Eur J Appl Physiol (1989) 58:395-399

European Journal of Applied Physiology and Occupational Physiology

Comparison of twitch potentiation in the gastrocnemius of young and elderly men

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Summary. The capacity for twitch potentiation in the gastrocnemius muscle was determined following maximal voluntary contractions (MVC) in 11 elderly ($\bar{x} \pm SD$; 66.9±5.3 years) and 12 young (25.7±3.8 years) men. Potentiation was observed by applying selective stimulation to the muscle belly, 2 s after a 5 s MVC. With this procedure, both groups showed significant ($P<0.05$) increases in twitch tension in the gastrocnemius (ratios of potentiated twitch to baseline were $\bar{x}=1.68 \pm 0.40$ for young vs $\bar{x}=1.40 \pm 0.20$ for the elderly, $P<0.001$). Time to peak tension of the twitch decreased from $\bar{x}=101.5 \pm 17.9$ ms to $\bar{x}=88.0 \pm 15.8$ ms in the young men following potentiation; the respective values for the older men were 136.7±17.9 ms and 133.1±28.6 ms. These changes resulted in a greater rate of tension development in the potentiated state. The elderly gastrocnemius thus showed qualitatively similar changes in the isometric twitch following potentiation, but reduced and prolonged responses in comparison to young adults. Slowed muscle contraction and reduced capacity for potentiation may be physiological correlates of the reported morphological changes in aged skeletal muscle.

Key words: Aging — Physical fitness — Muscle contraction — Strength

Introduction

The ability of human skeletal muscle to increase twitch tension after voluntary contractions (Belanger et al. 1983; Vandervoort et al. 1983; Vandervoort and McComas 1986; Alway et al. 1987) or following tetanic stimulation (Botelho and Cander 1953; Takamori et al. 1970; Vandervoort and McComas 1983) has been described. Observing the triceps surae, Vandervoort and McComas (1983) reported post-tetanic potentiation in the gastrocnemius muscle but an absence of potentiation in the soleus muscle, in young men and women. The differences in potentiating ability between these muscles has been attributed to their distinctive fibre type proportions, the gastrocnemius being a mixed muscle with approximately equal proportions of type I and type II fibres while the soleus has primarily slow twitch (type I) fibres (see Saltin and Gollnick (1983) for a review).

Functional characteristics of the triceps surae muscle group, studied as a whole, show changes with ageing toward an overall slower contraction, and reduced capacity for twitch potentiation (Davies et al. 1983; McDonagh et al. 1984; Vandervoort and McComas 1986), possibly reflecting a greater type II fibre atrophy compared to type I fibres (Tomonaga 1977; Larsson 1978; Aniansson et al. 1986; Lexell et al. 1988). This change could be related to a greater reliance on habitually slower movements (walking) in the elderly population (Cunningham et al. 1982). The performance of skeletal muscle may have important consequences in terms of the capacity of elderly individuals for independent living (Himann et al. 1986). The purpose of the present investigation was to provide a detailed comparison of potentiation capacity of the gastrocnemius muscle in young and elderly men.

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Material and methods

Subjects. The subjects were 11 elderly men aged 66.9 (±5.3) and 12 young men aged 25.7 (±3.8) years. The two groups were similar in body size. Height was 177.3±5.1 cm and 177.4±13.5 cm for the young and elderly respectively. Body weight was 76.5 kg±5.5 kg and 81.4±5.2 kg for the young and elderly respectively. All elderly subjects exercised approximately three times each week for 60 min in an aerobic training program (walk/jog) which met regularly over the past 3-5 year period (Cunningham et al. 1987). Young subjects were all physically fit individuals from the university student community. Subjects reported for testing in a rested state (no exercise for 24 h prior to testing), and were instructed to abstain from food and drink containing caffeine or alcohol for 24 h. Subjects reported to the lab on 3 separate occasions. All subjects signed an informed consent prior to the start of the experiments.

