

Relation between the direction of mechanical action of muscles and muscle activation level in force vector regulation by the upper limb

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Relation between the direction of mechanical action of muscles and muscle activation level in force vector regulation by the upper limb

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ABSTRACT

In exploring the factor for determining muscle coordination, it is important to investigate the relation between the muscle activation level and the mechanical action of muscles. Although many researchers have proposed the relation between muscle activity and the mechanical action of muscles, it remains an unsettled question whether there is definite relation between muscle activity and mechanical actions of muscles. In the present study, we investigated these relationships by comparing electromyographic (EMG) activity during force vector regulation tasks in the upper limb in humans with the mechanical action of muscles in a mechanical model simulated human arm. In particular, we calculated the preferred direction of muscle activity using a cosine regression, which represented the direction of the largest EMG activity, and compared its direction with the mechanical pulling direction when the weight was hanged out to the wire corresponding to the muscle in the mechanical model. Our major findings are that the preferred direction of muscle activity in which the largest EMG activity level was obtained, did not coincide with the mechanical pulling direction of muscles. We propose a theoretical view based on the direction of the action force at the endpoint exerted by the muscle in order to explain about the factor of these non-coincided relationships, and suggest that the direction of mechanical action of muscles is represented by the action force of muscles at the endpoint, but that the preferred direction of muscle activity is directed by another factors.

KEY WORDS

Muscle coordination, Mechanical model, EMG activity, Force vector regulation, Cosine regression

Introduction

A fundamental problem is that human musculo-skeletal system has inherent redundancy which the number of muscles acting a joint exceed the number of degrees of freedom of the joint. Therefore, as for performing a goal-directed movement, it exists various combinations for selecting activation of available muscles. Despite this redundancy, it is well known that the human selects similar activation patterns of muscles in movement within and between subjects. The reasons why this phenomenon arises have been as-

sumed that anatomical or neurological constraints are posed in human in order to reproduce the similar activation patterns. In other words, to control a redundant set of muscles, it seems that the human is equipped with the selective mechanism on muscle activations to obtain the optimal muscle coordination.

With regard to previous studies in muscle coordination, Buchanan et al.¹⁾ reported that the direction of force for which the electromyographic (EMG) activity of a given muscle reached a maximum value corresponded closely to the direction of greatest mechani-

cal advantage of the muscles. Buneo et al.²⁾ found that the mechanical action of each muscle, which specify the spatial and temporal aspects of muscle activation, changed substantially with arm posture when this action was defined either in the frame of reference of the insertion or origin. However, these findings made more complicated by the observation by van Zuylen et al.³⁾ They reported that certain muscles were activated for forces in directions in which their mechanical advantage was zero. These reports give us many opinions with regard to muscle coordination. However, it remains an unsettled question whether there is the determining factor in muscle coordination on the relation between muscle activations and mechanical actions of muscles.

In this manuscript, to explore the determining factor on muscle coordination, we compare the relation between the direction of the largest EMG activity (preferred direction of muscle activity) during force vector regulation tasks in humans and the direction of the mechanical pulling action of muscles in a human-like mechanical arm model. We hypothesize that muscle coordination is based on mechanical actions of muscles, if the preferred direction of muscle activity coincided with the pulling direction of muscles.

Methods

1. Human experiment

Eleven male subjects participated in this study. Their mean age was 24.0 ± 3.4 (SD) yr ; their mean height and weight was 170.4 ± 3.9 cm, and 62.5 ± 5.4 kg, respectively ; their mean upper arm and forearm length was 31.3 ± 1.0 cm, and 27.3 ± 1.9 cm, respectively. All subjects were right-handed, and had no known history of musculoskeletal or neurological disorders. Informed consent was obtained from all subjects prior to participation in this study.

