RESEARCH ARTICLE

Muscle fiber typology substantially influences time to recover from high-intensity exercise

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Lievens E, Klass M, Bex T, Derave W. Muscle fiber typology substantially influences time to recover from high-intensity exercise. *J Appl Physiol* 128: 648–659, 2020. First published January 30, 2020; doi:10.1152/japplphysiol.00636.2019.—Human fast-twitch muscle fibers generate high power in a short amount of time but are easily fatigued, whereas slow-twitch fibers are more fatigue resistant. The transfer of this knowledge to coaching is hampered by the invasive nature of the current evaluation of muscle typology by biopsies. Therefore, a noninvasive method was developed to estimate muscle typology through proton magnetic resonance spectroscopy in the gastrocnemius. The aim of this study was to investigate whether male subjects with an a priori-determined fast typology (FT) are characterized by a more pronounced Wingate exercise-induced fatigue and delayed recovery compared with subjects with a slow typology (ST). Ten subjects with an estimated higher percentage of fast-twitch fibers and 10 subjects with an estimated higher percentage of slow-twitch fibers underwent the test protocol, consisting of three 30-s all-out Wingate tests. Recovery of knee extension torque was evaluated by maximal voluntary contraction combined with electrical stimulation up to 5 h after the Wingate tests. Although both groups delivered the same mean power across all Wingates, the power drop was higher in the FT group (-61%) compared with the ST group (-41%). The torque at maximal voluntary contraction had fully recovered in the ST group after 20 min, whereas the FT group had not yet recovered 5 h into recovery. This noninvasive estimation of muscle typology can predict the extent of fatigue and time to recover following repeated all-out exercise and may have applications as a tool to individualize training and recovery cycles.

NEW & NOTEWORTHY A one-fits-all training regime is present in most sports, though the same training implies different stimuli in athletes with a distinct muscle typology. Individualization of training based on this muscle typology might be important to optimize performance and to lower the risk for accumulated fatigue and potentially injury. When conducting research, one should keep in mind that the muscle typology of participants influences the severity of fatigue and might therefore impact the results.

fatigue; muscle fiber type composition; training-recovery cycles; Wingate testing

INTRODUCTION

In humans, skeletal muscle fibers exist in two main categories: slow-twitch fibers, also called type I fibers, and fast-twitch fibers, or type II fibers. The latter are further divided into IIA and IIX subtypes. It is known that some individuals display a dominant fast typology (FT), whereas others have a mixed/intermediate typology (INT) or a dominant slow typology (ST) (10). The average human muscle fiber type composition follows a Gaussian distribution, and all people have both fast- and slow-twitch fibers. However, this distribution can range from 15% to 85% fast-twitch fibers (35). Notwithstanding the fact that the muscle fiber typology is mainly genetically determined (37), several studies indicate that exercise-induced muscle fiber shifting exists between the fast-twitch subtypes (1, 2). Contrarily, a bidirectional shift between slow- and fast-twitch fibers is less evident (16, 44). The muscle fiber type composition therefore underpins the "typology" of an athlete, as elite sprinters have predominantly fast-twitch fibers whereas elite endurance athletes have relatively more slow-twitch fibers (10, 45). Since fast-twitch fibers can generate more power, especially at high shortening speed (43), and as slow-twitch fibers are more fatigue resistant (36), it can be concluded that the muscle typology of an athlete is an important performance-determining factor in many sports. However, this information is rarely applied in daily sport science practice.

The use of the muscle typology in sport science and coaching is mainly hampered by the invasive nature of the current evaluation of muscle fiber type composition by biopsies. Therefore, a new noninvasive estimation of muscle typology based on calf muscle carnosine quantification with proton magnetic resonance spectroscopy (^{1}H-MRS) was developed (4). As carnosine, a muscle pH buffer, is highly abundant in fast-twitch fibers, athletes with high concentrations of carnosine are estimated to have a fast muscle typology. This technique enables noninvasive determination of muscle typology (type I vs. type II fibers), which can be used in talent identification and orientation (4, 6). It can be questioned whether this technique can also be used to individualize training and recovery cycles, as single fast-twitch motor units are known to have a higher fatigability as opposed to slow-twitch motor units (11).

Fatigue in whole muscles manifests as a loss of peak force, contraction velocity, and/or power, and there is some literature available indicating that muscle fatigue in humans is dependent on the muscle fiber type composition. Correlations demonstrated that athletes with predominantly fast-twitch fibers are more fatigable compared with athletes with mostly slow-twitch fibers during sustained isometric maximal voluntary contractions (MVCs) (17), 50–100 isokinetic maximal knee extensions (24, 41), and 60 s of continuous jumping (7). Next to fatigue, muscle fiber typology also seems to affect the recovery profile immediately following a fatiguing exercise. Colliander

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et al. (9) reported a lower recovery of initial peak torque during a 1-min rest period between 3×30 maximal isokinetic knee extensions in subjects with predominantly fast-twitch fibers compared with slow-twitch fibers. This is in accordance with Hamada et al. (18), who showed that recovery of an electrically induced twitch peak torque at 5 min after sixteen 5-s maximal voluntary isometric contractions of the knee extensors was significantly lower in subjects with predominantly fast-twitch vs. slow-twitch fibers. To date, the time course of recovery in subjects with divergent muscle fiber type composition beyond the first 5-min time frame of recovery remains to be investigated. Nevertheless, this information is key to individualizing training and recovery cycles, to ensure that every individual athlete can commence the next training session in a fully recovered state.

In this study we noninvasively assessed the muscle typology of 32 subjects and characterized them as ST, INT, and FT. Subsequently, we investigated the muscle fatigue and prolonged recovery profile in the a priori-determined ST and FT groups only. Fatigue was induced by three repeated Wingate tests, and the degree of fatigue and the course of recovery were assessed up to 5 h after Wingates by a combined voluntary and electrically stimulated knee extension contraction approach. We hypothesized that subjects with a FT are characterized by more pronounced fatigue and delayed recovery in the 5 h after the high-intensity exercise compared with subjects with a ST.

METHODS

Study design. Thirty-two male recreational athletes were recruited and invited for a proton magnetic resonance spectroscopy (^{1}H-MRS) scan to estimate their muscle typology based on their carnosine content in the gastrocnemius (Fig. 1). A higher carnosine content was considered as indicative of a FT and an underlying larger proportion of fast-twitch fibers (4). All carnosine concentrations were converted into z scores based on the normal distribution of our reference population. The absolute value of the z score represents the distance between the individual score of an athlete and the population mean in units of the standard deviation. The reference population consisted of 98 recreationally active male control subjects (average age: 22 ± 2 yr), gathered in our laboratory over the past 9 yr and was also used in Bex et al. (6). To divide the subjects into a slow typology (ST) group and a fast typology (FT) group, only athletes with a z score higher than 0.5 (FT, $n = 10$) or lower than -0.5 (ST, $n = 10$) were included in
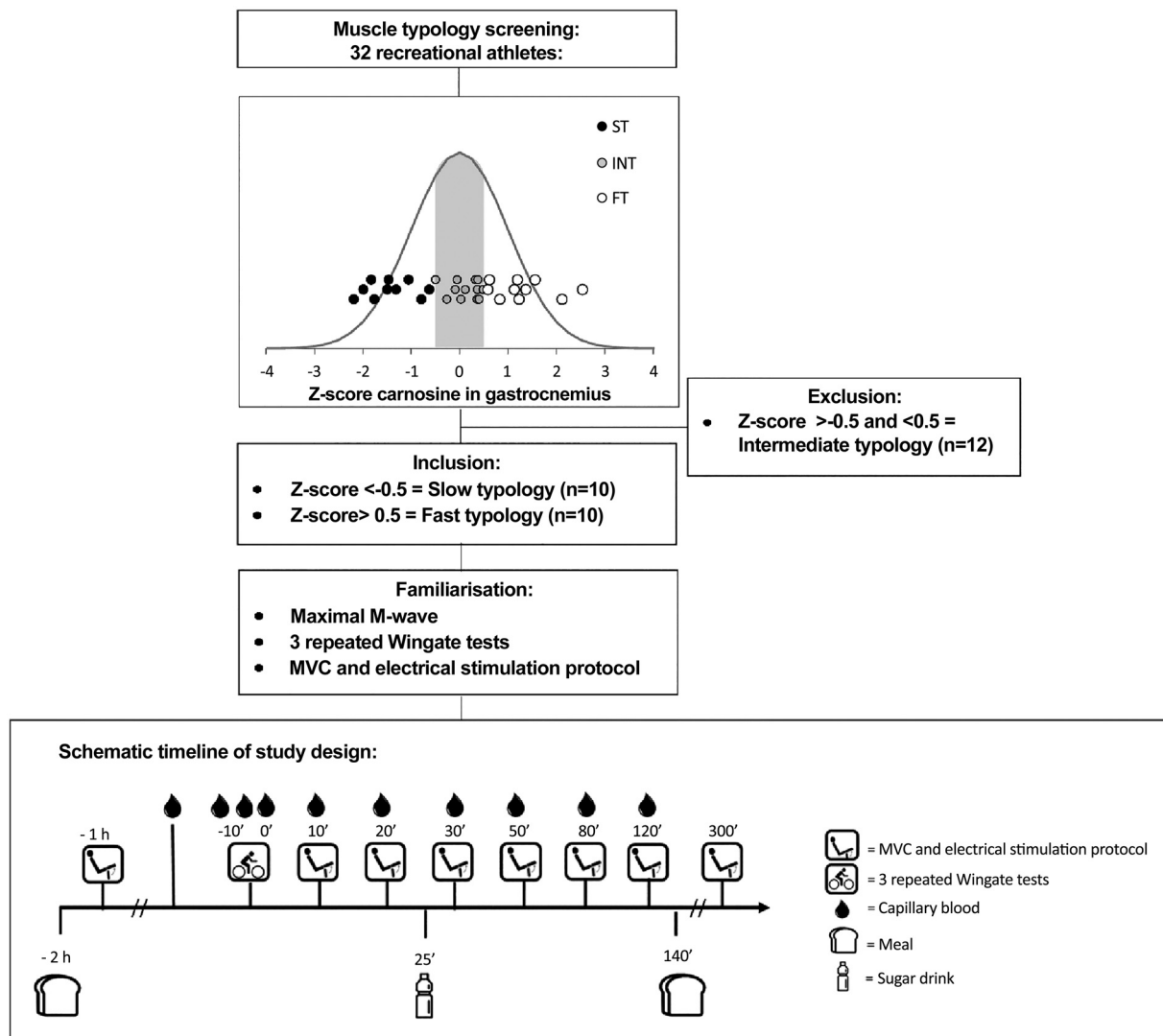