Muscle stimulation and recording. Description of the experimental arrangement has been detailed by Davies et al. (1982). Subjects were seated on a bench with their left leg immobilized by a transducing clamp placed above the knee with the thigh horizontal, the knee and ankle set at an angle of 85°. Ankle plantarflexion torques caused an upwardly transmitted force through the lower leg to the transducer. Twitches were elicited by pulses, produced with a high voltage stimulator (# 3072) triggered by a digitimer (# 4030) (both from Medical Systems Corp., New York) and transferred to the skin through aluminum stimulating electrodes (15 cm×9 cm) aligned in the longitudinal axis of the limb and placed over the gastrocnemius (anode) and soleus for activation of the whole triceps surae. For separate stimulation of the gastrocnemius, a narrower pair of 15 cm×3 cm electrodes was used. In order to confine the excitation to just the lateral and medial gastrocnemius, the anode was placed distally across these 2 muscle bellies and the cathode was located slightly above it over the region of lowest threshold for stimulation. The voltage and current across the electrodes were measured by a volt-ammeter.

The force output of muscle contraction was converted by strain gauges mounted on the transducer clamp. The wave form of the force output was displayed on a recorder and graphics and analysis performed (as subsequently described) by the Digital-Minc computer (PDP 11/23).

Testing procedures. Each test session consisted of 3 parts. First, twitch responses for the entire triceps surae were elicited by the application of rectangular wave pulses of 50 µs duration. Stimulation was given in 40 volt increments at 30 s intervals until supra-maximal twitch (Pt) responses were recorded. The criterion for Pt was a plateau in force with no further rise upon increased voltage. Time to peak tension (TPT) and half relaxation time (1/2 RT) of the criterion twitch were determined as the time elapsed from twitch onset to peak force and from peak to half force decay respectively. Average rates of twitch force development (dP/dtx) and relaxation to half force decay ($-dP/dtx$) were determined by computer software. Every 3.12 ms, in which 8 sample points were made, a slope was calculated (dP/dt). This process was continued until the maximum twitch tension was reached. From this file of slopes a mean slope value was calculated as dP/dtx. This program was repeated for the twitch relaxation phase to the time of 1/2 relaxation ($-dP/dtx$).

The second phase of the test session consisted of separate twitch response determination for the gastrocnemius muscle. Wave pulses of 50 µs duration, with increasing voltage at 30 s intervals, were given until suitable twitch responses were achieved. Criteria for these twitches were that (1) there was no visible contraction of the soleus when the gastrocnemius was being stimulated, (2) palpation also indicated the soleus was not activated and (3) the twitch Pt response was less than half the torque produced in a maximal twitch contraction of the entire triceps surae. An assumption was made that twitches which exceeded this 50% criterion could no longer be attributed to an isolated stimulation of the gastrocnemius.

Subjects then performed a 5 s maximal voluntary contraction (MVC), followed by a twitch stimulation 2 s later with the same pulse intensity. Comparison of the baseline and post-MVC twitch amplitudes was used to determine the potentiation. A MVC of short duration was chosen to maximize potentiation without inhibitory fatigue processes (Vandervoort et al. 1983).

Statistical analyses. The changes in Pt, TPT, 1/2 RT, dP/dtx and $-dP/dtx$ were compared pre- to post-potentiation in both

Table 1. Comparison of the contractile properties of gastrocnemius muscle in young and elderly subjects following a maximal voluntary contraction

Variable	Time of measurement	Young	Elderly	*P*-value
Twitch	BMVC	34.40 (13.00)	20.49 (8.96)*	0.001
Tension (N)	AMVC	55.33 (13.79)	27.95 (11.66)	
TPT (ms)	BMVC	101.46 (17.90)	136.68 (17.89)*	0.050
	AMVC	88.02 (15.83)	133.09 (28.63)	
dP/dtx (N/ms)	BMVC	0.44 (0.16)	0.24 (0.15)*	0.001
	AMVC	0.89 (0.18)	0.35 (0.25)	
1/2 RT (ms)	BMVC	98.57 (34.86)	122.79 (41.80)	0.491
	AMVC	88.25 (15.81)	95.81 (32.35)	
$-dP/dtx$ (N/ms)	BMVC	0.38 (0.11)	0.28 (0.04)*	0.068
	AMVC	0.47 (0.13)	0.31 (0.05)	

