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Del Vecchio, Alessandro; Negro, Francesco; Falla, Deborah; Bazzucchi, Ilenia; Farina, Dario; Felici, Francesco

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TITLE PAGE

Higher muscle fiber conduction velocity and early rate of torque development in chronically strength trained individuals

Authors:

A. Del Vecchio,[1,4] F. Negro,[2] D. Falla,[3] I. Bazzucchi,[1] D. Farina,[4] and F. Felici[1]

Affiliations:

[1]Department of Movement, Human and Health Sciences, University of Rome "Foro Italico", 00135 Rome, Italy

[2]Department of Clinical and Experimental Sciences, University of Brescia, 25123 Brescia, Italy

[3]School of Sport, Exercise and Rehabilitation Sciences, University of Birmingham, Birmingham, UK

[4]Neuromechanics and Rehabilitation Technology Group, Department of Bioengineering, Imperial College London, London, UK

Short title

Explosive torque neuromuscular assessment

Corresponding author:

Francesco Felici, Department of Movement, Human and Health Sciences, University of Rome "Foro Italico", Piazza de Bosis 6, 00135, Rome, Italy, phone: +39 06 36733540, francesco.felici@uniroma4.it

Key words: Explosive force contractions; Motor unit Conduction Velocity; Motor unit recruitment; Neuromuscular assessment; Size principle

ABSTRACT

Strength trained individuals (ST) develop greater levels of force when compared to untrained subjects. These differences are partly of neural origin and can be explained by training induced changes in the neural drive to the muscles. In the present study we hypothesize a greater rate of torque development (RTD) and faster recruitment of motor units with greater muscle fiber conduction velocity (MFCV) in ST when compared to a control cohort. MFCV was assessed during maximal voluntary isometric explosive contractions of the elbow flexors in eight ST and eight control individuals. MFCV was estimated from high-density surface electromyogram recordings (128 electrodes) in intervals of 50 ms starting from the onset of the EMG. The rate of torque development (RTD) and MFCV were computed and normalized to their maximal voluntary torque (MVT) values. The explosive torque of the ST was greater than in the control group in all time intervals analyzed ($p<0.001$). The absolute MFCV values were also greater for the ST than controls at all time intervals ($p<0.001$). ST also achieved greater normalized RTD in the first 50 ms of contraction (887.6 ± 152 vs. 568.5 ± 148.66 $\%MVT \cdot s^{-1}$, $p<0.001$) and normalized MFCV before the rise in force when compared to controls. We have shown for the first time that ST can recruit motor units with greater MFCV in a shorter amount of time when compared to untrained subjects during maximal voluntary isometric explosive contractions.

New & Noteworthy

Strength trained individuals show neuromuscular adaptations. These adaptations have been partly related to changes in the neural drive to the muscles. Here, we show for the first time that during the initial phase of a maximal isometric explosive contraction, strength trained individuals achieve higher levels of force and recruit motor units with greater conduction velocities.

INTRODUCTION

The human neuromuscular system has the ability to develop high forces in short time intervals (1). It takes approximately 150 ms to reach high levels of force (>70% maximal voluntary force) during a single-joint maximal voluntary isometric explosive contraction (7, 16, 30, 50). Explosive force is commonly measured during specific time intervals from the contraction onset or characterized by the slope of the joint torque-time curve (i.e., the rate of torque development, RTD) during the first 200 ms of force generation (1). Over the past decades there has been an increasing interest in the determinants of explosive force especially in relation to the implications for enhancing athletic performance and for the prevention of falls and injuries (1, 6, 30, 35, 42, 46, 50). Moreover, the RTD has been identified as an important parameter to detect changes in neuromuscular function in addition to the maximal voluntary force (35).

At the neuromuscular level, RTD is associated to the neural drive to muscles during the very early phase (first ~50 ms) of the contraction (9, 12, 14, 30, 47). The neural drive to muscles is the ensemble of motor neuron action potentials that reach the muscle per unit time (24). During rapid 'ballistic' contractions, the size principle of motor unit recruitment is maintained (11) but the motor unit recruitment thresholds decrease and discharge rates increase compared to slow-force contractions (12).

There is a strong association between the neural activity during the early phase of muscular contraction (0-50 ms) and explosive force (1, 30, 46, 47, 50). The greater RTD in the first 50 ms of the contraction observed in power athletes is partly associated to a greater EMG amplitude with respect to controls (50). Moreover, twelve weeks of isometric explosive training significantly increase the neural responses during explosive contractions when compared to isometric strength training (6). However, the specific neural adaptations in chronically strength/power trained individuals are largely unknown. The current evidences from cross-sectional studies that compared trained individuals vs. a control cohort (29, 50) relies on EMG features that are separated from the neural drive to the muscle (19, 54, 55).

At the motor unit level, short-term ballistic training increased motor unit discharge rate of the first four detected motor unit action potentials during isometric ballistic contractions (10). Similarly, six week of strength training increased the motor unit discharge rate during contractions at forces below 30% of maximum (57). It can be hypothesized that chronic strength training involving explosive tasks may also results in a faster recruitment of larger, fast-twitch motor units. A faster motor unit recruitment would increase the explosive force of a muscle because the size of the motor unit (i.e. the recruitment threshold (33)) is associated to the motor unit mechanical properties (peak force, force rise-time) (32, 52). However, direct or indirect data on motor unit recruitment strategies in chronically resistance trained individuals are lacking (15). Recently, Methenitis and colleagues reported significant associations between MFCV and rate of force development in strength trained individuals (39). However, the estimates of MFCV were obtained during electrical stimulation of individual muscle fibers (39) thus the time course of MFCV (when the muscle fibers are activated by the central nervous system) is unknown.

