Spike-triggered average torque and muscle fiber conduction velocity of low-threshold motor units following submaximal endurance contractions

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Submitted 7 October 2004; accepted in final form 5 November 2004

Farina, Dario, Lars Arendt-Nielsen, and Thomas Graven-Nielsen. Spike-triggered average torque and muscle fiber conduction velocity of low-threshold motor units following submaximal endurance contractions. J Appl Physiol 98: 1495–1502, 2005.—The motor unit twitch contraction is the smallest contractile event that can be measured in vivo during voluntary muscle activation. The net force of a motor unit is affected by many factors, including muscle fiber type (3), fiber length (37, 39), discharge rate (44), muscle temperature (24), [Ca\textsuperscript{2+}] concentration (38), sensitivity to Ca\textsuperscript{2+} (38), and muscle stiffness (42). With sustained activation, twitch force may increase due to potentiation (38) or decrease due to fatigue (2). Single-motor unit twitch torque can be measured by artificially activating single motor axons (48) or from the average of the joint torque potentiation (38) or decrease due to fatigue (2). Single-motor units after sustained contraction, it is not clear if conduction velocity depends on membrane depolarization, variations in conduction velocity may also affect the twitch force profile directly. Posttetanic force potentiation shortly after tetanic contractions seems to be associated with an increase in muscle fiber conduction velocity and, consequently, in increased M wave (15, 16, 29). Moreover, as the twitch force increases when a motor unit is activated at short time intervals (19, 44), conduction velocity increases with increasing motor unit discharge rate in voluntary contractions (10, 30). These mechanisms suggest an adaptive change in muscle fiber membrane properties during muscle contraction, which may have a direct effect on contractile properties.

With sustained muscle contraction, both contractile and membrane fiber properties change over time. It is generally accepted that muscle fiber conduction velocity decreases with sustained activation, due to increased extracellular potassium concentration (25). On the other hand, both increases and decreases in peak twitch force have been reported with fatigue (e.g., Ref. 5). Because there are no studies that assessed concomitantly twitch force and conduction velocity in single motor units after sustained contraction, it is not clear if contraction-induced modifications in twitch force are associated with changes in membrane fiber properties. Thus the present study aims at investigating twitch torque, conduction velocity, and action potential properties of low-threshold motor units following isometric submaximal contraction until endurance.

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Subjects

Eleven healthy male subjects (age, mean ± SE: 25.8 ± 1.7 yr; height: 179 ± 2 cm; weight: 73 ± 2 kg) participated in the study. None of the subjects reported symptoms of neuromuscular disorders or problems with the ligaments. The study was conducted in accordance with the Declaration of Helsinki, approved by the Local Ethics Committee, and written, informed consent was obtained from all participants before inclusion.

General Procedures

The subject sat in a reclined position on a chair of adjustable height with the back flexed at ~30°. The right leg (dominant for all subjects) was positioned over a support and flexed at ~160° (180° equal to full extension of the leg). The foot was fixed to a footplate (90° ankle joint angle). The maximal voluntary contraction (MVC) torque in dorsiflexion was recorded three times, separated by 2-min rest. The maximal measured MVC defined submaximal torque contraction levels. After the MVC measure, intramuscular and surface electrodes for electromyogram (EMG) signal detection were mounted on the right leg.

The subject was provided with auditory and visual feedback of the intramuscular EMG signals and was asked to modulate the torque during ankle flexion to identify a single motor unit (target motor unit). Once the subject could activate the target motor unit, he was asked to maintain its activity stable at the minimum discharge rate with visual and auditory feedback on the intramuscular recordings. The volunteer was given 10–20 min to train for this task.

Ten minutes after the training phase, the subject performed three contractions, each lasting 3 min (preendurance contractions, C1–C3), separated by 10-s rest, activating the target motor unit at the minimum discharge rate. Five minutes after the C1–C3 contractions, the subject sustained an isometric contraction at 40% MVC until endurance with visual feedback on the exerted torque provided by an oscilloscope.

When the torque level decreased to <35% MVC for >5 s, the subject could stop. Ten seconds after the endurance time, he then performed an additional five contractions, each lasting 3 min and separated by 10-s rest, where the target motor unit was kept at the minimum discharge rate (postendurance contractions, C4–C8). Contractions C1–C8 were identical but performed before (C1–C3) and after (C4–C8) the endurance contraction.

