The flexible recruitment of muscle synergies depends on the required force-generating capability

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Hagio S, Kouzaki M. The flexible recruitment of muscle synergies depends on the required force-generating capability. J Neurophysiol 112: 316–327, 2014. First published April 30, 2014; doi:10.1152/jn.00109.2014.—To simplify redundant motor control, the central nervous system (CNS) may modularly organize and recruit groups of muscles as “muscle synergies.” However, smooth and efficient movements are expected to require not only low-dimensional organization, but also flexibility in the recruitment or combination of synergies, depending on force-generating capability of individual muscles. In this study, we examined how the CNS controls activations of muscle synergies as changing joint angles. Subjects performed multidirectional isometric force generations around right ankle and extracted the muscle synergies using nonnegative matrix factorization across various knee and hip joint angles. As a result, muscle synergies were selectively recruited with merging or decomposition as changing the joint angles. Moreover, the activation profiles, including activation levels and the direction indicating the peak, of muscle synergies across force directions depended on the joint angles. Therefore, we suggested that the CNS selects appropriate muscle synergies and controls their activation patterns based on the force-generating capability of muscles with merging or decomposing descending neural inputs.

motor control; muscle synergy; electromyography; joint angle; human lower limb

A principal problem in motor control is how the central nervous system (CNS) selects the optimal solution from multiple sets of muscles and joints to execute a movement (Bernstein 1967). Research employing various motor tasks has provided some evidence that complex muscle activities can be explained by a few muscle synergies to simplify redundant motor control (Cheung et al. 2005; d’Avella et al. 2003; Ting and McKay 2007; Tresch et al. 1999). The recruitment of muscle synergies has been examined in many different tasks, including reaching (Cheung et al. 2009; d’Avella et al. 2006, 2008; Muceli et al. 2010), postural responses (Chvatal et al. 2011; Torres-Oviedo and Ting 2007, 2010), locomotion (Chvatal and Ting 2012, 2013, Clark et al. 2010) and cycling (Hug et al. 2010). In all of these cases, the tasks can low-dimensionally be completed using combinations of a limited number of muscle synergies (Nsymp), the activities of which are spatiotemporally modulated by descending neural commands (referred to as “synergy activation coefficients”) (Ting and Macpherson 2005). Despite such complicated or dynamic multijoint tasks requiring a wide range of motion, which enforces changes of mechanical property of individual muscles (Zajac 1989), how were the tasks achieved smoothly and low-dimensionally by using a few muscle synergies? It is critical to assess how the CNS could regulate the recruitment of muscle synergies by focusing on a muscle’s force-generating capability.

It is well known that the ability of a muscle to produce force varies, depending on its length and moment arm (Zajac 1989). During isometric knee extension, for example, the estimated muscle force of the vastus lateralis (VL) muscle, which directly contributed to knee extension torque, was maximal with the knee positioned at 110° from full flexion (i.e., optimal angle) and decreased away from the optimal joint angle (Ichinose et al. 1997). Additionally, during isometric knee flexion, maximal knee flexion torque increased with hamstrings lengthened and reached maximal at 135° and 90° of knee and hip joint angle, respectively (Mohamed et al. 2002). Other studies of lower limb muscles have revealed that the electromyographic (EMG) activity of a muscle is modulated as a function of the muscle’s length, indicating that the neural drive may be altered, depending on the muscle’s ability to generate force on the basis of its length-tension curve (Babault et al. 2003; Cresswell et al. 1995; Onishi et al. 2002).

Whether muscle synergies are of neural origin is still controversial (Bizzi and Cheung 2013). Some empirical findings, however, provided the suggestion that muscle synergies may be encoded in the brain stem (Roh et al. 2011) or intermediate zone of the spinal cord (Hart and Giszter 2010; Takei and Seki 2010). Furthermore, in impaired stroke survivors, it is reported that synergies extracted from stroke-affected arm were similar to those of the unaffected arm, although motor performance between the arms was remarkably different (Cheung et al. 2009). That study suggests that the CNS controls descending neural input to neurally structured muscle synergies, and the impaired motor performance was attributed to the descending signal affected by lesions in motor cortical area. Consequently, assuming that muscle synergies are not merely conjecture but of neural origin, the force-generating capabilities of individual muscles can affect the neural activity of muscle synergies.

