

Distribution of Muscle Fiber Conduction Velocity of M. Biceps Brachii During Voluntary Isometric Contraction with Use of Surface Array Electrodes

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Abstract. Surface electromyogram (EMG) was recorded in m. biceps brachii during the contractions of 20, 40 and 60% of maximum voluntary isometric contraction (MVC) in twelve healthy male subjects, using surface array electrodes. The distribution of muscle fiber conduction velocity (MFCV) was found directly using the averaging technique and the cross-correlation function technique. MFCVs in the region of 20~45 mm measured from end-plate denoted constant value of about 4 m/s in 20% MVC, while MFCVs in the region around end-plate and tendons showed about 10 m/s in 20% MVC. The values of MFCV depended on the contraction levels of muscle. The model for the generation of MFCV which considered the ensemble of muscle fibers with the shape of a cone was proposed. The theoretical values of MFCV by the muscle fiber ensemble model (MFE model) proposed in the paper showed in good agreement with the experimental results.

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Keywords: muscle fiber conduction velocity, voluntary isometric contraction, m. biceps brachii, surface array electrodes, muscle fiber ensemble model.

Introduction

The muscle fiber conduction velocity (MFCV) is the velocity of interference wave in the group of muscle fiber action potentials propagated from motor end-plate zone to both tendons. The methods of measuring muscle fiber action potential are divided by (a) contraction type of muscle (i.e., voluntary contraction or electric stimulation), (b) electrode (surface electrode or needle electrode). Several procedures for the evaluation of MFCV have been performed by the following four techniques: a) dip frequency technique (Lindstrøm et al., 1970), b) zero-crossing technique (Lynn, 1979), c) averaging technique (Nishizono et al., 1979), and d) cross-correlation function technique (Nishizono et al., 1979) were proposed. A detailed explanation was reviewed by Arendt-Nielsen and Zwarts (1989). The results of MFCV

of m. biceps brachii by various procedures are presented in Table 1. Many studies of MFCV have been performed especially for m. biceps brachii.

The first study of MFCV was performed by Denslow and Hassett (1943), who presented 24 measurements from human arm muscle of normal subjects by voluntary contraction. MFCV was determined from recording of motor unit (MU) potentials with two needle electrodes 0.7~7 cm apart along the direction muscle fibers. 24 values of MFCV were widely spread between 1.3 m/s and 12.5 m/s with the mean value of 4.95 m/s. No consideration was taken regarding the site of the end-plate in relation to recording electrodes. An attempt to reinvestigate these results was investigated by Buchthal et al. (1955a) who recorded the MU potentials of m. biceps brachii with three needle electrodes in the location except for the end-plate and tendon. MFCV varied between 3.3 and 5.2 m/s, and the average velocity and the standard deviation (SD) was 4.02 ± 0.13 m/s. Buchthal et al. (1955b) also measured MFCV in the location of motor end-plate zone in m. biceps brachii with six concentric needle electrodes. They reported that the conduction velocity of the action potential by voluntary effort varied over a narrow range, and that the mean value of MFCV was 4.7 m/s with SD value of 1.3 m/s. The value of MFCV did not so much depend on the location measured on muscle. Stålberg (1966) estimated MFCV of 12 healthy male subjects in m. biceps brachii during voluntary contraction. The value of MFCV was 3.69 ± 0.71 m/s. Thus, MFCV in m. biceps brachii found by Stålberg (1966) was 22% lower than that of the MU spike potentials studied by Buchthal et al. (1955b).

The first report by noninvasive method in the estimation of conduction velocity was based on a dip frequency technique (Lindstrøm et al., 1970) with use of surface electrode. Then, Lynn (1979) proposed a zero-crossing technique accompanied by bandpass digital filter preprocessing and determined MFCV of m. biceps brachii with surface array electrodes. Resultant value of MFCV ranged from 3.2 to 5.3 m/s with mean and standard deviation of 4.34 ± 0.61 m/s. They reported that the relationship between MFCV and the contraction force

Table 1 Estimation of MFCV in m. biceps brachii by various procedures

Condition of contraction	MFCV range (m/s)	MFCV mean $\pm$ SD (m/s)	Electrode and Procedure	Authors
Voluntary contraction	1.3–12.5	5.0 $\pm$ 2.8	Two needles (arm muscle)	Denslow and Hassett (1943)
	3.7–5.9	4.7 $\pm$ 0.5	Six needles, direct	Buchthal et al. (1955b)
	2.0–3.7	3.7 $\pm$ 0.7	One needle, multielectrode	Stålberg (1966)
	3.5–4.8		Surface, dip frequency analysis	Lindstrøm et al. (1970)
	3.2–5.3	4.3 $\pm$ 0.6	Surface, zero-crossings	Lynn (1979)
	4.2–5.5	4.6 $\pm$ 0.5	Surface, averaging and cross-correlation	Nishizono et al. (1979)
	1.1–6.7	3.8	Multielectrode needle, cross-correlation	Yaar et al. (1980)
		4.2	Surface, zero-crossings	Masuda et al. (1982)
		4.4 $\pm$ 0.4	Surface, cross-correlation	Naeije and Zorn (1983)
	4.1–4.3		Surface, zero-crossings	Sadoyama et al. (1983)
	2.0–7.1	4.1 $\pm$ 1.0	Multielectrode needle, cross-correlation	Yaar et al. (1984)
	3.9–5.0	4.4 $\pm$ 0.4	Surface, cross-correlation	Hilfiker and Meyer (1984)
	3.9–5.6	4.6 $\pm$ 0.6	Surface, cross-correlation	Eberstein and Beattie (1985)
	3.4–3.5		Surface, zero-crossings	Masuda et al. (1986)
		5.0	Surface, phase detection	Hunter and Kearney (1987)
		3.8 $\pm$ 0.4	Surface, cross-correlation	Yamada et al. (1987)
Electrical stimulation		4.6 $\pm$ 0.3	Surface, cross-correlation	Zwarts et al. (1988)
			Surface, averaging	Kossev et al. (1991)
		3.5 $\pm$ 0.5	Surface, cross-correlation	Yamada et al. (1991)
		4.4 $\pm$ 0.3	Surface, cross-correlation	Matunaga et al. (1993)
	3.3–5.2 variations	4.0 $\pm$ 0.5	3–5 needles, muscle fiber	Buchthal et al. (1955a)
			Multielectrode needle	Stålberg (1966)
	3.0–6.0	4.2 $\pm$ 0.6	Needles, muscle fiber	Hopf (1973)
		3.8 $\pm$ 0.3	Needles, muscle fiber	Troni et al. (1983)
			1 cycle/sec	
	2.8–5.5		Needles, muscle fiber	Kereshi et al. (1983)
		5.1 $\pm$ 0.8	Needles, muscle fiber	Chino et al. (1984)
		3.7 $\pm$ 0.3	Surface, single motor axon	Nishizono et al. (1989)
			1 cycle/sec	