Values are means (±standard deviation) TPT=time to peak tension; 1/2 RT=half relaxation time; dP/dtx=average rate of twitch development; $-dP/dtx$=average rate of force decay; BMVC=before maximal voluntary contraction; AMVC=after maximal voluntary contraction. The *P*-value refers to the age effect of the MVC in potentiating the muscle with the initial test value as a covariate and the test value after the MVC as the dependent variable. * Denotes a significant difference ($P<0.05$) between age groups at baseline the elderly and young groups and significant differences were determined using a t-statistic. To compare the effect of the MVC between the two age groups, analysis of covariance was used with the initial test value as a covariate and the test value after the MVC as the dependent variable.

Results

Baseline data showed that the elderly subjects had a significantly lower mean MVC ($\bar{x}=862 \pm SD=210$ N) compared to the young subjects ($\bar{x}=1508 \pm 326$ $P<0.01$). The elderly subjects also showed significantly slower development of baseline twitch tension in the gastrocnemius (Table 1); twitch times for both young and old men agreed closely with values published previously (Vandervoort and McComas 1986).

Twitch potentiation in the gastrocnemius was found to be significantly greater in the young men; their ratio of Pt after versus before MVC was $\bar{x}=1.68 \pm 0.40$ while the $\bar{x}$ for the elderly$=1.40 \pm 0.20$ ($P<0.001$, Fig. 1). Further, in the gastrocnemius, changes with potentiation in all variables measured, except 1/2 RT and $-dp/dtx$, were significantly different between young and elderly subjects. Twitch potentiation in young adults was achieved with an increase in the rate of tension development, rather than prolongation of the time to peak tension (Table 1). Elderly adults showed less change in these variables.

Discussion

In humans, the two muscles which make up the triceps surae complex are considered to have different functions. The soleus has an important postural role, serving to maintain a standing position,

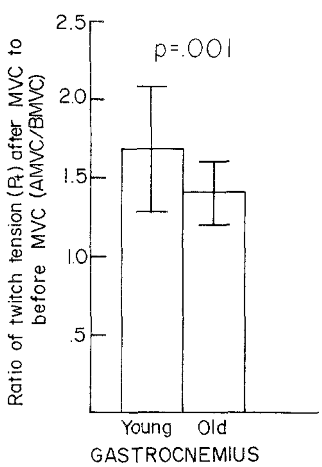

Fig. 1. Comparison of the ratio of twitch tension (Pt) after to before a 5 s MVC in the gastrocnemius muscles of young ($n=12$) and elderly ($n=11$) men. Values are means ±SD

whereas the gastrocnemius is more active in phasic activity (Campbell et al. 1973). These differences in function are reflected in the histochemical properties of the fibres in the two muscles; the soleus is composed mainly of type I fibres (70 to 90%) and the gastrocnemius has approximately equal proportions of type I and type II fibres (Saltin and Gollnick 1983). Capacity for twitch potentiation is pronounced in the gastrocnemius as demonstrated in the present study with voluntary contraction, and in the study of Vandervoort and McComas (1983), in which an involuntary tetanus was produced by stimulation at 50 Hz. This stimulation rate is similar to that found in human muscle with a maximal voluntary contraction (Bellemare et al. 1983). It is notable that just a brief but intense period of voluntary effort is necessary to induce potentiation (Vandervoort et al. 1983; Alway et al. 1987; present study).

