

# Association between regional differences in muscle activation in one session of resistance exercise and in muscle hypertrophy after resistance training

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**Abstract** The purpose of this study was to examine if the regional difference in muscle hypertrophy after chronic resistance training is associated with muscle activation after one session of resistance exercise. Twelve men performed one session of resistance exercise of elbow extensors. Before and immediately after the exercise, transverse relaxation time (T<sub>2</sub>)-weighted magnetic resonance (MR) images of upper arm were recorded to evaluate the muscle activation along its length. In the MR images, T<sub>2</sub> for the pixels within the triceps brachii muscle was quantified. The number of pixels with T<sub>2</sub> greater than the threshold (mean + 1SD of T<sub>2</sub> before the exercise) was expressed as the ratio to the number of pixels occupied by the muscle (%activated area). Another 12 subjects completed 12 weeks of training intervention (3 days per week), which consisted of the same program variables as used in the experiment for the T<sub>2</sub> measurement. The cross-sectional areas of the triceps brachii before and after the training intervention were measured from MR images of upper arm. The %activated

area of the triceps brachii induced by one session of the exercise was found to be significantly lower in the distal region than the middle and proximal regions. Similarly, the relative increase in muscle cross-sectional area after the 12 weeks of training intervention was significantly less in the distal region than the middle and proximal regions. The results suggest that the regional difference in muscle hypertrophy after chronic resistance training is attributable to the regional difference in muscle activation during the exercise.

**Keywords** Transverse relaxation time · Magnetic resonance image · Cross-sectional area · Triceps brachii muscle

## Introduction

Chronic resistance training induces an increase in muscle size (hypertrophy). The extent of hypertrophy is, reportedly, not uniform within a muscle along its length (Blazevich et al. 2007; Housh et al. 1992; Kanehisa et al. 2002; Kawakami et al. 1995; Melnyk et al. 2009; Narici et al. 1989; 1996; Roman et al. 1993; Seynnes et al. 2007; Smith and Rutherford 1995; Tracy et al. 1999). Narici et al. (1989) demonstrated that the relative increase in cross-sectional area (CSA) of the quadriceps femoris muscle, after 60 days of isokinetic knee extension training, was highly prominent in the proximal region and less prominent in the regions toward the knee. They also found that the relative increase in the muscle CSA was nonuniform for each head of the quadriceps femoris muscle. Although the underlying mechanisms for the nonuniform muscle hypertrophy remain unclear, the phenomenon might be explained by a regional difference in muscle activation during the resistance exercise (Narici et al. 1996). If the activation level

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during a given session of resistance exercise is higher in a certain region of a muscle than other regions, hypertrophy after chronic resistance training can be prominent in that region. However, there is little evidence that supports the assumption.

Immediately after a brief, high-intensity exercise, brightness of the agonist muscle in a magnetic resonance (MR) image increases (Adams et al. 1992; Fleckenstein et al. 1989; Shellock et al. 1991). This change can be quantified as an increase in the transverse relaxation time (T2) of the muscle. The increase in T2 of a muscle is related to the exercise intensity (Adams et al. 1992; Fisher et al. 1990), the number of repetitions of exercise with a given load (Yue et al. 1994) and the electrical activity of the muscle [integrated electromyogram (iEMG)] (Adams et al. 1992). In addition, the increase in T2 of the medial gastrocnemius muscle after a calf-raise exercise was different along the proximal–distal direction; the T2 increase was greater in the distal than in the proximal region (Kinugasa et al. 2005). In that study (Kinugasa et al. 2005), the iEMG during the calf-raise exercise was also greater in the distal region of the medial gastrocnemius than in the proximal region. These findings indicate that the quantification of the exercise-induced increase in T2 within a muscle is suited to evaluate the regional difference in muscle activation.

If the nonuniform muscle hypertrophy along its length after chronic resistance training is induced by the region-specific muscle activation during the exercise, it is hypothesized that the regional difference in the increase in muscle CSA after chronic resistance training corresponds to that in T2 increase after one session of the same exercise. The purpose of the present study was to test this hypothesis.

## Methods

### Study design

The triceps brachii muscle was selected for this study because of its high responsiveness to resistance training in size (Kawakami et al. 1995, 2006; Wakahara et al. 2010). The following two experiments were performed for the muscle. In the experiment I, acute changes in T2 of the muscle were investigated immediately after one session of resistance exercise. In the experiment II, an intervention program consisting of the resistance exercise used in the experiment I was applied for 12 weeks and chronic effect on the muscle CSA was examined.