Subjects were seated in a wooden chair with the right arm abducted at shoulder height and supported by arm-suspension equipment (SPR-191, Sakai, Japan) in the horizontal plane. To restrict the movement of the shoulder location, subjects were strapped to the chair by two belts on the upper and lower trunk. The wrist joint of the subjects was fixed by a thermoplastic splint (Aquaplast, Smith+Nephew, UK). Subject's right hand was grasped a handle which equipped two-

axis load cell (LSA-A-300NSA30, Kyowa, Japan) to measure the force vector. The line passing through both shoulders and the line between the handle and the shoulder were set up to cross perpendicularly, and the distance between the handle and the shoulder was set up approximately 46~49 cm.

The exerted force vector by subjects was measured by two-axis load cell in the handle, and the magnitude and direction of the force vector were calculated from the magnitude of x-axis or y-axis of the force. The force vector was monitored on the display (FlexScan E76F, Nanao, Japan) in front of the subjects in a fashion of bar graph. Each subject was instructed to regulate the force vector while monitoring that bar graph in which the magnitude of the force was specified at 20 N and the direction of the force was specified at one of eight directions among 0, 45, 90, 135, 180, 225, 270, 315° (Fig. 1). The magnitude of the force at 20 N, used in the present study, decided it as reliable magnitude can be exerted in the horizontal plane from both previous results⁴⁾ and our preliminary experiment. The 0° direction correspond to the direction to the right side along the trunk. During the experimental task as the desired force vector was maintained for 5 sec period within the range between ± 5 N in the magnitude and $\pm 5^\circ$ in the direction, then we judged that for obtaining the successful experimental task. For every experimental task, a total of 8 trials (1 magnitude \times 8 direction) was completed by each subject, after tested a few practice.

EMG activity of primary six muscles of the upper limb were recorded using surface electrodes. The EMG signals were recorded from the pectoralis major muscle (PMA) as shoulder flexor and the posterior deltoid muscle (DEL) as shoulder extensor ; from the brachioradialis muscle (BRD) as elbow flexor and lateral head of the triceps brachii muscle (TLA) as elbow extensor ; from the biceps brachii muscle (BIC) as bi-articular flexor and long head of the triceps brachii muscle (TLO) as bi-articular extensor. After cleansing of the subject's skin with alcohol and electrode paste, Ag/AgCl electrodes (P-00-S, Medicotest, Denmark) with 15 mm diameter were placed on each muscle belly in a bipolar configuration of 30 mm apart between center-to-center electrodes. The position of electrodes estimated by Perotto⁵⁾. The EMG

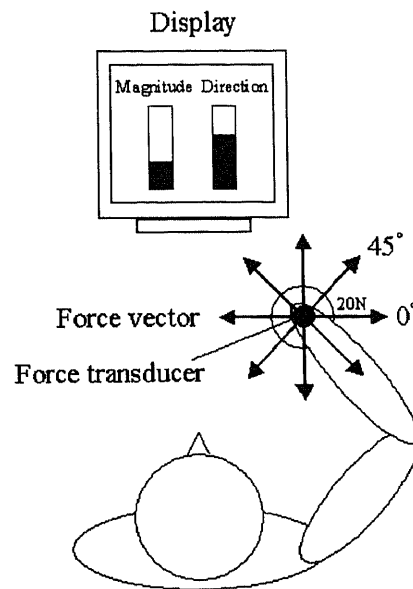


Fig. 1. Experimental setup for force vector regulation. Bars on the display illustrate the magnitude and direction of the force vector measured by the force transducer. The arrows denote the force vectors for exerting by subjects at the magnitude at 20 N and the direction of eight directions at 45° interval.

signals were measured of time-constant at 0.03 sec and of high-pass filtered at 100Hz (BA1008, TEAC, Japan). The resulting signals were full-wave rectified, and then low-pass filtered at 50 Hz using a 4th-orders Butterworth digital filter for smoothing.

