Effect of power, pedal rate, and force on average muscle fiber conduction velocity during cycling

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Farina, Dario, Andrea Macaluso, Richard A. Ferguson, and Giuseppe De Vito. Effect of power, pedal rate, and force on average muscle fiber conduction velocity during cycling. J Appl Physiol 97: 2035–2041, 2004. First published July 30, 2004; doi:10.1152/japplphysiol.00606.2004.—Muscle fiber conduction velocity (MFCV) provides indications on motor unit recruitment strategies due to the relation between conduction velocity and fiber diameter. The aim of this study was to investigate MFCV of thigh muscles during cycling at varying power outputs, pedal rates, and external forces. Twelve healthy male participants aged between 19 and 30 yr cyclic on an electronically braked ergometer at 45, 60, 90, and 120 rpm. For each pedal rate, subjects performed two exercise intensities, one at an external power output corresponding to the previously determined lactate threshold (100% LT) and the other at half of this power output (50% LT). Surface electromyogram signals were detected during cycling from vastus lateralis and medialis muscles with linear adhesive arrays of eight electrodes. In both muscles, MFCV was higher at 100% LT compared with 50% LT for all average pedal rates except 120 rpm (mean ± SE, 4.98 ± 0.19 vs. 4.49 ± 0.18 m/s; P < 0.001). In all conditions, MFCV increased with increasing instantaneous knee angular speed (from 4.14 ± 0.16 to 5.08 ± 0.13 m/s in the range of instantaneous angular speeds investigated; P < 0.001). When MFCV was compared at the same external force production (i.e., 90 rpm/100% LT vs. 45 rpm/50% LT, and 120 rpm/100% LT vs. 60 rpm/50% LT), MFCV was higher at the faster pedal rate (5.02 ± 0.17 vs. 4.64 ± 0.12 m/s, and 4.92 ± 0.19 vs. 4.49 ± 0.11 m/s, respectively; P < 0.05) due to the increase in inertial power required to accelerate the limbs. It was concluded that, during repetitive dynamic movements, MFCV increases with the external force developed, instantaneous knee angular speed, and average pedal rate, indicating progressive recruitment of large, high conduction velocity motor units with increasing muscle force.

Dynamic exercise; surface electromyogram; electrode arrays

Electromyographic (EMG) recordings provide a window into the nervous system, allowing the assessment of global muscle properties as well as single motor unit (MU) features (36, 38). Due to methodological issues, both surface and intramuscular EMG recordings have often been performed during standardized constrained conditions, such as isometric, constant force contractions (26, 37). However, the understanding of muscle functions and motor control during movement is more relevant than during static contractions in applied fields, such as sport and rehabilitation medicine.

The use of surface EMG in dynamic contractions has mainly been limited in the past to the detection of muscle activation timing or contraction intensity, thus providing a tool for investigating muscle coordination during movement (8). More recently, methods based on time-frequency analysis of surface EMG signals have been proposed for assessing dynamically induced muscle fatigue (4, 19) and to gain an insight into the properties of the muscle fiber membrane during movement. However, spectral frequencies are not direct physiological variables, and thus their elucidation is not straightforward and may lead to ambiguous interpretations of the results (11).

Among the information that can be extracted from surface EMG, muscle fiber conduction velocity (MFCV) is a physiological parameter that is related to the fiber membrane and contractile properties (1). Estimates of MFCV are obtained from the interference EMG signal without the separation of contributions of individual MUs. Thus MFCV is the average value of the conduction velocities of all active muscle fibers within the detection volume of the measuring electrodes (10). Because MU conduction velocity is a size principle parameter (1), estimates of MFCV may be used to infer MU recruitment/derecruitment strategies. Indeed, lower threshold MUs have a lower conduction velocity than higher threshold MUs, which results, during isometric contractions, in an increased average MFCV with progressive MU recruitment (e.g., Ref. 9).

