ORIGINAL ARTICLE

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Effect of strenuous strength training on the Na-K pump concentration in skeletal muscle of well-trained men

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Abstract This study examined how strenuous strength training affected the Na-K pump concentration in the knee extensor muscle of well-trained men and whether leg muscle strength and endurance was related to the pump concentration. First, the pump concentration, taken as 3H-ouabain binding, was measured in top alpine skiers since strength training is important to them. Second, well-trained subjects carried out strenuous eccentric resistance training either 1, 2, or 3 times · week−1 for 3 months. The Na-K pump concentration, the maximal muscle strength in a full squat lift (one repetition maximum, 1 RM), and the muscle endurance, taken as the number of full squat lifts of a mass of 70% of the 1 RM load, were measured before and after the training period. The mean pump concentration of the alpine skiers was 425 (SEM 11) nmol · kg−1 wet muscle mass. The subjects in part two increased their maximal strength in a dose-dependent manner. The muscle endurance increased for all subjects but independently of the training programme. From a mean starting value of 356 (SEM 6) nmol · kg−1 the mean Na-K pump concentration increased by 54 (SEM 15) nmol · kg−1 (+15%, P < 0.001) when the results for all subjects were pooled. The effect was larger for those who had trained twice a week than for those who had trained only once a week (P = 0.025), suggesting that the effect of strength training depended on the amount of training carried out. The muscle strength and endurance were not related to the pump concentration, suggesting that the pumping power of this enzyme did not limit the performance during heavy lifting. However, the individual improvements in the endurance test during the training period correlated with the individual changes in the pump concentration (rSpearman = 0.5; P = 0.01) which could mean that a common factor both increases the pump concentration and makes the muscles more adapted to repeated heavy lifting.

Key words Alpine skiing · Na+-K+-exchanging ATPase · Sodium-potassium pump · Squat lifting · Strength training

Introduction

Strenuous muscle activity requires high frequencies of action potentials in millions of muscle cells, leading to extracellular accumulation of potassium (Vyskocil et al. 1983). The potassium is pumped back into the muscle cells by the Na-K pump. If the pump rate is not high enough, the extracellular accumulation of potassium may lead to a depolarisation block, and an insufficient maximal pump rate or pump power (Kjeldsen et al. 1986; Clausen and Everts 1988; Clausen and Nielsen 1994) leading to depolarisation of the muscle cell membrane could be a cause of muscle fatigue (Clausen and Everts 1991). We have on the other hand suggested that the pump does have a sufficiently high maximal power and is never forced to work at rates higher than one-third of its maximal rate (Medbø and Sejersted 1990; Everts et al. 1997). If this is so, the pump concentration may not be closely related to the muscle performance.

The plasma potassium concentration increases at the onset of exercise, but after a training period of 1 week to a few months the effect is reduced in man (Tibes et al. 1974; Kjeldsen et al. 1990; Green et al. 1993; McKenna et al. 1993) and dogs (Knochel et al. 1985). This is compatible with a higher Na-K pump activity or that the
pump becomes more sensitive to activation-induced changes after training. Experiments on mammals have shown a higher pump concentration or maximal Na-K adenosine triphosphatase activity after training in dogs (Knochel et al. 1985), rats (Kjeldsen et al. 1986), guinea pigs (Leivestet al. 1992), and sheep (Jebens et al. 1995). Intense sprint-training (McKenna et al. 1993), endurance-training (Green et al. 1993, 1999; Madsen et al. 1994; Evertsen et al. 1997), or strength training (Green et al. 1999) may increase the pump concentration by around 15%, at least in untrained men. The effect of strenuous strength training in well-trained men is not known. If the pump's power is critical for physical performance, changed pump concentrations should be closely related to a changed performance.

We first examined the Na-K pump concentration in well-trained alpine skiers and found concentrations as high as ever reported for man (Evertsen et al. 1997). Since strength-training is central for alpine skiers, we hypothesised that strenuous strength-training may be particularly effective in raising the pump concentration, perhaps in a dose-dependent way. Therefore strength-trained athletes underwent 3 months of strenuous resistance-training. The pump concentration was measured before and after the training period and related to the subjects' muscle strength. Since repeated heavy lifting may lead to a continued release of potassium and perhaps cause fatigue unless the potassium is removed quickly, the pump concentration was also compared with the subjects' ability in repeated heavy lifting, that is with muscle endurance.