Torque Recordings

Two load cells mounted on the footplate measured the torque around the ankle joint. The signal from the first load cell was amplified (charge amplifier J011B10, Kistler Instrument, Winterthur, Switzerland), leading to a sensitivity of torque recording of 50 mV/mN·m (bandwidth 0.1–100 Hz). This signal was used to extract the single motor unit twitch torques by averaging, as described below. The signal from the second load cell was amplified (Amplifier Unit LAU 73.1, Soemer, Lennestadt, Germany) and used to provide a feedback on the exerted joint torque to the subject. Both torque signals were sampled at 2,048 Hz and synchronized with the EMG signal recordings.

EMG Signal Detection

Surface and intramuscular EMG signals were recorded simultaneously from the tibialis anterior muscle. The procedure for electrode positioning has been described and validated in previous work (8, 9).

Surface EMG. Surface EMG signals were recorded by a linear adhesive array (ELSCH008, SPES Medica, Salerno, Italy) of eight equally spaced electrodes (inter electrode distance 5 mm, electrodes 5 mm × 1 mm) (26, 27) (Fig. 1). The array was located between the most distal innervation zone and the distal tendon, along the direction of the muscle fibers. The innervation zone position was identified by multichannel surface EMG in preliminary short voluntary contractions of the tibialis anterior, as described in previous work (26).

The skin was slightly abraded in the location selected for array placement. To ensure proper electrode-skin contact, conductive gel (20–30 μl) was inserted with a gel dispenser (model AG-Multipette Plus, Eppendorf, Hamburg, Germany) into the cavities of the adhesive electrode array. Surface EMG signals were detected bipolarly and amplified (EMG amplifier, EMG-16, LISiN-Prima Biomedical and Sport, Trevisio, Italy; bandwidth 10–500 Hz), sampled at 2,048 Hz, and stored by a 12-bit analog-to-digital conversion.

Intramuscular EMG. Four wire electrodes made of Teflon-coated stainless steel (A-M Systems, Carlsborg, WA) were inserted with a 23-gauge needle, 10–20 mm proximal to the surface array top (Fig. 1). The angle of insertion of the needle was ~45°, and the depth was a few millimeters below the muscle fascia. The detection point of the wires was between the innervation zone and the proximal tendon region and corresponded to motor units with territory under the surface electrodes (Fig. 1). Approximately 1 mm of the wires was uninsulated at the tip to detect intramuscular EMG signals. The needle was removed with the wire electrodes left inside the muscle fibers. The main muscle innervation zone, identified in a preliminary test before electrode placement (see text for details), is located between the array top and the insertion point of the wires. The array is placed along fiber direction between the innervation zone and the distal tendon. In this region, the intracellular action potentials of the analyzed motor units present the same direction of propagation, which allows conduction velocity estimation.

**Table 1. Conduction velocity and power spectral frequency computed during the endurance test from 1-s signal epochs at 0, 25, 50, 75, and 100% of the endurance time**

<table>
<thead>
<tr>
<th>Endurance Time, %</th>
<th>Average CV, m/s</th>
<th>MPF, Hz</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>4.36 ± 0.56</td>
<td>142.2 ± 8.2</td>
</tr>
<tr>
<td>25</td>
<td>4.11 ± 0.54</td>
<td>132.6 ± 9.1</td>
</tr>
<tr>
<td>50</td>
<td>3.79 ± 0.57*</td>
<td>124.5 ± 7.8*</td>
</tr>
<tr>
<td>75</td>
<td>3.75 ± 0.61*</td>
<td>126.1 ± 8.5*</td>
</tr>
<tr>
<td>100</td>
<td>4.14 ± 0.67</td>
<td>134.9 ± 7.0</td>
</tr>
</tbody>
</table>

Values are means ± SE. CV, conduction velocity; MPF, mean power spectral frequency. *Conditions significantly different from the beginning of the contraction (0% endurance time; P < 0.05).
Intramuscular EMG signals were amplified (Counterpoint EMG, DANTEC Medical, Skovlunde, Denmark), band-pass filtered (500 Hz–4 kHz), sampled at 10,240 Hz, and stored after 12-bit analog-to-digital conversion.