There are methodological limitations in the identification of individual motor unit activities in time intervals of 20-50 ms during explosive force contractions. However, it is possible to indirectly assess the properties of active motor units by measuring their average muscle fiber conduction velocity (MFCV). MFCV is a size principle parameter (4) since muscle fibers of high threshold motor units have greater diameters than those of lower threshold motor units (4, 37, 54). There is a biophysical relation between MFCV and fiber diameter (41, 43) that has been demonstrated at the individual muscle fiber level (31). Moreover, we have recently shown that the increase in the average MFCV during increasing-force contractions is strongly associated with the increase in single motor unit conduction velocities when related to the progressive recruitment of motor units (55). It has also been shown that MFCV can be reliably estimated from EMG signals in intervals as short as ~25 ms (23, 25, 37, 53).

Therefore, estimates of MFCV may provide an indirect analysis of motor unit recruitment (4, 54, 55). Moreover, the time-course of MFCV during maximal voluntary isometric explosive contractions is unknown. In this study, we measure for the first time MFCV during explosive voluntary force contractions in chronically ST individuals when compared to untrained subjects. We hypothesized a greater early RTD in ST individuals that would be accompanied with a higher MFCV during isometric explosive force contractions.

MATERIALS AND METHODS

Participants

Sixteen healthy, non-smoking young men volunteered for this study which was approved by the University of Rome Ethical Advisory Committee and conducted according to the Declaration of Helsinki. The volunteers signed an informed consent, completed a standard health questionnaire, and were screened for their habitual physical activity. None had any previous history of neuromuscular disorders. Volunteers included those involved in regular strength training programs (strength training group (ST), n = 8, age, 22.2 ± 2.5 years; body mass, 85.2 ± 8.3 kg; height 181.2 ± 9.3 cm) and control individuals who were only involved in light to moderate aerobic activity (control group, n = 8, age, 23.4 ± 3.1 years; body mass, 73.2 ± 7.5 kg; height 177.3 ± 7.5 cm). All volunteers were students from the department of Human Movement Sciences, University of Rome ‘Foro Italico’, Rome, Italy. Before the first familiarization session, the volunteers were asked to report their physical activity habits. ST volunteers were required to be in a strength-training program that targeted strength and power for at least three years and for a minimum of three times per week. The training programs were classical models of progressive strength training for enhancing muscle strength and power that targets all major upper and lower muscle groups. The training protocols performed by the ST cohort closely matched the guidelines reported in (2) for enhancing strength and power. The individuals from the ST cohort also performed national and international competitions that involved explosive tasks, such as volleyball (4 subjects), javelin throw (1), boxing (1), karate (1). Controls were required to be involved in moderate to light aerobic exercise less than twice per week and were not involved in any form of regular strength or power training. All subjects were instructed to avoid strenuous exercise and caffeine, respectively 48 and 24-hour prior to their visit to the laboratory.

Study overview

Participants visited the laboratory on two occasions, one week apart. During the first visit, they performed a familiarization test to become acquainted with the experimental protocol. The familiarization session included elbow flexion maximal voluntary isometric contractions (MVC) and maximal voluntary isometric explosive contractions of their dominant arm (self-reported). During the second visit, the volunteers performed the experimental session with concurrent recordings of force (MVC and isometric explosive force contractions) and high-density surface electromyography (HDsEMG).

Measurements

Force Recording

Both the familiarization and measurement sessions were conducted using an isokinetic dynamometer (KinCom Dynamometer, Chattanooga, TN) with the elbow of the dominant limb flexed to 90°. The reliability and feasibility of this dynamometer has been described previously (27) and used in previous studies that assessed maximal RTD (1). The chair configuration was established during the familiarization session and replicated in the main trial. Waist and shoulder straps were tightly fastened to prevent extraneous movements. The waist strap was fastened across the pelvis and two other straps across the shoulders (35). This setup was comfortable and well tolerated by the participants of the study. The shoulder was in a neutral position with the upper arm parallel to the trunk (humerus in a pendent position), and the forearm was midway between pronation and supination. The elbow joint was secured in a padded brace with Velcro straps. The dynamometer load cell (KinCom Dynamometer, Chattanooga, TN) consisted of four strain gauges. The wrist strap was consistently secured to the styloid process of radius and was in series with a calibrated linear response from the dynamometer load cell that was positioned perpendicular to the radius. The center of the lever arm was aligned to the distal lateral epicondyle of the humerus. Subsequently, the lever arm length was measured as the distance between the distal lateral epicondyle of the humerus and the styloid process of radius. The analogue force signal was amplified and sampled at 2048 Hz with an external analogue to digital (A/D) converter (EMG-USB2+ OT Bio elettronica, Turin, Italy). Two personal computers recorded the data with the software OTbiolab (OT Bio elettronica, Turin, Italy) and Labview 8.0 (National Instruments, Austin, USA). The force signal was displayed for visual feedback during the tests. Force signals were corrected for the effect of gravity.

High-density surface electromyography recordings (HDsEMG)

Two bi-dimensional arrays (matrices) of 64 electrodes each [dimensions for one matrix: 1 mm in diameter, 8 mm inter electrode distance, 13 rows (10.9 cm) x 5 columns (3.7 cm), gold-coated; OT Biolettronica, Turin, Italy] (Fig.1 A) were used for recording HDsEMG signals. The skin was treated by shaving, light abrasion and cleansing with 70% ethanol. An experienced investigator identified the muscle belly of the biceps brachii (BB) through palpation and a surgical marker was used to delineate the perimeter of the muscle. Before placing the electrodes, the arm circumference and the skinfold thickness (Harpenden skinfold caliper, Milan, Italy) were measured. Successively, both matrices were placed over the BB using bi-adhesive foams (SpesMedica, Battipaglia, Italy). The grids were mounted closed to each other to form an array of 128 electrodes (Fig 1.A). The array was located between the proximal and distal region of the BB, along the direction of the muscle fibers, covering most of the BB area (26) (Fig 1.A). The large number of electrodes used allowed the accurate identification of the innervation zone and selection of channels with propagating action potentials. Moreover, the high-density configuration improves the reliability of MFCV estimates and of the EMG recordings considerably (26, 49). The ground electrode was placed on the wrist of the non-dominant arm. Two reference electrodes were placed on the vertebra prominens and on the acromion. The EMG signals were amplified and band-pass filtered and converted to digital data by a multichannel amplifier (3dB bandwidth, 10-500 Hz; EMG-USB2+ multichannel amplifier, OT Bioelettronica, Turin, Italy). The same multichannel amplifier synchronized the HDsEMG and force signals.