was not found during voluntary isometric contraction, and that MFCV decreased during sustained contraction. Also, other authors reported that the average MFCV declined during local muscle fatigue: m. biceps brachii reported by Naeije and Zorn (1982; 1983) and Sadoyama et al. (1983), and m. vastus lateralis by Arendt-Nielsen and Mills (1988). At low contraction levels, MFCV was found to increase during prolonged contraction (Arendt-Nielsen and Mills, 1988), possibly due to the recruitment of motor units with higher conduction velocities: that is, the motor unit conduction velocity was confirmed to denote a size principle parameter by Andreassen and Arendt-Nielsen (1987), who reported that the larger motor unit gives higher value of conduction velocity as compared with the conduction velocity for smaller motor unit. In all these studies, surface EMG methods were used to obtain MFCV. An important aspect, dealt with in some of the papers concerning muscle fatigue is that the relationship between the shifts of MFCV and the power spectrum was found (Naeije and Zorn, 1982; Sadoyama et al., 1983; Eberstein and Beattie, 1985). It

was also found that MFCV increased when the force of voluntary contraction increased (Naeije and Zorn, 1982; Sadoyama et al., 1983; Arendt-Nielsen et al., 1984; Sadoyama and Masuda, 1987; Zwarts et al., 1988). The notion that the augmentation is due to the high conduction velocity of larger motor units recruited at high contraction levels was supported by the study of Andreassen and Arendt-Nielsen (1987). MFCV has been expected to be a new index to estimate the function of human muscle.

On the other hand, the estimates of MFCV are very unstable in the same muscle. For example, the first study of MFCV (Denslow and Hassett, 1943) reported that MFCV ranged widely from 1.3 to 12.5 m/s during voluntary contraction in human arm muscle. Gydikov et al. (1976) measured the conduction velocity of motor unit action potential at different locations with monopolar and bipolar surface electrodes in m. triceps surae, m. gastrocnemius lateralis, and m. gastrocnemius medialis. They reported that MFCVs near the end-plate and the tendon of the muscle showed very a high value and that

MFCV at a different location on the same muscle showed a different value. Yaar et al. (1984) obtained MFCV during maximum voluntary isometric contraction in m. biceps brachii, using one multielectrode needle with neighbour recording separated by 1 cm. The value of MFCV was estimated by cross-correlation technique and it ranged widely from 1.09 to 6.7 m/s (mean 3.8 m/s). Sollie et al. (1985) determined the conduction velocity of m. biceps brachii with surface array monopolar electrode. They explained that if the electrodes are placed too close to the motor end-plate zone or the tendons, high values of conduction velocity was unexpectedly found during voluntary isometric contraction. Roy et al. (1986) investigated the effect of surface electrode location on the estimate of the conduction velocity in tibialis anterior muscle. They reported that large values of MFCV were found at the distal tendon in 8 out of 10 subjects. Also, they reported that MFCVs in different locations of different electrode on the same muscle were not constant. In the studies, MFCV shows large variations and this explains the reason that MFCV is not used extensively in clinical practice. Many authors except for Denslow and Hassett considered MFCV to be a constant value at various locations on one muscle, and have not reported clearly the relation between MFCV and the location measured.

In the present study, our main purpose is to investigate MFCV at different locations on m. biceps brachii during voluntary isometric contraction with surface array electrodes. Our aim is to make the distribution of MFCV located on the muscular surface clearly, that is to show that MFCV depend on the location measured. The other aim is to obtain the relation between MFCV

and the degree of voluntary contraction. Moreover, the mechanism of generation of MFCV in ensemble of muscle fibers are proposed, in which the group of muscle fibers is considered to be of the cone shape, i.e., the end-plate has a large cross section of muscle fibers and the tendon has a small cross section.

Method

Subjects and experimental procedure

Twelve healthy male volunteers, ranging from 22 to 33 years, served as subjects. All subjects were informed prior to experiment. Subjects were seated on a chair. The elbow joint was maintained at right angle as shown in the experiment system of Fig. 1. All experiments were performed under isometric contraction. The maximum voluntary isometric contraction (MVC) was taken as the largest value of 3 brief maximal contractions done at an interval more than 20 minutes.

MFCVs were evaluated from the motor unit potentials detected by array electrodes at 5 different zones on m. biceps brachii as shown in Fig. 2. The subjects were asked to keep a target line displayed on the oscillograph and maintain the torque for 30 seconds at a given percentage of MVC. The location of myoneural junctions (end-plate) was reasonably determined from the shape of the propagating potentials wave before starting the experiment (see the section of Data analysis). The preliminary experiments were performed on a different day. All experiments were performed under room temperature of 22~24°C and skin temperature of 30~33°C.

EMG recording

The surface array electrodes used in this study were composed of six stainless steel wires, with a diameter of 1 mm and a length of 10 mm. These were arranged on a flexible gum board (15×40 mm) and were used as longitudinal surface array electrode. The stainless steel wires were positioned parallel to each other with an inter-electrode spacing of 5 mm as shown in Fig. 3. They were assembled by referring to the design of Lynn (1979) and Masuda et al. (1983). During data acquisition, the array electrodes were placed perpendicularly to the direction of underlying muscle fibers. The gum plate was molded to fit the muscle shape and the electrode wires were then attached directly to the skin surface with approximately uniform pressure. The attachment of the array electrodes was not pasted to the skin. In the present study, the array electrodes were positioned on the surface of m. biceps brachii (caput breve) in the right arm. Myoelectric potential was derived by the use of differential amplifiers for each adjacent pair of electrodes as shown in Fig. 3. The frequency range of each bioelectric amplifier was set from 5.3 Hz to 1 KHz. Before the experiment, the skin was lightly abraded with sand

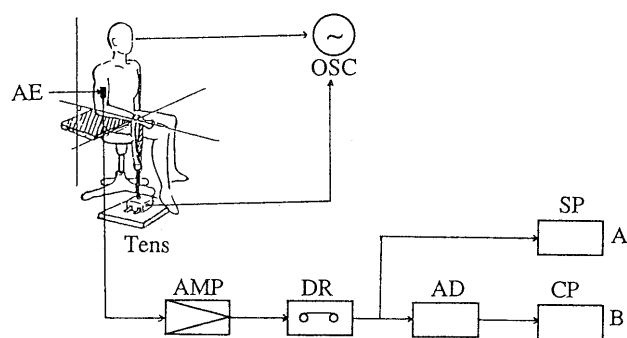


Fig. 1 Experimental system.