**Signal Analysis**

The times of occurrence of the action potentials of the target motor unit were identified from the intramuscular recordings by means of a decomposition algorithm previously described (8). The method is based on an amplitude threshold to detect action potentials and on potential classification based on cross-correlation. The four detected channels were decomposed independently, and the results were merged by identifying, from the estimated firing patterns, motor unit activities detected in common by different channels (8). Due to the feedback on single-motor unit activity, the decomposition of the intramuscular signals was not critical (in most cases only one motor unit was detected). Interpulse interval variability was computed as the ratio between standard deviation and mean interpulse interval and expressed in percentage. It was ensured that the target motor unit was maintained active at the minimum discharge rate. The extracted action potentials belonging to the target motor unit are shown on the right for the 3 contractions.

**Table 2. Discharge rate, interpulse interval variability, recruitment threshold, twitch time to peak, peak-to-peak amplitude, and duration of the surface potential for the target motor unit detected in the eight contractions with feedback.**

<table>
<thead>
<tr>
<th>Contraction</th>
<th>Discharge rate, pps</th>
<th>IPI variability, %</th>
<th>Threshold, %MVC</th>
<th>Twitch Properties</th>
<th>Surface Action Potential Properties</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Time to peak, ms</td>
<td>Peak to peak, µV</td>
</tr>
<tr>
<td>Prefatigue</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C1</td>
<td>6.0±0.3</td>
<td>39.0±9.5</td>
<td>3.6±0.5</td>
<td>80.4±11.6</td>
<td>25.2±2.4</td>
</tr>
<tr>
<td>C2</td>
<td>6.4±0.2</td>
<td>25.8±5.2</td>
<td>3.8±0.6</td>
<td>74.8±12.0</td>
<td>28.8±3.7</td>
</tr>
<tr>
<td>C3</td>
<td>6.7±0.2</td>
<td>23.1±7.5</td>
<td>3.7±0.5</td>
<td>69.3±7.3</td>
<td>24.9±2.7</td>
</tr>
<tr>
<td>Postfatigue</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C4</td>
<td>6.5±0.2</td>
<td>32.8±7.8</td>
<td>4.3±0.6*</td>
<td>69.8±12.6</td>
<td>26.2±4.6</td>
</tr>
<tr>
<td>C5</td>
<td>7.0±0.3</td>
<td>42.8±11.9</td>
<td>3.9±0.6</td>
<td>74.2±11.3</td>
<td>29.3±4.9</td>
</tr>
<tr>
<td>C6</td>
<td>6.9±0.3</td>
<td>41.2±11.6</td>
<td>3.8±0.5</td>
<td>77.2±8.5</td>
<td>24.1±4.4</td>
</tr>
<tr>
<td>C7</td>
<td>6.9±0.4</td>
<td>30.4±18.8</td>
<td>3.6±0.5</td>
<td>76.1±8.9</td>
<td>28.6±3.6</td>
</tr>
<tr>
<td>C8</td>
<td>6.9±0.3</td>
<td>31.6±13.3</td>
<td>3.5±0.5</td>
<td>73.6±8.6</td>
<td>29.4±3.6</td>
</tr>
</tbody>
</table>

Values are means ± SE, pps, Pulses per second; IPI, interpulse interval; MVC, maximal voluntary contraction. C1–C8, contractions 1–8. *Condition significantly different from all others (Student-Newman-Keuls: P < 0.05).
in conduction velocity (in the order of 0.1–0.2 m/s) (10) and that it is less sensitive to tissue inhomogeneities than two-channel approaches (11). From the averaged potentials, mean power spectral frequency, peak-to-peak amplitude, and potential duration were also computed. Action potential duration was estimated as the ratio between the area of the rectified potential and its peak-to-peak amplitude.

Mean power frequency and average conduction velocity were also computed as global variables from the interference surface EMG signal recorded during the endurance test. In this case, consecutive, nonoverlapping signal epochs of 1 s were considered. The surface channel selected for the estimation of global variables was the middle channel of those used for single motor unit multichannel conduction velocity estimation. The global EMG variables during the endurance test were analyzed at five time instants along the contraction, corresponding to 0, 25, 50, 75, and 100% of the endurance time.