Procedures

Before the measurements, the volunteers performed a standardized warm-up, which consisted in four contractions at 50% of their perceived maximal voluntary force, four at ~75%, and one submaximal ~90% contraction. Each contraction was separated by 15 s. Following the warm-up with a recovery time of 5 min, the subjects completed three MVC, with 1 minutes of rest in between. The volunteers were encouraged to "push as hard as possible" for at least 3 s while receiving feedback on the exerted force and on the force exerted in the previous MVC contractions. The greatest force was recorded as the maximum voluntary force (MVF). After 5 minutes of rest eight explosive force contractions were performed in two blocks of four contractions each. The blocks were separated by 5 min of rest and the individual contractions within each block were separated by 20 s of rest. For the explosive force contractions, volunteers were instructed to relax and flex the elbow "as fast and hard" as possible after hearing an auditory cue. Volunteers were instructed to exceed the 75% of MVF threshold, which was displayed with a horizontal cursor on the monitor, without performing any countermovement. Only contractions that did not show any counter movement (≤ 0.5 Newtons (N) from the baseline of force in the 150 ms before the onset of force) were included within each block and used for the analysis.

Force signal analysis

In the offline analysis, the analogue force signal was converted in N and multiplied by the respective lever arm in order to obtain torque (N*m). Successively, the torque signal was filtered with a low-pass fourth-order, zero-lag Butterworth filter with a cut-off frequency of 400 Hz. The torque onset (T_0) was determined with a visual detection method used in previous studies (50). After the onset detection was found, the torque was filtered with zero-lag Butterworth filter with a cut-off frequency of 20 Hz. This two-step filtering procedure allowed to first detect precisely the onset of torque in the 400 Hz low pass filtered signal (51) and then the 20 Hz filter removed all the non-physiological frequencies in the signal. The 20 Hz low pass filter guaranteed an undistorted signal in all cases with respect to the 400 Hz filtered signal, that was checked in all the explosive torque contractions. The onset value was used to determine the torque values at 50 ms (T_{50}), 100 ms (T_{100}), 150 ms (T_{150}), and 200 ms (T_{200}) after the onset (Fig. 1 C-D). The five contractions with the highest torque values at T_{150} were used for the analysis. The absolute torque values at different time points were normalized by the respective maximal torque (T / maximal voluntary torque (MVT)). The RTD (i.e., $RTD_{100\text{-}150} = T_{150} - T_{100} / 0.05$ s) was calculated in three-time intervals, $RTD_{0\text{-}50}$, $RTD_{50\text{-}100}$, and $RTD_{100\text{-}150}$ for both the absolute and relative torque values (e.g., RTD-$\text{rel}_{0\text{-}50}$) (Fig. 2 A-B). The torque analysis was completed with MATLAB 2015 (MathWorks Inc., Natick, MA).

EMG Processing

Single differential HDsEMG signals (SD) were calculated from the monopolar derivations for each column of the two bi-dimensional arrays. SD signals for each column were visually inspected and the six SD channels with the highest coefficient of correlation (CC) (CC ≥ 0.8) and clear MUAPs propagation without shape change from the nearest innervation zone to the distal tendon (Fig. 1 C-D) were chosen for the analysis. The columns of the matrix that were selected for the estimates of MFCV corresponded to the central part (between the first three central columns) of the two bi-dimensional arrays, as they corresponded to the channels with the highest quality (CC and propagation). MFCV was computed using an algorithm that allows highly accurate estimates of conduction velocities from multichannel EMG signals and whose reliability and validity has been previously assessed in both isometric and dynamic contractions, with robust intraclass coefficient of correlations (>75% ICC) (23, 25, 26). During isometric contractions the between day coefficient of variability in MFCV is lower than 2%, with ICC >88% (36). The use of ≥6 EMG channels allows to detect changes of MFCV as small as 0.1 m/s when compared to estimates from a pair of bipolar signals (>0.4 m/s) (18). The BB muscle was chosen in this study because it has been shown to provide estimates of MFCV with good reliability during submaximal (50% MVC) steady state contractions (26). It has been shown that MFCV can be accurately assessed also during dynamic explosive tasks (44). Maximal muscle fiber conduction velocity ($MFCV_{MAX}$) was estimated during the MVF contraction in time windows of 50 ms, from 500 ms before to 250 ms after peak torque during the MVF. The choice of this interval for the estimation of $MFCV_{MAX}$ was due to the delay between recruitment and motor unit peak twitch forces. After determining the maximal value of MFCV, MFCV was estimated during the explosive torque contractions in intervals of 50 ms. For each explosive contraction, the onset of EMG activity was assessed visually (Fig. 1. C-D) and MFCV was estimated from five intervals, corresponding to the electromechanical delay (EMD = T_0 (s) – EMG onset (s)), and the four 50-ms intervals following T_0 ($MFCV_{EMD}$, $MFCV_{0\text{-}50}$, $MFCV_{50\text{-}100}$, $MFCV_{100\text{-}150}$, $MFCV_{150\text{-}200}$). MFCV absolute and normalized values (MFCV (m/s) / $MFCV_{MAX}$, e.g., $MFCVrel_{0\text{-}50}$) were averaged over the five explosive contractions selected for the analysis.

Statistics

The Shapiro-Wilk test confirmed the normal distribution of the extracted variables. The number of participants needed for the study was estimated with a statistical power analysis test (function *sampsizepr* in MATLAB) using previous data on MFCV and RTD, and successively progressively tested with the data collected in the present study. The significance level of the power test was set with a P value of 0.05. Two-way repeated measures analysis of variance ANOVA (group x time) was used to assess differences in explosive force, RTD and MFCV for both absolute and normalized values. The ANOVA included the five-time intervals from EMG or torque onset during the explosive contractions. Bonferroni stepwise corrected paired t-tests were used to assess differences between groups at different time intervals. Moreover, Pearson product-moment coefficient of correlation was used to assess the linear relation between RTD and MFCV for each individual cohort and the coefficient of determination (R^2) was used as an index of prediction power. The Bonferroni correction was applied to the regression significance values. Independent sample t-tests were used to assess differences between groups for all other variables (MVF, $MFCV_{MAX}$, skinfold and arm circumference). Statistical analysis was completed using SPSS version 14 (SPSS Inc., Chicago, IL) and MATLAB. The significance level was set at $P < 0.05$. Data are reported as mean and SD.