Reliable estimation of MFCV requires the detection of surface EMG signals from at least two locations over the muscle between the innervation zone and the tendon endings (10). The delay between the two detected signals is inversely related to the velocity of propagation of the intracellular action potentials. The measure of MFCV implies a fixed distance between detection points and signals free of artifacts. These requirements are not easily satisfied in dynamic conditions involving fast limb movements, which in the past hindered the possibility of performing this measure during movement. Recently, advances in surface EMG detection and processing made the estimation of MFCV feasible during dynamic contractions (13, 14). The availability of MFCV estimates in these conditions opens important perspectives in the field of motor control and muscle assessment. Indeed, due to the association between muscle fiber diameter and conduction velocity (31), MFCV estimates provide indications on the changes in the active MU population during dynamic exercise. It is thus possible to understand how the population of active MUs evolves over time in a specific movement. Currently, no other
electrophysiological measure provides direct assessment of MFCV in dynamic conditions.

In the present work, we measured MFCV in two thigh muscles during dynamic cycling exercise. Cycling is a well-standardized movement that can be performed by varying a few parameters, such as pedal rate and force. Cycling at different velocities and forces implies changes in muscle control strategies that are revealed, for example, by oxygen uptake ($\dot{V}\text{O}_2$) responses (33). The measure of MFCV during cycling may provide a direct means for assessing modifications of the MU population in the different phases of the task. As an example, additional MU recruitment was supposed to be responsible for the so-called “slow component of $\dot{V}\text{O}_2$” (16), which has been recently confirmed using single muscle fiber analysis from muscle biopsies obtained before and after exercise (20). The possibility of noninvasively investigating these control mechanisms would have relevant applications in sport medicine and physiology.

The main objective of the study was thus to investigate 1) the feasibility of MFCV estimates at high contraction speeds (i.e., up to 120 rpm) during cycling and 2) the dependence of MFCV on power, average pedal rate, and external force. In particular, we tested the hypothesis that the order of MU recruitment from low to high conduction velocity with increasing force is maintained during cycling across a range of contraction speeds and forces.

METHODS

Subjects. Twelve healthy male subjects (mean $\pm$ SD: age, 26 $\pm$ 5 yr; stature, 1.77 $\pm$ 0.06 m; body mass, 70 $\pm$ 8 kg) participated in the study. Four of the 12 subjects were engaged in regular training activity (cycling). These trained cyclists had peak $\dot{V}\text{O}_2$ ($\dot{V}\text{O}_2\text{ peak}$) of 62 $\pm$ 3 ml·kg$^{-1}·$min$^{-1}$ and a lactate threshold (LT) corresponding to 241 $\pm$ 18 W (see LT and $\dot{V}\text{O}_2\text{ peak}$ for the description of the measurement of $\dot{V}\text{O}_2\text{ peak}$ and LT). The other participants were physically active but did not practice any kind of systematic training and had a $\dot{V}\text{O}_2\text{ peak}$ of 46 $\pm$ 7 ml·kg$^{-1}·$min$^{-1}$ and LT corresponding to 140 $\pm$ 36 W. The study was conducted in accordance with the Declaration of Helsinki and approved by the Local Ethics Committee, and written, informed consent was obtained from all participants before inclusion.

LT and $\dot{V}\text{O}_2\text{ peak}$. At least 3 days before the main experimental session, each participant undertook a standardized LT test that was combined with the measurement of $\dot{V}\text{O}_2\text{ peak}$. The protocol was modified from a treadmill test previously described by Jones (18). In the first part of the test, subjects exercised on an electronically braked ergometer (Excalibur Sport, Lode, The Netherlands) at an initial power output of 70 W at 15 pedal revolutions. Power output was increased every 3 min by 35 W. At the end of each stage, a capillary blood sample for the determination of lactate concentration (Lactate Pro, Arkray, Japan) was obtained. When lactate concentration had increased by >1 mM, at least three further stages were performed, after which a 10-min recovery period was allowed. In the second part of the test, $\dot{V}\text{O}_2\text{ peak}$ was determined with the subjects cycling, beginning at the power output of the penultimate stage, with power being increased by 35 W every minute until the subject reached volitional exhaustion. Pulmonary $\dot{V}\text{O}_2$ and CO$_2$ production was measured continuously during the exercise via an online gas-analysis system (Oxycon gamma, Mijnhardt, Netherlands), which had been calibrated with known values of oxygen, CO$_2$, and volume. Data points for blood lactate concentration were plotted against power output, with LT determined using linear regression analysis according to the intersection point of the two best-fitting lines (6).