Before every experimental task, we performed two measurements. EMG activity of the relaxed arm in the measurement position was recorded to exclude influence of background activation in which the horizontal arm posture was maintained. EMG activity during isometric, maximum voluntary contraction (MVC) was recorded to allow comparison of EMG activity across the subjects. The EMG activity levels of each muscle were calculated as percentage of EMG activity on MVC, through subtractions of background activation. EMG activity during the relaxed arm position, during MVC, and during the experimental task were integrated for 5 sec period, and each integrated EMG activity (*iEMG*) was normalized to calculate the EMG activity level is given by

$$\% iEMG = \frac{iEMG_{task} - iEMG_{relax}}{iEMG_{MVC}} \quad (1)$$

where %*iEMG* denotes normalized the EMG activity

level and its percentage is obtained by multiplying one hundred to Eq. 1. *iEMG_{task}*, *iEMG_{relax}*, and *iEMG_{MVC}* denote EMG activity during experimental tasks, in relaxed position, and in MVC, respectively.

To verify the joint angle of shoulder and elbow in the horizontal flexion/extension during the experimental task, the electrogoniometer (M180, Penny+Giles, UK) was used.

All data were digitally sampled with a 16-bit A/D converter (DaqBoard 2000, IOtech, USA) at 500Hz, were calculated using custom software programmed in DASyLab (ADTEK System Science, Japan) with DELL Dimension 2100 computer.

Statistical analyses of all data were performed using the SPSS package (SPSS, USA). A one-way ANOVA was used for any difference in the direction of the force vector. Statistical difference was determined as at least $P < 0.01$ level for all analyses.

Georgopoulos et al.⁶⁾ discovered that activity of single cells in motor cortex is a sinusoidal function of the direction of movement, and defined the peak of wave as the preferred direction. Similarly, Hoffman et al.⁷⁾ reported that the muscle activation of arm have been fitted the cosine tuning with regard to the

direction of the force and movement. In present study we were able to verify that muscle activation levels were fitted the cosine curve as the direction of the force. Thus, we represented a cosine regression on EMG activity levels during force regulation tasks, following the methodology of Georgopoulos et al.⁶⁾. The regression equation is

$$y = b_0 + b_1 \sin \theta + b_2 \cos \theta \quad (2)$$

where θ are the direction of the force, b_0 , b_1 , b_2 are regression coefficients. b_0 , b_1 , b_2 are given in the following from EMG activity level in Eq. 1,

$$b_0 = \sum \frac{\% iEMG}{8} \quad (3)$$

$$b_1 = \sum \frac{\% iEMG \sin \theta}{4} \quad (4)$$

$$b_2 = \sum \frac{\% iEMG \cos \theta}{4} \quad (5)$$

where θ are the direction of the force. $\% iEMG$ was used the value in subject's average of EMG activity levels for each direction of the force. The preferred direction which the largest EMG activity can be calculated as follows using Eq. 4 and 5,

$$\theta_{PD} = \tan^{-1} \left(\frac{b_1}{b_2} \right) \quad (6)$$

where θ_{PD} are the preferred direction of muscle activity. However, except $b_1 > 0$ and $b_2 > 0$, if $b_2 < 0$, then $\theta_{PD} + 180^\circ$ is θ_{PD} , and if $b_1 < 0$ and $b_2 > 0$, then $\theta_{PD} + 360^\circ$ is θ_{PD} .

2. Mechanical model

In order to investigate the mechanical action of muscles, we built a special apparatus which simulated the mechanical human arm with the modified Ball Bearing Feeder (BBF) as the upper limb arm and with the wire as the muscle (Fig. 2). The BBF had two ball bearing, to not resist to parts corresponding to the shoulder and elbow joint. The BBF length corresponding to the upper arm and forearm was 0.3 m and 0.31 m, respectively. The number of muscles modeled in the apparatus was four. The modeled muscle was PMA (shoulder flexor), DEL (shoulder extensor), BIC (bi-articular flexor) and TLO (bi-articular extensor). For structural restriction of the apparatus, BRD and TLA as elbow mono-articular