Fig. 1. Flowchart of study design. FT, fast typology; INT, intermediate typology; MVC, maximal voluntary contraction; ST, slow typology.

Table 1. *Baseline values of the 2 groups*

	ST	FT	P
Anthropometry			
Age, yr	23.8 ± 3.05	22.8 ± 3.01	0.470
Height, cm	177 ± 4.36	182 ± 9.88	0.131
Weight, kg	68.9 ± 2.97	78.9 ± 8.18	0.004*
Fat, %	12.6 ± 2.22	14.7 ± 2.40	0.059
Lean body mass, kg	61.2 ± 2.07	67.3 ± 6.68	0.009*
Circumference Quad, cm	52.9 ± 2.47	56.6 ± 2.54	0.004*
Skinfold Quad, mm	7.98 ± 1.76	7.54 ± 2.73	0.674
Corrected circumference			
Quad, cm	50.4 ± 2.37	54.2 ± 2.33	0.002*
Exercise performance			
during incremental test			
Peak power, W/kg	5.77 ± 0.711	5.34 ± 0.182	0.092
Peak power, W	398 ± 56.9	422 ± 49.2	0.338
$\dot{V}O_{2max}$, mL·min^{-1}·kg^{-1}	58.4 ± 7.40	53.0 ± 3.12	0.052
$\dot{V}O_{2max}$, mL/min	4,287 ± 964	4,757 ± 1,010	0.301
Gas exchange threshold,			
mL/min	2,412 ± 498	2,488 ± 402	0.463
Respiratory compensation			
point, mL/min	3,715 ± 571	3,897 ± 494	0.145
Maximal heart rate, beats/min	183 ± 9.85	196 ± 7.28	0.004*
Muscle typology			
Muscle carnosine in Gastro,			
z score	−1.43 ± 0.496	1.29 ± 0.595	<0.001*

Data are presented as means ± SD. FT, fast typology; Gastro, medial head of gastrocnemius muscle; Quad, quadriceps muscle; ST, slow typology; $\dot{V}O_{2max}$, maximum oxygen consumption. *Significant difference between ST and FT.

the study. Characteristics of both groups are displayed in Table 1. All subjects were in good health and took part in some form of recreational sports (running, cycling, triathlon, martial arts, badminton, swimming, gym, football, and volleyball) three to six times per week, but no differences in training hours per week were found between groups. Twelve athletes with an intermediate muscle typology (INT; z score higher than −0.5 and lower than 0.5; Fig. 1) did not meet the inclusion criteria.

Body height was measured with a portable stadiometer (model 213; Seca). Body weight, fat percentage, and lean body mass were determined with a bioelectrical impedance analyzer (BC-420SMA; Tanita) in all subjects. Circumference of the quadriceps and midthigh skinfold (Harpenden skinfold caliper; Baty) was taken in the middle of the line between the inguinal crease and the proximal border of the patella (26). Corrected circumference for the thigh was calculated with corrected thigh circumference (cm) = thigh circumference (cm) – π × skinfold (cm) (27). To determine medical eligibility, screening was performed by a medical doctor, after which an incremental cycling protocol to exhaustion was performed. The test was performed on an electrically braked cycling ergometer (Excalibur; Lode), and oxygen consumption ($\dot{V}O_2$) was measured continuously via a computerized breath-by-breath system (Jaeger Oxycon Pro; Jager). After a 3-min warm-up at 40 W, the workload was increased by 35 W every min until the point at which the subjects failed to continue to pedal at 60 rpm.

All subjects took part in a familiarization session, which was performed at least 1 wk before the start of the study. Subjects were familiarized with electrical stimulation, and intensity for maximal M wave was obtained. Afterwards, subjects were familiarized with the maximal voluntary contraction (MVC) and electrical stimulation protocol at rest and in a fatigued state. To achieve this fatigued state, subjects were asked to perform the 3 × 30-s all-out (repeated Wingate tests) on a cycle ergometer.

Participants refrained from exhaustive physical activity and caffeine consumption for 24 h and 12 h, respectively, before the experimental session. The evenings before the test days, subjects were asked to have a carbohydrate-rich dinner. The actual test days consisted of a standardized breakfast 2 h before the start of the repeated Wingate tests. One hour before the start of the repeated Wingate tests, two baseline measurements of the MVC and electrical stimulation protocol were obtained. A baseline capillary blood sample was collected before the repeated Wingate tests and 3 min after every Wingate. To evaluate the recovery pattern of muscles, the MVC and electrical stimulation protocol was performed at the following time points: 10, 20, 30, 50, 80, 120, and 300 min after the repeated Wingate tests. Up to 120 min, capillary blood was taken from the fingertip at the same time points. A sugar drink (1 g carbohydrate/kg body wt) and a standardized meal consisting of 20 g of proteins were provided 25 and 140 min, respectively, after Wingate tests (Fig. 1). The experimental protocol was repeated on 2 separate days to minimize day-to-day variation, and the means of the results of the 2 test days are presented, except for the capillary blood sampling, which was only performed during the first test day.

Ethical approval. All subjects gave their informed consent for the described experiments, and the studies were approved by the Local Ethics Committee (Ghent University Hospital, B670201628807). Written informed consent was obtained from all individual participants included in the study. This study was performed in accordance with the standards of ethics outlined in the Declaration of Helsinki.

Muscle typology screening. Muscle carnosine content was measured by proton magnetic resonance spectroscopy (^{1}H-MRS) in the right gastrocnemius medialis of 32 subjects. All ^{1}H-MRS measurements were performed on a 3-T whole body MRI scanner (Trio; Siemens), as described by Baguet et al. (4). The subjects were lying in a supine position, and the lower leg was fixed in a spherical knee coil. Single-voxel point-resolved spectroscopy sequence with the following parameters was used: repetition time (TR) of 2,000 ms, echo time (TE) of 30 ms, number of excitations equal to 128, 1,024 data points, spectral bandwidth of 1,200 Hz, total acquisition time of 4.24 min, and a voxel size of 40 mm × 12 mm × 30 mm. The absolute carnosine content (mM) was calculated as described by Baguet et al. (4) with the phantom replacement technique.

Fatigue induction. The three repeated Wingate tests were preceded by a 10-min warm-up at 100 W on the cycle ergometer (Cyclus 2; Avantronic). At *minute 6* and *minute 7* of the warm-up, a 5-s sprint was performed. The repeated Wingate tests were performed with a pedal force (N) of 0.85 × body weight (kg)/crank length (m) (= 0.173 m) and interspersed with 4 min of rest. Three minutes after each Wingate, capillary blood samples were administered from the fingertip and analyzed by an automated cartridge-based blood gas analyzer (ABL 90; Radiometer).