For the current muscle synergy model, robustness and low dimensionality, which simplify redundant motor control, have been proposed to be advantageous (Berniker et al. 2009; Chvatal and Ting 2013; Roh et al. 2012). However, not only low-dimensional organization, but also high flexibility of controlling synergy activations to adapt to some changes of physiological parameters, is speculated to be necessary to achieve smooth and efficient multijoint movements. We, therefore, hypothesized that the CNS may select the most relevant muscle...
synergies and control their activation patterns based on the force-generating capability of individual muscles.

The aim of the present study was to examine how the CNS recruits appropriate muscle synergies as changing force-generating capability of individual muscles. To this end, subjects performed multidirectional isometric force-generating tasks across various joint angles. Our results demonstrated the flexible recruitment of various synergies and the diverse states of descending neural input from the CNS to these synergies.

**METHODS**

**Subjects.** Five male subjects voluntarily participated in this study. Their mean (±SD) age, height and body mass were 23.8 ± 0.45 yr, 174.4 ± 4.6 cm and 64.8 ± 8.3 kg, respectively. All subjects were healthy, had no history of any neurological disorder and had corrected-to-normal vision. Subjects provided written, informed consent to participate in the study after receiving a detailed explanation of the purposes, potential benefits and risks associated with participation. All procedures used in this study were in accordance with the Declaration of Helsinki and were approved by the Committee for Human Experimentation at the Graduate School of Human and Environmental Studies, Kyoto University.

**Experimental setup.** Subjects lay on their left side on a bed with the right leg supported horizontally by a sling (Fig. 1A). Six patterns of flexion were applied to the knee and hip joints from full flexion as follows: 50°/180°, 50°/90°, 90°/180°, 90°/90°, 130°/180° and 130°/90° (knee/hip). Isometric endpoint forces surrounding the right ankle were produced for a total of 10 s at 2 different intensities (20 N and 40 N) in each of 12 different directions on the sagittal plane (Fig. 1B). The force intensities were determined so as not to change the joint configuration of the knee, hip and trunk. The directions were equally distributed in 30° increments to cover the entire sagittal plane. We then measured isometric endpoint forces, which were composed of two force vectors, \( F_x \) and \( F_y \), anatomically referring to knee flexion-extension and hip flexion-extension directions, respectively, using a triaxial force transducer (LSM-B-500NSA1, Kyowa, Tokyo, Japan) attached to the subject’s right ankle (Hagio et al. 2012; Kouzaki et al. 2002) (Figs. 1C and 2). In each trial, the subjects viewed the produced and target forces on a visual display.

**Fig. 1.** Experimental setup. A: an overhead view of the experimental setup. Subjects lay on their left side on a bed with the right leg supported horizontally by a sling. Both knee and hip joint angles were changed in 6 patterns. Visual feedback of produced and target forces was displayed to the subject on a computer screen. B: the 12 target directions in which isometric force generations were obtained are shown. +\( F_y \) and +\( F_x \) anatomically refer to knee flexion and hip flexion directions, respectively. C: using a triaxial force transducer attached to the subject’s right ankle, two-dimensional forces, \( F_x \) and \( F_y \), anatomically referring to knee flexion-extension and hip flexion-extension directions, respectively, were measured.