General procedures. After a warm-up of 5–10 min of cycling at a freely chosen pedal rate on the ergometer, electrodes for surface EMG detection were placed over the vastus lateralis and vastus medialis muscles of the right thigh, as detailed below. The knee joint angle was recorded by means of an electronic goniometer (model GON2A30144, DEM, Torino, Italy). The subject then performed a total of eight cycling bouts, in a random order, by varying 1) average pedal rate (45, 60, 90, and 120 rpm) and 2) power output (50 and 100% of external power output corresponding to LT) (Table 1). The selection of the average pedal rate and power output allowed the comparison of exercises performed at the same average external force with different average pedal rates (e.g., exercises at 60 and 120 rpm with power output of 50 and 100% LT, respectively, led to the same average external force; Table 1). Thus it was possible to independently investigate the effect of average pedal rate and force on MFCV.

The intensity of exercise was defined according to LT, as opposed to absolute power outputs or a relative percentage of $\dot{V}\text{O}_2\text{ peak}$, to normalize the metabolic stress at which the subjects were analyzed. This minimized the potential confounding effect of different levels of training and fitness. The importance of this normalization was previously underlined by Meyer et al. (27), who claimed that exercise intensity should be defined in relation to individual anaerobic threshold. LT corresponds to the upper limit of the aerobic/anaerobic metabolic transition, where production and elimination of lactate are in equilibrium. Over this point, there is a net accumulation of lactate both in the muscle and in the blood that alters the pH and leads to muscle impairment. Thus the intensity of the exercise corresponding to LT implies the recruitment of type II MUs that have a high glycolytic capacity (7, 33). Cycling at 50 or 100% LT will therefore imply a significant change in the population of active MUs. If the MUs are activated with increasing conduction velocity, the increase in power output should determine larger MFCV.

The acquisition of surface EMG signals started when the subject reached the target pedal rate and power output and lasted for the duration of 15 pedal revolutions in all instances. The subject was provided with a visual feedback of the average pedal rate, and a 3-min rest was given after each exercise.

Surface EMG recordings. Multi-channel surface EMG signals were detected from the right (dominant in all cases) vastus lateralis and vastus medialis muscles, with two linear adhesive arrays (model EL50908, SPES Medica, Salerno, Italy) consisting of eight electrodes with 5-mm interelectrode distance in bipolar configuration. EMG signals were amplified (16-channel surface-EMG amplifier, EMG-16, LISIN-Prima Biomedical & Sport, Treviso, Italy), band-pass filtered (−3-dB bandwidth, 10–500 Hz, 40 dB/decade), and sampled at 2 kHz.

Before electrode placement, muscle activity was assessed in three to four test contractions with a dry array of eight electrodes (silver...
bars, 5 mm long, 1 mm in diameter, 10-mm interelectrode distance). The array was placed along the estimated fiber orientation. From visual inspection of the multi-channel EMG signals, the main muscle innervation zone was detected, as described in Ref. 23, and marked on the skin. The detection of the innervation zone location was performed at 90 and 170° knee joint angles (with 180° being the full extension of the leg). The position of the innervation zone over the skin surface could change at the two joint angles due to the shift of the muscle underlying the skin (12). The adhesive arrays were located between the most distal location of the innervation zone and the distal tendon region. This procedure of electrode placement allowed the detection of signals between the innervation zone and tendon at all joint angles involved in the exercise (13).

Before array placement, the skin was slightly abraded with abrasive paste (Meditec-Every, Parma, Italy). Conductive gel (20–30 μl) was used for each electrode of the array to ensure proper electrode-skin contact and was inserted with a dispenser (Eppendorf, Multipette plus, Hamburg, Germany) into the grooves of the adhesive electrode arrays. This detection modality (adhesive array of electrodes) was recently proposed for the detection of multi-channel surface EMG signals during movement to estimate average MFCV in these conditions (13, 14). Representative signals are shown in Fig. 1 for the four pedal rates.