RESULTS

Electromechanical Delay, Anthropometry, and Statistical Power

The EMD did not differ between the two groups (ST 62.42 ± 10.81 vs controls 60.24 ± 12.12 ms, $p>0.05$). Moreover, there was no difference in the subcutaneous fat layer thickness between groups (ST 4.11 ± 0.71, control group 4.45 ± 1.05 mm, $p>0.05$) as assessed by skinfold measures, whereas the arm circumference was greater for the ST (36.01 ± 1.51 vs 29.3 ± 2.58 cm, $p<0.05$). The power analysis indicated that 7 subjects per cohort were needed to obtain a power of 90% for MFCV and RTD estimates.

Torque

Maximal torque was significantly greater for the ST compared to controls (99.64 ± 21.62 vs 60.56 ± 8.74 (N·m), $p<0.001$). The ST also developed higher torques at 50, 100, 150, and 200 ms from contraction onset ($p<0.001$). When torque at different time points was expressed relative to the MVT, the ST achieved higher relative torques in the first two phases of contraction (T_{50} and T_{100}, 43.84 ± 5.29 vs 17.12 ± 4.61 T_{50}, 63.45 ± 10.02 vs 33.25

± 4.42 T_{100} %MVT, $p<0.001$). The relative explosive torque at T_{150} and T_{200} was similar for both cohorts ($p>0.05$).

The absolute RTD during the initial phase (T_{50}) of the contraction was greater for the resistance trained individuals than controls (861.82 ± 104.60 vs 342.05 ± 93.08 $N \cdot m \cdot s^{-1}$, $p<0.001$; Fig 2A). The absolute RTD over the consecutive time windows did not differ (Fig 2A). In addition, the normalized RTD was greater only in the first 50 ms of contraction for the ST (887.66 ± 152.08 vs. 568.54 ± 148.66 $\%MVT \cdot s^{-1}$, $p<0.001$ $\%MVT \cdot s^{-1}$, $p<0.001$; Fig 2B). Conversely, the normalized $RTD_{50\text{-}100}$ and $RTD_{100\text{-}150}$ was greater for the controls (536.48 ± 112.08 vs 404.91 ± 96.36 $MVT \cdot s^{-1}$, 356.21 ± 110.48 vs 271.41 ± 69.44, $MVT \cdot s^{-1}$; $p<0.001$; Fig 2B).

Muscle fiber conduction velocity

Maximal MFCV at MVT ($MFCV_{MAX}$) ranged from 5.05 to 5.82 m/s in ST and from 4.93 to 5.26 m/s in the controls with the ST group having a significantly higher $MFCV_{MAX}$ compared to controls (5.37 ± 0.27 vs 5.04 ± 0.11 m/s $p<0.001$).

MFCV during the explosive torque contractions (from the EMD to T_{200}) ranged from 3.44 to 5.45 m/s (and the lowest value of MFCV corresponded to the time interval during the electromechanical delay, $MFCV_{EMD}$) when grouping all participants. The average MFCV values across subject at each time window can be observed for the two cohorts in Fig 3. The MFCV value consistently increased in the second-time interval ($MFCV_{0\text{-}50}$) (Fig 3, $p<0.01$). This indicates recruitment of motor units with progressively larger diameter fibers with increase in torque (37, 54, 55), that is related to the progressive recruitment by size (33, 54). However, the ST achieved a higher $MFCV_{EMD}$ compared to the controls (4.44 ± 0.13 vs 3.83 ± 0.20 m/s, $p<0.001$; Fig 3A), even when $MFCV_{EMD}$ was normalized to $MFCV_{MAX}$ (82.57 ± 3.13 vs 75.86 ± 3.55 $MFCV\text{-}rel_{EMD}$, $p<0.001$; Fig. 3B). Moreover, the early phase of absolute and normalized MFCV estimates was correlated to RTD (Fig. 4; *RTD and MFCV correlations paragraph).*

The ST cohort maintained a greater absolute and normalized MFCV value throughout the full duration of the explosive contractions ($p<0.001$; Fig. 3A). Interestingly the time-MFCV curve had a similar pattern for the ST compared to the controls (Fig 3A-B). MFCV indeed increased linearly from EMD until reaching a plateau at $MFCV_{50\text{-}100}$ ($p<0.001$) for both groups (Fig. 3A-B). This observation indirectly indicates that the muscle full motor unit recruitment may have been completed before the first 100 ms of explosive torque production.

RTD and MFCV correlations

The estimates of MFCV were positively correlated with RTD only in the time window $RTD_{0\text{-}50}$ (Fig. 4). For the resistance trained individuals, a negative correlation was found between normalized RTD_{100_150} and absolute MFCV (average R^2 for all MFCV estimates when plotted as a function of RTD_{100_150} values = -0.59 ± 0.24, $p < 0.001$). During the same RTD time window, the correlation for the controls was not significant ($p>0.05$).

DISCUSSION

MFCV was measured during explosive force contractions in a group of resistance trained individuals and a control cohort. ST exhibited greater explosive torque, early rate of torque development (RTD), and greater MFCV with respect to controls throughout the contraction. When explosive torque was normalized to maximal torque, ST had a higher RTD at the beginning of the contraction (0-50 ms). Moreover, a greater absolute and normalized conduction velocity ($MFCV_{MAX}$) during the electromechanical delay (EMD) and in the first 50 ms of torque generation was observed for the ST group. This result indicates a recruitment of motor units with greater conduction velocities. This is the first study showing that ST may recruit larger motor units in a shorter amount of time.