**Fig. 2.** Force trajectory. Force trajectory across 6 joint patterns, 12 force directions and 2 force levels in a representative subject are shown. The force traces were low-pass filtered at 20 Hz using a zero-phase-lag fourth-order Butterworth filter. Angles (ang) 1–6 represent 50°/180°, 50°/90°, 90°/180°, 90°/90°, 130°/180° and 130°/90° (knee/hip) joint patterns, respectively. ext, Extension; flex, flexion.
Electromyography. Surface EMGs were recorded from the following 15 muscles spanning knee and hip joints: the rectus femoris (RF), VL, vastus medialis obliquus (VMO), vastus medialis longus (VML), vastus intermedius (VI), sartorius (SR), adductor longus (AL), biceps femoris long head (BFL), biceps femoris short head (BFS), semitendinosus (ST), semimembranosus (SM), gluteus maximus (GMax), gluteus medius (GMed), gastrocnemius lateralis (LG) and gastrocnemius medialis (MG) (Rainoldi et al. 2004, 2008; Watanabe et al. 2009; Watanabe and Akima 2011). EMGs were recorded using bipolar Ag-AgCl electrodes. Each electrode had a diameter of 5 mm, and the interelectrode distance was 10 mm (Imagawa et al. 2013). A small interelectrode distance was used to prevent cross talk between neighboring muscles. A reference electrode was placed on the lateral epicondyle of the femur. The EMG signals were amplified (MEG-6116M, Nihon-Kohden, Tokyo, Japan) and band-pass filtered between 5 and 1,000 Hz. All electrical signals were stored at a sampling frequency of 2,000 Hz on the hard disk of a personal computer using a 16-bit analog-to-digital converter (PowerLab/16SP; AD Instruments, Sydney, Australia). Raw EMG traces were high-pass filtered at 35 Hz using a zero-phase-lag fourth-order Butterworth filter, after which they were demeaned, digitally rectified and low-pass filtered at 40 Hz (Chvatal et al. 2011). The filtered traces were then divided into 10 time bins and averaged across each bin. This procedure took account of fluctuations of muscle activations, despite the constant period. In this way, EMG signals were treated across the hold period of each trial and across each corresponding rest period, and the difference between the two traces represented the net EMG. The averaged muscle activity data for each muscle were assembled to form an EMG data matrix (see the following description).

Extracting muscle synergies. We extracted muscle synergies from the data matrix of EMG recordings using nonnegative matrix factorization (NMF), which has previously been described as a linear decomposition technique (Lee and Seung 1999; Ting and Macpherson 2005; Tresch et al. 1999). This method assumes that a muscle activation pattern (\( M \)) evoked to achieve an isometric endpoint force in a particular direction is composed of a linear combination of a set of muscle synergies (\( W_i \)), each of which is recruited according to a synergy activation coefficient (\( c_i \)). Therefore, the particular muscle activation pattern for a given direction is represented by the following equation:

\[
M = \sum_{i=1}^{N} c_i W_i \geq 0 \quad W_i \geq 0
\]

where \( W_i \) specifies the muscles that are involved in the synergy \( i \) and their relative contributions. Each component of \( W_i \) represents the contribution of one particular muscle to that synergy, and an individual muscle may contribute to multiple synergies. The composition of the muscle synergies does not change between conditions, but each synergy is multiplied by a scalar activation coefficient (\( c_i \)) that does change between conditions. The synergy weighting and activation

Fig. 3. Using variability accounted for (VAF) to determine the number of global synergies. Top: the global VAF for global synergy extraction as a function of the number of global synergies used for reconstruction was based on the original (black solid line) and shuffled (gray dashed line) electromyographic (EMG) datasets. In all cases, the VAF values for the reconstruction of the original data using the identified synergies were definitely higher than the VAF for the shuffled datasets. Second row: the VAF across muscles for global synergy extraction. Different lines indicate the different number of muscle synergies. Third row: the VAF across tasks for global synergy extraction. Different lines indicate the different number of muscle synergies. Bottom row: the global synergies for separate synergy extraction across joint angle patterns as a function of the number of synergies. Muscle names are indicated in an abbreviated form: RF, rectus femoris; VL, vastus intermedius; VL, vastus lateralis; VMO, vastus medialis obliquus; VML, vastus medialis longus; SR, sartorius; AL, adductor longus; BFL, biceps femoris long head; BFS, biceps femoris short head; ST, semitendinosus; SM, semimembranosus; GMed, gluteus medius; GMax, gluteus maximus; LG, gastrocnemius lateralis; MG, gastrocnemius medialis. Ang 1–6 represent 50°/180°, 50°/90°, 90°/180°, 90°/90°, 130°/180° and 130°/90° (knee/hip) joint patterns, respectively. Syn, synergy; ID1–5, subjects 1–5.
Coefﬁcient matrices were normalized such that the individual muscle-weighting vector was unit vector.

