The aim of this work was to study the electromyographic characteristics of two ankle extensors during treadmill locomotion after hindlimb unloading. The studied muscles were the soleus which contains mainly slow fibres, and three parts (red, mixed and white) of the heterogeneous gastrocnemius. Our results showed that the cycle duration was significantly increased (+26%) after 14 days of unloading; the burst duration was increased in the soleus (+18%) and in the red gastrocnemius (+20%). The mean EMG (burst area divided by burst duration) was decreased when treadmill speed was increased in the soleus (-11%) and the red part (-5%) of the gastrocnemius after unloading; in contrast, it was greatly increased in the white part (+46%). These data suggest that hindlimb unloading shifts the normal speed-related increase in muscle effort from the red to the white compartment of the muscle.

Key words: ATPase, fibre-type, gastrocnemius, microgravity, soleus.

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The physiological properties of hindlimb skeletal muscles are known to adapt to a variety of experimental conditions like immobilization [12], denervation [11], exercise [4], and hindlimb unloading (HU) [10, 34]. The latter model has been shown to cause deleterious effects on rodent skeletal muscles [19, 31, 33]. Antigravity muscles, such as the slow-twitch Soleus (SOL), are affected more than fast muscles such as the Gastrocnemius (GAST) [26]. The SOL and GAST show considerable histochemical differences with the former containing ~ 85% slow type I fibres, and the latter a mixture of slow and fast fibre types. The GAST is a very heterogeneous muscle, composed of two heads (medial and lateral) innervated by different branches of the tibial nerve. In addition to this *compartmentalization*, there exists a *regionalization*, to use Kernell's terms [20]. This term signifies the presence of regional intramuscular differences in fibre-type composition. The deep region of the lateral head contains slow oxidative and fast oxidative glycolytic fibres, and is referred to as the red GAST (r-GAST). The superficial white region of the lateral head, referred to as the white GAST (w-GAST), has been shown to contain a majority of fast glycolytic fibres. The deep part of the medial head has intermediate histological properties, and is named mixed GAST (m-GAST) [8]. The segregation between the different types of fibres, and thus of motor units, is particularly well defined in the rat [2]. Knowledge about regionalization is essential for studies of the neuromuscular system, since the electromyographic activity (EMG) may depend on the intramuscular localization of recording electrodes. Many functional studies have been conducted on the comparison between the simultaneous activity of these two ankle extensors, in cat [17, 32, 35], guinea-pig [13] and rat [18] . A "division of labour" has been reported for the two muscles in these three species. The SOL is active during all activities where a stable support is required; it can produce during quiet standing as much force as during locomotion. The GAST, conversely, is anatomically and physiologically suited for more forceful and rapid ankle extensions; it produces low force during standing, and is mainly recruited for higher locomotor speeds or during jumping.

The EMG activity recorded via intramuscular electrodes can be used to quantify various parameters of the locomotor pattern. Using this method, a study performed on the SOL during treadmill locomotion has revealed subtle changes induced by 14 days of HU [5, 6]. For example, in control conditions, the mean EMG (burst integrated area / burst duration), reflecting in certain limits the force developed by the muscle [35], increased with speed, while it was stable after HU. This change in mean EMG and the decrease in the maximal tetanic tension observed in the whole muscle [12] sug-

gested that, after an episode of HU, the SOL was no longer able to produce the normal level of force needed for the propulsion during locomotion and for the body support. As the SOL capacity to participate in movement is altered, our hypothesis is that the division of labour between the SOL and its agonist the GAST may be perturbed.

The purposes of this work were therefore to study the EMG characteristics of the SOL and of the three regions of the rat GAST during treadmill locomotion after HU, and then 1) to compare the simultaneous activity of the fast and slow synergists, in order to determine if a functional reorganization occurred in response to HU; 2) to determine if changes in EMG activity were correlated to structural alterations. Our main conclusion is that there is a specific increase in the activation of the w-GAST.