Signal analysis. The goniometer signal was low-pass filtered (anti-causal Butterworth filter of order 4, cutoff frequency of 10 Hz) and differentiated for estimating the instantaneous knee angular speed. For each revolution, the maximum and minimum joint angles were detected from the goniometer signal. The interval of time between the minimum and the consecutive maximum joint angle (half of the revolution) was divided by nine to compute the interval of time \( t_1 \). Six time instants (referred in the following as instants of time within the revolution) spaced by \( t_1 \) were considered for MFCV estimation, starting from the minimum joint angle (Fig. 2). The surface EMG average rectified value (ARV) was computed in the interval of time between the first and sixth time instant identified for MFCV estimation.

Average MFCV was estimated with the method proposed in Ref. 13. This technique allows a high-resolution, low-variance estimate of MFCV that is local in time. MFCV is estimated as the average of the conduction velocities of the action potentials occurring close to the selected time instant, weighted by a Gaussian window whose standard deviation (set to 30 ms in this study) can be tuned according to the

![Fig. 1. Representative signals detected from the vastus medialis muscle from 1 subject at the 4 average pedal rates [power output = 100% lactate threshold (LT) in all cases]. The 7 bipolar recordings detected by the linear array as well as the joint angle are shown. The 7 bipolar signals are similar in shape and delayed between each other, reflecting detection between the innervation zone and the distal tendon region. The array records the surface potentials corresponding to the traveling of the intracellular action potentials along the muscle fibers. au, Arbitrary units.](image1)

![Fig. 2. Surface electromyographic signals detected from the vastus lateralis muscle with the surface array and corresponding joint angle. The exercise in this case was performed at 45 rpm and 100% LT. •, Time instants where muscle fiber conduction velocity (MFCV) was estimated.](image2)
desired localization in time of the MFCV estimation. The MFCV estimates were obtained at the six time instants defined above. The values in the 15 revolutions of each exercise were averaged to obtain, for each of the six time instants within a revolution, a MFCV value representative of the average conduction velocity of the MUs active close to that specific instant of the revolution. Thus six MFCV values were obtained for each of the eight conditions reported in Table 1. The method allowed monitoring MFCV of the active MU population along the different phases of the exercise for different knee angular speeds within each revolution (Fig. 2).

Statistical analysis. Data are presented as means and standard errors. Three- and four-way ANOVA were used for data analysis. When appropriate, the Student-Newman-Keuls post hoc test was used for multiple comparisons. Statistical significance was set at $P < 0.05$.

RESULTS

Joint angle and instantaneous knee angular speed. Joint angle and instantaneous knee angular speed were analyzed with three-way ANOVA (factors: average pedal rate, power output, and time instant within the revolution). For each of the six selected time instants, the joint angle at which MFCV was estimated did not depend on average pedal rate or power output. Thus, for all pedal rates and power outputs, MFCV was estimated at the same joint angles corresponding to the six time instants previously defined. Average joint angles (over the 2 powers and pedal rates) were $99.5 \pm 0.8, 104.5 \pm 0.8, 117.3 \pm 0.6, 134.3 \pm 0.8, 153.0 \pm 1.1$, and $171.7 \pm 1.3^\circ$ for the six time instants, respectively. The instantaneous knee angular speed at each of the six time instants within the revolution was not statistically different between 50 and 100% LT. Instantaneous speed increased with average pedal rate ($P < 0.001$). Furthermore, at all average pedal rates, instantaneous speed increased ($P < 0.001$) between the first three selected time instants and thereafter remained the same (Table 2).

Surface EMG amplitude. Surface EMG ARV was analyzed by a three-way ANOVA (factors: average pedal rate, power output, and muscle). In both muscles, ARV was higher ($P < 0.01$) during cycling at 100% LT than at 50% LT. There was, however, no effect of pedal rate and muscle on ARV (Fig. 3). When ARV was compared at the same external average force production (i.e., conditions 1 vs. 7 and 2 vs. 8 in Table 1), ARV was higher ($P < 0.001$) at the faster pedal rate in both muscles, except for the vastus lateralis at the average pedal rate of 120 rpm (Fig. 4).