In the present study, muscle synergies were extracted from two different data pools: the global and separate data sets. The global data sets represented all data pools from a subject, including all directions, joint patterns, force levels and time bins. The global EMG matrix consisted of 15 muscles \( \times \) 1,440 variables (12 directions \( \times \) 6 joint patterns \( \times \) 2 force levels \( \times \) 10 time bins), and this extraction was based on the assumption that all of the data sets could be accounted for by a few muscle synergies (global synergy). The separate EMG matrix was constructed from 15 muscles \( \times \) 240 variables (12 directions \( \times \) 2 force levels \( \times \) 10 time bins) across joint patterns to calculate the specific muscle synergies in each joint pattern (separate synergy). These two different constructions of EMG data matrix assumed the following: that the global synergies are the minimum units, the combinations of which makes it possible to explain all of the datasets; however, the data reconstruction overestimates the data across joint angle patterns; and the separate synergies can demonstrate the specific structure of synergies across joint angles. The EMG values of each muscle were normalized to the maximum value for that muscle across all desired directions such that each value was between 0 and 1. Then each muscle data vector was normalized to have unit variance to ensure the activity in all muscles was equally weighted.

To select the \( N_{\text{syn}} \) that could best model our data, we extracted between 1 and 15 synergy matrixes and synergy activation coefficient matrixes from the EMG data matrixes that were obtained from each subject. Then we verified the goodness-of-ﬁt between the original and reconstructed data matrixes; the data matrixes were calculated using NMF analysis to select the smallest \( N_{\text{syn}} \) that resulted in an adequate reconstruction of the muscle responses. We first calculated the variability accounted for (VAF) as \( 100 \times \) the coefﬁcient of determination from the uncentered Pearson correlation coefﬁcient (Torres-Oviedo et al. 2006; Zar 1999), which was based on the entire dataset (global VAF). VAF is sensitive to both the shape and magnitude of the variation.

Fig. 4. EMG activities. The rectiﬁed and averaged EMG activities across 12 force directions and joint patterns are shown. Each dot represents the muscle activations averaged across 10 different time bins, and the 12 values of the averaging for each direction are connected by a periodic cubic spline interpolation curve (solid line). Ang 1–6 represent 50°/180°, 50°/90°, 90°/180°, 90°/90°, 130°/180° and 130°/90° (knee/hip) joint patterns, respectively. The activation proﬁles are shown for the force level of 40 N. deg, Degree.

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original and reconstructed datasets. The $N_{\text{syn}}$ underlying each dataset was defined as the minimum number of synergies required to achieve a mean global VAF > 90% and a mean VAF for each muscle (muscle VAF) that exceeded 80%, and, in the case of the global synergies extraction, a mean VAF for each joint angle pattern (task VAF) > 80%. For $N_{\text{syn}}$, both synergy weighting and synergy activation coefficient matrices were defined.

**Data analysis.** We quantified the similarity between the global and separate synergy structures. An initial comparison was performed between each global synergy and the individual separate synergy across the joint patterns. Similarity was defined using cosine similarity. Additionally, we compared a summation of a few selected global synergies (for example, $W_i + W_j$), that is “merging,” with the individual separate synergy and determined the combination having the highest correlation as the similar.

Functional sorting of the global synergies across each subject was initially performed by grouping muscle synergies based on the values of cosine similarity ($r > 0.60$) to that of an arbitrary reference subject using an iterative process. If two synergies in one subject were assigned into a same synergy group, we defined a pair of synergies with highest correlation as the same group of synergies. Subsequently, an averaged set of similar muscle synergies for all subjects was computed, and the similarity between the averaged muscle synergies and each synergy grouped across subjects was quantified (Torres-Oviedo and Ting 2007).

The statistical analysis for the force directions, which is represented by angles in the polar coordinate, indicates the peak synergy activations was based on the statistical analysis of circular data (Fisher 1993). The average values of the force directions were calculated from the vector in the Cartesian coordinates, which translated from the polar coordinate. Data variability was defined as a magnitude of the averaging vector; the value is into 1, if there is high data variability, and the value is into 0, if not.