Recovery monitoring. The degree of fatigue induction and time course of recovery were monitored by repeated knee extension dynamometry and electrical stimulation of the quadriceps over 5 h. Testing consisted of a 5-s MVC performed on a dynamometer (Biodex System 3 Pro; Biodex Medical Systems). Subjects were seated with a knee angle of 90° and a trunk-thigh angle of 100°. Extraneous movements of the upper body were limited by two shoulder harnesses and by crossing the arms before the body. Supramaximal electrical stimulation (pulse duration of 1 ms) was delivered to the femoral nerve by a high-voltage constant-current stimulator (DS7A; Digitimer). Pulses were given through self-adhesive electrodes (Ag-AgCl, 10-mm diameter). The cathode was positioned over the nerve in the femoral triangle and the anode on the greater trochanter. During familiarization, stimulus intensity was increased gradually by steps of 5 mA until the M-wave amplitude reached a plateau in the vastus lateralis. This intensity was increased by a further 20% (i.e., supramaximal) and kept constant for all subsequent tests. Voluntary and evoked torques developed by the knee extensors were recorded by custom-made software on a computer at a sampling rate of 3 kHz. During the experimental sessions, paired stimuli at 100 Hz were given during the plateau of the MVC (= superimposed doublet; SID) and 2 s after MVC to test the voluntary activation. These stimuli were followed by

paired stimuli at 10 Hz and a single stimulus, to obtain the resting mechanical responses (doublets and singlet) and the M wave, at 2-s intervals (Fig. 2). The electromyographic (EMG) activity of the vastus lateralis, vastus medialis obliquus, and rectus femoris were recorded through self-adhesive surface electrodes (Ag-AgCl, 10-mm diameter) positioned lengthwise over the middle part of the muscle belly with an interelectrode (center to center) distance of 2 cm, according to SENIAM guidelines (19). These electrodes were connected with wireless transmitters to the Noraxon device (3 kHz, ZeroWire; Noraxon).

Data analysis. As test days were performed twice, every baseline parameter was measured four times (2 baseline measurements at each test day). We calculated the average of the four results, or on three results if the baseline value in one of the occasions deviated by >10% from the average of the other three values.

The Wingate peak and minimum power were considered as the highest and lowest instantaneous values achieved during each Wingate. To have an idea of the course of each repeated Wingate test, power output during the repeated Wingate tests (30 s) was divided into six parts of 5 s. Power drop (= fatigue index) was measured as (highest 5-s power output from 1st Wingate − lowest 5 s of 3rd Wingate)/highest 5-s power output from 1st Wingate × 100.

Surface EMG was band-pass filtered (10–500 Hz) and rectified with Visual 3D software (C-Motion, Maryland). For the integrated EMG (iEMG), a moving root mean square (RMS) with a window of 50 ms was applied and the 5-s MVC period was integrated. As we did not want to include the SID in this measurement, values 1 ms before SID to 9 ms after SID were substituted by the mean of the 10 ms before this period. Maximal EMG signals during the MVCs were quantified as RMS amplitudes for a 500-ms interval around maximum torque (250-ms periods either side of the maximum torque). Maximal RMS values were then normalized to the peak-to-peak amplitude of the M wave to obtain the RMS-to-M wave ratio. This normalization was performed to account for peripheral influences including neuromuscular propagation failure and changes in the impedance from the EMG recordings (33).

MVC torque was considered as the peak torque attained during the voluntary contraction. Biodex data were filtered with a 20-Hz low-pass filter. Pre- and postexercise torque of the 10-Hz and 100-Hz doublets, 10 Hz-to-100 Hz ratio, rate of torque development of the 100-Hz doublet (maximum from first derivative, dP/dt), as well as the contraction time, half-relaxation time, and rate of torque relaxation (minimum from first derivative, $-dP/dt$) of singlets were quantified to assess changes in contractile properties. Paired stimuli at 100 Hz were given superimposed on and immediately after MVCs to assess the voluntary activation level (VAL), which was used as an index of central fatigue and assessed as VAL = [1 − (SID torque/potentiated doublet torque)] × 100. A correction was consistently applied when the SID was given slightly before or after the real maximal voluntary torque. In these cases, VAL was calculated as [1 − (SID amplitude × voluntary torque level just before the SID/maximal voluntary torque)/ potentiated doublet amplitude] × 100 (40).

Statistical analysis. Data are reported as means ± SD. $P \leq 0.05$ was considered statistically significant. All statistical analyses were performed with SPSS, version 25.0 (IBM, Armonk, NY). Normality of the data was assessed with a Shapiro–Wilk normality test. Population characteristics and absolute baseline values of isometric knee extension were analyzed by an independent t test.

Wingate data were analyzed with repeated-measures MANOVA (2 groups × 3 Wingate tests), and differences in fatiguing profile between groups (split file: group) were assessed. Also, differences between groups on each separate Wingate and on each 5-s part of the Wingate (independent sample t test) were further analyzed.

For the recovery data (torque, EMG, blood) a repeated-measures MANOVA [2 groups × 8–10 time points (8 for torque and EMG; 10 for blood)] was performed both on the relative data (% compared with baseline values) and on the absolute values. Repeated-measures MANOVA on the relative values (% of initial value) was used to analyze the differences in recovery between groups (interaction effect). If the interaction effect was significant, differences in recovery profile between groups (split file: group) and differences between groups on each time point (independent sample t test) were further analyzed. The main effects of time were analyzed by repeated-measures MANOVA on the absolute data. If the main effect of time was significant, pairwise comparison per group was used to analyze at which time point a post-repeated Wingate test measurement was significantly different from baseline. In contrast to the method described above, ratios were only analyzed on the absolute values (VAL, RMS-to-M wave ratio, etc.). Therefore, a repeated-measures MANOVA on the absolute data was done to look for differences in recovery profile between groups. If the interaction was significant, differences in recovery profile between groups were further analyzed (split file: group). Likewise, differences between groups on each time point were further analyzed by an independent sample t test. If a significant main effect of time was present, pairwise comparison per group was used to analyze at which time point a post-Wingate measurement was significantly different from baseline.
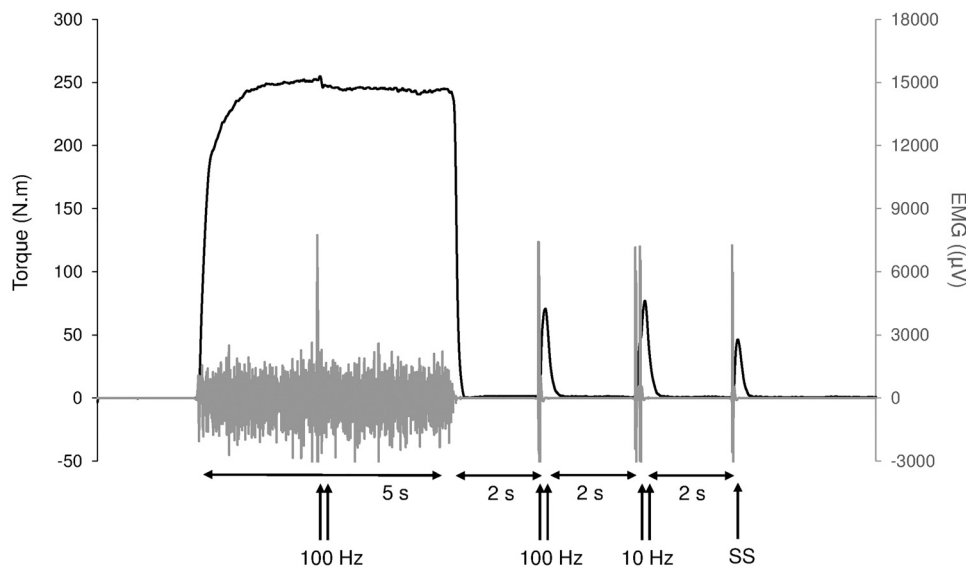

Fig. 2. Example of a representative 5-s maximal voluntary contraction (MVC). MVC was performed with superimposed 100-Hz paired stimuli at the plateau, followed by 3 stimulations at 2-s intervals: paired stimuli at 100 Hz and 10 Hz and a single stimulus (SS). Torque output of the quadriceps and EMG output of the vastus lateralis are displayed.

Table 2. *Baseline values of isometric knee extension*

	ST	FT	*P*
MVC			
Max torque, N·m	204 ± 48.9	293 ± 46.5	0.001*
iEMG of vastus lateralis, μV	2,140 ± 832	2,338 ± 859	0.528
Electrical stimulation			
100-Hz doublet torque, N·m	79.5 ± 15.0	98.3 ± 16.3	0.015*
100-Hz doublet rate of			
torque development, N·m·s^{-1}	1,639 ± 325	2,143 ± 447	0.010*
10-Hz doublet torque, N·m	85.1 ± 17.3	101.5 ± 13.3	0.028*
Singlet torque, N·m	50.5 ± 11.3	61.1 ± 8.96	0.032*
Singlet contraction time, ms	213 ± 15.6	197 ± 11.9	0.308
Singlet rate of torque			
development, N·m·s^{-1}	1,102 ± 276	1,473 ± 329	0.014*
Singlet half-relaxation			
time, ms	88.0 ± 14.4	79.9 ± 13.4	0.211
Singlet rate of torque			
relaxation, N·m·s^{-1}	−442 ± 117	−644 ± 178	0.008*
M-wave area. mV·ms	63.1 ± 13.0	57.9 ± 12.8	0.380
Voluntary activation level, %	85.7 ± 5.90	89.7 ± 6.87	0.182

Data are presented as means ± SD. FT, fast typology; iEMG, integrated electromyography; MVC, maximal voluntary contraction; ST, slow typology. *Significant difference between ST and FT.