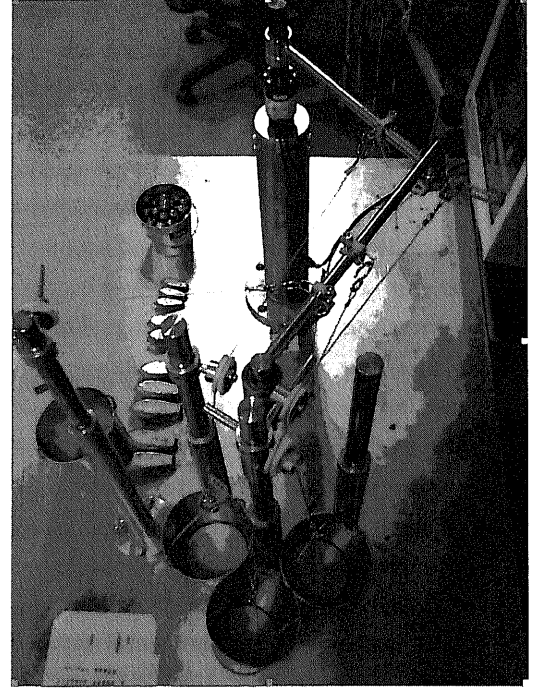


Fig. 2. Top view of a special apparatus which simulated the mechanical human arm with the modified Ball Bearing Feeder as the upper limb and with the wire as the muscle.

muscles were unable to do modeling. Four muscles were constructed by wire with 0.1 mm radius. By hanging out various weights of the fishing sinker to each wire, the wired muscle was able to generate the virtual muscle force corresponding to the weight. The position of the origin and insertion of each wired muscle was determined based on the anatomical data in cadavers was reported by Wood et al.⁸⁾, after modified as an adaptation for this study. As the origin of coordinate was the shoulder joint, the origin and insertion for each muscle were set up in the following. The origin coordinate of PMA, DEL, BIC, TLO is (-20.5, 5.0) cm, (2.5, -7.0) cm, (-3.0, 0.0) cm, (3.0, -2.0) cm, respectively. The insertion coordinate of PMA, DEL, BIC, TLO is (2.6, 8.8) cm, (8.2, 11.7) cm, (8.8, 32.6) cm, (15.9, 24.0) cm, respectively. The distance between the endpoint and the shoulder was set up 49cm. The force generated by the wired muscle was recorded as the force vector at the endpoint of BBF. The force vector at the endpoint of BBF was measured by same handle with two-axis load cell used in human experiment.

We investigated the direction of the force at the

endpoint of BBF, which represents the pulling direction by the wired muscle by hanging out the weight to each muscle. The pulling direction, therefore, corresponds to the direction of the maximum muscle force exerted by each muscle. No change of the magnitude of the force was obtained in case of we hanged out various weight of the fishing sinker to the wired muscle within tolerance level of the apparatus. Therefore, the weight by the fishing sinker to the wired muscle was set up 3 kg as a constant for exerting the pulling force. The pulling direction was recorded by the system with same computer environment in human experiment.

In order to investigate the reproduction of muscle coordination, we predicted the muscle forces based on muscle activation level in Eq. 1 and calculated the weight for each wired muscle of the mechanical model under the coordinated state. We assumed that calculated weight based on muscle activation level allowed the mechanical model to exert the force vectors similar to human experiment. The predicted muscle force f by using muscle activation levels is expressed by

$$f = PCSA \cdot k \cdot \% iEMG \quad (7)$$

where $PCSA$ denote the physiological cross-sectional area. We decided these parameters for each muscle to refer from Gomi⁹⁾. PMA, 19.36 cm²; DEL, 38.71 cm²; BRD, 10.30 cm²; TLA, 7.75 cm²; BIC, 3.23 cm²; TLO, 3.87 cm². The constant k denote the strength per unit area as the maximum muscle strength is taken from Ikai et al.¹⁰⁾ at 62N/cm². Furthermore, we used subject's average data as $\% iEMG$. In this equation, multiplying $PCSA$ and k mean to calculate the maximum muscle force, and multiplying the above and $\% iEMG$ mean to calculate the coordinated ratio against the maximum muscle force exerted by muscle base on muscle activation levels, which represent movement activity/maximum activity in Eq. 1. Because the unit of muscle forces predicted using Eq. 7 is Newton, we divided the predicted muscle force by $g = 9.8 \text{ m/sec}^2$ of the gravitational acceleration for converting to kilogram unit. In addition, because the predicted muscle forces at kilogram unit exceed tolerance level of the apparatus, we divided its force by value 10. The weight of fishing sinkers corresponding