Materials and Methods

Animals

Experiments were performed on male Wistar rats (n = 34) weighing about 250 g at the beginning of the experiment. All the rats were individually caged on a 12:12 light-dark daily cycle at a 25°C room temperature. The rats were divided randomly into 4 groups: CON (control, n = 7), UNL (unloaded, n = 6), and I-UNL (unloaded implanted, n = 18). To test whether the presence of electrodes may change the locomotor characteristics, sham rats were treated identically as the I-UNL rats, except for unloading. No changes were observed for all studied parameters in this group. Therefore, the changes observed in the I-UNL were due to unloading and were not an epiphenomenon linked to the presence of electrodes.

All procedures described below were approved by both the Agricultural and Forest Ministry and the National Education Ministry (Veterinary service of health and animal protection, authorization 03805).

Electrodes

Bipolar electrodes were made from two insulated multistranded stainless steel wires (7 strands, 50 µm gauge, A.M. Systems). The recording surfaces were standardised by removing with a scalpel blade a 0.5 mm length of insulation under a dissecting microscope along the part of each wire implanted in the muscle. The ends of the cut wires were insulated by pulling the Teflon coating over the ends. The electrode wires were connected to leads attached to a six-pin amphenol connector (Plastics One) with acrylic cement (TAB 2000, Kerr).

Surgical procedure

Before surgery, the rats were trained to walk on a motor driven treadmill (Letica) at variable speeds from 20 to 50 $cm.s^{-1}$. Following training (one week), the animals were implanted with chronic bipolar electrodes. The rats were anaesthetised with pentobarbital (60 $mg.kg^{-1}$ I.P.), supplementary doses were administered when necessary. A skin incision was made along the sagittal plane of the skull. The scalp musculature and the connective tissue were tilted laterally. Three screws were secured to the skull and the connector was firmly attached to the screws and the skull using dental acrylic (TAB 2000, Kerr). The GAST and the SOL of the right hindlimb were exposed via a 1 cm incision made on the surface on the calf. The electrode wires were led subcutaneously from the connector to the muscles with two loops, positioned one in the thigh and the second on the neck. The common earth wire was positioned in the back musculature. Two pairs of electrode wires were inserted in each rat. Among the 18 rats of the I-UNL group, 9 had electrodes in both the SOL and m-GAST (deep part of the medial head), and the other 9 had electrodes in the r-GAST (deep part of the lateral head) and w-GAST (superficial part of the lateral head). The electrodes were inserted longitudinally through a 23-gauge 1.5 inch hypodermic needle. The two wires were separated by 1 mm. Sutures (Crinercé, 0.08 mm diameter, Autosuture) were tied tightly around the proximal and distal ends of the wires at their entry and exit sites in the muscle to secure the position of the electrodes in the muscle. A test was made by back-stimulating (Pulsemaster A300, WPI) the muscle through the electrode wires to make sure that they were in the good position. At the end of the experiment, the position of the electrode tracks was verified by histological sections (see "histological and morphological analyses" paragraph).

Hindlimb unloading

The I-UNL group was subjected to unloading using the tail suspension model adapted from Morey [24]. Briefly, the tail of each rat was cleaned, dried and wrapped in adhesive plaster. The rats were unloaded by the tail at 30° head down angle in order to avoid a contact of the hindlimb with the ground. The animals were free to move on their forelimbs and they had free access to food and water.

EMG recording and analysis

Recording began 5 days after surgery. In the I-UNL group, the EMG activity was recorded during treadmill locomotion before (HU-0) and after 7 days (HU-7) of unloading on 100 steps. After the HU-7 recording session, the rats were unloaded again for another week, and a third recording session was then performed (HU-14). Treadmill speed range was 20, 22, 24, 26, 28 and 30 $cm.s^{-1}$, since the animals had difficulties to walk at speeds greater than 30 $cm.s^{-1}$ after unloading as previously described [5]. HU-7 and HU-14 recordings were performed just after reloading. To evaluate if there is a rapid neural adaptation, the analysis was performed on the first 100 steps. The head connector was linked to a low friction connector (Plastics One) fixed on the lateral

wall of the treadmill by a flexible cable. The second connector was linked to a pre-amplifier (model P511J, Grass Instruments) with shielded cable. The raw EMG signal was amplified (x1000, band pass 30 Hz – 3 kHz). The signal was visualised on an oscilloscope (Hameg) and stored on a digital tape recorder (DTR 1802, Biologic) for further analyses. The data were then transferred to a personal computer (PC 486) with a data acquisition system (CED 1401). The burst onset and offset times were determined using a SPIKE 2 software (Cambridge Electronic Design). The cycle (period from the onset of a burst to the onset of the next burst) and burst duration were calculated from these data. Mean EMG (mEMG) was calculated (burst integrated area divided by burst duration) and normalised to the value observed at the slowest speed (i.e. 20 $cm.s^{-1}$) (Fig. 3A) in each rat. It was expressed in percent.