**Methods**

**Subjects**

The subjects in the first part of the study were 8 male alpine skiers who were studying at the Norwegian High School for Top Athletes at Hovden, Norway. Their mean age was 19 (SD 1) years, mean height 1.81 (SD 0.05) m, and mean body mass 76 (SD 4) kg. Their maximal O₂ uptake was 43 (SD 2) μmol·s⁻¹·kg⁻¹ [58 (SD 2) ml (standard temperature and pressure, dry) · min⁻¹ · kg⁻¹], and their maximal strength in full squat lifting (defined below) was 1.87 (SD 0.27) kg · kg⁻¹ body mass. The subjects in the second part of the study were 23 well-trained male athletes who had trained regularly at The National Olympic Training Centre in Oslo. Their mean age was 27 (SD 7) years, mean height 1.82 (SD 0.06) m, and mean body mass 91 (SD 12) kg. Their maximal strength in a full squat lift was 1.79 (SD 0.15) kg · kg⁻¹ body mass before the study. In addition to these 23 subjects who completed the second part of the study, there were 7 subjects who dropped out. Of these, 3 left the study because they were unable to fit the training to their daily life, 1 dropped out because of back pain – it appeared that he had suffered from similar problems earlier, and 3 subjects dropped out for medical reasons unrelated to the training. No further information is given on these 7 subjects.

Each subject was informed orally and in writing about the purpose of the experiments and experimental procedures involved before giving his written consent to participate. The subjects in series 2 were in particular told that they were allowed to leave the study at any stage. The studies were approved by the Ethics Committees of Health Region I in Norway, and were carried out according to Norwegian laws.

**Inclusion criterions for series 2 and previous training**

To be accepted as a subject in the study each participant was required to be able to lift at least 1.5 times his own body mass in a full squat lift. Novice lifters show a fast improvement in strength during the first few weeks of training, probably because of a significant neural adaptation (for review, see Enoka 1988; Sale 1988). To minimize possible neural adaptation during the training period, it was required that each subject should have carried out strength training, including squat lifting, regularly for at least 1 year. Subjects who had previously suffered from injuries that might have influenced the results or whose condition might have become worsened by the training, were excluded. However, as stated above, 1 subject who dropped out had not reported his former back problems.

**Tests and measurements**

Full squat lifts were carried out according to the current rules of power-lifting, which state that a lift shall not be accepted unless the lifter's hip joints in the deepest position are at the same level as, or lower than, his knee joints. During the tests the subjects wore shoes, shorts and T-shirts. They were instructed to use a powerlifter belt around the waist to secure the lower spine, but they were not allowed to use straps or bandages around their knees or any other means that could improve a lift.

The one repetition maximum (1 RM) was taken as the maximal mass lifted on the shoulders during a full squat lift; loads were added in steps of no less than 2.5 kg. For these tests the subjects were allowed several attempts separated by a few minutes. The endurance test was taken as the maximal number of lifts of a mass equal to 70% of a subject's 1 RM before the training period (termed series of 70%; S 70 score). For these lifts the subject was allowed a pause for one deep breath between each lift. Lifts not carried out according to the rules of power lifting were not accepted and thus not counted. More specifically, if the hip joint was not lowered to the level of the knee joint, the lift was not accepted. There were 2 subjects who did not carry out the S 70 test after the training period, and therefore data from only 21 subjects are given for the S 70 score after the training period. The variability of these tests was no larger than the lower limit of resolution of 2.5 kg (1 RM) and one lift (S 70), respectively.

**Training during this study**

The subjects in series 2 were randomly assigned to groups 1, 2, and 3 who trained one, two, or three times a week, respectively. Each training session consisted of five series of four heavy full squat lifts. These lifts were carried out in a specially designed apparatus that allowed repeated lifts where the load was higher in the eccentric lowering phase than in the concentric raising phase of a full squat lift (Refsnæs, to be published). In short, in the deepest position part of the mass was taken off the subject's shoulders, lifted up by a hydraulic engine while the subject carried out the concentric part of the lift, and the mass was again placed on his shoulders before the next lift. During the concentric phase the load was 50% of the subject's pretest 1 RM throughout the study. The load during the eccentric phase was 110% of the pretest 1 RM during the 1st week of the training period. This latter load was raised stepwise by approximately 2.5% of the 1 RM every week, ending at 135% of the pretest 1 RM at week 12. The subjects regularly reported to their training, and the only deviation from the scheduled programme was that some of the subjects had a 1 week rest half-way through the training period.