Muscle fiber conduction velocity

The average MFCV values are in agreement with previous reports of MFCV during steady state contractions. For example, Farina and colleagues reported estimates of MFCV in the biceps brachii during isometric steady state contractions at 50% MVC of ~4.6 m/s (26). Zwarts and Arendt-Nielsen estimated MFCV at high contraction forces of the biceps brachii and reported values ranging between 3.22 and 5.11 m/s (58). MFCV average values in the present study were also in agreement with estimates of single motor unit conduction velocities (MUCV) using intramuscular electromyography recordings during voluntary and electrical activation of the biceps brachii muscle. Moreover, the present estimates are also in accordance with other studies involving different muscular contractions and protocols (21, 22, 28, 37, 38, 44, 45).

Interestingly, only two studies assessed MFCV in power athletes and only during electrical stimulation and maximal voluntary contractions (39, 48). Sadoyama and colleagues reported a significantly higher maximal MFCV in a group of trained sprinters compared to endurance runners (4.84 vs 4.31 m/s) (48). Moreover, they reported a significant relation between the relative area of fast twitch fibers and conduction velocity (48).

Recently, Methenitis and colleagues estimated MFCV during electrical stimulation of muscle fibers in endurance runners, power trained and ST individuals, and measured separately RTD (39). They reported significant relations between MFCV, muscle fiber cross-sectional area and rate of force development (39). However, estimates of MFCV were assessed during electrical stimulation and thus separately from the voluntary generation of explosive force. Therefore, it was not possible to associate the underlying neural strategies of muscle control to explosive force performance. Collectively, these previous results indicate that MFCV may be an indicator of muscle explosive performance, although no previous study assessed MFCV during explosive torque generation.

Explosive torque and RTD

The RTD was significantly greater for the ST during the early phase of explosive torque generation (Fig 3A). However, when the moment-time curve was normalized to the maximal strength, the RTD for the resistance trained subjects was significantly different only in the first 50 ms of the contraction (Fig 3B). Because the relative explosive torque at 150 and 200 ms from contraction onset was similar between the two groups, the controls developed higher RTD during the second and third time window from force onset (Fig 3B).

Previous studies found an increase in the EMG amplitude and rate of force development in the initial phase of contraction after four weeks of explosive training (7). In addition, a greater normalized rate of force development in the first 50 ms of contraction was found for power athletes during knee extensor explosive torque (50). Because the first 50 ms of contraction strongly reflect neural activation (9, 11, 12, 46), strength or power training presumably increase RTD by a faster recruitment of motor units, as discussed in the following.

MFCV during the explosive phase of contraction

ST individuals have the ability to develop higher levels of force in the first 50 ms of contraction. This seems to be associated to greater MFCV in the same time interval which indicates recruitment of motor units with greater conduction velocity. The role of motor unit recruitment during explosive force contraction is not well understood because it is not possible to identify representative populations of motor units in very short time intervals.

The primary determinant of motor unit twitch force is the number of muscle fibers innervated by the axon (13, 52). Motor unit peak twitch forces in humans range from ~6 to ~78 mN•m with maximal tetanic forces ranging from ~30 to ~200 mN•m (32, 34). Therefore, one of the mechanisms that determined the increase in RTD during the first 0-50 ms interval in the ST may have been the recruitment of larger motor units with greater and faster twitches. There is evidence showing correlations between electrically evoked twitch torque and early voluntary rate of force development, that could be associated to the differences in muscle fiber composition and/or Ca^{2+} saturation for the trained individuals (3, 30).

Interestingly, the two groups showed similar EMD values, which is in accordance with a previous study that compared the EMD in a power trained and untrained cohort (50). This finding is however contradictory with a higher MFCV during the EMD. A higher absolute MFCV value should theoretically anticipate the release of Ca^{2+} and thus the rise in force. However, these problematics may be related to the techniques employed in assessing the delay between the neural and muscular apparatus. The EMD during explosive contractions may not be sensitive to differences in neural activation due to a compressed recruitment (11, 56). We have recently shown, that when the electromechanical delay is assessed as the time difference between the neural drive and force during the sustained contractions the central nervous system modulates the delay broadly and according to the rate of force development (56). Indeed, the neuromechanical delay seems to be predominantly influenced by the type of recruited motor units and to the intrinsic properties of the motor neuron (5, 56). Future studies assessing the neuromechanical delay in strength/power trained individuals may be warranted.

MFCV increases with voluntary force production due to the relation between motor unit recruitment thresholds and fiber diameter (4, 8, 31, 54). This association implies that the ordered recruitment of motor units may be assessed by estimates of conduction velocity (55). We have recently reported that large, high-threshold motor units innervate fibers with large diameter (54), which explains the association between motor unit mechanical properties and conduction velocity, previously reported (4). Moreover, we have recently demonstrated that the increase in average MFCV during voluntary force contractions is associated to the progressive recruitment of motor units with increasing conduction velocity and predicts recruitment thresholds at the individual subject level (55).

In the present study, MFCV was the average of the conduction velocities of the active motor units during explosive force contractions, in time intervals of 50 ms following EMG onset. We showed that there may be significant differences in the recruited motor units during explosive tasks in ST compared to moderately active individuals. Absolute MFCV values were greater in ST throughout the full duration of the explosive contractions (Fig. 3.A). Moreover, the early absolute and normalized MFCV were positively associated to RTD (Fig. 4). Because absolute MFCV values are linearly related to the diameters of muscle fibers, higher absolute conduction velocity values may indicate that ST have muscle fibers with larger diameters due to the strength training induced hypertrophy (39), as compared to controls (20, 40).