Histochemical and morphological analyses

Adenosinetriphosphatase (ATPase) staining analysis was performed for each rat in the four groups: in the CON and UNL groups for characterization of fibres, and in the I-CON and I-UNL groups to verify on histological sections that the electrode tracks were localised on the proper part of the muscle. After experiments, animals were killed with a letal dose of pentobarbital.

The GAST and the SOL were removed from the animals, frozen in isopentane cooled with liquid nitrogen and stored at -80°C until analysis. Cross-sections (10 µm) were obtained with a cryostat at -20°C. These cross-sections were stained for myosin ATPase activity, using the combined methods of Brooke & Kaiser [3] and Guth & Samaha [15] with alkaline (pH = 10.4) and acid preincubations (pH = 4.3 and 4.45). By using a combination of the three staining procedures, it was possible to identify type I, IIA, IID/X, IIB and IIC fibres. Type I fibres stained dark after preincubation at pH 4.3 and 4.45 and very light at pH 10.4; the reverse was true for IIA fibres. Type IID/X and IIB fibres both stained very light at pH 4.3 and medium at pH 4.45, but IID/X fibres stained medium at pH 10.4, whereas IIB fibres stained light. The composition of the three parts was expressed as the percentage of each fibre-type in an examined section. Cross-sectional area (CSA) was obtained for each fibre-type using an image analyser (SAMBA 2000, Alcatel TITN). A sample of 200 fibres was visualised in each part of the muscle.

Statistics

Results are presented as the mean of *n* rats ± SD. The main interests of this study are in the changes of each variable from control (HU-0) to unloading (HU-7 and HU-14). Therefore, for the EMG study, a repeated measures ANOVA was performed to compare values before and after unloading within I-UNL group. For the histochemical study, the difference between the two groups (CON and UNL) was tested by a one-way analysis of variance (ANOVA). Bonferroni's *t*-test was used as a post-hoc test to determine the significance. The 0.05 level of probability was established for statistical significance.

Results

As already described [5, 6], rats had some difficulties in moving after HU (disequilibrium, poor lateral stability). They exhibited some anomalies of locomotor movement: abduction of hindlimbs, elevation of hindquarter, hyperextensions of the ankle. A walking gait was used throughout by the rats for the speed range used (20-30 $cm.s^{-1}$). No gait shift from walking to trotting was observed over this speed increase in normal rats or after HU.

Cycle and burst duration

The burst and the cycle duration of both muscles decreased when the treadmill speed increased in control as well as after unloading. This is a characteristic feature of extensor muscles and it is in accordance with the results of Clarke and Parker [7].

To determine the effect of unloading on the locomotor activity, cycle and burst duration were compared before, after 7 days, and after 14 days of hindlimb unloading. First, concerning the cycle duration, its value was increased after 14 days of unloading whatever the speed used. A representative example at 26 $cm.s^{-1}$ is given Figure 1. No difference was observed between HU-0 and HU-7, but at HU-14, a 26% increase was obtained ($P<0.01$). Second, when considering the burst duration, a significant increase was observed in all parts except m-GAST, the higher values being observed at HU-14 for the SOL and r-GAST. The comparison of the values indicates that there was no difference between HU-0 and HU-14 for the m-GAST (+8%, non significant); in contrast, burst duration was increased in the w-GAST (+10%, $P<0.05$), in the SOL (+18%, $P<0.01$) and in the r-GAST (+20%, $P<0.05$). Note that in 4 animals out of 9 that were implanted in