AE: Array electrode.

AMP: amplifier (NEC San-ei, BIOELECTRIC AMPL-4124).

DR: data recorder (SONY, PC-108M).

AD: DC amplifier (NEC, AD-641G).

CP: mini-computer (NEC, PC-9801DA).

SP: signal processor (NEC San-ei, 7T17).

OSC: oscillograph (Iwasaki, HIOKI 3251).

Tens: sensor of tension (Shinkoh, Type-U3B1).

A: averaging technique.

B: cross-correlation function technique.

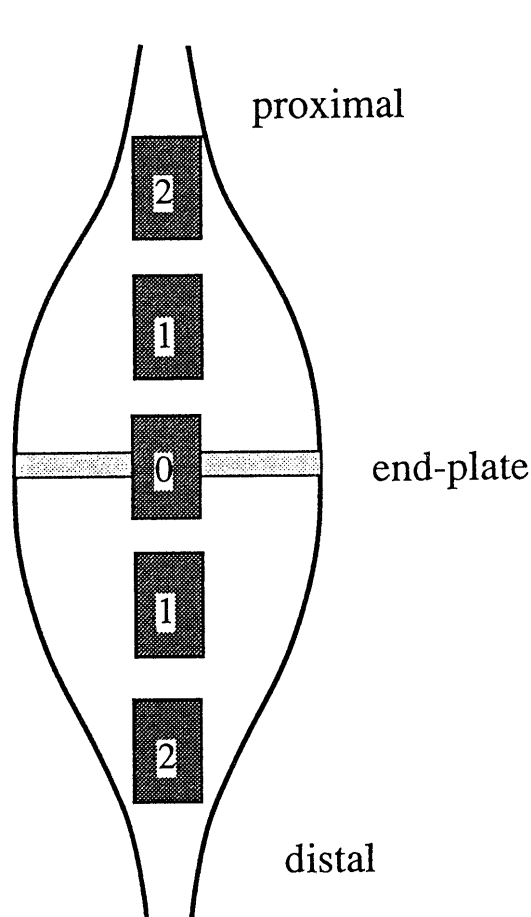


Fig. 2 Array electrodes were placed on the surface of the skin in one location of 5 different locations on m. biceps brachii, and was placed perpendicular to the direction of muscle fiber. Location 0 includes end-plate, location 1 is the position between the end-plate and proximal tendon or the position between the end-plate and distal tendon, location 2 means the position near proximal tendon or the position near distal tendon.

paper and then cleaned with alcohol. The myoelectric analog signals were stored into data recorder as shown in Fig. 1.

Data analysis

After recording the muscle fiber action potential, MFCV was calculated using the analytical techniques of both the averaging technique and the cross-correlation function technique.

In the averaging technique, recorded EMG signals were analyzed by signal processor (Fig. 1). Myoelectric signals were presented by the use of a triggered averaging program based on motor unit action potential as shown in Fig. 4. The channel of amplifier for the determination of the trigger level was used to be the number 1 in Fig. 3. The position of channel 1 in array electrode always pointed to the proximal side in the five locations

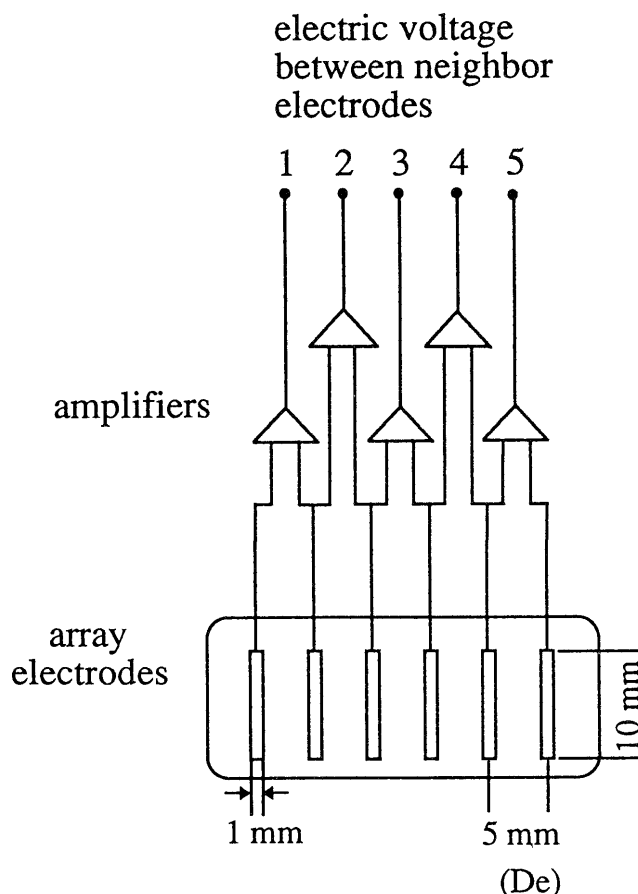


Fig. 3 Schematic diagram of array electrodes connected to the amplifiers. The electric potential between adjacent electrodes was amplified. The ground terminals for respective amplifiers were connected commonly to the earth.

used as in Fig. 2. The trigger level was decided around the maximum action potential in the force set by % MVC for the array electrode put at the location of distal side and around the minimum one at that of proximal side. As for the array electrode on the end-plate, the trigger level was taken as around the minimum. The signal processor in the analysis detected the trigger level only in the descending time series of the action potentials as shown in Fig. 4.

The existence of end-plate could be estimated from the example shown in Fig. 4(a), in which the peaks of action potentials around end-plate became inverse to each other, because the action potential propagate to both tendons and the direction of propagation was opposite. To detect the conduction delay between adjacent electrodes, we digitized the surface EMGs with 0.012 ms sampling from 1024 data points. The surface EMG signals were superimposed 200 times in order to detect clearly the position peak action potential. The total time required for the computer-assisted processing was 2.5 sec. The time delay was evaluated by the time