**Statistical Analysis**

Data are reported as means ± SE. One-way repeated-measures ANOVA was used to assess the dependency of the extracted variables on the contraction (C1–C8) or on the time instant of the endurance test (0–100% of the endurance time, 25% increments). The post hoc Student-Newman-Keuls (SNK) test for pairwise comparisons was applied when necessary. The Wilcoxon matched-pairs test was used for comparing the percent variations in the variables extracted from the single motor unit activities. Pearson correlation coefficient was computed to assess relations between variables. Significance was accepted for \( P \) values <0.05.

**RESULTS**

**Endurance Contraction**

The mean endurance time was 231 ± 30 s. Average conduction velocity and mean power frequency were lower at 50 and 75% endurance time than in the beginning of the contraction (0% endurance time) (Table 1; ANOVA: \( F > 2.30, P < 0.05; \) SNK: \( P < 0.05 \)). The percent decreases in the two variables at 50% endurance time with respect to the beginning of the contraction were positively correlated (\( R^2 = 0.58, P < 0.01 \)) and not significantly different.

**Target Motor Unit Recruitment Threshold, Discharge Rate, and Interpulse Interval Variability**

All subjects were able to recruit the target motor unit in the eight contractions. In most cases, the target motor unit was the only motor unit detected by the intramuscular wires (Fig. 2). The recruitment threshold was higher in contraction C4, after the endurance test, than in all other contractions (Table 2;

![Fig. 3. The twitch torque assessed during the 8 contractions from 1 subject. The estimated conduction velocity of the target motor unit and the joint torque are also reported at the bottom for each contraction. Note the increase in peak twitch torque, which corresponds to a decrease in conduction velocity and an increase in joint torque in C4. After C4, the peak twitch torque and conduction velocity return to preendurance values. C1 and C2, preendurance contractions; C6–C8, postendurance contractions.](image1)

![Fig. 4. Mean (±SE) peak twitch torque of the target motor units for the 8 contractions. After the third contraction, the subject was asked to perform an endurance contraction. The last 5 contractions follow the endurance contraction. *Significant difference with respect to all of the other contractions (\( P < 0.05 \)).](image2)
ANOVA: $F = 2.33, P < 0.05$, SNK: $P < 0.05$). The percent increase in recruitment threshold in C4 with respect to the preendurance contractions was $11.5 \pm 4.5\%$. Neither average discharge rate nor interpulse interval variability was different through the eight contractions (Table 2).

**Target Motor Unit Twitch Torque**

The number of triggers ($309 \pm 25$, over the eight contractions) used for averaging the twitch torque responses and the surface EMG (according to the criterion of a minimum distance of 150 ms between discharges) was not significantly different in the eight contractions. The peak twitch torque was significantly higher in the contraction after the endurance test (C4) than in all of the others (Figs. 3 and 4; ANOVA: $F = 2.46, P < 0.05$; SNK test: $P < 0.05$). The percent increase in C4 with respect to the preendurance contractions was $93 \pm 29\%$. Time to peak of the twitch was not different among the eight contractions (Table 2).

**Target Motor Unit Surface Action Potential**

The similarity in shape of the average surface potentials recorded at the different detection points along the array was assessed by cross-correlation analysis. The maximum of the cross-correlation function between pairs of signals detected by consecutive electrode pairs of the array (i.e., signals detected along the propagation of the action potentials) was $0.83 \pm 0.02$, indicating similar shape among potentials detected along the muscle fibers (Fig. 5). This condition ensured reliable conduction velocity estimates (28).