Elderly individuals had prolonged contraction and half relaxation times of the gastrocnemius muscle in comparison to young men and corresponding lesser increases in twitch tension following MVC. As well, the MVC's obtained in this study in the elderly subjects were also reduced; this reduction was comparable to that reported in other papers on strength differences between young and old men (Davies et al. 1983; McDonagh et al. 1984; Vandervoort and McComas 1986; Cunningham et al. 1987). Loss of strength in highly motivated old people is a clear indication of reduced muscle mass (Vandervoort and McComas 1986), caused by a decrease in the total number of fibres in aged muscle (Caccia et al. 1979; Lexell et al. 1988). Further, elderly muscle shows preferential atrophy of the Type II fibres in studies of gastrocnemius (Tomonoga 1977) and quadriceps (Larsson 1978; Aniansson et al. 1986; Lexell et al. 1988). If one assumes that it is mainly the Type II fibres that potentiate (Brown and von Euler 1938; Close and Hoh 1968; Burke 1981), then the muscle mass present in the aged would be expected to show a reduced capacity for this process. Analysis of muscle fibre composition in the gastrocnemius of old people would provide valuable information to relate to contractile properties. It would also be of interest to observe whether strength-training induced hypertrophy of Type II muscle fibres can lead to greater twitch potentiation in the elderly.

Several other factors could also contribute to the reduced twitch potentiation in the elderly muscle. Structure and function of the sarcoplasmic reticulum (SR) may change with age (Tomonaga 1977), thus influencing the amount of Ca^{2+} available to the contractile apparatus for potentiation. Froelich et al. (1978) and Narayanan and Tucker (1986) reported that the slowed relaxation of cardiac muscle with advanced age was related to a decrease in the rate at which the SR can accumulate calcium. The trend to prolonged half relaxation time of the elderly gastrocnemius muscle, ($\bar{x}$BMC = 122.8 ms VS 98.6 ms for young adults, Table 1) is one indicator of reduced efficiency in SR function. Another possibility of a change mediated at the cellular level with aging could be in regard to the binding of Ca^{2+} to myosin (Carlsen and Walsh 1987). Houston et al. (1985) have shown that myosin becomes phosphorylated during repetitive contractions and in this state is more receptive to Ca^{2+} activation. The enhanced efficiency is reflected by an increased rate of tension development in the potentiated twitch (MacIntosh and Gardiner 1987). It remains to be determined by direct biochemical analysis if the capacity for this phosphorylation process decreases in old muscle. An additional factor which may have influence on contractile properties of elderly muscle, that of tendon composition series elastic compliance has yet to be evaluated.

In summary, the present study has described the difference in twitch potentiation observed between young and elderly groups of men after the gastrocnemius muscle underwent a maximal voluntary contraction lasting 5 s. Lower potentiation in the elderly may be due to a reduced contribution of type II muscle fibres during twitch contractions. Whether contractile properties of elderly muscle such as decsreased speed and potentiation can be modified by alterations in exercise pattern remains to be determined.

Acknowledgements. The authors wish to thank M. Ginty and E. Nowicki for their assistance. The study was supported by a grant from NSERC (A2787). A. A. Vandervoort was supported by a Gerontology Research Council of Ontario Post-Doctoral Fellowship.

References

Alway SE, Hughson RL, Green HJ, Patla AE, Frank JS (1987) Twitch potentiation after fatiguing exercise in man. Eur J Appl Physiol 56:461–466

Aniansson A, Hedberg M, Henning G-B, Grimby G (1986) Muscle morphology, enzymatic activity, and muscle strength in elderly men: a follow-up study. Muscle Nerve 9:585–591

Belanger AY, McComas AJ, Elder GBC (1983) Physiological properties of two antagonistic human muscle groups. Eur J Appl Physiol 51:381–393

Bellemare F, Woods JJ, Johansson R, Bigland-Ritchie B (1983) Motor unit discharge rates in maximal voluntary contractions of three human muscles. J Neurophysiol 50:1380–1392

Botelho SY, Cander L (1953) Post-tetanic potentiation before and during ischemia in intact human skeletal muscle. J Appl Physiol 6:221–228

Brown GL, von Euler US (1938) The after effects of a tetanus on mammalian muscle. J Physiol (Lond) 93:39–60