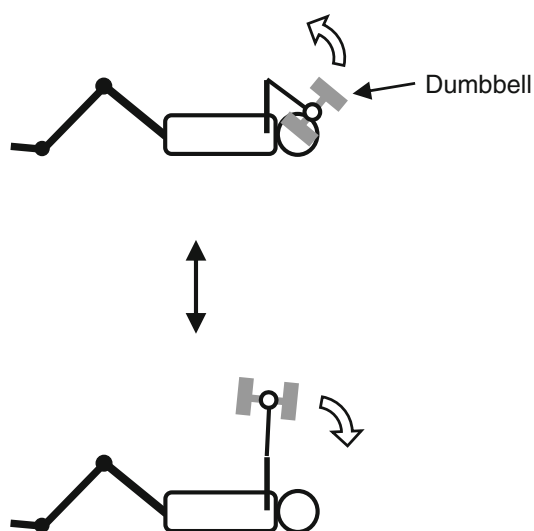
### Experiment I: acute effects of resistance exercise

Twelve healthy young men ( $25.2 \pm 3.0$  years,  $172.8 \pm 5.0$  cm,  $65.3 \pm 7.8$  kg; mean  $\pm$  SD) voluntarily participated

in the experiment I for examining the acute effects of resistance exercise. They were physically active, but had not participated in a regular resistance training program for the upper extremity for at least 6 months before the experiment. They were informed of the purpose and risks of the experiment and provided written informed consent. Each subject was instructed to refrain from drinking alcohol from 24 h before MR image recordings. The present study was approved by the human research ethics committee of the Faculty of Sport Sciences, Waseda University.

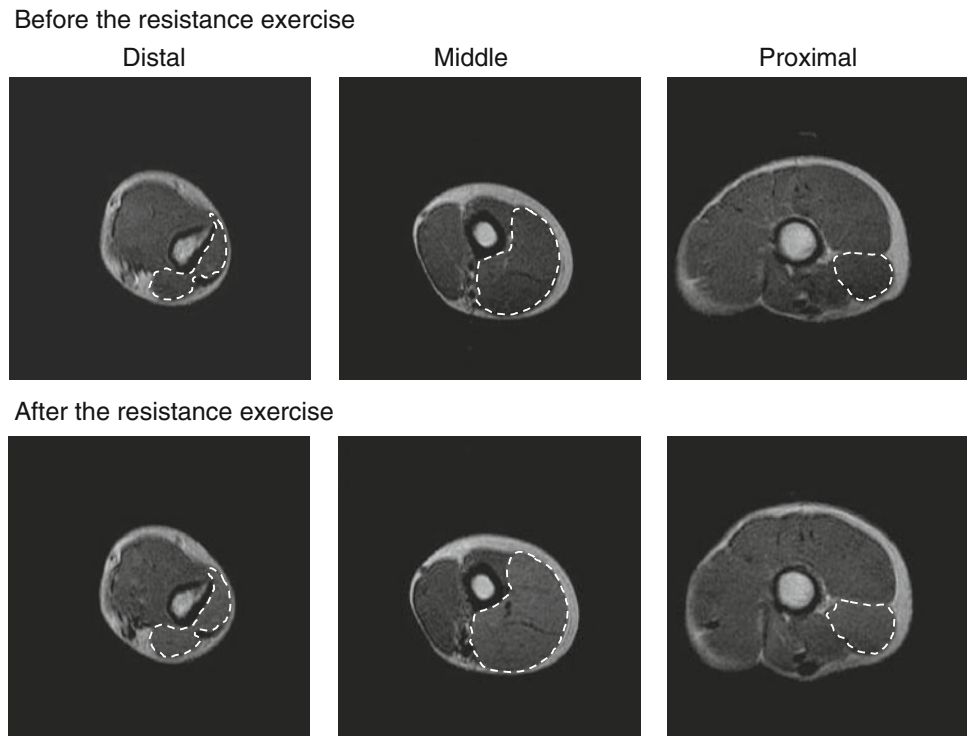
The subjects performed one session of “lying triceps extension” exercise (Fig. 1). They lay supine with the shoulder flexed at 90° and the examiner stabilized the upper arm by supporting the elbow. Each subject was then instructed to extend the elbow concentrically (for 2 s), and then flex eccentrically (for 2 s) with a dumbbell in his hand. The mass of the dumbbell was adjusted to 80% of one repetition maximum (1RM). The 1RM of the exercise was measured 2–4 days before the measurement of T2 to minimize potential effects of contractions in the 1RM test on the T2. One session of the resistance exercise consisted of five sets of eight repetitions. A rest period of 90 s was provided between the sets. These program variables (duration of contraction, load and number of sets and repetitions) were the same as those of Kawakami et al. (1995), who reported remarkable hypertrophy (32% increases in muscle volume) for the triceps brachii muscle after 16 weeks of resistance training.