**Methodological identification.** To confirm that the synergies extracted by the NMF algorithm were due to the inherent organization of muscle activation based on neurophysiological evidence rather than artifacts of the NMF method, the VAF levels for the synergies extracted from the original data were compared with the VAF values for synergies extracted from shuffled datasets. For the shuffled procedure, the data for each muscle were shuffled independently; therefore, this shuffled data matrix contained the same values, range and variance for each muscle, but the relationships among muscle activations were removed (Chvatal et al. 2011). Figure 3 (top row) shows the plots of both the original (black solid line) and shuffled (gray dashed line) global VAF values in the condition extracting global synergy as a function of the number of synergies across subjects. This
comparison showed that the VAF values with the appropriate number of synergies extracted from the original data were definitely higher than those for the same numbers of synergies extracted from the shuffled data. This was consistently observed in separately extracted conditions for all subjects. These results provide evidence that the structures of the synergies extracted from the original data reflect the actual spatial organization of the muscle activation around the knee and hip joints. Furthermore, Fig. 3 also represents VAF across muscles (second row) and joint angles (third row) in global condition and global VAF in separate conditions across joint angles (bottom row).

RESULTS

Muscle activations. We recorded the EMG activity from up to 15 muscles acting on the knee and hip joints, and the EMG traces for 10 s were divided into 10 time bins and averaged across each time bin. Figure 4 shows the muscle activations directionally tuned across 12 force directions in a representative subject (ID1). Each dot represents the muscle activations averaged across 10 different time bins, and the 12 values of the averaging for each direction are connected by a periodic cubic spline interpolation curve (solid line). We observed small fluctuations of the individual muscle activations with low frequency. The activation profiles of individual muscles specifically depended on force directions, which are approximately normally distributed centering on the peak activation. Furthermore, the force direction indicating the peak activation was changed across joint angles.

Flexible recruitment of muscle synergies. In this study, entire muscle activities were accounted for by 6.4 ± 0.89 global synergies, which were extracted from the entire data set of 6 joint angle patterns [50°/180°, 50°/90°, 90°/180°, 90°/90°, 130°/180° and 130°/90° from full flexion (knee/hip)]. Figure 5 shows the global muscle synergies in the six joint patterns for a representative subject (ID1). Each dot represents the synergy activations averaged across 10 different time bins, and the 12 values of the averaging for each direction are connected by a periodic cubic spline interpolation curve (solid line). In this subject, characteristic patterns of muscle activation required to produce the multidirectional forces for all joint patterns were reconstructed with six synergies. The synergy $W_1$ mainly comprised biarticular muscle (RF) spanning the knee and hip joints and contributed to knee extension/hip flexion torques. The synergy $W_3$ included biarticular muscles (BFL, ST and SM) spanning the knee and hip joints and monoarticular knee flexor (BFS) and was activated to generate knee flexion/hip extension torques. The synergies $W_2$ and $W_4$, which produce the knee extension and flexion torques, elicited relatively isolated activation of the monoarticular knee extensors (VI, VL, VMO and VML) and a flexor (BFS), respectively. The synergy $W_5$ was dominated by activation of GMed (a hip abductor) in addition to the activation of ST (contributing to knee flexion and hip extension) and GMax (a hip extensor). This synergy presumably contributed to reduce force fluctuations in lateral direction, and in the 50°/180°, 50°/90°, 90°/180° joint angle patterns, seemed to be activated to produce hip extension torque. The synergy $W_6$ contained MG and LG, which may produce knee flexion torques for the design in this study, in addition to BFL, and approximately activated over all directions.

As comparing the activations of the global synergies among the six different joint patterns, we observed changes of the profiles (Fig. 5). The force directions indicating the peak synergy activations across the groups of similar synergies (detail below) for all subjects are shown in Table 1 (the synergies $W_1$ to $W_6$ correspond with the synergies in Fig. 5). For example, on synergy $W_1$ functioning as knee extensor and hip flexor, the direction indicating the peak activation in the 50°/180° (knee/hip) joint angle pattern was 121.3° (averaging for all subjects and 2 force levels) and is mainly shifted to the 180° (Table 1). The peak activation direction of knee extension synergy $W_2$ and knee flexor and hip extensor synergy $W_3$ mainly distributed around 200° and 330°, respectively, depending on the joint patterns. The synergy $W_4$ showed the distribution of peak activation direction around 350°. Therefore, the activation profiles, such as amplitude and the direction indicating the peak activation, were different among the six joint patterns. These results suggest that the CNS controls the activations of individual muscle synergies, depending on the joint angle.