**Biopsy sampling and enzyme analysis**

Each biopsy was taken at rest several hours or more after a giant slalom contest (series 1) or any training (series 2). Thus, the pos-
sible exercise-induced recruitment of internal pumps that has been described by Tsakiridis et al. (1996) has probably not influenced the results given here. Local anaesthesia (Xylocain, 10 g · 1−1) was induced before two incisions in the skin and muscle fascia were made over the lateral portion of the quadriceps muscle of one thigh. Muscle tissue was taken from both incisions by muscle biopsy needles using the technique of Bergström (1962). The muscle tissue was immediately frozen in isopentane precooled with liquid N2. The leg the biopsies were taken from was randomly chosen, but for each subject in series 2 biopsies were taken from the same leg before and after the training period.

Tissue samples for enzyme analysis were dissected free from connective tissue, blood and fat under a light microscope. The concentration of Na-K pumps (Enzyme Commission no. 3.6.1.37) in biopsies of 3–10 mg was determined as described elsewhere (Evertsen et al. 1997). These authors used the method described by Nørgaard et al. (1983, 1984) and Kjeldsen (1986) but used N-2-hydroxyethylpipеразине-N′-2-ethanesulfonic acid (HEPES) as buffer rather than TRIS in agreement with the recommendations of Good et al. (1966). Separate control experiments showed that incubation in HEPES gave as high ouabain binding as in TRIS but that the variability was reduced (not shown). The variability (SD) of single analyses by the 3H-ouabain method used here was 24 mmol · kg−1 · wet muscle mass, giving a coefficient of variation of 6%; the error in the weighted mean of parallel analyses was around half this value. The 3H-ouabain, having a specific activity of 2.15 PBq · mol−1 and a radiochemical purity of 96.5%, was purchased from Nycomed Amersham plc. (Little Chalfont, England; batch 62A).

The 3H-ouabain binding values reported are the means of parallel measurements on three biopsies from each subject. The value from one biopsy was excluded because of a low biopsy mass (< 1 mg).

Statistics

The data on the Na-K pump concentration in series 2 showed very large values in all biopsies for 3 subjects (1 subject before the training period and 2 other subjects after). These high values would have seriously influenced the statistics and inferences if standard tests based on normal distributions were used. The data have therefore been presented as trimmed means together with Winsorised SEM and have been tested according to Bickel and Doksum (1977), an approach that according to these statisticians is superior to the use of rank tests and ordered statistics. We used the Bonferroni correction for repeated comparisons.

Correlations between the Na-K pump concentration and other parameters have first been expressed by Spearman’s rank correlation coefficients (rS) where all data have been used. Rank correlations hold for a wider class of distributions, but for normally distributed data this correlation coefficient is almost identical to Pearson’s correlation coefficient (Diem and Seldrup 1982). After possible outliers were excluded (see the criteria below) the common Pearson’s product-moment correlation coefficient (r) has also been calculated. In Fig. 4b regression analysis (geometric mean; Riggs et al. 1978) has been carried out after values regarded as outliers were excluded. Tests of statistical significance were calculated by SPSS for Windows 7.5.1 (SPSS Inc., Chicago).

Exclusion criteria

For normally distributed data only one out of 400 values is more than three standard deviations from the expected value. Therefore, values deviating by more than three standard deviations from the mean were regarded as outliers and excluded from analyses assuming normally distributed data. Moreover, for least square regression analyses extreme values have what in statistics is called a high potential or leverage, meaning that these values may affect the analysis considerably (Weisberg 1985). One extreme value in Fig. 4 was therefore not included in that analysis.

Results

Study 1

The trimmed mean of the Na-K pump concentration, taken as the binding of labelled ouabain, in the 8 male top alpine skiers was 425 (Winsorised SEM 11) nmol·1·kg−1·wet muscle mass (Fig. 1). This is higher than we measured on young, male elite cross-country skiers before a 5 months strenuous training period (P < 0.001) but not significantly higher than the value of the same subjects after the training period (P = 0.2; Evertsen et al. 1997). It is also higher than the value of our strength trained subjects in series 2 before their 3 months training period (P < 0.001) but not after that training period (P = 0.2). It is also higher than the values from other studies given in Fig. 1 (P < 0.05).