However, when MFCV values were normalized to the maximal value during MVF (full motor unit recruitment), ST had a significantly greater MFCV-rel during the initial phase of the explosive contractions. Specifically, MFCV-rel$_{EMD}$ and MFCV-rel$_{0\text{-}50}$ were on average ~9% greater (Fig 4B). This suggests that during the early phase of explosive force, ST have the ability to recruit motor units with faster conduction velocities in a shorter time. It takes ~100ms more for the controls to reach similar values of normalized MFCV compared to the ST group. Interestingly, the changes in conduction velocity did not differ between groups (Fig. 4A-B) and the MFCV plateaued in the interval 50-100 ms that can be interpreted as full motor unit recruitment (55). This interpretation is in agreement with previous studies reporting that most motor units are recruited at 1/3 of maximal force during explosive contractions (11, 12). Moreover, MFCV increased in all subjects from the EMD to 0-50, indicating that the ordered recruitment according to the size of the motor unit was preserved during the explosive tasks in both groups.

The underlying mechanism that may determine an increase in explosive force for the ST individuals may be an anticipated recruitment of high threshold motor units with high conduction velocities. The difference between MFCV of high and low threshold motor units within a muscle is ~2 m/s (54). A faster motor unit recruitment (and conduction velocity) would achieve greater peak mechanical torques in a shorter time. The release of calcium from the sarcoplasmic reticulum is correlated to the speed the action potential on the fiber membrane (17). Indeed, MFCV is related to motor unit time-to-peak twitch forces (4). The increase in MFCV may potentially allow a faster calcium uptake and thus anticipating the rise in force.

Van Cutsem and colleagues reported an increase in motor unit discharge rates following ballistic training (10) and concluded, in agreement with other studies, that RTD depends on motor unit discharge rate (10, 12, 14). On the other hand, the recruitment threshold of motor units significantly influences the discharge rate at a given absolute force (Duchateau & Baudry, 2014). Anticipating the recruitment of high threshold motor units would result in reaching motor unit peak discharge rate and motor unit peak RTD in a shorter time. Accordingly, in the present study, MFCV was positively associated with RTD (Fig 4A), suggesting that motor unit recruitment may play an important role in explosive force production.

Interestingly, the correlation between RTD_{0-50} and early MFCV values ($MFCV_{EMD,0-50}$) was different for the ST and untrained individuals. $MFCV_{0-50}$ was not correlated with RTD_{0-50} in the ST group (Fig. 4). This result indicates that ST completed the motor unit recruitment during the very early phase of explosive force, i.e. between the EMD and the first 50 ms from contraction onset (Fig. 4B). The increase in MFCV during the explosive force at the time points 50 and 100 (ms) for the ST is presumably due to some subjects continuing the recruitment, whilst the subjects with higher RTD achieving a faster plateau in MFCV (Fig. 4). Indeed, it took more time for the untrained individuals to reach high MFCV (and full motor unit recruitment) values (Fig 3,4).

It must be noted that the number of subjects in the present study may be too low for a correlation study. Moreover, the cross-sectional design cannot isolate the innate and environmental factors that contributed to the explosive force and MFCV differences found between the cohorts. However, in the present study the trained individuals performed combined strength and explosive training for more than three years. Recent evidence showed a significant increase in explosive force production after twelve weeks of isometric explosive training when compared to isometric sustained-contraction strength training (6). The large differences in the early RTD for the trained subject in the present study may also indicate that the neural contributors to explosive strength could be related to chronic exposure to explosive/strength training and that the neural adaptations may continue over time. Future studies assessing the neural contributors to explosive force in large cohorts and longitudinal (>1yr) interventions are warranted.

Conclusion

Resistance trained individuals showed higher RTD and explosive force in the very early phase of contraction that was accompanied by an increase in absolute and normalized MFCV, when compared to controls. These observations may be explained by recruitment of fast twitch motor units (i.e., large motor units with large muscle fibers diameters) in a shorter amount of time in the resistance trained cohort than controls. In addition to the functional implications in the study of human explosive force, the study also presents a methodology that may be applied in the assessment of the neural strategies of muscle control in health, training, and pathology.

Conflict of interest

The authors declare no conflict of interest

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FIGURE CAPTIONS

Fig. 1. A: Two high-density surface EMG arrays of 64 of electrodes each. **B:** Time-torque curve during an isometric explosive contraction (black line) and the activity of 128 monopolar channels recorded from the biceps brachii muscle. **C.** Ten single differential EMG signals during an explosive force contraction from a control subject. The innervation zone (IZ) and several motor unit action potentials (MUAPs) propagating in the distal direction can be seen. **D.** In these signals recorded from a strength trained individual, several MUAPs propagating at a significant higher velocity can be seen compared to the control subject. The dotted line indicates the time-torque curve.

Fig 2. Rate of torque development (RTD) in absolute (A) and normalized (B) values. Black bars represent the strength trained individuals and white bar for the controls. Data are reported as mean and SD. * = $p< 0.001$

Fig. 3. Muscle fiber conduction velocity (MFCV) in absolute (A) and normalized (B) values. Filled circles for the strength trained individuals. Correlation coefficients (R2 and regression lines are given). Data are reported as mean and SD. * = $p<0.01$.

Fig. 4. Correlation between the rate of torque development during the first 50 ms of contraction ($RTD_{0\text{-}50}$) and muscle fiber conduction velocity during the electromechanical

delay and in the first 50 ms of contraction ($MFCV_{EMD,0-50}$). Filled circles for the control individuals. Correlation coefficients (R^2 and regression lines are given) * = $p<0.05$.