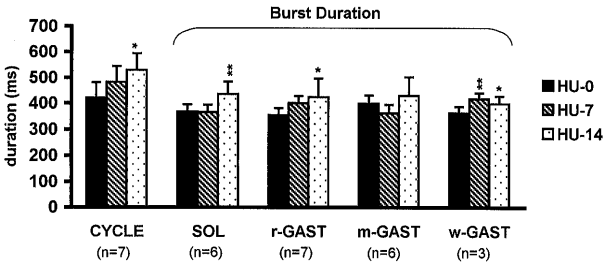

Figure 1. Burst and cycle duration before and after HU. Values were obtained when walking at 26 $cm.s^{-1}$. Error bars indicate standard deviation. Asterisks indicate a significant increase in burst or cycle duration with respect to HU-0 (: $P<0.05$; **: $P<0.01$).*

the w-GAST, the activity in this part was sometimes too low to determine with precision the burst onset and offset, and therefore these recordings did not permit an accurate evaluation of burst duration.

SOL–m-GAST relationships

When recording simultaneously the SOL and the m-GAST, the time interval between the onsets (TI on) of both agonist muscles, or the time interval between their offsets (TI off) have been evaluated. This parameter was independent of the treadmill speed. At HU-0, the m-GAST began 13.08 ± 8.84 ms after the SOL, and ended 35.75 ± 21.30 ms after the SOL offset (Fig. 2). After an episode of unloading, no significant modification was observed for TI on. Values were respectively 14.40 ± 13.28 ms at HU-7 (non significant) and 10.84 ± 13.32 ms at HU-14 (non significant). In contrast, TI off was significantly reduced at HU-7 (21.45 ± 22.47 ms, $P<0.01$) and at HU-14 (7.66 ± 15.29 ms, $P<0.001$). This observation indicates that the relative onset of both muscles was not altered.

Burst and cycle relationships

The correlation coefficient and the slope of the regression line between the cycle duration and the burst duration were analysed by linear regression (least square method) (Table 1). A strong correlation existed between the cycle and the burst duration in each part of the GAST and in the SOL before and after unloading. This is a characteristic feature of extensor muscles [25]. No obvious difference was noticed between the different recording sites nor between pre- and post-unloading. The slope was comprised between 0.59 and 0.99, and the correlation coefficient between 0.78 and 0.98.

Mean EMG

The values obtained for the mEMG (burst integrated area / burst duration) were normalised to the value observed from the same recording session at the slowest treadmill speed (i.e. 20 $cm.s^{-1}$) and the values were expressed in percent. So, the value obtained at low speed corresponds to 100%. All values presented above correspond to a moderate speed (30 $cm.s^{-1}$). When it was higher than 100%, this indicates that the muscle was more active at moderate than at low speed, and when it was under 100%, that the muscle decreased its activity when the speed was increased.

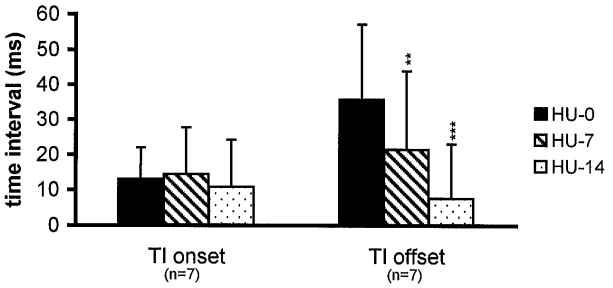

*Figure 2. Time interval between SOL and m-GAST bursts of activity. TI onset was not affected by HU, while TI offset was significantly decreased after 7 and 14 days of HU. Bars correspond to standard deviation. ** and ***: significant decrease with respect to HU-0 ($P<0.01$ and $P<0.001$, respectively).*

At HU-0, mEMG increased with the increase of the treadmill speed in both muscles (Fig. 3). Values were comprised between 110.1 ± 14.7% and 116.7 ± 14.8%. No statistical difference was noticed between the different recording sites. The increase was not significantly different between the SOL and the three parts of the GAST.

At HU-7, mEMG was decreased with respect to HU-0 in all recording sites; it varied between 92.2 ± 18.6% and 106.8 ± 14.6%. Nevertheless, the reduction was only significant for the SOL (116.7 ± 14.8% at HU-0; 96.2 ± 17.6% at HU-7, $P<0.05$). The values of the different sites were similar. The four recording sites presented the same evolution at HU-7.