There was no relationship between the subjects’ Na-K pump concentration and their maximal leg muscle strength or race time during a giant slalom race (rS < 0.5; P > 0.15). On the other hand, the race times correlated with their maximal leg muscle strengths taken as a full squat lift (rS = −0.6; P = 0.04).

![Graph showing Na-K pump concentration with training](image-url)
Study 2

**Na-K pump**

Before the training period the trimmed mean of the subjects’ Na-K pump concentration was 356 (Winsorised SEM 6) nmol·kg⁻¹ wet muscle mass, and there was no statistically significant difference between subjects assigned to the different groups ($P = 0.2$). When pooling data from all of the subjects, the pump concentration rose by 54 (Winsorised SEM 15) nmol·kg⁻¹ wet muscle mass ($+15\%$, $P < 0.001$; Figs. 1, 2). For training group 1 there was no systematic effect of training ($P = 0.1$), while for training groups 2 and 3 the value rose during the 3 months training period ($P = 0.001$). The increase for group 2 was higher than for group 1 ($P = 0.025$), while the effect seen for group 3 did not differ significantly either from that of group 1 ($P = 0.20$) or from that of group 2 ($P = 0.27$). Consequently, while training 2 days · week⁻¹ increased the pump concentration more than training only 1 day · week⁻¹, we cannot decide whether increasing the training further from two to three times a week led to a levelling off or a reduction in the effect on the Na-K pump concentration.

**Strength**

The subjects increased their maximal strength in full squat lifting by a mean of 0.13 (SEM 0.02) kg·kg⁻¹ body mass ($+7\%$, $P < 0.001$) when values for all subjects were pooled. The effect was largest for training group 3 and least for group 1, which means that the muscle strength was increased by the amount of training. Thus, there was no relationship between muscle strength and the Na-K pump concentration either before the training period ($r_S = 0.1$), after the training ($r_S = -0.3$, $P = 0.2$; Fig. 3) or for the change in the pump concentration versus the increase in the maximal muscle strength ($r_S = -0.2$).

**Endurance**

Before the training period the subjects were able to lift 70% of their 1 RM for a mean of 13.9 (SEM 0.5) times in full squat lifts. After the training period this value rose by a mean of 4.0 (SEM 0.6) lifts [mean relative increase, 29 (SEM 4)%; $P < 0.001$], and there was no difference between subjects who trained 1, 2, or 3 times · week⁻¹. There was no relationship between the muscle endurance taken as the maximal numbers of lifts in this test and the Na-K pump concentrations either before the training period ($r_S = -0.2$, $P = 0.4$) or after the training period ($r_S = 0.2$, $P = 0.4$) when all data were pooled. After excluding three outliers the remaining post-training data correlated positively ($r = 0.5$, $P = 0.02$; Fig. 4 a). Moreover, the change in the pump concentration correlated with the increase in muscle endurance expressed both as the absolute and the relative number of lifts ($r_S = 0.5$, $P = 0.01$; Fig. 4b). When four outliers were excluded, the remaining changes during the training period seemed to be linearly related with a relative error of regression of 0.1, corresponding to 1.5 lifts in absolute terms.

**Discussion**

The main findings in this study were first that the Na-K pump concentrations in these top alpine skiers were among the highest values reported for skeletal muscles of humans. The period of 3 months of strenuous

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*Fig. 2* Effect of 3 months of strenuous strength training on the Na-K pump concentration for subjects who trained 1 ($n = 7$), 2 ($n = 9$), or 3 times week⁻¹ ($n = 7$). a Significant training effect for groups 2 and 3, b the effect for group 2 was larger than that for group 1. The data are trimmed means and Winsorised SEM.