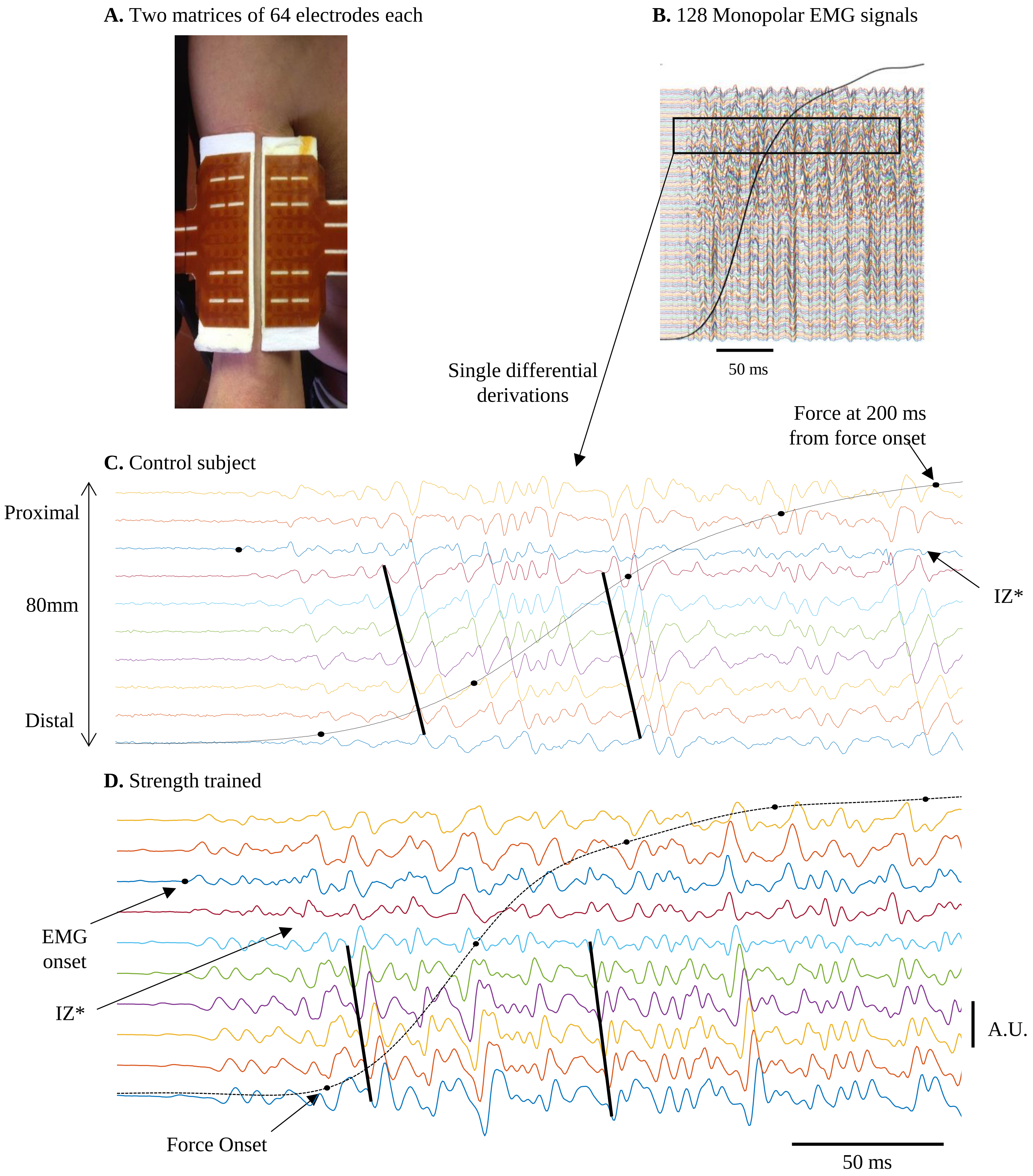
A. Two matrices of 64 electrodes each
B. 128 Monopolar EMG signals
50 ms
Single differential derivations
Force at 200 ms from force onset
C. Control subject
Proximal
80mm
Distal
IZ*
D. Strength trained
EMG onset
IZ*
A.U.
Force Onset
50 ms

Fig 1.

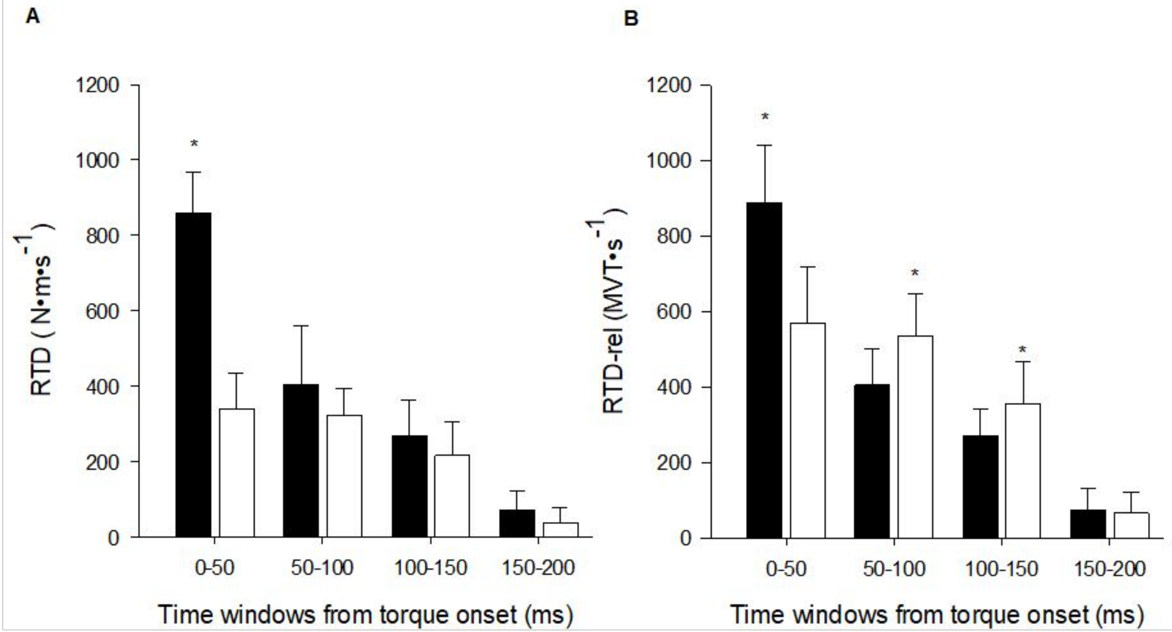
A
B
RTD (N•m•s^{-1})
RTD-rel (MVT•s^{-1})
1200
1000
800
600
400
200
0
*
0-50
50-100
100-150
150-200
Time windows from torque onset (ms)

Fig 2.