Before and immediately after the resistance exercise, T2-weighted MR images of the upper arm (Fig. 2) were obtained with an MR scanner (Signa 1.5T, GE, USA). The subjects lay prone in a bore of the scanner. Ink marks on the



**Fig. 1** Schematic illustrations of the “lying triceps extension” exercise. The subjects concentrically extend, and then eccentrically flexed the elbow with a dumbbell in the hand

**Fig. 2** Examples of T2-weighted MR (magnetic resonance) images at distal (6 cm from the elbow joint), middle (16 cm from the elbow joint) and proximal (26 cm from the elbow joint) regions of the upper arm before (*upper*) and after (*lower*) one session of resistance exercise



surface of upper arm aligned with crosshairs of the scanner allowed for similar positioning for the repeated scans. The images were acquired with following parameters; echo times 25, 50, 75, 100 ms, repetition time 2,000 ms, matrix  $256 \times 256$ , field of view 180 mm, slice thickness 10 mm, gap 10 mm. The time from completion of the exercise to initiation of the scanning was  $72 \pm 21$  s. In each MR image, the outline of the triceps brachii muscle was traced to determine the CSA using a software package (Image J, National Institute of Health, USA). Care was taken to exclude noncontractile tissues such as intramuscular fat and blood vessels. The T2 for each pixel within the triceps brachii was calculated, and its mean value was computed for each slice. Within the triceps brachii region, the number of pixels with a T2 greater than the threshold (mean + 1SD of T2 before the exercise) was determined and expressed as the ratio to the total number of pixels of the muscle CSA (%activated area) (Adams et al. 1993). A total of 13 images from 4 to 28 cm from the elbow joint were analyzed. For each head (long, medial and lateral heads) of the triceps brachii muscle, an area of approximately  $100 \text{ mm}^2$  was selected in the middle of the CSA in each slice and then the %activated area of the head was calculated. Not the entire CSA, but a small region of head was arbitrary selected for this computation because the boundaries between heads were not clearly visible in several slices. The %activated area of each head was calculated as the ratio of the number of pixels with the T2 greater than the threshold to the total number of pixels within the area. The above analyses were

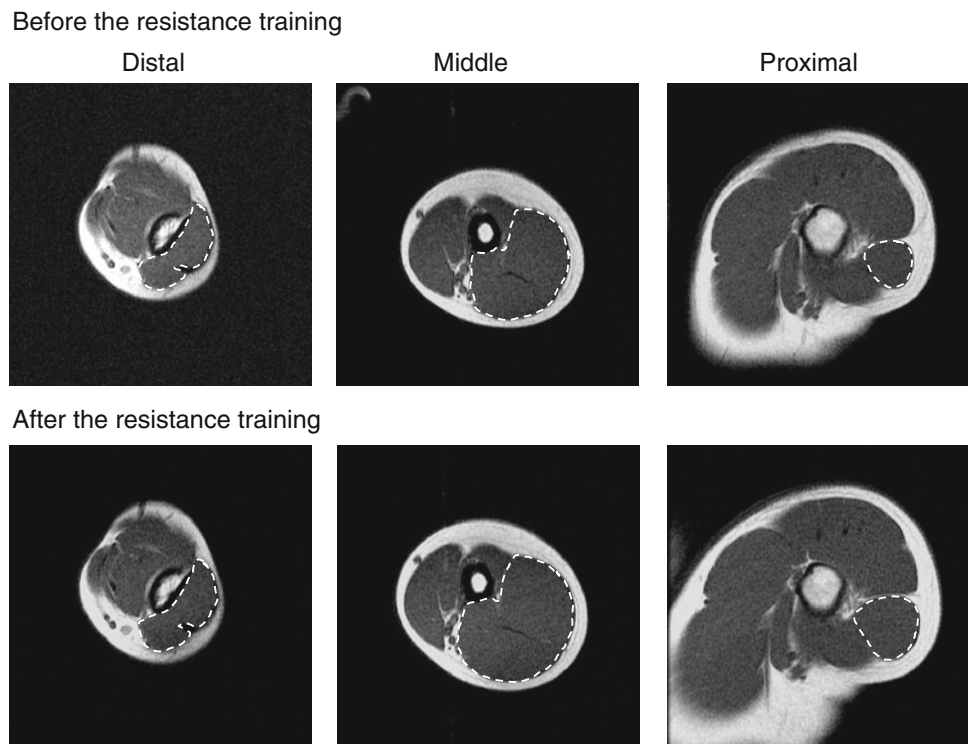
performed two times for each slice, and an averaged value was used for further analysis. The coefficient of variation (CV) of the two measurements for the %activated area was  $0.3 \pm 0.3\%$ . The intraclass correlation coefficient (ICC) of the measurements was higher than 0.999.