Table 1. The force direction indicating the peak synergy activation

<table>
<thead>
<tr>
<th>Synergy</th>
<th>No. Samples</th>
<th>Index</th>
<th>Angle 1</th>
<th>Angle 2</th>
<th>Angle 3</th>
<th>Angle 4</th>
<th>Angle 5</th>
<th>Angle 6</th>
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<tr>
<td>$W_1$</td>
<td>10</td>
<td>Average</td>
<td>121.31</td>
<td>135.01</td>
<td>146.22</td>
<td>157.17</td>
<td>171.84</td>
<td>158.76</td>
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<td></td>
<td></td>
<td>Variability</td>
<td>0.059</td>
<td>0.016</td>
<td>0.035</td>
<td>0.064</td>
<td>0.040</td>
<td>0.045</td>
</tr>
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<td>$W_2$</td>
<td>10</td>
<td>Average</td>
<td>185.32</td>
<td>199.88</td>
<td>212.79</td>
<td>217.49</td>
<td>243.15</td>
<td>225.64</td>
</tr>
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<td></td>
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<td>Variability</td>
<td>0.022</td>
<td>0.015</td>
<td>0.010</td>
<td>0.113</td>
<td>0.260</td>
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<tr>
<td>$W_3$</td>
<td>10</td>
<td>Average</td>
<td>338.94</td>
<td>326.36</td>
<td>355.05</td>
<td>8.79</td>
<td>357.37</td>
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<td></td>
<td></td>
<td>Variability</td>
<td>0.249</td>
<td>0.103</td>
<td>0.017</td>
<td>0.010</td>
<td>0.080</td>
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<td>$W_4$</td>
<td>6</td>
<td>Average</td>
<td>337.32</td>
<td>353.46</td>
<td>328.28</td>
<td>348.50</td>
<td>359.71</td>
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<td>Variability</td>
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<td>0.225</td>
<td>0.317</td>
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<td>$W_5$</td>
<td>8</td>
<td>Average</td>
<td>302.43</td>
<td>299.16</td>
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<td>22.50</td>
<td>320.23</td>
<td>225.18</td>
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<td>Variability</td>
<td>0.283</td>
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<td>0.217</td>
<td>0.967</td>
<td>0.440</td>
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<tr>
<td>$W_6$</td>
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<td>Average</td>
<td>357.62</td>
<td>25.92</td>
<td>50.44</td>
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<td></td>
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<td>Variability</td>
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<td>$W_7$</td>
<td>8</td>
<td>Average</td>
<td>320.67</td>
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<td>282.99</td>
<td>290.15</td>
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<td>0.000</td>
<td>0.044</td>
<td>0.048</td>
<td>0.039</td>
<td>0.821</td>
</tr>
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</table>

Values are in degrees. The averaging force direction indicating the peak synergy activations and their variability for all subjects and 2 force levels are shown. The synergies $W_1$ to $W_6$ correspond with the synergies in Fig. 7. The nos. of samples were different across subjects and are indicated next to the designation of the synergies. Angles 1–6 represent 50°/180°, 50°/90°, 90°/180°, 90°/90°, 130°/180° and 130°/90° (knee/hip) joint patterns, respectively.
Merging of muscle synergies. We separately extracted muscle synergies for each force intensity and joint pattern. Typically, three to six muscle synergies were required to reproduce the datasets for each joint pattern (4.6/H11006 0.89, 4.0/H11006 0.71, 4.0/H11006 1.00, 5.0/H11006 0.00, 4.2/H11006 1.30 and 4.4/H11006 0.89 synergies for the six joint patterns of 50°/180°, 50°/90°, 90°/180°, 90°/90°, 130°/180° and 130°/90°, respectively (knee/hip)).

Figure 6 shows the global synergies (left) and separate synergies (remaining) in a representative subject (ID1). In this subject, four or five synergies were required to reconstruct the discrete datasets of the joint patterns. Comparing separate synergies with the global synergies, the spatial structures of some synergies were similar to each other; for example, the first synergy in the 130°/90° joint pattern is highly corresponding to the global synergy W1 (r = 0.964, defined as cosine similarity), whereas some synergies seemed to have a little difference between global and separate synergies. This divergence of structures, however, was the result of merging of some of the muscle synergies. For example, the r value between the global synergy W3 and the third 50°/180° synergy was 0.876, but if we compared the second 50°/180° synergy to the merged global synergies W3 and W4, the r value increased to 0.987. Furthermore, the r value was 0.390 comparing W2 with the first 50°/180° synergy, whereas it increased to 0.881 as merging the synergies W1, W2 and W4. This result suggests that, although the spatial structures of synergies were altered as changing the joint patterns, the essential structures were preserved. Consequently, we propose that the merging of synergies is dependent on the joint angles.