RESULTS

Baseline group characteristics. As a result of the baseline screening and selection, the FT group had a higher *z* score in carnosine content for the gastrocnemius (1.29 ± 0.595) than the ST group (−1.43 ± 0.496) (Table 1). As no other inclusion criteria were established, it was expected that other characteristics would be randomly distributed between groups. Nevertheless, body weight (+13%), lean body mass (+11%), and corrected circumference of the quadriceps (+7%) were higher in the FT group compared with the ST group (Table 1). This difference in body weight was reflected in a nonsignificantly (*P* = 0.052) higher relative maximum V̇O₂ (V̇o₂ₘₐₓ) in the ST group (+9%) compared with the FT group, whereas no difference in absolute V̇o₂ₘₐₓ was found during the incremental cycling protocol. Gas exchange threshold, respiratory compensation point, as well as maximal power were also not different between groups (Table 1).

All presented results on the repeated Wingates, the MVC, and electrical stimulation are the average of both test days, although the results were not different when test days were analyzed separately. The FT group was able to produce a higher maximal voluntary torque (+43%), 100-Hz doublet torque (+24%), 10-Hz doublet torque (+19%), and singlet twitch (+21%) compared with the ST group (Table 2). At baseline no differences between groups were seen in the VAL, the iEMG of the vastus lateralis over the duration of the MVC, RMS-to-M wave ratio, and M-wave area after a single stimulus (Table 2). We only chose to present EMG data from the vastus lateralis because this muscle is a representative muscle for the whole quadriceps and produces reproducible data during both MVC and electrical stimulations (33). Moreover, results did not differ between muscle parts for baseline values or for fatigue measurements.

Fatigue during Wingate. Fatigue profile during three repeated Wingate tests was different between groups (Fig. 3*A*). The peak power of the first Wingate was significantly higher in the FT group compared with the ST group (FT 11.8 ± 0.0765/kg vs. ST 10.7 ± 1.13 W/kg, *P* = 0.018); however, this was not the case in the second and third Wingates. The highest peak power reached during the three Wingates correlated with the muscle typology *z* score (*r* = 0.545, *P* = 0.013). Minimum power was the same in both groups in the first Wingate but was lower in the FT group compared with the ST group in the second and third Wingates [FT 4.98 ± 0.522 vs. ST 6.19 ± 0.876 W/kg (*P* = 0.002) and FT 4.12 ± 0.808 vs. ST 5.92 ± 1.01 W/kg (*P* < 0.001, respectively]. Therefore, total power drop over three repeated Wingate tests was significantly higher in the FT group (−61%) compared with the ST group (−41%) (Fig. 3*A*; *P* < 0.001). Moreover, the total power drop was correlated with the muscle typology *z* score (*r* = 0.677, *P* = 0.001). Despite different fatiguing profiles, total work done over the three repeated Wingate tests was the same in both groups (FT 729 ± 32.5 vs. ST 746 ± 75.8 J/kg, *P* = 0.53; Fig. 3*B*).

Recovery monitoring. Complete recovery was defined as being no longer significantly different from absolute baseline
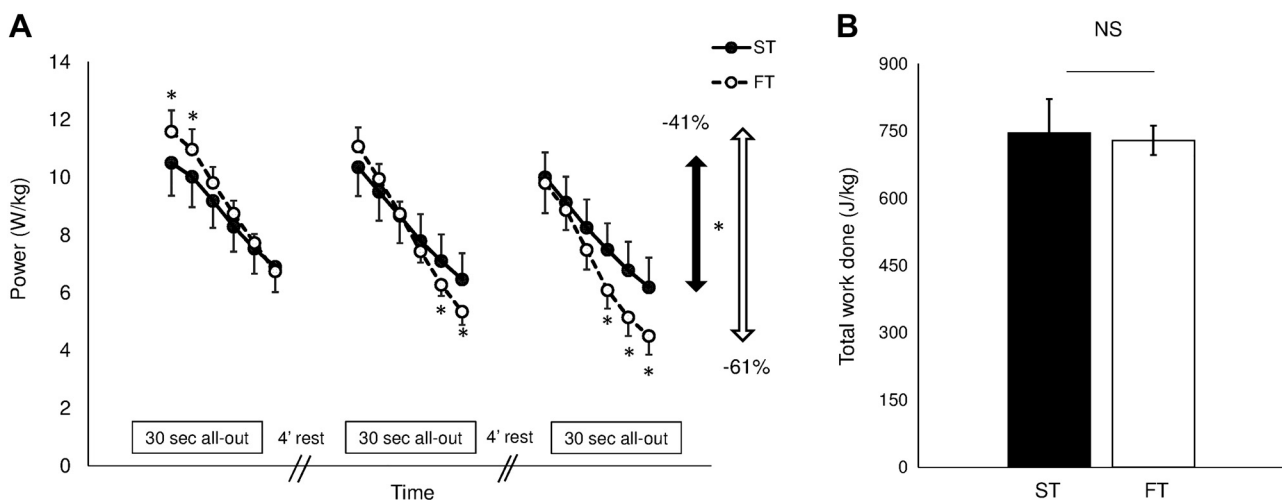

Fig. 3. Fatigue profile of slow typology (ST) and fast typology (FT) groups during 3 repeated Wingate tests interspersed with 4 min of rest. *A*: power drop was significantly higher in FT (−61.0%) compared with ST (−40.9%). *B*: total work done over repeated Wingate tests was equal between groups. Means ± SD are presented. *Significantly different between groups. NS, nonsignificant.
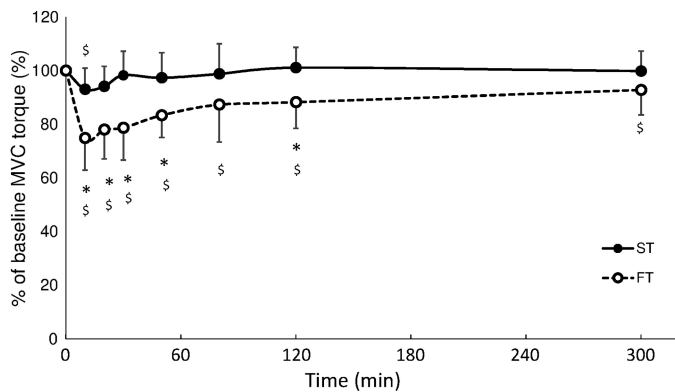
Fig. 4. Recovery of maximal voluntary contraction (MVC) torque after 3 repeated Wingate tests. Values are mean ± SD % of maximal baseline torque. *Significantly different between groups; $significantly different from baseline. ST, slow typology; FT, fast typology.

value. Peak torque, generated during the MVC, was decreased when measured 10 min after the three repeated Wingate tests in both groups ($P = 0.023$ in ST and $P < 0.001$ in FT). The FT group had a significantly higher decline (25%) compared with the ST group (7%) ($P = 0.001$) (Fig. 4). Moreover, this decrease in torque after 10 min (%) was correlated with the muscle typology z score ($r = 0.600$; $P = 0.005$). After 20 min the recovery of the MVC peak torque in the ST group was completed ($P = 0.106$), whereas the FT group displayed a sustained torque deficit throughout the evaluation period and did not recover even after 5 h ($P = 0.024$).

Activation of the knee extensor was assessed with the VAL method and RMS-to-M wave ratio to see if central fatigue was present. As no decline in the VAL was seen after the three repeated Wingate tests (Fig. 5A; main effect of time $P = 0.077$, interaction effect $P = 0.064$) and the RMS-to-M wave ratio was constant over time and between groups (Fig. 5B; main effect of time $P = 0.551$, interaction effect $P = 0.905$), we assume that no central fatigue was present during the recovery period going from 10 min to 5 h after the repeated Wingate tests. Despite unaltered central command, 20 min after the repeated Wingate tests a 38% higher EMG/mean torque during MVC was seen in the FT group, whereas this ratio was unaltered in the ST group. The FT group was unable to produce the same amount of torque despite the same activation of the knee extensors (Fig. 5C; interaction effect $P < 0.001$).