One-way analysis of variance (ANOVA) with repeated measures was used to analyze the effects of region (13 regions) on the %activated area of the triceps brachii muscle. For the %activated area of each head, one-way ANOVAs with repeated measures were performed to analyze the main effects of region (long head: ten regions, medial head: seven regions, lateral head: three regions). Two-way ANOVA with repeated measures was conducted to test the main effects of head (three heads) and region (three regions) on the %activated area of each head at 12–16 cm from the elbow joint where all heads could be analyzed. The ANOVAs were followed by post hoc comparisons with Bonferroni correction. Statistical significance for each analysis was set at  $P < 0.05$ .

#### Experiment II: chronic effects of resistance training

Nineteen healthy men participated in this intervention study. They were physically active, but had not participated in a regular resistance training program for the upper extremity for at least 6 months before the initiation of the experiment. They were informed of the purpose and risks of the experiment and provided written informed consent. Twelve men ( $26.3 \pm 3.7$  years,  $172.3 \pm 5.3$  cm,  $71.6 \pm 7.4$  kg) completed 12 weeks

**Fig. 3** Examples of T1-weighted MR (magnetic resonance) images at distal (6 cm from the elbow joint), middle (16 cm from the elbow joint) and proximal (26 cm from the elbow joint) regions of the upper arm before (*upper*) and after (*lower*) the chronic resistance training



(3 days per week) of resistance training (36 sessions). The period and frequency of the training intervention were determined from previous findings that 8–16 weeks of resistance training at a frequency of 3 days per week induced sufficient increases (more than 10%) in the CSA and/or volume of the triceps brachii muscle (Housh et al. 1992; Kanehisa et al. 2002; Kawakami et al. 1995). The other seven men ( $26.9 \pm 3.9$  years,  $172.1 \pm 5.5$  cm,  $65.5 \pm 6.3$  kg) were allocated to the control group. The training session consisted of the same program variables as in the experiment I. The 1RM was measured every 2 weeks to adjust the training load throughout the period. All training sessions were supervised and controlled by the examiners. Both groups of subjects maintained their dietary habits during the control or intervention period. All subjects were instructed to refrain from drinking alcohol from 24 h before MR image recordings.

T1-weighted MR images (Fig. 3, echo time: 11 ms, repetition time 520 ms, matrix  $256 \times 192$ , field of view 180 mm, slice thickness 10 mm) of the upper arm were obtained before and after 12 weeks of the training. The CSAs of the triceps brachii were measured using an image analysis software package (SliceOmatic, Tomovision, Canada) in the 13 images that corresponded to the experiment I (4–28 cm from the elbow joint). The series of MR images of three subjects were analyzed two times to evaluate the reproducibility of the measurements. The CV of the CSA measurements was  $1.2 \pm 1.2\%$ . The ICC of the measurements was higher than 0.998.

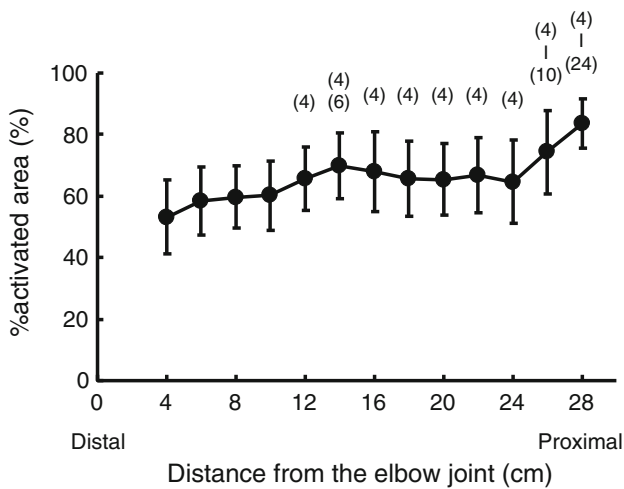
Paired *t* tests were used to test the significance of the difference in the mass of 1RM before and after the training intervention. Two-way ANOVA with repeated measures was used to analyze the effects of time (before and after the training) and region (13 regions) on the absolute values of muscle CSA. One-way ANOVA with repeated measures was used to analyze the effects of region (13 regions) on the relative change in CSA induced by the training. The ANOVAs were followed by post hoc comparisons with Bonferroni correction. Statistical significance for each analysis was set at  $P < 0.05$ .