Conduction velocity and mean power frequency of the target motor unit were significantly smaller in C4 than in all other contractions (Fig. 6 and Table 2; ANOVA: $F > 2.08, P < 0.05$, SNK: $P < 0.05$). The percent decreases in conduction velocity and mean power frequency in C4 with respect to the preendurance contractions ($6.3 \pm 1.8$ and $7.2 \pm 1.4\%$, respectively) were correlated ($R^2 = 0.66, P < 0.001$) and not significantly different. Peak-to-peak amplitude of the average

![Fig. 5. Top: intramuscular action potentials classified as belonging to the target motor unit in the 8 contractions from 1 subject. Bottom: averaged multichannel surface EMG potentials belonging to the target motor unit in the 8 contractions. Note that the surface potentials detected by the array are delayed between each other due to the propagation of the action potential along the muscle fiber from the innervation zone to the distal tendon region. The distance between detection points (5 mm) divided by the propagation delay provides an estimate of conduction velocity.](image-url)
velocity (duration was correlated to the relative decrease in conduction 0.05, SNK: P 0.001). There was no correlation between the percent changes in C4 with respect to C1–C3 of conduction velocity, potential duration, or mean power frequency and the percent changes in peak twitch torque (R² = 0.04, 0.10, and 0.06, respectively).

**DISCUSSION**

This study presents for the first time concomitant measure of low-threshold motor unit twitch torque and conduction velocity after a voluntary submaximal contraction sustained until endurance. The main result is that peak twitch torque increased, whereas conduction velocity decreased, after the endurance test with respect to the preendurance values. The relative changes in conduction velocity and action potential properties after the sustained contraction were not correlated to those in peak twitch torque. The recruitment threshold of the investigated motor units increased after the prolonged contraction.

**Global EMG Variables**

The average conduction velocity during the endurance test decreased until 50–75% of the contraction duration and then increased. The increase in average conduction velocity in the second half of the endurance contraction has been reported previously (13, 18). Because average muscle fiber conduction velocity reflects the mean conduction velocity of all active motor units, its increase was interpreted with the recruitment of additional motor units as fatigue progressed (7). Houtman et al. (18) hypothesized, from multichannel surface EMG analysis, motor unit derecruitment during sustained contractions. Neither in the study by Houtman et al. nor in the present work was it possible to directly follow single motor unit activities during the endurance contraction. However, evidence for motor unit substitution during sustained submaximal isometric contractions is scarce, and most studies report additional recruitment with fatigue without derecruitment of previously active motor units, with unaltered recruitment order (e.g., Ref. 1). Thus it is likely that the low-threshold target motor units analyzed in this study were active for the entire duration of the endurance contraction.

**Twitch Torque**

The peak and time to peak twitch values obtained in this study are in agreement with previous reports on the tibialis anterior muscle (3, 47). Van Cutsem et al. (47), for example, reported peak torque of 0.7–1 mN·m and time to peak of 80–90 ms for the lowest threshold motor units in the tibialis anterior. Peak twitch torque increased after the endurance contraction, in agreement with findings on other muscles (5, 31, 41). Moreover, we observed that the peak twitch torque returned to preendurance levels in the second contraction following the endurance test. The time to peak of the twitch was unchanged with fatigue, as also previously reported for low-threshold motor units of the first dorsal interosseus muscle (5).

The difference in motor unit twitch torque before and after fatigue cannot be due to a change in discharge rate of the target motor unit and in the number of triggers used, as they were the same in the eight contractions. One methodological issue possibly affecting the results is the eventual increase in motor unit short-term synchronization with fatigue. If the degree of synchronization was significantly larger after the endurance contraction with respect to preendurance levels, the twitch torque amplitude estimated by spike-triggered averaging might be increased (43). Although this issue cannot be completely excluded, there are observations making it unlikely. A significant increase in motor unit synchronization would have led to a larger relative decrease in mean power frequency with respect to conduction velocity during the endurance contraction (14, 22), which was not observed in this study. Moreover, motor unit synchronization would have increased the amplitude of the averaged surface EMG potentials (20), in contrast to the actual findings. It has also to be noted that the contractions with feedback on the target motor unit were at a very low torque level with a small number of active motor units. Finally, the observed increase in recruitment threshold is in agreement with an increased twitch torque because it reflects an adaptation of the control strategy.

The increase in twitch torque could be due to potentiation (33) or to the enhancement of muscle stiffness (42), although the present results do not allow us to explain which of the two factors was the most relevant. For extracellular potassium concentrations observed in the fatigued muscle, the twitch torque may be enhanced with respect to the control condition due to potentiation (49). On the other hand, an increase in muscle stiffness is consistent with the finding that peak twitch torque returned to the initial values after 3 min from the endurance test, which is a shorter time than that usually reported for the duration of twitch potentiation (on average, 10 min) (17, 32). Moreover, there are several reports suggesting a
prolonged time to peak of the twitch torque with potentiation (e.g., Ref. 36) that was not observed in this study.