*Fig. 3* Maximal leg muscle strength measured as the one repetition maximum (1 RM) of a full squat lift versus muscle Na-K pump concentration. The data are individual values from 23 subjects after 3 months of regular eccentric resistance training either 1, 2, or 3 times-week⁻¹ (○, □) and from 7 well-trained alpine skiers (▲). Two possible outliers (○) were detected by the exclusion criteria given in the method section. There was 1 skier who did not carry out the 1 RM test. The two parameters do not correlate significantly ($r_S = -0.3$, $P = 0.12$)
Fig. 4 a Leg muscle endurance taken as the maximal number of lifts, of a mass equal to 70% of the 1 RM (S 70 score) versus muscle Na-K pump concentration after 3 months of strenuous eccentric resistance training. The two parameters do not correlate significantly ($r_S = 0.2, P = 0.4$) when all data (●, ○) are included. When the three outliers are excluded ( ○), the remaining values correlate ($r = 0.5; P = 0.02, n = 18$). b Increase in leg muscle endurance versus change in the muscle Na-K pump concentration during 3 months of strenuous eccentric resistance training. The two entities correlated ($r_S = 0.5; P = 0.01$) when all values (●, ○) were included. Four values were regarded as outliers ( ○) and not included in the subsequent regression analysis (●) giving $y_{GM} = 0.18 + 1.85 \times 10^{-5}x$, $n = 17$, $S_{yx} = 0.10$, $r = 0.7$, $P = 0.002$, where $y_{GM}$ denotes the regression taken as the geometric mean and $S_{yx}$ is the error of regression (residual variation) (Riggs et al. 1978). The increase in muscle endurance was taken as the relative increase in the maximal number of deep squat lifts in one series with a load of 70% of the 1 RM before the training period (S 70 score). The data are individual values from 21 subjects who trained regularly for 3 months either 1, 2, or 3 times-week$^{-1}$. There were 2 other subjects who did not carry out the S 70 test after the training period, and thus no data from these 2 subjects were available for the analyses in this figure.

Eccentric strength training increased the pump concentration in well-trained men by 15%, and training twice a week was more effective than training only once a week. Finally, the muscle strength or endurance was not related to the pump concentration, but changes in the pump concentration during the training period correlated positively with increases in the muscle endurance.

Effect of training on the Na-K pump concentration

Our subjects were strong and well-trained before the study, as shown by their maximal performance in a full squat lift. The period of 3 months of strenuous training in part 2 of this study increased the subjects’ muscle strength by 7% on average. The Na-K pump concentration of our subjects was similar to that of the top, well-trained cross-country skiers reported by Evertsen et al. (1997). Despite the high performance level of the subjects in part 2 of this study, the Na-K pump concentration of nearly young men (Kjeldsen et al. 1990; Green et al. 1993, 1999; McKenna et al. 1993; Madsen et al. 1994) was only 5%–27% less than that of our subjects (see Fig. 1). Consequently, a high pump concentration may not be important for a high muscle performance. This conclusion should be drawn with some caution since possible variations in the techniques used by different laboratories have not been examined. However, since all studies have used the approach of Norgaard et al. (1984) and Kjeldsen et al. (1986) for optimal binding of $^3$H-ouabain, these variations may probably be quite small.

The pump concentration of our subjects in series 2 rose on average by 15%. This is to our knowledge the first study to show that strenuous strength training increases the pump concentration in already strength-trained men. Training twice a week was more effective than training only once a week in raising the pump concentration, suggesting that the effect may depend on the amount of training within the range used in this study. Similar increases have been found in several other studies using either aerobic types of endurance-training (Green et al. 1993, 1999; Madsen et al. 1994; Evertsen et al. 1997), high-intensity training involving also anaerobic energy release (McKenna et al. 1993), or strength-training of untrained subjects (Green et al. 1999). Regular physical activity or training at low intensity does not on the other hand seem to affect the pump concentration (Kjeldsen et al. 1990). Thus, it may be that training of sufficiently high amounts and intensities increases the pump concentration independently of the kind of training (endurance, high-intensity, or strength training).

The highest pump concentrations were found in biopsies taken from top alpine skiers late in the competition season. These athletes include strenuous strength training as part of their off-season training. Our subjects in series 1 had included two 6 week periods with intense resistance-training in the months before their competition period, and during these periods they gained maximal muscle strength. Normally subjects lose strength during the weeks and months after such a training period. However, separate tests have shown that our subjects lost no strength during the competition period (Hans Blattmann, personal communication). Thus, regular alpine skiing at the highest level may be an adequate stimulus for maintaining the maximal leg
muscle strength. Our data further suggest that this training may also maintain a high Na-K pump concentration.