## Results

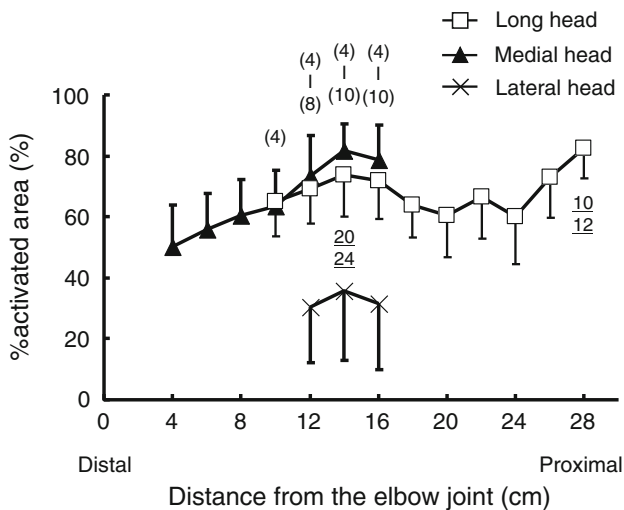
### Experiment I: acute effects of resistance exercise

The ANOVA revealed a significant main effect of the region on the %activated area of the triceps brachii (Fig. 4). The %activated area of the triceps brachii was significantly lower in the distal region than the proximal and middle regions.

The %activated areas of each head of the triceps brachii are shown in Fig. 5. The main effect of the region was significant for the long and medial heads, but not for the lateral head. For the long head, the %activated areas at 14 and 28 cm from the elbow joint were significantly higher than several other regions. The %activated area of the medial head was increased proximally toward the shoulder. Significant main effects of the head and region with no



**Fig. 4** The %activated area of the triceps brachii muscle along its length induced by one session of the resistance exercise. The number in parentheses indicates the position (distance from the elbow joint), where a significant difference was found

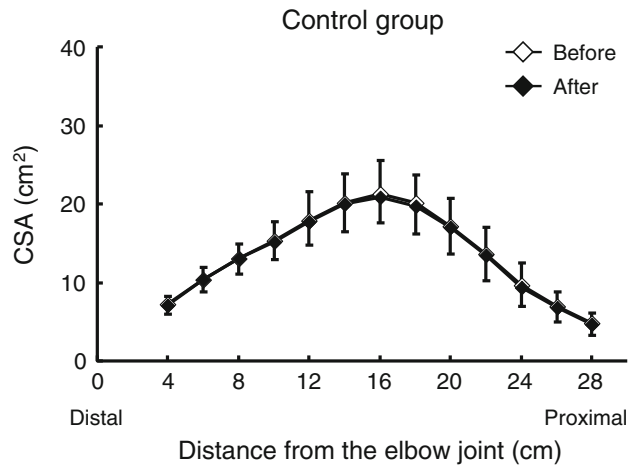
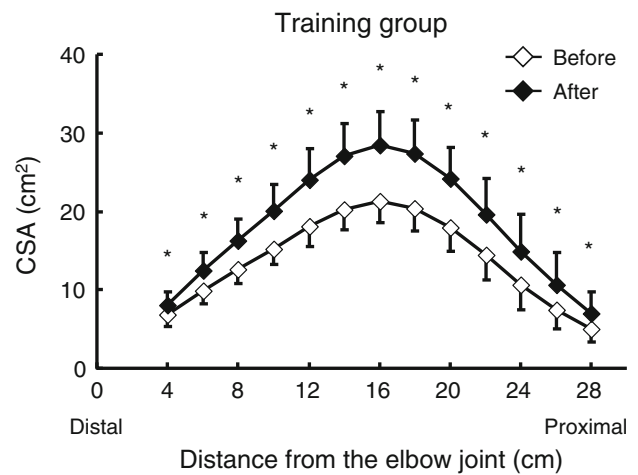


**Fig. 5** The %activated area of each head of the triceps brachii muscle along its length induced by one session of the resistance exercise. The numbers with underline and in parentheses denote the position (distance from the elbow joint), where a significant difference was found in the %activated area of the long and medial heads, respectively

interaction were found for the %activated areas of each head at 12–16 cm from the elbow. In those regions, the %activated area of the lateral head was significantly lower than that of the long and medial heads.

**Experiment II: chronic effects of resistance training**

Following the training intervention, the dumbbell mass of 1RM of the exercise significantly increased from  $11.0 \pm 2.0$  to  $17.3 \pm 2.9$  kg. This corresponded to a relative increase of  $58 \pm 26\%$ .