**DISCUSSION**

In this study, we applied a recently developed method for assessing muscle fiber membrane properties through the estimation of MFCV during fast dynamic exercises. The study reports estimates of MFCV during cycling for a number of average pedal rates and external forces. We showed that MFCV increased as external force or pedal rate increased. Furthermore, during each single concentric contraction, MFCV increased as the instantaneous knee angular speed increased. Because average MFCV is related to the population of recruited MUs (1), these results provide direct information on MU recruitment in the different phases of cycling exercise.

Average MFCV during cycling. The estimates of MFCV obtained in the present study were within the range of physiological values previously reported. The only study in which MFCV was estimated from the vastus lateralis and vastus medialis muscles in conditions similar to the present work is by

<table>
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<th>Average Pedal Rate, rpm</th>
<th>Power, %</th>
<th>$t_1$</th>
<th>$t_2$</th>
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<td></td>
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<td>0</td>
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<td>323±11</td>
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<tr>
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<td>395±23</td>
<td>498±17</td>
<td>533±15</td>
<td>517±16</td>
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<tr>
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<td>0</td>
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<td>429±28</td>
<td>510±24</td>
<td>540±17</td>
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<td>508±21</td>
<td>677±21</td>
<td>728±18</td>
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<td>522±30</td>
<td>677±25</td>
<td>730±17</td>
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Values are means ± SE. $t_1$–$t_6$, Time instants within the revolution. $t_1$ Corresponds to the minimum joint angle, i.e., to null instantaneous knee angular speed.
Farina et al. (13), who reported MFCV measures at an average pedal rate of 60 rpm and power output of 150 W in sedentary subjects. In these conditions, MFCV for both vastus lateralis and vastus medialis was in the range of 4.25–4.45 m/s, similar to the present results. In the same muscles, Pozzo et al. (32) reported similar MFCV values that were estimated during explosive contractions of leg extension. There are no other studies that assessed MFCV during fast dynamic tasks.

The MFCV values obtained in this study were in agreement with those reported during static contractions. Arendt-Nielsen et al. (2) found MFCV in the vastus lateralis muscle to be on average 4.2 m/s at 10% of the maximal voluntary contraction. At 50% maximum voluntary contraction, Rainoldi et al. (34) provided higher estimates (5.5–6.1 and 6.2–6.6 m/s for the vastus lateralis and vastus medialis muscles, respectively). Using transcutaneous electrical stimulation, Merletti et al. (25) obtained values between 4 and 6 m/s in the vastus medialis. Similar MFCV values were reported for the vastus lateralis by Arendt-Nielsen et al. (3), Sadoyama et al. (35), and Bazzucchi et al. (5), among others. Nishizono et al. (29) estimated conduction velocity of single MUs from the vastus lateralis muscle and observed a mean value of 4.6 m/s. The range of MFCV values measured from other muscles is similar (e.g., Refs. 24, 28, 30). The agreement of the present results with those from previous studies in more constrained conditions underlines the reliability of the approach. These data also provide further validation of the method for MFCV estimation during dynamic muscle contractions proposed by Farina et al. (13). Indeed, in the present study, MFCV could be estimated at a pedal rate of up to 120 rpm, which resulted in bursts of EMG activity of only 120–150 ms in duration.

**Dependence of MFCV on average external force.** We were able to independently assess the effect of pedal rate and external force production on MFCV. Because pedal rate was kept constant at the different exercise intensities and the instantaneous knee angular speed did not depend on the power output (Table 2), there was an increase in average force requirement at the higher power output. At all pedal rates, except 120 rpm, MFCV was higher at the greater power output; thus the increase in MFCV with external force was independent of the pedal rate. The increased pedal resistance would require a larger muscle force, which, according to size principle (17), would result in the progressive recruitment of additional larger MUs. The increase in MFCV indicated that, in the dynamic contractions analyzed, MUs were progressively recruited from those with low to those with high conduction velocity, as shown by Andreassen and Arendt-Nielsen (1) during static conditions. Factors affecting estimates of MFCV other than average force, such as the joint angle, could be excluded since the comparisons were done at the same joint angles for each average pedal rate (Table 2). Thus the relative location of the recording electrodes with respect to the muscle fibers was similar in the conditions compared.