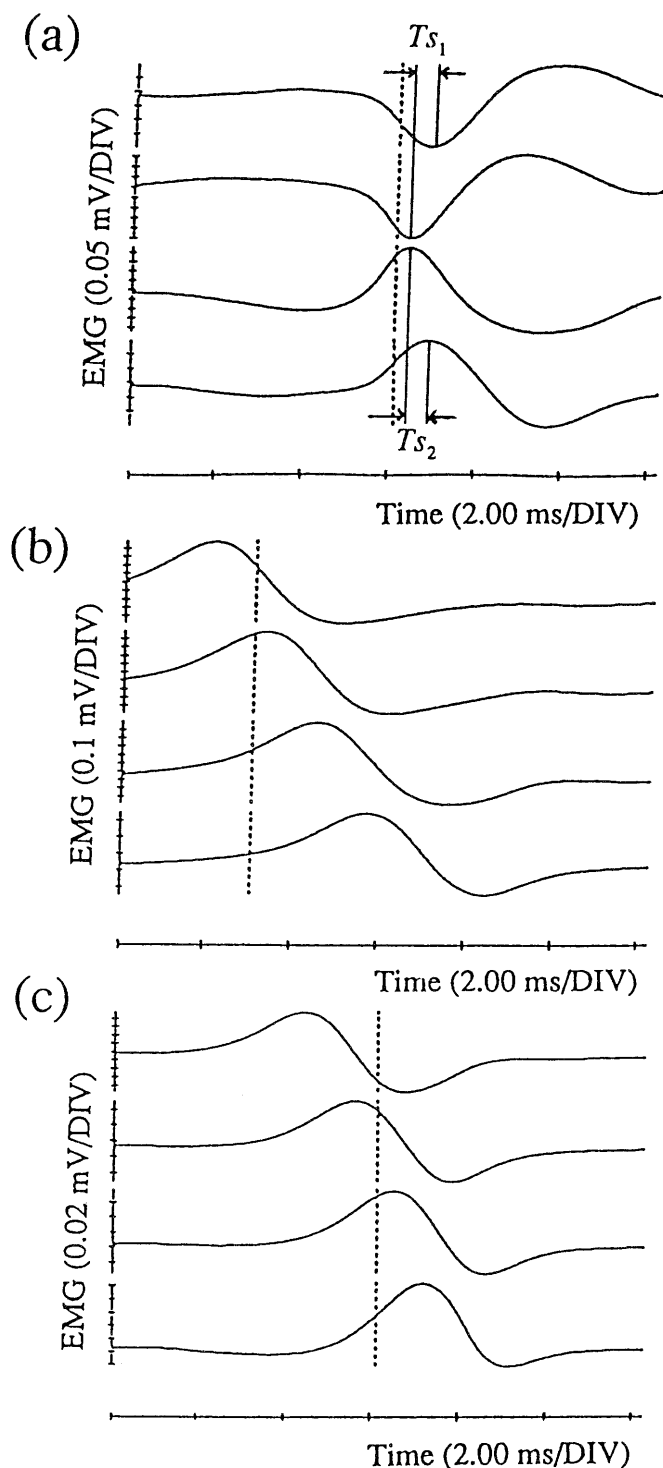


Fig. 4 Examples of averaging muscle fiber action potential. Averaged myoelectric signals at 3 different locations in 20% MVC: (a) location of end-plate, (b) location 1 in distal side, (c) location 2 in distal side. The clear differences in the time delay are shown. The end-plate was estimated between the positions of action potential peaks with the opposite sign to each other in (a) by way of example. The perpendicular dash line in each figure means trigger point for the top curve.

difference for peaks of action potentials of respective channels by averaging technique as shown in Fig. 4. MFCV could be calculated using the time shift (T_s) and the distance (De) between electrodes.

$$MFCV = De / T_s \quad (1)$$

where De was taken to be the distance between any two channels taken. In the paper, the value of De between the neighbouring channels was 5 mm.

For the evaluation of T_s , the cross-correlation function for two action potentials of two channels was employed by equation (2).

$$R_{xy}(\tau) = (1/k) \int x(t+\tau) y(t) dt \quad (2)$$

where $x(t)$ was the EMG signal for one channel, $y(t)$ was one for other channel, was the time shift between $x(t)$ and $y(t)$, and k was the normalizing constant to place the correlogram between -1 and $+1$. Provided the electrode was positioned correctly, a high correlation between the two signals was obtained as shown in Fig. 5 (e.g., cross-correlation coefficient, $R_{xy} > 0.8$). The peak in the correlogram displaced from zero time is a time lag T_s reflecting the conduction time between the two channels. Thus, there were two ways to obtain T_s , but the values obtained were similar, so that averaging technique was employed in the paper.

Statistical analysis

The values of MFCV in different locations and different contraction levels (i.e., 20, 40, 60% MVC) for respective subjects were compared by t test with the paired data.

Results

The time shift T_s between action potentials for two channels was measured by the averaging technique. MFCVs were estimated from the difference in arrival time (T_s) of the motor unit potentials for electrodes by the distance separated (De), using equation (1). Resultant value of MFCV was not constant for the location measured: MFCV was found to depend on the location measured as shown in Fig. 6. MFCV also depend on the degree of the contractions as shown in Fig. 7. MFCVs near to the end-plate zone (i.e., $|Ld| \leq 5$ mm in Fig. 6) and both tendon zones (i.e., $|Ld| \leq 60$ mm in Fig. 6) gave large values of about 10 m/s. However, comparatively smaller and steady values of MFCV were obtained in the region of 20~45 mm measured from the motor end-plate zone. The values of MFCV seemed to be almost constant at the region. Minimum values were obtained in the region: The means and SD for MFCV in the flat region of 20~45 mm in 20% MVC were 4.13 ± 0.23 m/s for distal side region and 4.03 ± 0.23 m/s for proximal side region. The values obtained showed similar values which other

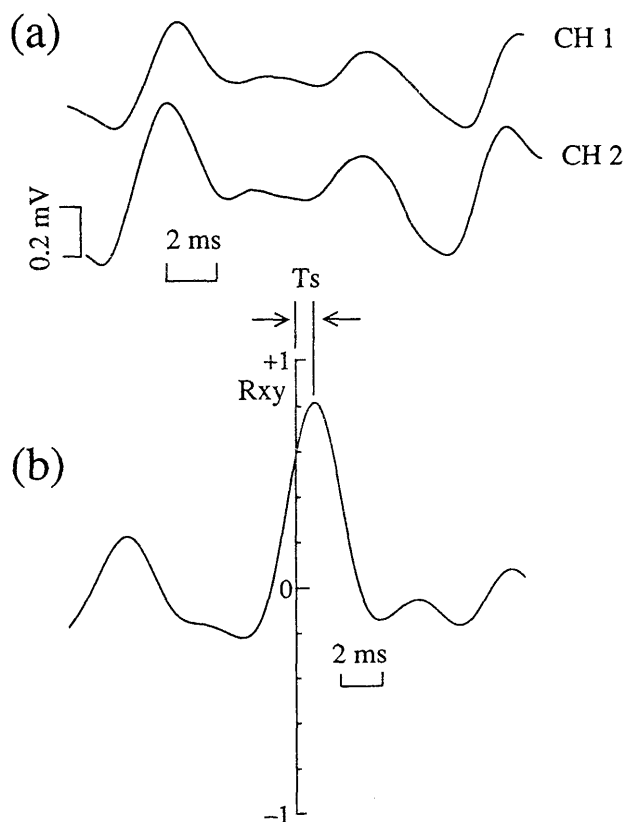


Fig. 5 Examples of surface-recorded EMGs (upper) from location 1 in distal side of m. biceps brachii during 20% MVC. (a) action potentials for two channels, (b) cross correlation of two EMG signals show a peak reflecting the time delay (T_s). R_{xy} is correlation coefficient.