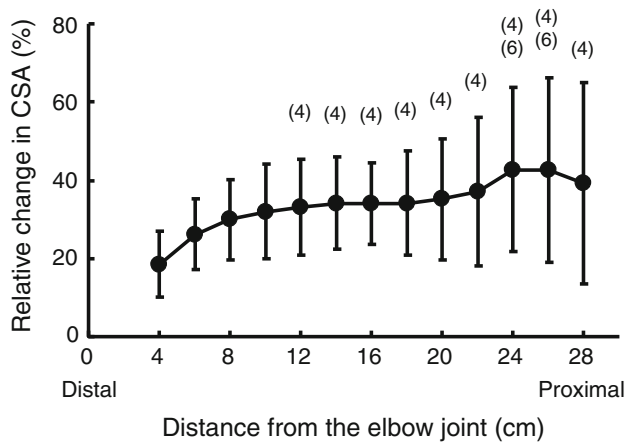


**Fig. 6** Distribution of the CSA (cross-sectional area) of the triceps brachii muscle in the training (upper panel) and control (lower panel) groups. Asterisk denotes a significant difference between before and after the training

Figure 6 shows the distribution of CSA of the triceps brachii muscle along its length before and after the intervention period. In the training group, significant main effects of time and region on the CSA were found with a significant interaction between the two factors. The CSAs were increased significantly throughout the entire length of the muscle. Relative change in CSA significantly differed among the regions (Fig. 7). The relative change in CSA in the distal region was significantly less than the middle and proximal regions. In the control group, no significant differences were observed in the CSA measured before and after the same period.

**Discussion**

The present study demonstrated that both the %activated area induced by one session of resistance exercise and the relative increase in CSA after 12 weeks of resistance training



**Fig. 7** Relative change in CSA (cross-sectional area) of the triceps brachii muscle along its length induced by training intervention. The number in parentheses indicates the position (distance from the elbow joint), where a significant difference was found

were lower in the distal region of the triceps brachii than the middle and proximal regions. The result supports the hypothesis that the regional difference in the increase in muscle CSA after chronic resistance training corresponds to that in T2 increase after one session of the exercise. Although the physiological mechanism for the exercise-induced T2 increase in the MR image has not been fully understood, many previous studies indicated that the T2 increase reflected the extent of muscle activation (Adams et al. 1992; Fisher et al. 1990; Kinugasa et al. 2005; Yue et al. 1994). Thus, our data suggest that the region-specific muscle hypertrophy after chronic resistance training is attributable to the regional difference in muscle activation during the exercise.

The %activated area induced by one session of the resistance exercise was found to be nonuniform within the triceps brachii muscle (Fig. 4). This could be attributed to the inter- and intra-head differences in the %activated area. In the middle region, the %activated areas of the lateral head were lower than the other heads. Buchanan et al. (1986) recorded the intramuscular EMG from the three heads of the triceps brachii during isometric contractions of the elbow in different directions. In their results, the EMG of the lateral head was lower when the force was exerted in the pure elbow extension direction compared with the combination of the elbow extension and humeral internal rotation (varus). On the other hand, the EMG of the long and medial heads during the pure elbow extension was greatest or similar to the greatest value among the directions. The resistance exercise was performed in the pure extension direction in the present study, which could be the reason for the lower %activated areas of the lateral head than the other heads. Within the head, the %activated areas of the medial and long heads increased toward their proximal ends

(Fig. 5). Nonuniform increase in T2 was also demonstrated within the medial and lateral gastrocnemii (Giordano and Segal 2006; Kinugasa et al. 2005; Segal and Song 2005) and the rectus femoris (Akima et al. 2004) muscles. As a possible explanation for the nonuniform change in T2, these studies suggested the existence of neuromuscular compartments (anatomical subdivision of a muscle according to the architecture, innervation and/or histochemical composition, Segal et al. 1991). To our knowledge, no study has ever confirmed the existence of the neuromuscular compartments within the heads of the triceps brachii. However, if such compartmentalization exists within the same head, it might be a reason for the observed intra-head differences in the %activated areas of the medial and long heads. Further research is needed to clarify this point.

Another factor that should be considered for interpreting the present results is the possible difference in the muscle fiber type composition within the triceps brachii. For the human triceps brachii muscle, the percentage of the type II fibers was reported to be about 60% for the long and lateral heads and about 40% for the medial head (Elder et al. 1982). It has been shown that the increase in T2 induced by high-intensity exercise is affected by the muscle fiber type (Prior et al. 2001). The T2 increase in the rat triceps surae muscle after a nerve stimulation was higher in the gastrocnemius, which consists predominantly of type II fibers, and lower in the soleus, which consists mainly of type I fibers (Prior et al. 2001). It should be noted that, at 12–16 cm from the elbow joint, the %activated area of the medial head was higher than the lateral head (Fig. 5). Thus, the data on the %activated area did not correspond to the difference in the muscle fiber composition among heads (Elder et al. 1982). On the other hand, several studies (Aagaard et al. 2001; Harber et al. 2004; Kuno et al. 1990; MacDougall et al. 1980) found a greater hypertrophy in the type II fibers than in the type I fibers after chronic resistance training. Hence, the relatively small increase in the CSA in the distal region (Fig. 7) might be related to the lower percentage of type II fiber of the medial head (Elder et al. 1982), which accounted for the major part of the triceps brachii CSA in this region. The prominent increase in the CSA in the proximal region might be due to the higher percentage of type II fiber in the long head, which occupied almost all of the CSA in this region. Even if the fiber type composition is not so markedly different among the three heads, the difference would, at least in part, contribute to the region-specific muscle hypertrophy after the chronic resistance training.