Possible alterations at the neuromuscular junction and the transmission of the action potential on the sarcolemma were investigated using the M-wave area in response to the single stimulus. The M-wave area was unchanged in both groups at 10 min after Wingate ($P = 0.159$ in ST and $P = 0.435$ in FT); then it was decreased in the ST group from 20 min (-10.7%, $P = 0.006$) to 50 min (-8.71%, $P = 0.006$) and in the FT group from 20 min (-10.4%, $P = 0.002$) to 2 h (-9.12%, $P = 0.025$) after the repeated Wingate tests (Fig. 6).
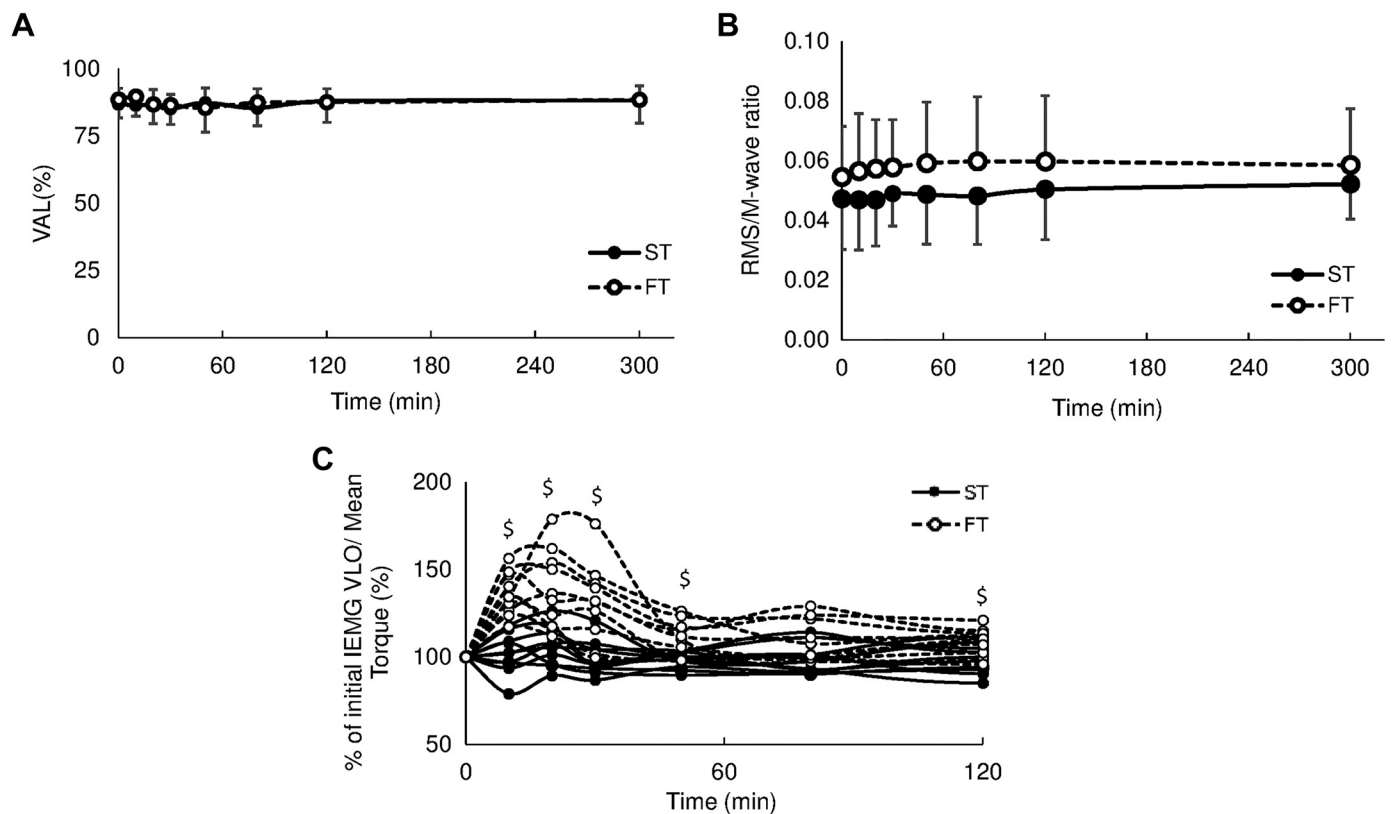

Fig. 5. A and B: there is no central fatigue present after 3 Wingates, as there is no decline in voluntary activation level (VAL) (A) and root mean square (RMS)-to-M wave ratio (B) in both groups and no differences between groups are present. C: the FT group cannot maintain torque level during maximal voluntary contraction, despite unaltered central command. Means ± SD are presented. $Significantly different from baseline. FT, fast typology; ST, slow typology; iEMG VLO, integrated electromyography of vastus lateralis muscle.
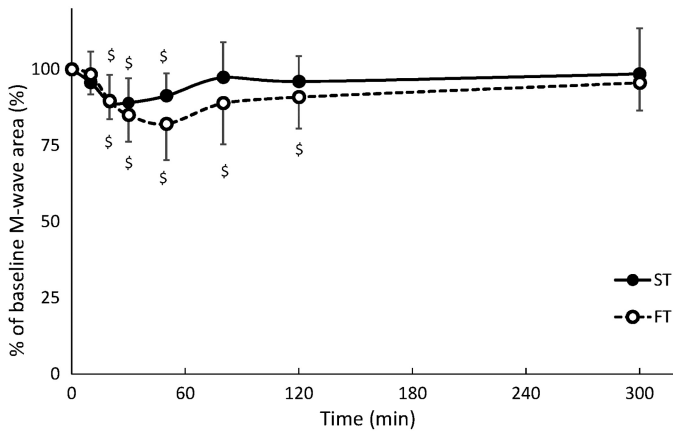
Fig. 6. Fatigue is present in both groups during transmission of action potential along the neuromuscular junction and muscle fiber, as indicated by the decline in the M-wave area. Slow typology (ST) group is different from baseline until 50 min after the Wingates and fast typology (FT) group until 120 min. Means ± SD are presented. $Significantly different from baseline.

At the muscle level, 100-Hz doublet torque was decreased after the repeated Wingate tests in both groups (Fig. 7A and Fig. 8; $P < 0.001$), although the decrease was higher in the FT group (-22% after 10 min) compared with the ST group (-14% after 10 min; $P = 0.039$). Differences between groups occurred up to 50 min of recovery ($P = 0.009$). The decrease in 10-Hz doublet was even greater compared with the 100-Hz

doublet (Fig. 7B and Fig. 8; FT -40% and ST -29% after 10 min). Up to 2 h into recovery, the FT group had a higher decrease in the doublet torque compared with the ST group ($P = 0.011$). In both 100-Hz and 10-Hz doublets, all time points were significantly different from baseline, suggesting that muscle fatigue was still present after 5 h in both groups. Because of a higher decrease in 10 Hz compared with 100 Hz, the 10 Hz-to-100 Hz ratio (Fig. 7C) was decreased up to 5 h in both groups (main effect of time $P < 0.001$). Moreover, the ratio was significantly lower in the FT group compared with the ST group (main effect of group $P = 0.028$).