The significant increase in MFCV between 50 and 100% LT power output indicated that full MU recruitment was never reached at 50% LT for average pedal rates lower than 120 rpm, suggesting that progressive recruitment of larger MUs occurred with either increasing pedal rate (33) or external force or both. Furthermore, the additional MU recruitment with increasing average force was indirectly indicated by surface EMG ARV, which increased with power output at all average pedal rates (Fig. 3). The lack of change of MFCV with increasing power output at 120 rpm may indicate a smaller effect of external force on the population of recruited MUs when the speed of the contraction is very high. However, the present data do not allow full validation of this hypothesis.

**Dependence of MFCV on instantaneous knee angular speed and average pedal rate.** An increase of MFCV with the instantaneous knee angular speed was observed for both muscles. Within each pedal revolution at constant external force, MFCV resembled the trend of the instantaneous knee angular speed (Fig. 4 and Table 2). By maintaining a constant average external force, the increase in instantaneous speed could be due to an increase in the inertial power to accelerate the limbs (21), which required increased muscle force (without increased external force) and thus additional MU recruitment.

The dependence of MFCV on the instantaneous speed could, however, be due to methodological rather than physiological factors since the joint angle in this case was different for the different instants selected within the revolution. If the joint angle changes, the relative location of the electrodes with respect to the muscle fibers may change (12), and this can affect estimates of MFCV. Nevertheless, the dependence of MFCV on the instantaneous speed was in agreement with the dependence of MFCV on the average pedal rate (with fixed
average external force) when MFCV was estimated at fixed joint angles. MFCV increased with average pedal rate when compared with the same average external force (conditions 1 vs. 7, and 2 vs. 8; Table 2). Instantaneous speed at a specific joint angle increased with average pedal rate (Table 1) as did MFCV. Thus the dependence of MFCV on instantaneous knee angular speed (and, as a consequence, on the average pedal rate) was most probably due to the increased inertial power and muscle force rather than to methodological masking factors.

These data indicate that a larger number of MUs with increasing conduction velocity (fast-twitch MUs) are active at a higher pedal rate with respect to slower movements, which could explain the greater skeletal muscle energy turnover that has been observed at high contraction frequencies (15). Furthermore, Pringle et al. (33) recently showed that the amplitude of the VO₂ slow component was significantly higher at 115 rpm than at 35 rpm. These authors could not provide direct evidence of the fact that the increase in pedal rate was responsible for additional recruitment of faster MUs, although they strongly advocated such a mechanism to support their results.

Dependence of MFCV on power output. Because EMG ARV and MFCV depended on both average pedal rate and external force, they did not change when the pedal rate was varied at a fixed power output. This was observed at both 50 and 100% LT power output (Figs. 3 and 4). Constant EMG amplitude with varying pedal rate at constant power output was previously reported for the vastus medialis muscle by MacIntosh et al. (22). The indication provided by EMG amplitude has been confirmed in the present study by the estimate of MFCV, which indicated that the pool of recruited MUs is similar at constant power despite the average pedal rate being different. As pedal rate increases, the inertial power required also increases, which is counteracted by a decrease in average external force to maintain a constant power output.

In conclusion, estimation of MFCV during movement provides a unique insight into muscle fiber membrane properties in dynamic tasks. In this study, we have demonstrated that MFCV during cycling exercise depends on the external force developed, instantaneous knee angular speed, and average pedal rate. The measure proposed was feasible at pedal rates up to 120 rpm, which represents a burst of EMG activity of ~120 ms. These results provide evidence that MFCV is a size-principle parameter during cyclic dynamic contractions, and as such it can be used to assess progressive MU recruitment and derecruitment in the different phases of a dynamic exercise. This may be relevant in studies where an accurate identification of recruitment patterns [which previously needed to obtain muscle biopsy samples from the working musculature to identify the population of MUs that had been active (e.g., Ref. 7)] is important.

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