to the muscle force, which was predicted thought above processing, was hanged out to each wired muscle as the coordinated state of muscles. As noted above, for structural restriction of the apparatus, muscles modeled in the mechanical model were four (PMA, DEL, BIC and TLO). Thus, instead of the wired muscle of BRD and TLA as mono-articular elbow muscles, the weight to these wired muscles were added to BIC and TLO, i.e. as BIC+BRD and TLO+TLA. We investigated the force vectors exerted by the weight as the coordinated state in the mechanical model, and compared that with the force vectors by human experiment.

Results

The magnitude and direction of the force vectors during experimental tasks, shows as mean \pm SD in all subjects. There was no significant difference at the magnitude of the force in ANOVA ($p < 0.01$). The exerted magnitude were $19.4 \pm 1.0 \text{ N}$, $20.2 \pm 1.2 \text{ N}$, $19.8 \pm 1.1 \text{ N}$, $19.9 \pm 1.2 \text{ N}$, $20.0 \pm 0.7 \text{ N}$, $20.9 \pm 1.1 \text{ N}$, $20.5 \pm 1.0 \text{ N}$, $19.5 \pm 1.0 \text{ N}$ for 0, 45, 90, 135, 180, 225, 270, 315° of the direction of the given force, respectively. On each direction of the force exerted, the desired direction of the force were observed; $-0.4 \pm 1.6^\circ$ at 0°, $45.2 \pm 1.6^\circ$ at 45°, $90.7 \pm 1.8^\circ$ at 90°, $135.8 \pm 1.9^\circ$ at 135°, $181.8 \pm 1.4^\circ$ at 180°, $225.7 \pm 1.0^\circ$ at 225°, $270.5 \pm 2.6^\circ$ at 270°, $314.7 \pm 1.4^\circ$ at 315°. There was significant difference at the direction of the force in ANOVA ($p < 0.01$). From the above results, it is obvious that both the magnitude and direction of the force vectors were obtained as values we intended.

Figure 3 shows the polar plot of the EMG activity level and the preferred direction of six muscles during force vector regulation in eight directions of the force vectors. The EMG activity levels was indicated by all subject's average data. The direction indicates as a function of the direction of the force vectors and the radius of that indicates as the amplitude of the activity level. A solid line as the EMG patterns connects the top of the amplitude of the EMG activity level in 8 directions. The arrow depicts the preferred direction calculated using Eq. 6. The EMG patterns showed same diamond-shaped patterns at the peak of the preferred direction for each muscle. Similar results were