The Na-K pump and performance

We found that the increase in muscle endurance during the training period correlated with the change in pump concentration. If the pump is of critical importance for muscle endurance, one would have expected an even clearer relationship between muscle endurance and pump concentration, but that was not found. We found no relationship before the training period. After the training period we saw a weak relationship but only after three outliers were excluded. Random errors could have masked a possible relationship, but if so, these random effects would presumably have been more pronounced on the observed differences during the training period than on the scores per se. An alternative explanation is that there was a common underlying factor that was responsible both for the increase in muscle endurance and for the increased pump concentration in response to training. It has in line with this been shown that if a transcription factor like myogenin is overexpressed in transgenic mice, the activity of several enzymes is upregulated or downregulated in parallel (Hughes et al. 1999). It could therefore be that strenuous strength training through a common genetic mechanism leads to upregulation of both the Na-K pump concentration and factors important for muscle endurance. Our study gives no answer as to which factors are important for muscle endurance.

Does the power of the Na-K pump limit muscle performance during exercise?

Intense electric activity in muscle cells has been shown to lead to an extracellular accumulation of potassium (Vyskocil et al. 1983) that could lead to a depolarisation block. The Na-K pump is the only known enzyme that can actively restore the potassium balance and thus prevent the problem. If the maximal pumping power of the protein is exceeded during strenuous exercise, it may limit the performance. In vitro studies have shown that a high extracellular potassium concentration or a reduced pump power leads to a reduced muscle force, while a raised pump power has been found to delay fatigue (Juel 1988; Clausen and Everts 1991). It has therefore been proposed that an insufficient pump power leading to extracellular accumulation of potassium may be a cause of muscle fatigue (for a review, see Clausen and Nielsen 1994).

Each pump may be able to remove around 100 μmol K⁺ · s⁻¹ · kg⁻¹ wet muscle mass. As detailed elsewhere (Evertsen et al. 1997) the peak rate observed in real life may be only one-third of that (Medbø and Sejersted 1990). During less extreme activities the pump rate may be only 15% of its maximum (Hällén et al. 1994). Thus, the pump seems to have a large reserve pumping power that may not be needed even during intense activities. The calculations above should be viewed with some caution since possible local variations in the pump concentration or in the potassium accumulation have not been considered. However, even when using the lowest pump concentration seen in more than 200 biopsies measured in our laboratory, the calculated elimination rate of extracellular potassium is less than 50% of the maximum. Possible variations in the extracellular potassium accumulation are more difficult to evaluate quantitatively. However, data from exercise experiments too suggest that extracellular potassium does not limit the performance. Human subjects have been shown to be able to exercise at a high intensity even with a plasma potassium concentration above 8 mmol · l⁻¹ (Medbø and Sejersted 1990). While the plasma potassium concentration has been found to recover within 1 to 2 min (Hermansen et al. 1984; Medbø and Sejersted 1990), recovery of muscle function is much slower.

Methodological considerations

There were 3 subjects who showed very high pump concentrations that may or may not be methodological artefacts. We used robust statistical methods that should have minimized the influence of gross errors. Thus, a few possible wild values would not have affected our conclusions.

Our subjects trained at most three times a week during the training period. Nevertheless, that training was felt as being very demanding, particularly for the subjects in group 3 who trained three times a week. Some of these subjects reported a muscle soreness that was maintained between each training session during the later stages of the training period. It could be that they became overtrained and that this may have caused a smaller development of the pump concentration. Despite this possible reaction, these subjects increased their maximal muscle strength, suggesting that any cell damage was minimal. We chose eccentric resistance exercise as the means of training because that may be the most efficient way of raising the muscle strength further in already well-trained subjects (Refsnes, to be published).

Our interpretation of the Na-K pump data and the leg muscle strength should be taken with some caution. The pump concentration was measured on biopsies from the knee extensor muscle. This is only one of several muscles working during a squat lift. It cannot be ruled out that different muscles active during a squat lift developed differently and that this may have masked a
systematic relationship between muscle strength or endurance and the pump concentration. However, if so, one would not expect a relationship between the increase in muscle endurance and the increase in the pump concentration either.

Conclusions

Strenuous strength training may increase the Na-K pump concentration by 15% in well-trained athletes. The pump concentration was not related to maximal muscle strength or endurance. The increase in the subjects’ score on the muscle endurance test correlated positively with the increase in the pump concentration.

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