The contraction time of the singlet was equal between groups at baseline (Table 2) and was significantly shorter in the fatigued state in both groups [-22.8% in ST from 10 min onward ($P = 0.003$) and -17.7% in FT from 20 min onward ($P = 0.014$); Fig. 8]. The contraction time stayed significantly shorter in the ST group up to 80 min ($P = 0.020$) and in the FT group up to 2 h ($P = 0.010$). No differences were present between groups at any time point. The rate of torque development ($+dT/dt$) of the 100-Hz doublet was 31% higher in the FT group compared with the ST group at baseline (Table 2). Ten minutes after the repeated Wingate tests the decrease in $+dT/dt$ (100 Hz) was more pronounced in the FT (-27%) than the ST (-7%, $P = 0.001$) group, and this difference between groups was present until 30 min after the Wingate tests. In the ST group, $+dT/dt$ (100 Hz) was significantly different from baseline until 50 min (-7%, $P = 0.018$), then returned to
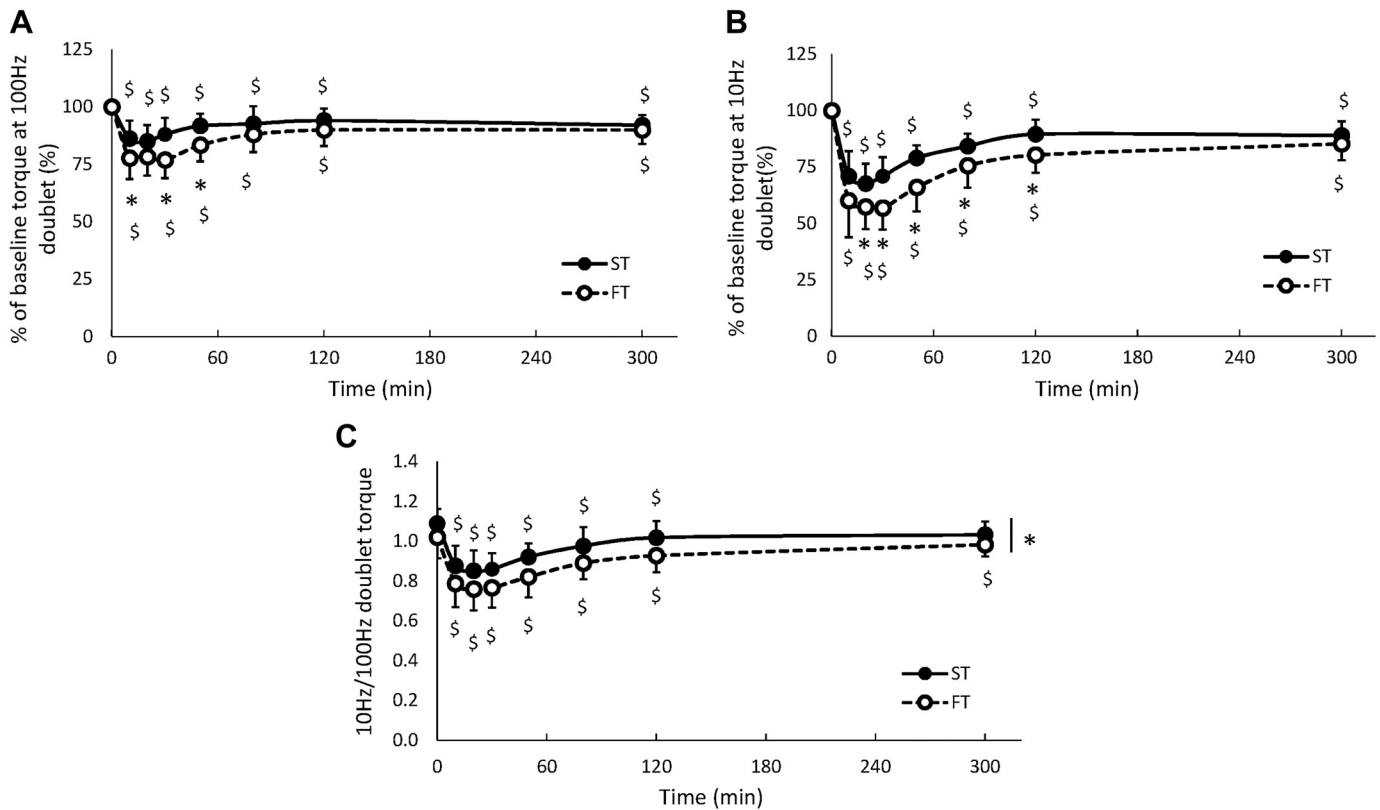

Fig. 7. A and B: peak torque at 100-Hz (A) and 10-Hz (B) doublets is decreased in both groups up to 5 h after the repeated Wingate test. The decrease is bigger in the fast typology (FT) group compared with the slow typology (ST) group up to 50 min in 100 Hz and up to 120 min in 10 Hz. C: as the 10 Hz-to-100 Hz ratio is negative, the 10-Hz doublet is more affected by fatigue than the 100-Hz doublet. Moreover, the 10 Hz-to-100 Hz ratio is lower in the FT group compared with the ST group. Means ± SD are presented. *Significantly different between groups; $significantly different from baseline.
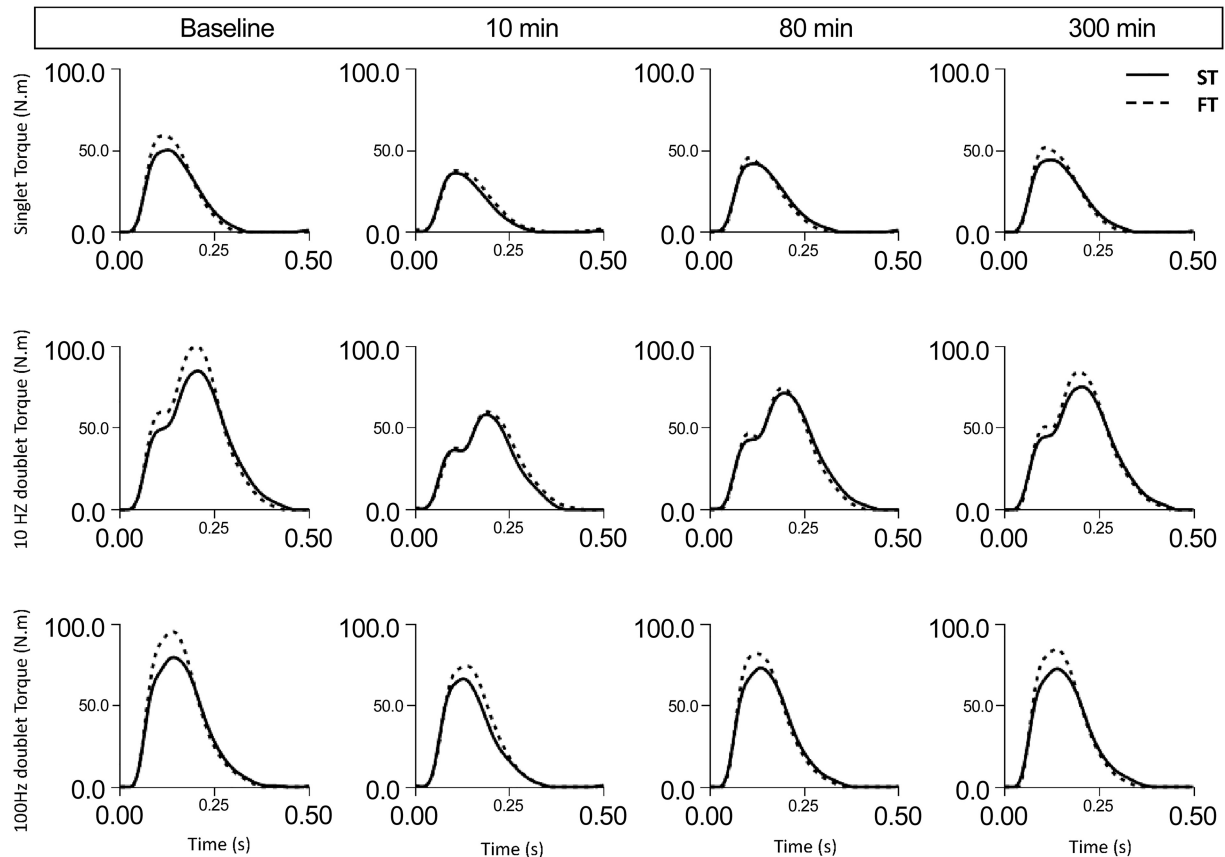
Fig. 8. Mean traces of the singlet 10-Hz and 100-Hz doublets of all subjects before and 10, 80, and 300 min after Wingate. ST, slow typology; FT, fast typology.

baseline values up to 2 h (-6%, $P = 0.074$), and decreased again after 5 h (-9%, $P = 0.009$). In the FT group, $+dT/dt$ (100 Hz) was significantly decreased up to 5 h (-8%, $P < 0.001$). The half-relaxation time (HRT) of the singlet was not significantly different between groups at baseline ($P = 0.211$) or at any fatigued time point. Nevertheless, the HRT was significantly increased in the FT group 10 min after the Wingates ($P = 0.038$). At baseline, the rate of torque relaxation of the singlet was 46% higher in the FT than ST group (Table 2). Ten minutes into recovery the reduction in the rate of torque relaxation was more pronounced in the FT group (-47%) compared with the ST group (-17%; $P = 0.001$), and this difference remained present until 80 min after the Wingate tests. Moreover, the rate of torque relaxation was significantly different from baseline until 5 h in both groups.

Blood variables. During the three repeated Wingates, disturbances in capillary blood lactate and pH appeared in both groups (Fig. 9). Lactate increased to a higher level in the FT group compared with the ST group only after the first Wingate (FT 14.95 ± 2.74 vs. ST 12.47 ± 1.52 mmol/L; $P = 0.022$) and not after the second and third Wingates ($P = 0.090$ and $P = 0.239$, respectively). In the FT group lactate continued to rise until 7 min after the repeated Wingate tests (23.1 ± 2.92 mmol/L), whereas in the ST group the maximal lactate was already reached 3 min after the Wingates (21.0 ± 2.11 mmol/L). Maximal lactate was not significantly different between groups ($P = 0.082$). Full return to baseline blood lactate was observed after 2 h for both groups. The pH decreased to a lower level in the FT group compared with the ST group after the first, the

second, and the third Wingate ($P = 0.009$, $P = 0.004$, and $P = 0.016$, respectively). The lowest pH was reached 3 min after the third Wingate in both groups (FT pH = 7.06, ST pH = 7.12). Recovery of blood pH was complete at 80 min in the FT group ($P = 0.361$) but only after 2 h in the ST group ($P = 0.621$).

DISCUSSION

The present study aimed to clarify whether an a priori division of athletes into either a fast or a slow muscle typology group, based on noninvasive measurement of the carnosine concentration by ^{1}H-MRS in the gastrocnemius, was associated with the fatigue during a high-intensity exercise and, more importantly, the recovery profile following this fatiguing exercise. Despite the moderate limits of inclusion for muscle typology (z score lower than -0.5 or higher than $+0.5$), marked differences in the fatigue and recovery profiles were present between groups.