authors gave as constant under various degrees of contraction as shown in Table 1. The distribution of MFCV was almost similar for both proximal and distal regions, but strictly it was not the same as shown in Fig. 6(a). The minimum and the maximum values of MFCV for other muscular contraction levels presented to be similar values as shown in Table 2. The feature of MFCV obtained is as follows. The value for both regions increased as the muscular contraction increased from 20% MVC to 60% MVC, but the increase rate was less than 10%. The value for distal region was greater than that for proximal region. On the other hand, the maximum value of MFCV was found around the end-plate as shown in Fig. 6. The maximum value also increased with the increase of muscular contraction. The maximum value around the end-plate in distal region side was larger than that in proximal region. The values of MFCV between neighbouring locations were significant by different in the region except for the flat region of 20~45 mm measured from the end-plate, so that MFCV was not constant for all the locations measured and MFCV indicated the distribution as shown in Fig. 6.

The maximum values of MFCV (9~10 m/s) were

near to the value 12.5 m/s which Denslow and Hassett (1943) obtained by the use of needle electrode. They, however, did not make the location measured clear. Many authors gave MFCV as constant value around 4~5 m/s as shown in Table 1, where the constant values did not depend on the condition of contraction, the kinds of electrode, and the analyzing technique. These results (Table 1) were close to the minimum MFCV for flat region as shown in Table 2.

MFCVs for some contraction level at the same location were compared with MFCV for other contraction levels as shown in Fig. 7. The values of MFCV between different contraction levels in all the region of proximal side gave similar values and were not significantly different, while for the values in distal region the significant difference was recognized around the flat region 20~45 mm measured from end-plate, and the quantitative difference was given as the minimum MFCV in Table 2.

The relation between MFCV and location (mm) measured from end-plate was obtained by multiple regression analysis. The relation could be evaluated empirically as an equation of the fourth degree:

$$MFCV = \sum_{i=0}^4 a_i x^i \quad (3)$$

The proportion of the relations was obtained to be 0.79~0.88 under various conditions of measured sides and muscular contraction levels. For example, for the relation of distal side and 20% MVC [see right side curve of Fig. 6(a)] MFCV (m/s) was calculated with the location (mm) measured from the end-plate.

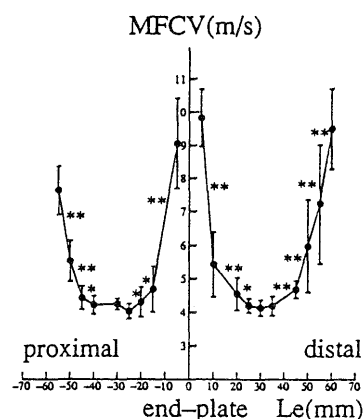
$$MFCV = 15.2 - 1.44x + 0.0667x^2 - 0.00132x^3 + 0.00000960x^4 \quad (4)$$

where respective regression coefficients were presented with the use of two significant figures. The proportion for the regression curve (4) was 0.80, and degree of freedom was 111.

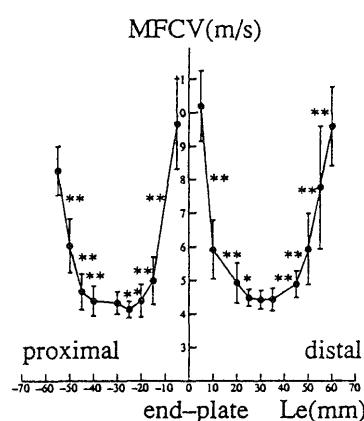
Discussion

Distribution of muscle fiber conduction velocity

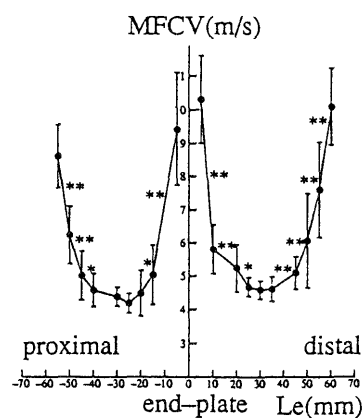
Muscle fiber action potential is generated at the motor end-plate zone (innervation zone) and then propagates to both tendons along the muscle fiber. Masuda et al. (1983) investigated the location of end-plate zone of m. biceps brachii during voluntary contraction by surface array electrodes. They found the end-plate zone was located on nearly the middle length of the muscle. In our paper, the end-plate was searched by the use of propagation wave form of action potential as shown in Fig. 4(a). When the sign of the peaks of action potential was inverse and the relation $T_{s1} = T_{s2}$ in Fig. 4(a) was obtained by moving the array electrodes along muscle fibers, it was estimated that the location of the end-plate



(a) 20%MVC



(b) 40%MVC



(c) 60%MVC

Fig. 6 Distribution of averaged MFCV during (a) 20%, (b) 40% and (c) 60% MVC for twelve subjects: The perpendicular line at each MFCV is SD. The significant difference between neighbouring MFCVs position was recognized. * and ** means statistical significant level of 5% and 1%, respectively. Le denotes the distance between end-plate and midpoint for bipolar electrodes. The measured mean length between proximal and distal side tendons for *m. biceps brachii* was 130.0 mm, so the mean length between the end-plate and tendon was 65.0 mm.

exactly existed between two electrode pairs (i.e., 5 mm). The location of end-plate was actually obtained around the middle point of the muscle.