Training-induced hypertrophic pattern of the triceps brachii muscle along its length differed among the previous studies (Housh et al. 1992; Kanehisa et al. 2002; Kawakami et al. 1995). Housh et al. (1992) demonstrated that the triceps brachii CSA increased significantly in the proximal

and middle regions, but not significantly in the distal region after concentric training with an isokinetic machine. In their results, the relative increase in the CSA was greatest in the middle region among the three regions examined. Kanehisa et al. (2002) found the significant hypertrophy only in the middle regions of the triceps brachii after isometric elbow extension training. Kawakami et al. (1995) showed significant increases in CSA in the middle regions after “french press” training. Although they did not calculate relative increases in the CSA for each slice, it could be read from the graph of absolute values of CSA (Fig. 2 in their study) that the relative increase in the CSA was greater in the proximal region than the distal region. Therefore, the hypertrophic pattern in Kawakami et al. (1995) was similar to that of the present study. The training exercise of the present study (lying triceps extension) is very similar to the french press exercise except for the shoulder joint angle. In addition, the program variables of the training (load, contraction time, sessions per week and number of sets and repetitions) in the present study were the same as that of Kawakami et al. (1995). The similarity of the training exercise with the same program variables may result in the similar pattern of muscle hypertrophy between the two studies.

We found the similar region-specific changes in T2 increase induced by one session of resistance exercise and muscle hypertrophy after 12 weeks of resistance training. The findings raise a possibility that region-specific muscle hypertrophy following a few months of resistance training can be predicted from T2 changes induced by just one session of resistance exercise. Such a prediction would be beneficial for athletes who want to increase a specific region of a muscle (e.g., bodybuilders). However, it remains to be studied whether the correspondence between the T2 and hypertrophic changes can be extrapolated to other populations (athletes), exercise modes and muscles.

In the present study, the %activated area and CSA were determined at the same absolute distance from the elbow joint. Therefore, the relative distance to the upper arm length was not the same for all the subjects. However, coefficient of variation of humerus length (distance from the most proximal to distal ends in the MR images) was 3.3 and 5.7% for the Experiment I and II, respectively. Such low variations in humerus length should not alter the main results of the present study.

## Conclusion

The present study demonstrated that the regional difference in T2 increase induced by one session of resistance exercise within the triceps brachii muscle was similar to that in muscle hypertrophy after 12 weeks of resistance training. The results suggest that nonuniform muscle hypertrophy after

chronic resistance training is attributable to the region-specific muscle activation during the exercise used.

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**Conflict of interest** None of the authors have a conflict of interest.

## References

- Aagaard P, Andersen JL, Dyhre-Poulsen P, Leffers AM, Wagner A, Magnusson SP, Halkjaer-Kristensen J, Simonsen EB (2001) A mechanism for increased contractile strength of human pennate muscle in response to strength training: changes in muscle architecture. *J Physiol* 534:613–623
- Adams GR, Duvoisin MR, Dudley GA (1992) Magnetic resonance imaging and electromyography as indexes of muscle function. *J Appl Physiol* 73:1578–1583
- Adams GR, Harris RT, Woodard D, Dudley GA (1993) Mapping of electrical muscle stimulation using MRI. *J Appl Physiol* 74: 532–537
- Akima H, Takahashi H, Kuno SY, Katsuta S (2004) Coactivation pattern in human quadriceps during isokinetic knee-extension by muscle functional MRI. *Eur J Appl Physiol* 91:7–14
- Blazevich AJ, Cannavan D, Coleman DR, Horne S (2007) Influence of concentric and eccentric resistance training on architectural adaptation in human quadriceps muscles. *J Appl Physiol* 103:1565–1575
- Buchanan TS, Almdale DP, Lewis JL, Rymer WZ (1986) Characteristics of synergic relations during isometric contractions of human elbow muscles. *J Neurophysiol* 56:1225–1241
- Elder GC, Bradbury K, Roberts R (1982) Variability of fiber type distributions within human muscles. *J Appl Physiol* 53:1473–1480
- Fisher MJ, Meyer RA, Adams GR, Foley JM, Potchen EJ (1990) Direct relationship between proton T2 and exercise intensity in skeletal muscle MR images. *Invest Radiol* 25:480–485
- Fleckenstein JL, Bertocci LA, Nunnally RL, Parkey RW, Peshock RM (1989) Exercise-enhanced MR imaging of variations in forearm muscle anatomy and use: importance in MR spectroscopy. *AJR Am J Roentgenol* 153:693–698
- Giordano SB, Segal RL (2006) Leg muscles differ in spatial activation patterns with differing levels of voluntary plantarflexion activity in humans. *Cells Tissues Organs* 184:42–51
- Harber MP, Fry AC, Rubin MR, Smith JC, Weiss LW (2004) Skeletal muscle and hormonal adaptations to circuit weight training in untrained men. *Scand J Med Sci Sports* 14:176–185
- Housh DJ, Housh TJ, Johnson GO, Chu WK (1992) Hypertrophic response to unilateral concentric isokinetic resistance training. *J Appl Physiol* 73:65–70
- Kanehisa H, Nagareda H, Kawakami Y, Akima H, Masani K, Kouzaki M, Fukunaga T (2002) Effects of equivolume isometric training programs comprising medium or high resistance on muscle size and strength. *Eur J Appl Physiol* 87:112–119
- Kawakami Y, Abe T, Kuno SY, Fukunaga T (1995) Training-induced changes in muscle architecture and specific tension. *Eur J Appl Physiol Occup Physiol* 72:37–43
- Kawakami Y, Abe T, Kanehisa H, Fukunaga T (2006) Human skeletal muscle size and architecture: variability and interdependence. *Am J Hum Biol* 18:845–848
- Kinugasa R, Kawakami Y, Fukunaga T (2005) Muscle activation and its distribution within human triceps surae muscles. *J Appl Physiol* 99:1149–1156