During the repeated Wingate tests, the power drop through each Wingate was much higher in the FT group compared with the ST group. This observation is in agreement with the invasive biopsy-based findings of Bar-Or et al. (5) and Inbar et al. (21), who found a positive relationship between the power drop during a single Wingate and the average fast-twitch area/average slow-twitch area ($r = 0.75$) and between the power drop during a single Wingate and the percentage of fast-twitch muscle fibers in vastus lateralis ($r = 0.52$), respectively. Accordingly, in this study, the total power drop over
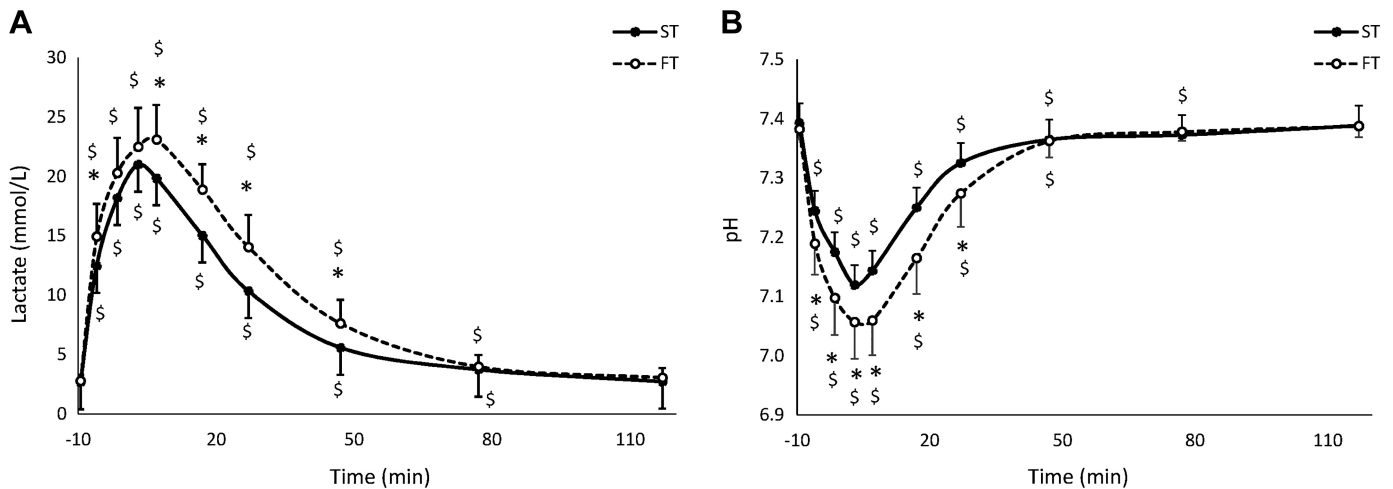
Fig. 9. Disturbance in blood lactate (*A*) and pH (*B*) during and 2 h after 3 repeated Wingate tests. Measurements were taken at baseline (time point -9.5 min), 3 min after each Wingate test (at -6 min, -1.5 min, and 3 min), and just before the maximal voluntary contraction and electrical stimulation protocol (at 7 min, 17 min, 27 min, 47 min, 77 min, and 117 min). Means ± SD are presented. *Significantly different between groups; $significantly different from baseline. ST, slow typology; FT, fast typology.

three repeated Wingates showed the strongest relationship with the muscle typology ($r = 0.677$). Moreover, the ST group showed hardly any accumulation of fatigue throughout the Wingates, as the peak power was equal between the first and the second Wingate and decreased only 3.2% from the second to the third Wingate. In contrast, the peak power of the FT group decreased with each consecutive Wingate (-4.0% from *Wingate 1* to *Wingate 2* and -12% in from *Wingate 2* to *Wingate 3*). The higher amount of accumulated fatigue in FT subjects, as demonstrated by the higher total power drop and the decreased peak power, is in accordance with the literature showing a higher accumulated fatigue in subjects with predominantly fast-twitch fibers after three bouts of maximal unilateral knee extensions (-18%) and after sixteen 5-s lasting MVCs (-26%) (9, 18).

Despite the different fatiguing profiles, total work done was the same in both typologies, enabling us to investigate the course of muscle torque recovery after an identical amount of performed work. Ten minutes after the repeated Wingate tests, the recovery of MVC torque was 18% lower in the FT group compared with the ST group. This difference in recovery was in accordance with Hamada et al. (18), who found a 16% lower state of recovery in their fast-twitch group compared with their slow-twitch group, 5 min after sixteen 5-s maximal voluntary isometric contractions. Up to now, it was unknown whether this difference between typology groups was only present in the first minutes of the recovery phase or would be lasting several hours. This study demonstrates for the first time that 2 h after a high-intensity exercise bout the difference in maximal torque recovery between typology groups was still 11%. The ST group had fully recovered to baseline 20 min after the Wingates, whereas the FT group had not yet recovered 5 h into recovery and their time to recover thus exceeded the time frame of this study. These findings have implications for further research, as it was formerly believed that MVC is rapidly recovered after a high-intensity cycling exercise (14, 39). Yet this might have been misleading if muscle fiber type was not taken in consideration, as in this study a fast recovery was seen in ST but not in FT. Moreover, if this study focused

on the effect of the three repeated Wingates on, for example, the HRT after a 10-Hz stimulation without any division in typologies, no effect would be found for this parameter ($P = 0.177$; Fig. 10). However, the high standard deviation 10 min after the repeated Wingate tests is explainable by opposing effects in both groups, with an increase of HRT in the FT group and a slight decrease (significant at 20 but not 10 min recovery) in the ST group. Differentiation between the muscle typology groups might thus lead to new insights regarding human muscle fatigue and recovery mechanisms.

The recovery of voluntary parameters was combined with electrically induced responses in order to get insights in the origin of fatigue (central vs. peripheral). By administering a SID during the MVC, the VAL was conducted. This measurement, combined with the RMS-to-M wave ratio, showed that central fatigue was not present in both groups from 10 min to 5 h after the fatigue-inducing task. This is in agreement with the current literature, as central fatigue is mostly present after long endurance but not after short intense exercises (8). It is possible that central fatigue was present during the Wingates, as the literature on fatigue during all-out repeated cycling typically shows that central motor command is limiting the performance in order to prevent excessive locomotor muscle fatigue. Because in this investigation central fatigue was only measured 10 min after the Wingates, it might have recovered in this time frame (20, 34). When iEMG/torque was analyzed 10 min after the Wingates, it became clear that, despite unaltered central activation, the FT group was not able to produce the same amount of torque after the repeated Wingate tests. The higher iEMG-to-torque ratio in FT was also observed by Nilsson et al. (31), who found a positive correlation between the increase in EMG-to-torque ratio and the percentage of fast-twitch fibers, indicating that local factors in fast-twitch fibers cause the development of fatigue (31). Before being able to interpret the peripheral fatigue, changes at the neuromuscular junction were investigated. The M-wave area showed fatigue during the transmission of the action potential along the neuromuscular junction in both groups from 20 min after the repeated Wingate tests. Based on the literature, no difference
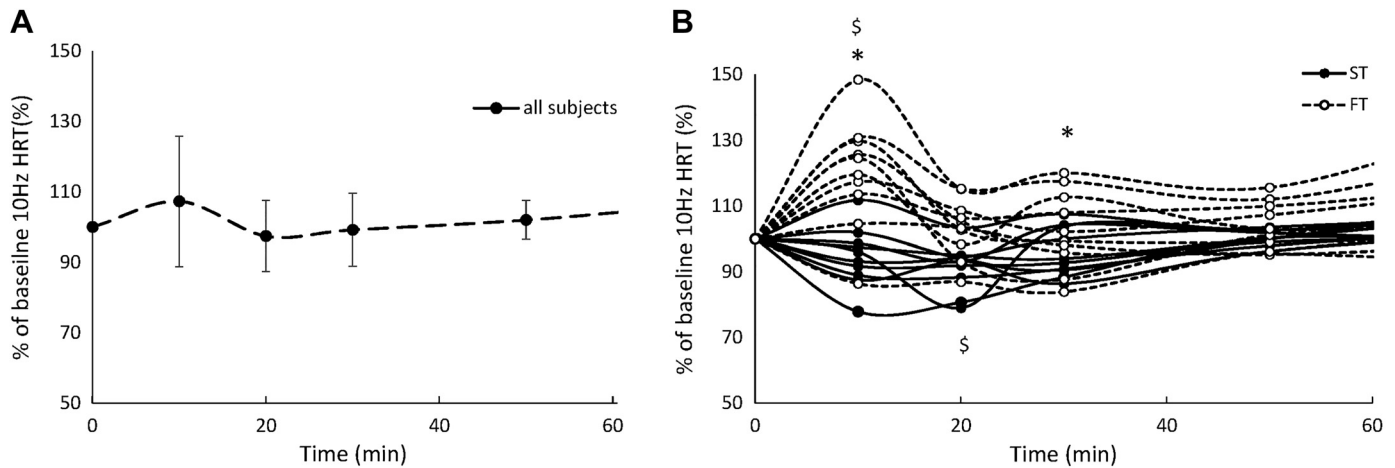
Fig. 10. Opposing effects of fatigue on half-relaxation time (HRT) of the 10-Hz doublet in both typology groups: increase in HRT in fast typology (FT) 10 min after the repeated Wingates and decrease in slow typology (ST) 20 min after the repeated Wingates. *A*: results for all subjects (ST and FT). *B*: results for individual subjects. *Significantly different between groups; $significantly different from baseline.