The increase in twitch torque was not correlated with the changes in conduction velocity or in surface action potential properties, such as amplitude or duration. Thus the changes in intracellular action potential and its propagation velocity did not significantly contribute to the twitch increase.

The recruitment threshold of the target motor unit increased after the endurance test. This suggests that control strategies adapt to the actual level of torque produced by the specific motor unit, as observed previously (5, 21). It has, however, to be noted that the measure of recruitment threshold was based on the net joint torque, and it cannot be excluded that this was influenced by a modification in the synergistic/antagonist muscle activity during the endurance task. Analysis of the relative contributions of the different muscles involved in the contraction to the net joint torque is not possible from the present data.

On the other hand, previous data on surface EMG amplitude from synergistic/antagonist muscles during endurance contractions of the tibialis anterior (e.g., Ref. 6) cannot be used to indicate the relative force, as EMG amplitude depends on fiber membrane properties, which change during the task.

Surface Action Potential Properties

In the unfatigued muscle, increased peak twitch torque may be related to an increase in conduction velocity, as indirectly observed in studies on electrical muscle stimulation (15, 16, 29, 35). In this study, conduction velocity of the target motor units decreased after the endurance contraction and returned to the initial value within 3–6 min. Accordingly, conduction velocity of low-threshold motor units activated at their minimum discharge rate for up to 5 min in hand muscles decreased (10).

The decrease in muscle fiber conduction velocity with sustained activation is due to the increased extracellular potassium concentration. The increase in action potential duration and the decrease in mean power frequency are mediated by the decrease in conduction velocity (28). The increase in twitch torque was probably not determined by the increase in potential duration, because Yensen et al. (49) observed similar increases in action potential duration with or without twitch potentiation, underlying that an elongated potential does not determine a potentiated twitch. Moreover, the absence of correlation between the increase in potential duration (or the decrease in conduction velocity) and the increase in twitch torque indicates that contractile and action potential properties changed independently. Thus the modifications of conduction velocity, leading to a longer action potential, did not have a major role in the twitch changes.

Because the increased twitch torque was not related to changes in conduction velocity, analysis of contraction-induced modifications in muscle properties by electrophysiological recordings may provide different information than the analysis of torque responses. The decrease in conduction velocity found in previous studies, both at the global (e.g., Refs. 4, 28) and at the single-motor unit level (10), does not necessarily imply a reduction in peak twitch torque in all active motor units. Thus the adaptation of control strategies to modifications in the contractile fiber properties cannot be predicted by the analysis of electrophysiological properties only. Similarly, unchanged motor unit twitch torque does not imply unaltered fiber membrane properties. Contraction-induced modifications in fiber membrane properties are consistent over many experimental conditions and result in decreased muscle fiber conduction velocity (8, 10). On the other hand, the measure of twitch torque is affected by the way in which the muscle fiber contractile force is transmitted at the joint, in addition to the specific contractile and membrane motor unit properties, which change with fatigue and potentiation. Thus modifications of peak twitch torque with sustained moderate-force contractions in low-threshold motor units may be mainly determined by mechanisms not related to muscle fiber electrophysiological properties.

The results reported in this study are limited to low-threshold motor units. Investigation of high-threshold units is critical due to limitations in the intramuscular EMG decomposition and in the number of triggers required to extract the surface EMG and twitch torque from the averaging process. The control properties and the relation between membrane and contractile properties in high-threshold units following the endurance test may be significantly different from those reported for low-threshold units.

Conclusion

Low-threshold motor unit peak twitch torque and recruitment threshold increased, with a concomitant decrease in conduction velocity, after a fatiguing contraction until endurance. The investigated variables returned to preendurance values after 3–6 min. Changes in twitch torque and conduction velocity or action potential duration were not correlated. It is concluded that modifications in twitch torque of low-threshold motor units, following medium-high-force contractions until endurance, are not induced and cannot be predicted by modifications in the depolarization of muscle fibers and its propagation.

GRANTS

The Danish Technical Research Council supported this work.

REFERENCES