- Kuno S, Katsuta S, Akisada M, Anno I, Matsumoto K (1990) Effect of strength training on the relationship between magnetic resonance relaxation time and muscle fibre composition. *Eur J Appl Physiol Occup Physiol* 61:33–36
- MacDougall JD, Elder GC, Sale DG, Moroz JR, Sutton JR (1980) Effects of strength training and immobilization on human muscle fibres. *Eur J Appl Physiol Occup Physiol* 43:25–34
- Melnyk JA, Rogers MA, Hurley BF (2009) Effects of strength training and detraining on regional muscle in young and older men and women. *Eur J Appl Physiol* 105:929–938
- Narici MV, Roi GS, Landoni L, Minetti AE, Cerretelli P (1989) Changes in force, cross-sectional area and neural activation during strength training and detraining of the human quadriceps. *Eur J Appl Physiol Occup Physiol* 59:310–319
- Narici MV, Hoppeler H, Kayser B, Landoni L, Claassen H, Gavardi C, Conti M, Cerretelli P (1996) Human quadriceps cross-sectional area, torque and neural activation during 6 months strength training. *Acta Physiol Scand* 157:175–186
- Prior BM, Ploutz-Snyder LL, Cooper TG, Meyer RA (2001) Fiber type and metabolic dependence of T2 increases in stimulated rat muscles. *J Appl Physiol* 90:615–623
- Roman WJ, Fleckenstein J, Stray-Gundersen J, Alway SE, Peshock R, Gonyea WJ (1993) Adaptations in the elbow flexors of elderly males after heavy-resistance training. *J Appl Physiol* 74:750–754
- Segal RL, Song AW (2005) Nonuniform activity of human calf muscles during an exercise task. *Arch Phys Med Rehabil* 86:2013–2017
- Segal RL, Wolf SL, DeCamp MJ, Chopp MT, English AW (1991) Anatomical partitioning of three multiarticular human muscles. *Acta Anat (Basel)* 142:261–266
- Seynnes OR, de Boer M, Narici MV (2007) Early skeletal muscle hypertrophy and architectural changes in response to high-intensity resistance training. *J Appl Physiol* 102:368–373
- Shellock FG, Fukunaga T, Mink JH, Edgerton VR (1991) Acute effects of exercise on MR imaging of skeletal muscle: concentric vs eccentric actions. *AJR Am J Roentgenol* 156:765–768
- Smith RC, Rutherford OM (1995) The role of metabolites in strength training. I. A comparison of eccentric and concentric contractions. *Eur J Appl Physiol Occup Physiol* 71:332–336
- Tracy BL, Ivey FM, Hurlbut D, Martel GF, Lemmer JT, Siegel EL, Metter EJ, Fozard JL, Fleg JL, Hurley BF (1999) Muscle quality. II. Effects of strength training in 65- to 75-yr-old men and women. *J Appl Physiol* 86:195–201
- Wakahara T, Takeshita K, Kato E, Miyatani M, Tanaka NI, Kanehisa H, Kawakami Y, Fukunaga T (2010) Variability of limb muscle size in young men. *Am J Hum Biol* 22:55–59
- Yue G, Alexander AL, Laidlaw DH, Gmitro AF, Unger EC, Enoka RM (1994) Sensitivity of muscle proton spin–spin relaxation time as an index of muscle activation. *J Appl Physiol* 77:84–92