was expected in the M-wave properties after the three repeated Wingate tests (32). In the ST group this decrease was present up to 50 min, whereas it was present up to 2 h in the FT group. This pattern was already observed by Mc-Fadden and McComas (28), who hypothesized that this decrease did not appear because of an impaired neuromuscular transmission but because of a problem in the membrane potential initiated by, for example, sarcolemmal damage. Although damage is not expected after the repeated Wingate tests, because this is mainly characterized by concentric contractions (32) it cannot be fully excluded in some fast-twitch fibers.

Because the maximal fatigue-induced deficits at the 100-Hz doublet (-23%), 10-Hz doublet (-43%), and singlet (-37%) are bigger than the alterations in the M wave (-18%) and these deficits in electrically evoked torque are already present at the beginning of the recovery in contrast to the deficit in the M wave, important torque-depressing alterations will have taken place beyond the muscle membrane as well. Early peripheral fatigue can be attributed to an increase of by-products of P_i, H^+, and ADP and local energy deprivation (3). The accumulation of these products might be higher in fast-twitch fibers because of the greater reliance on anaerobic processes to supply energy (29). Moreover, the accumulation might affect torque production differently in the FT compared with the ST group. For example, there is a bigger effect of increased P_i on the efficiency of a fast-twitch fiber compared with a slow-twitch fiber (25) and the detrimental effect of increase in H^+ on the transition to high-force state is present in fast- but not slow-twitch fibers (30). Furthermore, a local depletion of ATP might have been present around the sarcoplasmic reticulum Ca^{2+} pumps in fast-twitch fibers, as these have a higher density of sarcoplasmic reticulum Ca^{2+} pumps and therefore consume higher amounts of ATP (13, 22). Theoretically, all by-products should be recovered after 2 h and thus cannot explain the finding that recovery takes longer than 5 h in all stimulated frequencies.

During fatigue, the relative decrease in torque production is often bigger at high compared with low activation frequencies, because during fatigue a prolongation of the Ca^{2+} transient is present, which results in an increased fusion of stimulations at lower frequencies and consequently results in higher torque

production (23). Contrarily, in this study the 10 Hz-to-100 Hz ratio is decreased in the fatigued state; thus 10 Hz is depressed to a higher degree than 100 Hz. This phenomenon could be explained by the presence of prolonged low-frequency force depression, which might be the origin of the long-lasting fatigue (12). During prolonged low-frequency force depression, changes in Ca^{2+} handling will affect the torque production more at lower frequencies, as lower stimulation frequencies are on a steeper part of the force-intracellular Ca^{2+} concentration ($[Ca^{2+}]_i$) relationship than higher stimulation. The mechanisms behind prolonged low-frequency force depression are either a decreased sarcoplasmic reticulum Ca^{2+} release or a reduced myofibrillar Ca^{2+} sensitivity. More precisely, the origin of the different Ca^{2+} handling after three repeated Wingates in recreationally trained subjects might be the fragmentation of the sarcoplasmic reticulum Ca^{2+} release channel (32). As the 10 Hz-to-100 Hz ratio was significantly lower in the FT group, this fragmentation might have been higher in this group.

The present study provides evidence of a long-lasting deficit in maximal voluntary muscle force in some but not all individuals, which seems to be mainly attributable to distinct muscle typology. As the maximal voluntary (isometric) contraction requires the simultaneous recruitment of almost all muscle fibers, it can be hypothesized that slow-twitch fibers fully recover from all-out Wingate tests within a few minutes, whereas fast-twitch fibers would probably need hours to regain full initial contractile potential. In that case, individuals with a predominant slow-twitch fiber distribution will display little force deficit and fast recovery, whereas individuals with a predominant fast-twitch fiber distribution will have a greater proportion of their muscle fibers in a prolonged deficient state, leading to a compromised whole muscle torque for several hours. To test this hypothesis, we compared the absolute contractile kinetic properties in three electrically stimulated conditions both in rest and in a fatigued state. At baseline, the rate of torque development, peak torque, and rate of torque relaxation were higher in the FT group compared with the ST group. Despite these profound baseline differences, the mean trace of the FT group was no longer distinguishable from the trace of the ST group 10 min after the repeated Wingate test

(Fig. 8). Moreover, most of these contractile kinetic properties stayed equal between groups up to 5 h in recovery, except for the peak torque at 100 Hz and the rate of torque relaxation at singlet, which were significantly different after 2 h, and the rate of torque development at 100 Hz, which was significantly different after 50 min. As these traces reflect a compound of all muscle fibers that contribute to the torque production, all fast-twitch muscle fibers were possibly fatigued and therefore only the less fatigued slow-twitch muscle fibers were contributing to the electrically induced muscle torque.

We must acknowledge that the differences in baseline characteristics in weight, lean body mass, and quadriceps muscle mass (estimated by corrected circumference) between the muscle typology groups were a limitation of the study, which might have introduced differences in the torque at MVC and electrical stimulations at rest, although we do not expect these differences to induce the entire baseline differences in rate of torque development and relaxation. The latter might be explained by a different muscle fiber typology and therefore confirm that the measurement of carnosine is related to muscle typology. Moreover, it also proves the presence of an across-muscle phenotype, as carnosine was measured in the gastrocnemius but differential baseline responses to electrical stimulation were found in the quadriceps. This across-muscle phenotype suggests that the fiber type proportion of one muscle is indicative for the proportion of the total body (42). We chose to measure the muscle typology in the gastrocnemius, as this allowed us to compare the carnosine concentration to a large reference database (98 male recreationally active control subjects), in order to divide the group into representative slow and fast typology groups.

Next to functional measures via electrical stimulation, other attempts have been conducted to noninvasively estimate the muscle fiber typology, such as a countermovement jump (7) and tensiomyography (38). However, all these measurements have the same disadvantages: they can be influenced by warm-up, training, technique, fatigue, motivation, and acute food intake. Our noninvasive estimation of muscle typology, based on the measurement of carnosine via ^{1}H-MRS, is performed at rest and therefore not subjected to effects of technique, motivation, or fatigue. Moreover, carnosine is a very stable metabolite, not influenced by training or by acute daily food intake (4).

Although the fatiguing exercises in this study (3 repeated Wingates) were mainly concentric, we hypothesize that the higher fatigability and time to recover in the FT group would also be present after exercises with an eccentric component, like running. Moreover, an eccentric component might even exaggerate differences between groups, as it has been suggested that fast-twitch fibers are more easily damaged after eccentric exercises than slow-twitch fibers (15). Therefore, this information is important for athletes, especially if characterized by a high heterogeneity in muscle typology within one team. Until now, training has not been adjusted for muscle fiber typology and all athletes thus perform the same training and recovery cycles, although this induces distinct responses in athletes with different muscle typology. Some athletes might thus be at risk for accumulated fatigue, overtraining, and potentially injury. The proposed approach for noninvasive estimation of muscle typology can therefore be a meaningful tool for individualization of training and recovery cycles.

In summary, the present study shows that distinct muscle typology groups fatigue differently during three repeated Wingate tests, with a higher degree of fatigue during the Wingates in subjects with a FT compared with subjects with a ST. Moreover, a total of only 90 s of high-intensity exercise induced long-lasting fatigue and impairments in the contractile function after these Wingates. This postexercise fatigue was expressed more in the FT group and resulted in a noncomplete recovery of the voluntary contraction up to 5 h after Wingate. The voluntary torque of the ST group, on the other hand, had already recovered 20 min after the repeated Wingates. These results can be relevant for training and recovery cycles and might open opportunities to better individualize training of athletes on the basis of their muscle typology.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

E.L., M.K., T.B., and W.D. conceived and designed research; E.L. and T.B. performed experiments; E.L. analyzed data; E.L., M.K., T.B., and W.D. interpreted results of experiments; E.L. and W.D. prepared figures; E.L., M.K., and W.D. drafted manuscript; E.L., M.K., T.B., and W.D. edited and revised manuscript; E.L., M.K., T.B., and W.D. approved final version of manuscript.

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