Global synergies across subjects. For each subject, five to seven global synergies were identified in all conditions (Fig. 7). The synergies W1, W2 and W3, which were mainly dominant for biarticular knee extensor and hip flexor (RF), monoarticular knee extensor (vasti muscles) and biarticular knee flexor and hip extensor (BFL, SM and ST), respectively, were common among all subjects. Additionally, the monoarticular knee flexor synergy W4 and the synergy W6 including gastrocnemius muscles were extracted in three subjects, and the synergies W5 and W7, which was mainly composed of hip abductor (GMed) and SR, respectively, were observed in four subjects. In contrast, subject-specific synergy was found in one subject, who had hip adductor (AL). These results suggest that the primary coordination of muscle synergies to accomplish the motor tasks were similar among subjects in various joint angles.

Fig. 6. Global and separate synergies. The muscle weightings of global (left) and separate (remaining) synergies are shown for a representative subject (ID1). The separate synergies are shown in all joint patterns. Ang 1–6 represent 50°/180°, 50°/90°, 90°/180°, 90°/90°, 130°/180° and 130°/90° (knee/hip) joint patterns, respectively. The designation and value in each separate synergy represent the similar (combination of or independent) global synergies to the separate synergy and the cosine similarity, respectively. For example, the first separate synergy in 50°/180° joint pattern was similar to the merged structure of the global synergies W1, W2 and W4 (r = 0.881).
DISCUSSION

In the present study, we hypothesized that the CNS selects the most relevant muscle synergies and controls their activations based on the force-generating capability of individual muscles. To this end, we examined the recruitment of muscle synergies around the knee and hip joints as varying the joint angles during multidirectional isometric force generation tasks. We found five to seven global synergies in all conditions for each subject, and the activation profile of each global muscle synergy depended on the joint angles. Interestingly, we demonstrated merging of the synergies in some of the joint patterns. These results suggest that the CNS select the appropriate muscle synergies and control their activations based on the force-generating capability of individual muscles during multidirectional isometric force generation.

Fig. 7. Global synergies for all subjects. The muscle weightings of global synergies across each subject are shown. The r value represents cosine similarities between the averaged muscle synergies from the initial sorting and each original synergy grouped across subjects (see METHODS).

Merging of synergies is joint pattern specific. We observed the merging structures of muscle synergies depending on the joint patterns as varying the knee and hip joint angles to alter the force-generating capability of relevant muscles (Fig. 6). In addition, this merging seemed to be further prompted as the joint angle was far away from the optimal to produce maximal joint torque during isometric contraction, i.e., 130° and 90° (knee and hip joint angles, respectively) for both knee extension and flexion torques in the case of this study (Ichinose et al. 1997; Mohamed et al. 2002). The optimal joint angle was determined by the interaction between the moment arm and the length in the active length-tension curve of the muscles that span the relevant joint (Lieber 1992). Moreover, Shinohara et al. (2006) reported that the ability to generate steady force during plantar flexion force-matching task was greater in a
knee-extended position, which was near the optimal knee joint angle for plantar flexor muscles, than in a knee-flexed position. Thus the optimal joint angle involves more sophisticated force production, and movement control accuracy may depend on the force-generating capability. As for the merging of muscle synergies, previous studies reported functional merging of muscle synergies in the affected limb of poststroke subjects (Cheung et al. 2012; Clark et al. 2010), and such merging of muscle synergies is thought to be compatible with the poststroke co-contractions of muscles described in the literature (Beer et al. 1999; Dewald et al. 1995). Consequently, the merging of synergies could lead to a reduction in the complexity of locomotion or the range of joint motion. However, we suggested the constraints should also contribute to stabilizing the force generations.