After 14 days of unloading, mEMG slightly decreased when treadmill speed was enhanced in the SOL and in two parts of the GAST. The values were 88.8 ± 11.5% in the SOL ($P<0.05$), 95.1 ± 12.9% in the r-GAST ($P<0.01$), 97.8 ± 16.2% in the m-GAST (non significant). In contrast, in the w-GAST, a great increase was observed (146.2 ± 15.9%, $P<0.05$). The comparison of values of the different sites at HU-14 indicates that mEMG was significantly higher in the w-GAST than in other sites ($P<0.001$).

Table 1. Ranges of the slopes of the regression lines (a) and of the coefficients of correlation (r) relating the burst duration to the cycle duration before (HU-0) and after (HU-7 and HU-14) unloading.

	SOL		r-GAST		m-GAST		w-GAST	
	a	r	a	r	a	r	a	r
HU-0	0.80-0.98	0.89-0.98	0.74-0.99	0.93-0.98	0.80-0.97	0.85-0.98	0.60-0.98	0.94-0.98
HU-7	0.79-0.95	0.88-0.97	0.76-0.95	0.93-0.97	0.77-0.97	0.80-0.98	0.71-0.96	0.87-0.96
HU-14	0.82-0.98	0.85-0.98	0.78-0.95	0.91-0.94	0.59-0.98	0.78-0.98	0.79-0.96	0.87-0.87

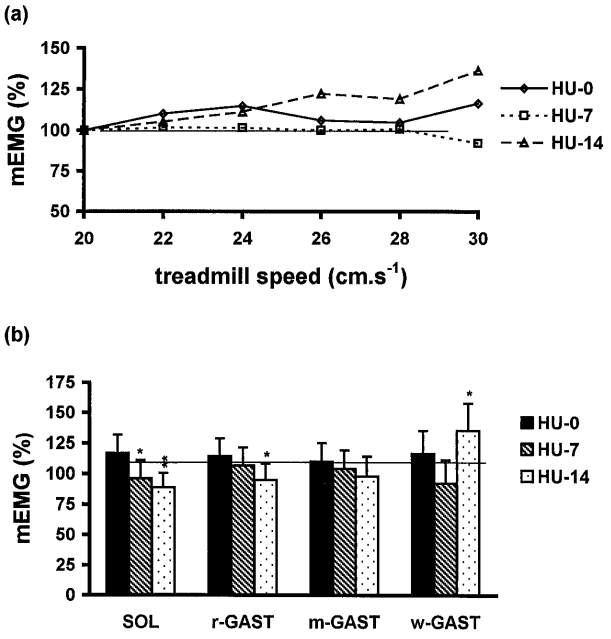

*Figure 3. Variation in mEMG before and after unloading. (a) presents the relative level of mEMG vs treadmill speed for the w-GAST. mEMG is normalized with respect to 20 cm.s^{-1} and is therefore expressed in percent. (b) The histograms report values obtained at 30 cm.s^{-1}. * and ** indicate a significant difference with respect to HU-0 (P<0.05 and P<0.01, respectively).*

Histochemical and morphological analyses

The histochemical and morphological analyses allowed verification of electrode placement, and quantification of muscle atrophy (Table 2).

In control rats, the SOL contained type I, IIA and IIC fibres, and the r-GAST type I, IIA, IID/X and IIC fibres. All 5 fibre types were observed in the m-GAST, while the w-GAST contained only type IID/X, IIB and IIC fibres. After 14 days of unloading, no significant change was noticed in the m-GAST or w-GAST. In contrast, in the r-GAST, a highly significant decrease in the proportion of type I fibres was detected (-37%, P<0.001), while type IID/X fibres were more numerous (+106%, P<0.001). In the SOL, the proportion of type I fibres also decreased (-16%, P<0.001), with a concomitant increase in type IIA (+19%, P<0.01) and IIC (+160%, P<0.001) fibres.