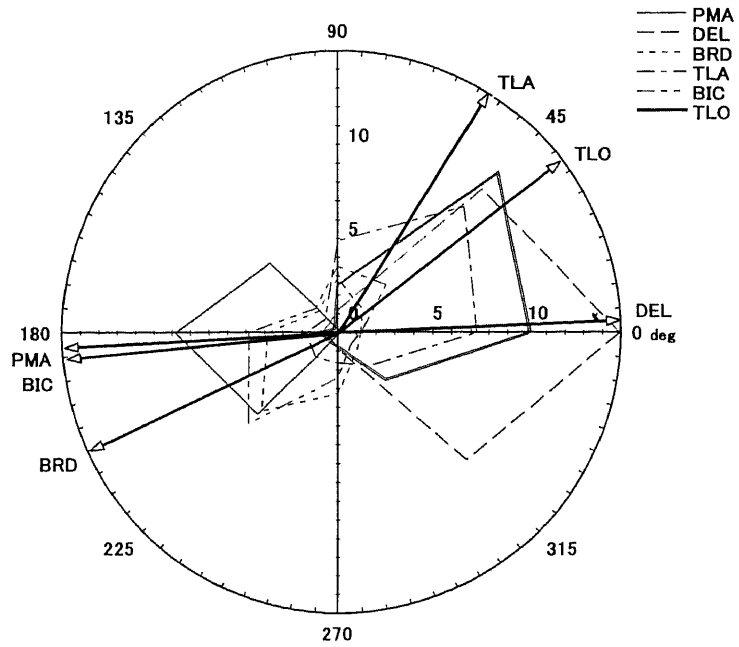


Fig. 3. Polar plot of the EMG activity level as a function of the direction of the force vectors. The arrows denote the preferred direction for each muscle. The preferred direction was determined by the cosine fit for all subject's average data. Outer circle indicates the amplitude of the EMG activity level.

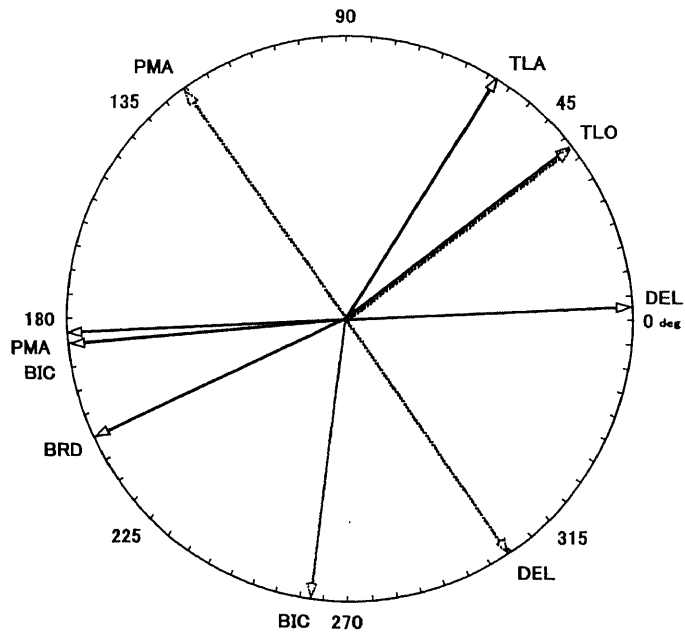


Fig. 4. Pulling directions measured by the mechanical model. The dotted arrows denote the mechanical pulling direction, and the solid arrows denote the preferred direction similar to Fig. 3.

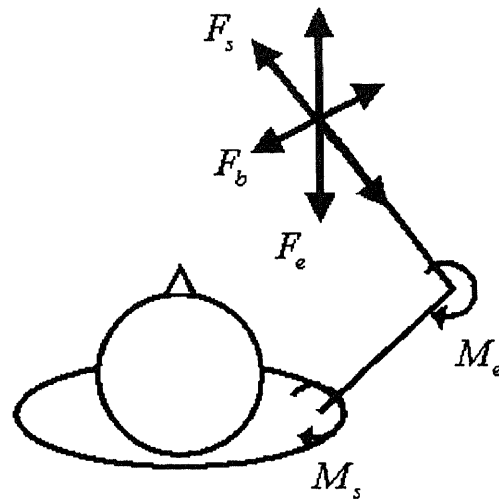


Fig. 5. Schematic drawing of the theoretical direction of muscle action forces. F_s , F_e , F_b denote the action force of mono-articular shoulder muscles, mono-articular elbow muscles, and bi-articular muscles, respectively. M_s , M_e denote the moment of shoulder joint, elbow joint, respectively.

also obtained by van Bolhuis et al.¹¹⁾ or Gomi⁹⁾. The preferred direction for each muscle were 182.2° in PMA ; 5.7° in DEL ; 204.8° in BRD ; 58.6° in TLA ; 184.8° in BIC ; 38.6° in TLO. In this figure, double peaks shows in BRD and TLO. However, we calculated the preferred direction included the second peak in BRD and TLO.