The main purpose of our paper is to study MFCV at various location on the muscle. MFCVs in the paper were found to have the distribution from end-plate to both tendons as shown in Fig. 6, where the values of MFCV in the region 20~45 mm measured from end-plate denoted constant values and they were in good agreement with the past results of Lynn (1979), Naeije and Zorn (1983), Nishizono et al. (1989) and Yamada et al. (1991) (Table 1). In the past many investigators did not explain the experimental results for distribution of conduction velocity (Fig. 6). They treated MFCV as a constant value for all the location on the muscle for a long time (Table 1). One of the reasons that MFCV has a constant value is due to the use of the electrode with a long inter-electrode distance of more than 10 mm. Almost all the authors listed in Table 1 except for Hilfiker and Meyer (1984) and Masuda and Sadoyama (1986) employed such electrode. The authors who employed array electrodes with short inter-electrode distance also considered MFCV to be a constant value over muscle measured: Hilfiker and Meyer (1984) did not refer to MFCV to have the distribution of conduction velocity. Masuda and Sadoyama (1986) did not pay attention to the distribution of MFCV, because their aim was to look for the location of the end-plate. Examples of results of MFCV around the end-plate are shown in Fig. 8, in which Nishizono et al. (1979) used inter-electrode distance De of 20 mm which was larger than the value of 5 mm for array electrodes used here. There were small number of locations measured for De of 20 mm, so the relation between the location and time delay obtained were estimated to be roughly linear as shown in Fig. 8. On the other hand, in case of using array electrodes with short inter-electrode of De 5 mm, many points of T_s on muscle were measured, so that various values of MFCV were obtained. MFCV depended much on the location measured as shown in the present study of Fig. 8. The present study denoted that both the region around less than about 20 mm measured from the end-plate point and the region around the tendons of more than 45 mm gave larger values of MFCV (i.e., curves a, c, a', c' in Fig. 8) as compared with the values of MFCV in the region from 20 mm to 45 mm (i.e., lines b and b'). The region around 20 to 45 mm showed constant MFCV. It was recognized that the too narrow inter-electrode distance could detect the influence of interference of action potential waves.

Sollie et al. (1985) and Gydikov et al. (1976) reported large values of MFCV around end-plate and tendon. However, these reports did not insist the distribution of conduction velocity on the muscle measured.

Table 2 Minimum and maximum value of MFCV in various contraction levels*

Muscular contraction (%MVC)	Minimum MFCV (m/s)		Maximum MFCV (m/s)	
	distal region (mean±SD)	proximal region (mean±SD)	distal region (mean±SD)	proximal region (mean±SD)
20%	4.13±0.23	4.03±0.23	9.83±0.86	9.06±1.37
40%	4.42±0.33	4.12±0.25	10.12±1.05	9.66±1.35
60%	4.58±0.27	4.18±0.29	10.23±1.30	9.42±1.68

*Minimum and Maximum values of MFCV are obtained in the region of 20~45mm measured from end-plate and in the region around end-plate, respectively.

Model for generation of muscle fiber conduction velocity

In the past studies of model of the conduction velocity for muscle and nerve, the diameter D and internal resistance were treated as important factor (Katz, 1948; Hodgkin and Nakajima, 1972): The theoretical conduction velocity was proportional to square root of the diameter of muscle or nerve (D) per internal resistance (R_i) (Table 3):

$$\text{Conduction Velocity for muscle and nerve} \propto \sqrt{D/R_i} \quad (5)$$

In these derivations of conduction velocity, muscle fiber or nerve or these groups were treated as forming cylindrical shape. They did not considered collective effect for muscle fibers or nerves.

The cylinder does not display the actual shape of m. biceps brachii consisting of a gathering of muscle fibers, since the cross section around the end-plate for the actual muscle has the maximum area, while that around tendons has the minimum area. In the paper, the shape of muscle was treated as a cone (Fig. 9) in order to express actual shape of the muscle. All the physical quantities except for electron charge is treated as the function depended on the position x . Using the cone shape of muscle, the model to generate MFCV was considered as follows.

On the basis of electromagnetism, the current in the conductor $I(x)$ is the product of current density $J(x)$ and cross section at each different position of the conductor $S(x)$.

$$I(x) = J(x) \cdot S(x) \quad (6)$$

$J(x)$ is expressed by number of electron per unit volume $n_e(x)$, electron charge e , and velocity of electron $V_e(x)$:

$$J(x) = -n_e(x) \cdot e \cdot V_e(x) \quad (7)$$

The minus sign means that the direction of velocity of electron is opposite to the direction of current density. The velocity of electron $V_e(x)$ is also in proportion to the electric field $E(x)$ at x of the conductor,

$$V_e(x) = -\mu(x) \cdot E(x) \quad (8)$$

where $\mu(x)$ is mobility.

From the equations (7) and (8), current density $J(x)$ is

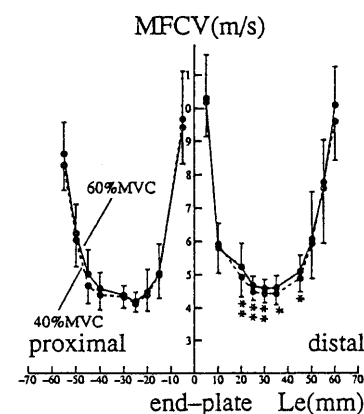
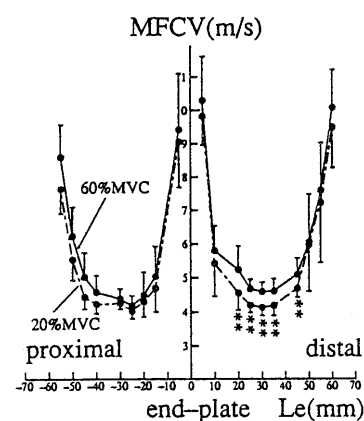
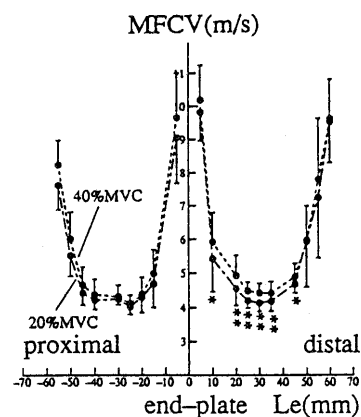


Fig. 7 Difference of MFCV in different contractions: The values of MFCV in flat regions 20~45 mm from end-plate increased when the contraction forces increased (---, 20% MVC; ---, 40% MVC; —, 60% MVC). * and ** means statistical significant level of 5% and 1%, respectively. Le denotes the distance between end-plate and midpoint for bipolar electrodes.