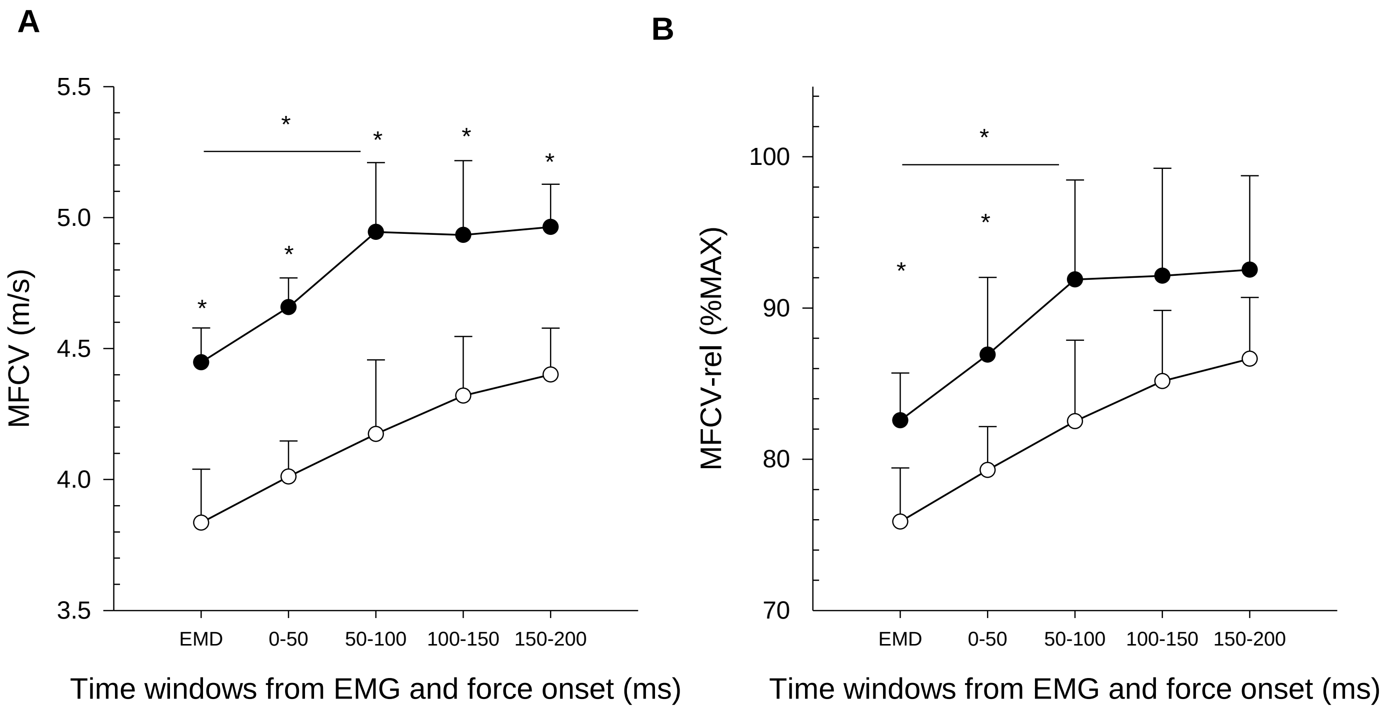
A
B
5.5
5.0
4.5
4.0
3.5
MFCV (m/s)
100
90
80
70
MFCV-rel (%MAX)
*
EMD
0-50
50-100
100-150
150-200
Time windows from EMG and force onset (ms)

Fig 3.

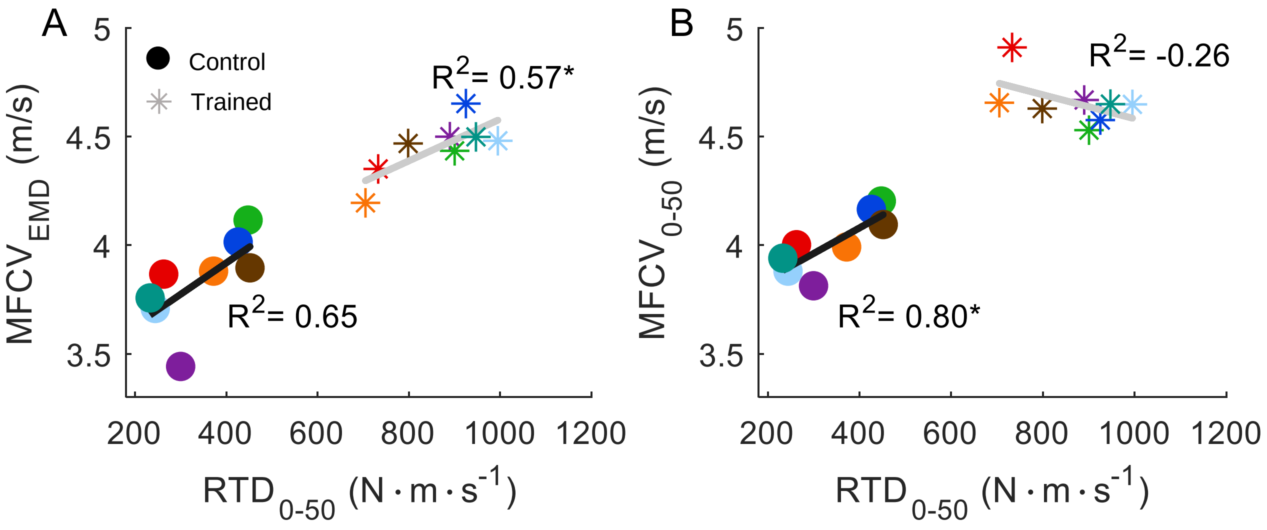
A
B
Control
Trained
R^2= 0.57*
R^2= 0.65
R^2= -0.26
R^2= 0.80*
MFCV$_{EMD}$ (m/s)
MFCV$_{0-50}$ (m/s)
RTD$_{0-50}$ (N·m·s^{-1})
5
4.5
4
3.5
200
400
600
800
1000
1200

Fig 4.