Pulling directions measured by the mechanical model shows in Fig. 4 in conjunction with preferred directions presented in Fig. 3. Solid arrows denote preferred directions and dot arrows denote pulling directions. The pulling direction of PMA, DEL, BIC, TLO were 124.9° , 304.1° , 262.5° , 38.4° , respectively. Disparities between the pulling direction and the preferred direction were 57.3° in PMA, 61.6° in DEL, 77.7° in BIC, 0.2° in TLO. Except for TLO, notable differences were remarked in another muscles.

The reproduction of muscle coordination was executed by the mechanical model, by hanging out the weight to each wired muscle corresponding to the predicted muscle force based on muscle activation levels. We expected that the magnitude of the force vectors may not indicate at 20 N in human experiment, because the weight to the wired muscle was corrected as 1/10 times for tolerance level of the apparatus. However, the magnitude of the force vectors in 90° , 135° , 180° , 225° , 270° indicated approximately

same value from 1.3 N to 1.8N. The direction of the force vectors that we intended were obtained in 135° , 180° , 225° , 270° , 315° direction, but not in 0° , 45° , 90° direction. Exerted directions were 144.2° , 159.9° , 210.8° , 274.6° , 300.9° for 135° , 180° , 225° , 270° , 315° direction, respectively.

Discussion

In this manuscript we describe the relation between the preferred direction of muscle activity and the mechanical action of muscles. Estimates of muscle mechanical actions were obtained by the mechanical human arm model. The preferred direction of muscle activity was compared with the pulling direction as the mechanical action at the endpoint of BBF exerted by wired muscles. Our major findings are that, the preferred direction did not coincide with the pulling direction. In this discussion, we first will examine the theoretical direction exerted by each muscle action in the upper limb at the endpoint in order to explain the reason that did not coincide in these relationships. We then will discuss what are differences between the preferred direction and the pulling direction, based on previous studies. Last, we will discuss several implications for our understanding of the determining factor on muscle coordination in the present study.

1. Theoretical directions of the action force of muscles

In this section, we sought that action force directions of each muscle at the endpoint. Hof⁽²⁾ presented theoretically the principal direction of action forces at the endpoint exerted by mono- or bi-articular muscles in lower limb. Following the methodology of Hof⁽²⁾, the action force at the endpoint in the upper limb can be calculated. Figure 5 shows the schematic drawing of the theoretical direction of muscle action forces. The action force F_s , originating from a shoulder mono-articular like PMA generates a moment about the shoulder joint. However, the elbow moment M_e by F_s is zero because the line of action of the force F_s should pass through the elbow joint. Thus, the action force of a shoulder mono-flexor is given the parallel direction with forearm. Similarly, that of a shoulder mono-extensor is given the reverse parallel direction with forearm. The line of action force F_e pass through the shoulder joint generates the elbow moment M_e , but not the shoulder moment M_s . Thus, the direction of F_e for mono-elbow flexor and extensor exist the line toward the shoulder joint at the endpoint. The line of the action force F_b of bi-articular muscles like BIC or TLO is given a resultant force vector of F_s and F_e . However, to calculate the magnitude of the action force, it is necessary to consider about moment arms in shoulder and elbow joint. Because bi-articular muscles generate a moment in both joints, the magnitude of the action force of F_s and F_e are influenced by the moment arm about the shoulder and elbow joint, respectively. Considering above, the action force for each muscle at the endpoint in this study can be examined theoretically. Theoretical directions of the action force for each muscle are 118.1° in PMA, 298.1° in DEL, 270.0° in BRD, 90.0° in TLA, 253.7° in BIC, 67.3° in TLO in human experiment and, 124.9° in PMA, 303.8° in DEL, 254.3° in BIC, 68.7° in TLO in mechanical model. Based on the theoretical direction, we compare that with the preferred direction or the pulling direction in Fig. 4. As a consequence, the theoretical direction coincided is not the preferred direction, but the pulling direction. Therefore, we support the results by van Zuylen et al.⁽³⁾ who reported muscles in relation to the elbow joint can be

activated even if their mechanical action does not contribute directly. In conclusion, we suppose that the direction of mechanical action of muscles is represented by the action force of muscles at the endpoint, but that the preferred direction of muscle activity is directed by another factors.