The CSA of each fibre type was decreased in each part of the GAST and in the SOL after unloading (P<0.001). When pooling all fibre types, we observed that the decrease in CSA was less pronounced in the w-GAST (-27%) than in the SOL (-44%) or in the r-GAST and m-GAST (-41% and -56%, respectively). Now, when pooling all parts and considering the fibre type, type IIB and IID/X fibres were slightly less atrophied (-32% and -38%, respectively) than the other types (between -46% and -48%).

Discussion

The present study has shown that after HU: 1) cycle duration and burst duration were increased in all but one

Table 2. Distribution of fibre types and cross-sectional area (in mm^2) in control rats (CON) and after 14 days of unloading (UNL).

	TYPE I		TYPE IIA		TYPE IID/X		TYPE IIB		TYPE IIC	
	CON	UNL	CON	UNL	CON	UNL	CON	UNL	CON	UNL
					Distribution of fibre type (%)					
SOL	80.7±5.3	67.8±1.3 ***	12.8±3.6	15.3±2.4 **					6.5±2.5	16.9±2.7 ***
r-GAST	44.9±4.8	28.4±8.4 ***	29.8±8.8	26.0±4.6	18.5±7.0	38.2±9.8 ***			7.0±2.2	7.4±4.8
m-GAST	15.3±6.2	11.1±3.7	19.6±6.3	21.6±2.7	35.7±12.4	44.0±10.4	25.7±12.5	19.3±13.9	3.4±2.7	3.7±2.8
w-GAST					22.1±12.2	29.1±13.3	72.3±14.1	70.5±14.1	5.4±6.0	1.0±0.5
					Cross-sectional area (mm^2)					
SOL	3269±241	1798±124 ***	3070±193	1700±198 ***					3370±289	1854±152 ***
r-GAST	2705±369	1361±316 ***	1919±222	1134±240 ***	2117±164	1733±149 ***			2149±183	937±173 ***
m-GAST	2090±657	1017±197 ***	2453±328	916±204 ***	3931±610	1549±467 ***	4653±475	2453±1014 ***	1684±252	703±101 ***
w-GAST					2336±274	1465±429 ***	3717±868	3069±657 ***	1559±306	1146±126 ***

** and *** indicate a significant difference with respect to CON values (P<0.01 and P<0.001 respectively).

(m-GAST) muscle parts and 2) mEMG was reduced when compared with before-HU controls, for locomotion speed of 30 $cm.s^{-1}$, except for w-GAST in which it was increased. These data indicate that a disruption of the SOL motor activity occurred after a period of HU. The results concerning the effects of HU on the SOL EMG activity are compatible with published data [6]. It is suggested that the EMG activity of the GAST, an agonist of the SOL, was changed in order to counteract the subtle changes observed in the SOL.

Mean EMG

The increased burst duration contributed to the increased cycle duration after HU. This suggests that the lengthening of cycle is primarily linked to a reinforced stance phase. The stance phase is composed of two factors: body support and development of the propulsive force. It is well established that the tetanic tension developed by the SOL and the GAST *in situ*, or isolated skinned fibres is reduced following HU [16, 30, 31, 36]. The force developed by the muscle during locomotion is proportional, to a certain extent, to the integrated EMG [35], i.e. the frequency and number of motor units recruited. In these conditions, it can be suggested that the force production, evaluated by mEMG, was decreased during the stance phase at HU-14, in the SOL and in the r-GAST. Conversely, force production was unaltered or even slightly increased in the w-GAST. The higher level of mEMG activity in w-GAST could reflect either an increase in the number of motor units recruited during the stance phase, and/or an increase in the firing rate of already recruited units. This increase in mEMG in the w-GAST, as well as the increase in burst duration in the entire calf, could compensate for the fibre atrophy and the decrease in peak active force (P_0) in both muscles, and help to restore an adequate function.

It is of interest to note that, in the w-GAST, the increase in mEMG was particularly important at HU-14 while no change or even a tendency to decrease was observed at HU-7. Such a tendency was also observed in the r-GAST and m-GAST, and the decrease was significant in the SOL. Our data suggest that at HU-7, the decrease in force production was not sufficient to set an adaptative mechanism in action. The increase in mEMG in the w-GAST occurred only when the force decrease reached a certain level in the other parts.