Burke RE (1981) Motor units: anatomy, physiology and functional organization. Handbook of physiology. The nervous system. Am Physiol Soc Bethesda, MD Sect 1, vol 2, chapt. 10, p 345–422

Caccia MR, Morris JB, Johnson MA (1979) Morphology and physiology of skeletal muscle in rodents. Muscle Nerve 2:202–212

Campbell KM, Biggs NL, Blanton PL, Lehr RP (1973) Electromyographic investigation of the relative activity among four components of the triceps surae. Am J Phys Med 52:30–41

Carlsen RC, Walsh DA (1987) Decrease in force potentiation and appearance of α-adrenergic mediated contracture in aging rat skeletal muscle. Pflügers Arch 408:224–230

Close RI, Hoh JFY (1968) The after-effects of repetitive stimulation on the isometric twitch contraction of rat fast skeletal muscle. J Physiol (Lond) 197:461–477

Cunningham DA, Morrison D, Rice CL, Cooke C (1987) Ageing and isokinetic plantar flexion. Eur J Appl Physiol 56:24–29

Cunningham DA, Rechnitzer PA, Pearce ME, Donner AP (1982) Determinants of self-selected walking pace across ages 19 to 66. J Gerontol 37:560–564

Davies CTM, Mecrow IK, White MJ (1982) Contractile properties of the human triceps surae with some observations on the effects of temperature and exercise. Eur J Appl Physiol 49:255–269

Davies CTM, White MJ, Young K (1983) Electrically evoked and voluntary maximal isometric tension in relation to dynamic muscle performance in elderly male subjects, aged 69 years. Eur J Appl Physiol 51:37–43

Froelich JP, Lakatta EG, Beard E, Spurgeon HA, Weisfeldt ML, Gerstenblith GB (1978) Studies of sarcoplasmic reticulum function and contraction duration in young adult and aged rat myocardium. J Mol Cell Cardiol 10:427–438

Himann JE, Cunningham DA, Rechnitzer PA, Paterson DH (1986) Determinants of choice of walking speed. Can J Appl Sport Sci 11:18P

Houston ME, Green HJ, Stull JT (1985) Myosin light chain phosphorylation and isometric twitch potentiation in intact human muscle. Pflügers Arch 403:348–352

Larsson L (1978) Morphological and functional characteristics of the ageing skeletal muscle in man. A cross-sectional study. Acta Physiol Scand suppl 36:457

Lexell J, Taylor CC, Sjostrom M (1988) What is the cause of the ageing atrophy? J Neurol Sci 84:275–294

MacIntosh BR, Gardiner PF (1987) Posttetanic potentiation and skeletal muscle fatigue: interactions with caffeine. Can J Physiol Pharmacol 65:260–268

McDonagh MJN, White MJ, Davies CTM (1984) Different effects of ageing on the mechanical properties of human arm and leg muscles. Gerontology 30:49–54

Narayanan N, Tucker L (1986) Autonomic interactions in the aging heart: age-associated decrease in cholinergic receptor mediated inhibition of β-adrenergic activation of adenylate cyclase. Mech Ageing Dev 34:249–259

Saltin B, Gollnick PD (1983) Skeletal muscle adaptability: significance for metabolism and performance. In: Handbook of Physiology, Sect. 10. American Physiological Society, Bethesda, pp 555–631

Takamori ML, Gutmann L, Shane SR (1970) Contractile properties of human skeletal muscle. Arch Neurol 25:535–546

Tomonoga M (1977) Histochemical and ultrastructural changes in senile human skeletal muscle. J Am Geriat Soc 25:125–131

Vandervoort AA, McComas AJ (1983) A comparison of the contractile properties of the human gastrocnemius and soleus muscles. Eur J Appl Physiol 51:435–440

Vandervoort AA, McComas AJ (1986) Contractile changes in opposing muscles of the human ankle joint with aging. J Appl Physiol 61:361–367

Vandervoort AA, Quinlan J, McComas AJ (1983) Twitch potentiation after voluntary contraction. Exp Neurol 81:141–152

Accepted September 16, 1988