2. Differences between preferred direction and pulling direction

Hoffman et al.⁽⁷⁾ reported the pulling direction of the wrist joint in the monkey stimulated by the electrical stimulation, and showed there is the disparity between the preferred direction and pulling direction. In addition, Fagg et al.⁽¹³⁾ considered a computational model of the wrist joint based on the study by Hoffman et al.⁽⁷⁾ and suggested that the deviation between the preferred direction and pulling direction may result from a process of movement optimization. Furthermore, Shah et al.⁽¹⁴⁾ extended the computational model by Fagg et al.⁽¹³⁾ to the cortical level, and demonstrated that a simple linear network is capable of representing the transformation from an extrinsic space to the muscle-recruitment patterns implementing the movements. From these reports, our results in Fig. 4, it may be said that disparities between the preferred direction and pulling direction have been represented the difference between the selective mechanism (optimized in the cortical level) of muscle activity and pure mechanical actions of muscles. According to another model, Pellionisz et al.⁽¹⁵⁾ have proposed a tensorial model in neck muscles, relating to the difference between anatomical pulling directions and maximal excitation directions. In that model, the authors have discussed that the divergence between directions can be explained by using the distinction between covariant (projection) and contravariant (parallelogram) representations in nonorthogonal coordinate systems, in order to transform the frame of reference. Therefore, it is suggested that the difference between the preferred direction and pulling direction is that the difference of the representation in the frame of reference between geometrical muscle arrangement and cortical coordinate involved muscle activation sets.

3. Determining factor on muscle coordination

In order to investigate the coordinated arm by the mechanical model, we calculated the weight to the

wired muscles based on muscle activation level in human experiment. The calculated weight, therefore, correspond to the muscle force in the coordinated arm. By reproducing the force vectors by the mechanical model, we could understand that the coordinated state of muscles was not completely able to be reproduced by the mechanical model, similarly to human experiment. However, force directions in 135, 180, 225, 270, 315° resulted in correct directions. The reason that the coordinated state in all directions did not be reproduced by the mechanical model may be that only four muscles was modeled, or the accuracy of the mechanical model was not full, or the predicted muscle force was not accuracy. Although we must examine cause of the reason in detail in the future, from the fact that we were able to obtain similar magnitudes in 90, 135, 180, 225, 270° and correct directions in 135, 180, 225, 270, 315°, we suggest that it was possible to reproduce muscle coordination by the mechanical model according to the distribution of weights for each wired muscle. Therefore, finding out the appropriate weight for each wired muscle might be similar to solving the optimal load sharing of muscles in the coordinated arm. Within the optimal load sharing, the answer that we demand might be found with regard to the determining factor on muscle coordination.

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上肢の力ベクトル制御における筋活動レベルと筋の機械的な作用方向との関係

犬丸 敏康

要 旨

筋の協調性を決定づける要因を探る上で、筋活動レベルと筋の機械的な作用の関係を調べることは重要である。これまでの研究では、筋活動レベルと筋の機械的な作用の関係は、一致するとの報告と一致しないとの報告に意見が分かれている。本研究では、ヒトによる上肢の力ベクトル制御課題中の筋活動レベルとヒト腕を模した機械モデルによる筋の機械的な作用を比較することで、それらの関係を調べた。特に、ヒトの課題遂行中の筋活動が最大となる方向（筋活動の最適方向）を余弦回帰により求め、その方向を機械モデルの筋に相当するワイヤに負荷をかけた時の筋の機械的な牽引方向と比較した。その結果、最大の筋活動レベルとなる筋活動の最適方向は、機械モデルによる筋の機械的な牽引方向とは一致しなかった。一致しなかった要因について、終端で発揮される筋の作用力に基づいた理論的な観点から検討し、筋の機械的な作用方向は終端での筋の作用力を表現していたが、筋活動の最適方向はそれとは別の要因によって方向づけられていることが示唆された。