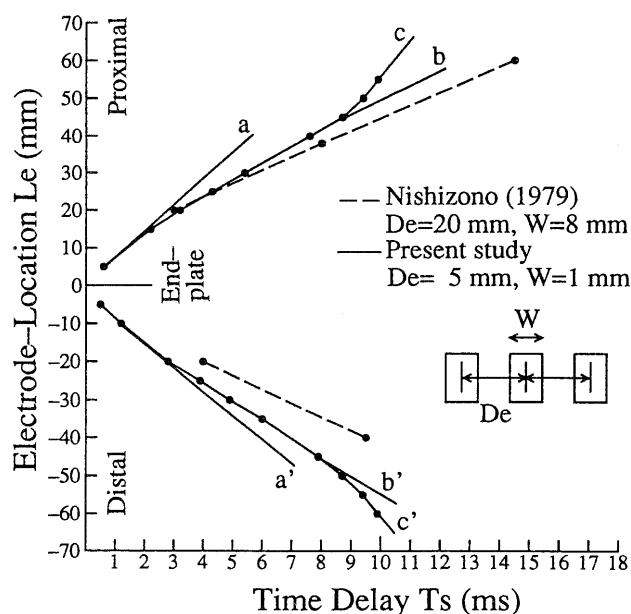


Fig. 8 Time delay of EMG measured around the end-plate in m. biceps brachii. De and W denote distance between neighboring electrodes and diameter of one electrode. a~c and a'~c' mean similar slopes (i.e. MFCV) for the inter-electrodes distance per time delay for the inter-electrodes distance; a sharp slope means a larger value of MFCV. As for Le, see Fig. 6.

obtained in equation (9)

$$J(x) = n_e(x) \cdot e \cdot \mu(x) \cdot E(x) = \sigma(x) \cdot E(x) \quad (9)$$

where $\sigma(x)$ is electric conductivity:

$$\sigma(x) = n_e(x) \cdot e \cdot \mu(x) \quad (10)$$

Using the equations (8) and (9),

$$\begin{aligned} V_e(x) &= -\mu(x) \cdot E(x) \\ &= -\frac{\mu(x) \cdot J(x)}{\sigma(x)} \\ &= -\frac{\mu(x) \cdot J(x) \cdot S(x)}{\sigma(x) \cdot S(x)} \\ &= -\frac{\mu(x) \cdot I(x)}{\sigma(x) \cdot S(x)} \end{aligned} \quad (11)$$

The equation (11) was employed as a model to study the mechanism of conduction velocity of muscle, that is, muscle is treated here to be a conductor. $V_e(x)$ is considered as MFCV. Moreover, the following two quantities, the numerator and the denominator in the equation (11), were supposed to be other useful functions: the numerator $-\mu(x) \cdot I(x)$ was in proportion to the cross section of muscle $S(x)$, x being the distance measured from the end-plate (Fig. 9), and the denominator $\sigma(x) \cdot S(x)$ was in proportion to electric energy which is presented by the function of position x , i.e., $f(x)$. Since the quantity $\sigma(x) \cdot S(x)$ denotes the degree of conductivity of electron in cross section at the position

Table 3 Conduction velocity for nerve and muscle

Author (year)	Conduction velocity (CV)
Katz (1948)	$CV = (S'D^{1/2}) / [(2R'_m)^{1/2} \cdot C_m \cdot (R_i)^{1/2}]$ S' safety factor D diameter R'_m active membrane resistance C_m membrane capacity R_i internal resistance
Hodgkin and Huxley (1952)	$CV = (K_a / (2R_2 C_M))^{1/2}$ K_a radius of axis cylinder ($= D/2$) R_2 specific resistance of axoplasm C_M capacity per area of membrane
Hodgkin and Nakajima (1972)	$CV = \frac{1}{2} \sqrt{R_2 k D G_1}$ G_1 internal conductivity ($1/R_2$) k parameter of membrane properties (e.g. $k = 30 \times 10^8 \Omega \text{cm}^2 / \text{sec}^2$)

The meaning of symbols is common to all the equations of CV listed. The form of fiber was considered to be a cylindrical model for CVs stated above.

x , it is considered that $\sigma(x) \cdot S(x)$ means the quantity like electric potential.

Around the end-plate, median power frequency is higher than that at the location 20 to 45 mm measured from the end-plate (Roy et al., 1986). The higher frequency was due to the interference of ensemble of the action potentials with time delay to generated from the end-plate region. The action potentials around the end-plate were also at a lower level as compared with the region of constant MFCV of about 4 m/s, because of the interference of the action potentials. The result was reported by Masuda and Sadoyama (1986) and Morimoto (1986). It should be noted that Masuda and Sadoyama (1986) presented the lower action potential around the end-plate for the case of the array electrodes stepping over the end-plate, while Morimoto (1986) showed the similar lower action potential for the case of the bipolar electrodes putting on the position between the end-plate and tendon without stepping over the end-plate. The action potentials around the tendons were also lower than that at the location with the constant MFCV, since the conductivity of tendon was lower as compared with the conductivity of the muscle fiber. The result was reported by Gydikov et al. (1976). The action potentials had the minimum values around both end-plate and tendon. Therefore, the quantity $\sigma(x) \cdot S(x)$ could be presented by $f(x)$ with the minimum value stated above.

Thus MFCV is expressed by the equation (12):

$$MFCV \equiv V_e(x) = \frac{S(x)}{f(x)} \quad (12)$$

It should be noted that the quantity MFCV meant the conduction velocity for ensemble of muscle fibers with the shape of a cone. The present procedure for m. biceps

brachii is called here as muscle fiber ensemble model (MFE model) with cone shape. In the model, it is supposed that the physical quantities in the cone indicate heterogeneous character, that is, they depend on the location x . In the muscle, there are various kinds of diameters of the section of muscle fiber, that is, the diameters distributed in the range of $30\sim 80\mu\text{m}$. The position of the junction of motor nerve for these muscle fibers are different, so that the action potentials in these muscle fibers have different phases from each other. Although MFCV for each muscle fiber depends on the diameter and has the constant value, the action potential observed consisted of the group of action potentials for respective muscle fibers. The resultant action potential was measured from the surface of skin on the muscle, and it was affected by the interference of respective action potentials and the volume conductance between the skin and respective muscle fibers. Therefore, the resultant MFCV was regarded as "appearance value of MFCV".

In the model, all the physical quantities treated here except for electron charge e were considered to be a function of x . The electrons which were generated by many generated muscle fibers at end-plate zone propagate to the direction towards tendons. The propagation of electrons around end-plate has different phase, so that the electric potential around the end-plate is considered to be low due to the interference. The electric potential in the tendon is low since the tendon has a scanty part of contraction component. The function of $f(x)$ presented as the electric energy is taken mathematically to be zero at both the end-plate ($x=0$) and the tendon ($x=h$), so the following function is employed.

$$f(x) = k_m \{x(h-x)\}^m \quad (13)$$

where m is order of x and $(h-x)$. Provided that k_m is a parameter with the dimension $L^{-(2m-1)} \cdot s$, the dimension of $f(x)$ becomes $L \cdot s$, where L and s mean the dimension of length and time.