Time interval

The time interval analysis indicates that the SOL was usually activated prior to GAST during stance. This has also been described in humans [9]. In early stance, the triceps surae is involved in supporting the body, and the SOL is well-suited for this postural action. In contrast, the SOL activity ended before the GAST. The end of the stance phase corresponds to the propulsion, and the GAST, which is commonly recruited in movements requiring considerable effort (high speed of treadmill locomotion, jump) [29], is more suited for this task.

The relative initiation of the two muscles was not affected by suspension. This indicates that both muscles were activated by a common mechanism, resulting in a resetting of the step cycle, possibly by the activation of ankle extensor group I afferents [14]. In contrast, since the burst increase was more pronounced in the SOL than in the GAST, the time interval between burst offsets was changed. This result indicates that a different regulation of the ankle extensors occurs.

Histology

We observed a decrease in the fibre CSA of all fibre types. This decrease in CSA was due to a decrease in protein content [19] or to a decrease in the number of myonuclei [1]. Miu *et al*. [23] have shown that the decrease in force and in CSA could be correlated. So, our results obtained for the CSA can be considered as arguments to support the hypothesis that the EMG changes reflect modifications of the force level developed by the different parts of the GAST.

Concerning the proportion of fibres, our results showed that muscles containing a high proportion of type I fibres, i.e. the SOL and the r-GAST, were transformed (decrease in the percentage of slow fibres associated with a concomitant increase in the IIC fibres), while no change was observed in the m-GAST and the w-GAST, mainly composed of fast fibres. This observation can be related to electromyographic parameters: the burst duration was mainly affected in the SOL and r-GAST; mEMG was decreased in these two parts while it was not affected in the m-GAST or was increased in the w-GAST. Consequently, we formulate the hypothesis that HU had the same effects on the transitory disruption of the electromyographic characteristics of muscles having neighbouring histological characteristics. Before HU, the mEMG was similar whatever the fibre type composition and whatever the muscle; by contrast, after HU, mEMG was proportional to the proportion of fast fibres.

Microgravity

HU bears some analogy with microgravity in that it totally suppresses weight-bearing function and strongly reduces the sensory and motor functions. A few studies have focused on the locomotor capacity of human [22] and non-human [27] primates when returning from space-flight to a normal gravitational environment. Riley *et al*. [28] have studied the rat locomotor behaviour during and after space-flight but to our knowledge, no study has been aimed at determining the electromyographic activity during locomotion in rats after space-flight. Comparison between species having very different locomotor behaviour (for instance bi- vs quadrupedal) is hazardous. Nevertheless, some common fea-

tures are observed: less stable standing posture, tremor-like activity. From the data of Recktenwald *et al* [27] as in ours in simulated microgravity, differential adaptation in motor-unit recruitment pattern of fast and slow motor pools has been shown since specific changes in the excitability of the pool of motoneurons appeared after a period of suppression of the afferent activity. The H-reflex method has provided evidence for a higher excitability of the motoneuronal pool after space-flight in humans [21]. The absence of sensitive nervous message from plantar or proprioceptive muscular receptors during unloading (real or simulated microgravity) likely plays a role in the change of the motoneurone excitability and consequently in the alteration of the neuromuscular pattern during walking.

Conclusion

To conclude, a reorganization of the motoneuron activity occurs after an episode of HU. We support the hypothesis that the increase in cycle duration and the specific increase in the EMG activity in the w-GAST is a consequence of the disruption of the motoneuron pool activity caused by the modifications in muscular properties and/or the decrease in the control afferent input in or after HU conditions. Motoneurons of the different ankle extensors may belong to different groups separately controlled [18], or they may belong to a single recruitment group that could be recruited more intensely after atrophy of the muscle, causing it to shift activation towards whiter compartments that had previously had little recruitment at the gait speeds studied.

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Address correspondence to:

M.H. Canu, Laboratoire de Plasticité Neuromusculaire, Université des Sciences et Technologies de Lille, Bâtiment SN4, F-59655 Villeneuve d'Ascq cedex, France, tel. (33) 3 20 33 70 87, fax (33) 3 20 43 68 88, Email canu@univ-lille1.fr.

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