$S(x)$ is obtained exactly from the cone model in Fig. 9:

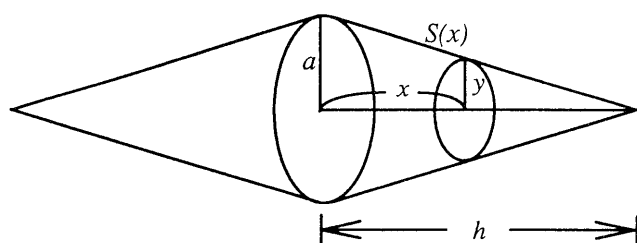


Fig. 9 Cone model for the generation of MFCV. a and h are the radius of cross section at end-plate (max. circle) and the distance between end-plate and tendon. x is the distance measured from end-plate. $S(x)$ is the area at x , and y is the radius of cross section at x .

$$S(x) = \pi (a/h)^2 \cdot (h-x)^2 \quad (14)$$

Therefore, MFCV is expressed by the above two equations.

$$MFCV = \frac{\pi (a/h)^2 \cdot (h-x)^2}{k_m \cdot \{x(h-x)\}^m} \quad (15)$$

The dimension of $S(x)$ is L^2 , so that the dimension of MFCV in equations (12) and (15) is presented to be L/s with the unit meter/second. Namely, the dimension of MFCV becomes to that of velocity. Expressing equation (15) by the ratio x/h , it is transformed to equation (16).

$$MFCV = \frac{\pi (a/h)^2 \cdot (h)^{2-2m} \cdot (1-\frac{x}{h})^2}{k_m \cdot \{\frac{x}{h} \cdot (1-\frac{x}{h})\}^m} \quad (16)$$

In order to fit the equation (16) to the experimental result, MFCV is taken to be 4 m/s at $x=h/2$ (i.e., constant region of MFCV) for the model calculation. In the case of $m=1$ and 2, MFCV denotes monotone decreasing function as shown in Fig. 10. These cases did not explain the experimental results of Fig. 6. However, for the case of $m=3$, when the value of x comes near to 0 (end-plate) or h (tendon), the values of MFCV come near to infinite. The theoretical result reflects the experimental result. These results for $m=1\sim 4$ are plotted in Fig. 10. As the value of parameter m increases, the shape of the theoretical function (16) approaches to the experimental result. For the case of $m=4$,

$$MFCV = \frac{4(\frac{1}{2})^6}{(\frac{x}{h})^4 \cdot (1-\frac{x}{h})^2} \quad (17)$$

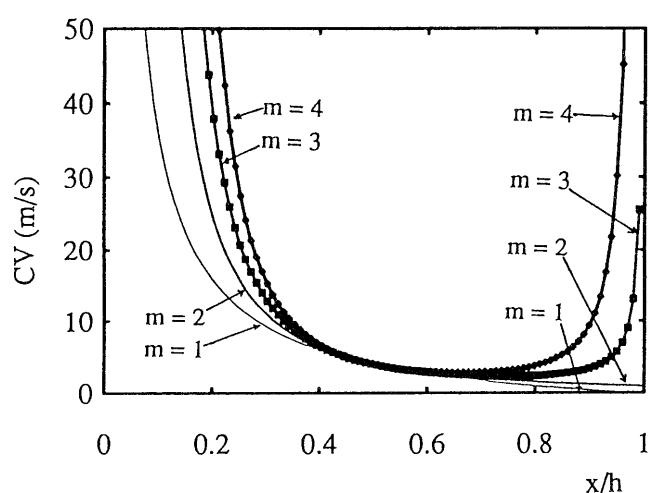


Fig.10 Theoretical curve of MFCV. m denotes order of x in function $f(x)$ [eq.(13) or (16)].

$$k_4 = \frac{\pi(\frac{a}{h})^2 \cdot (h)^{-6}}{4(\frac{1}{2})^6} \quad (18)$$

The parameter k_4 in the equation (18) is determined when MFCV at the region with the relation $x/h=1/2$ is taken to be 4 m/s. The theoretical curve for $m=4$ in Fig. 10 denotes the feature of experimental curve in Fig. 6. The complete fitting of model equation to experimental result is considered by taking different orders m_1 and m_2 for x and $(h-x)$ instead of m in the equation (16).

The conduction velocity for the cylindrical model which Katz (1948) and Hodgkin and Nakajima (1972) proposed was in inverse proportion to the square root of internal resistance R_i , and they treated the feature of many muscle fibers as that of single muscle fiber in the model while our model shows to be in inverse proportion to $\sigma(x) \cdot S(x)$ which is treated as the quantity to be in proportion to electric potential. Since there is the relation which $\sigma(x)$ is in reverse proportion to $R_i(x)$, it is estimated apparently that MFCV of the equation (15) gives the opposite tendency to equation (5) as $\sigma(x)$ increases. However, the denominator of equation (15) presents $\sigma(x) \cdot S(x)$ instead of $\sigma(x)$ and the quantity is the function of x and denote the quantity like electric potential. The experimental facts which the electric potential decreases at end-plate and tendon denotes the decrease of the denominator, so that the large value of MFCV at end-plate and tendon was obtained. In the muscle fiber region between the end-plate and tendon, it is considered that electric potential after interfering in end-plate propagates smoothly towards the tendon. The action potential in the region is assumed to be high as compared with the end-plate and tendon, so that MFCV denotes constant minimum value. The cone model could explain well to the experimental result of MFCV over the muscle. The difference of two equations (5) and (15) originates in the models taken and depends on the character of physical homogeneity for equation (5) or heterogeneity for equation (15) in ensemble of muscle fibers.

Relation between muscle fiber conduction velocity and degree of contraction

In the present study, the value of MFCV increased when the degree of the contraction of muscle increased, and the resultant values were in good agreement with the results of the previous studies (Naeije and Zorn, 1982; Sadoyama et al., 1983; Sadoyama and Masuda, 1987; Arendt-Nielsen et al., 1984; Zwarts et al., 1988). The increase of MFCV is due to the recruitment of muscle fibers by increase of contraction: The muscle fibers having higher level of contraction generate a larger conduction velocity. This function was supported by Andreassen and Arendt-Nielsen (1987).

The augmentation of MFCV in higher degree of contraction could also be explained in the proposed model: The increase of contraction results in the increase of both $S(x)$ and the action potential corresponding to $\sigma(x) \cdot S(x)$ due to the recruitment. The degree of increase of action potential is considered to be not so much duets the interference of action potentials. Since the charge of $S(x)$ is physical, the degree of increase is considered to be larger than the change of action potential. Therefore, it is considered that the value of MFCV in the equation (12) increases at a higher level of contraction.

It is found here that the value of MFCV depends on the location measured, so that in the measurement of MFCV the location of end-plate zone should be monitored by the action potential wave and the location measured from the end-plate should be pointed out clearly.

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