In this study, as described above, knee and hip angles of 130° and 90° were optimal for both knee extension and flexion torques (Ichinose et al. 1997; Mohamed et al. 2002), and the recorded knee extension and flexion force fluctuations were less than in the remaining joint patterns. Around this optimal joint pattern, we observed the decomposition of functionally similar synergies that resulted in an improvement in movement flexibility, which made it possible to produce the required force. Moving away from the optimal knee and hip joint angles (for example, 50°/180° and 50°/90° of the knee/hip joint angles) resulted in a reduced ability to generate force, as determined by the changes of interaction between the moment arm and muscle fiber length. Thus, to reduce force fluctuations, the CNS controls a few synergies together, i.e., the co-contraction of synergies, which leads to improved force stabilization. Consequently, the functionally merged synergies were extracted in these joint patterns.

The force maintenance tasks in this study required spatially fixed muscle synergies, whose activations were temporally modulated on a case-by-case basis. To simplify redundant motor control, however, reduction of neural input might have been considered, not only spatially but also temporally. The temporally fixed activation patterns of modular organization were observed in cyclic locomotion (Cappellini et al. 2006; Ivanenko et al. 2004). Additionally, in fast-reaching movement, spatiotemporally fixed synergies, referred to as time-varying muscle synergies, further simplified redundant motor control (d’Avella et al. 2006, 2008). The temporally fixed pattern of activations, however, could not allow flexible and continuous force generations required in such as force maintenance, so the CNS might plan a different strategy for reducing neural command. Therefore, the merging of muscle synergies might be one of the most efficient strategies, which could lead to reduction of control variables in the CNS.

Neurophysiologically, we suggest that this merging of synergies should represent a merging of motor commands, i.e., activation coefficients, from the CNS to the functionally similar synergies. Comparing the activation coefficients of global synergies with separate synergies, which was constructed by the merging of the global synergies, across joint angles, functionally similar neural inputs in the global synergies were integrated (Fig. 8). For example, in 50°/180° (knee/hip) joint angle, global synergies W3, W4 and W5, which similarly contributed to knee flexion, were merged into two separate synergies, sW3 and sW4. If the common neural inputs to individual synergies were separated (i.e., the merging of synergies was caused by the synchronization of their independent signals), this may lead to a higher degree of freedom and resulting unstable force generation. Moreover, only independent inputs cannot simplify the complex merging conditions for a certain synergy (W4 or W5) belonging to different merging groups in the 50°/180° and 50°/90° joint patterns (knee/hip), as shown in Fig. 8; the global synergy W4 was the component of both separate synergies sW3 and sW4. Therefore, the synergies should be affected by the descending motor command through independent and common (i.e., merged) neural inputs, and these commands and the subsequent merging or decomposition of synergies in the neural circuitry were dependent on the joint pattern. Moreover, we examined which combinations of synergies were merged or not, as shown in Fig. 9, which represents the number of the combination of merged synergies. The synergies W1 and W2, which function as knee extensors, and W3 and W4, which contribute to knee

Fig. 8. Directional tuning of global and separate (sW1–5) synergy activations. Directional tunings across 12 force directions for the global (top) and separate (bottom) synergy activations are shown. The 12 values of the averaging of activation traces across each direction (dots) are connected by a periodic cubic spline interpolation curve (solid line). Ang 1–6 represent 50°/180°, 50°/90°, 90°/180°, 90°/90°, 130°/180° and 130°/90° (knee/hip) joint patterns, respectively.

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flexion, had higher relationship and were allowed to merge each other. On the other hand, the functionally unconcerned combinations of synergies, such as $W_1/W_7$ or $W_3/W_5$, were also frequently integrated with each other. This result suggests that the merging of neural inputs to some synergies could contribute to making a relationship among, not only functionally similar synergies, but also unconcerned synergies, and stable multidirectional force generations.

Whether the merging of muscle synergies reflects realistic physiological events or methodological characteristics is an important topic in this study. As describing in the METHODS section, the constructions of global and separate EMG data matrices assumed the following: that the global synergies are the minimum units for overall datasets; however, the data reconstruction probably overestimated the data across joint angle patterns; and the separate synergies can demonstrate the specific structure of synergies across joint angles. Although this assumption resulted in the finding that the several structures of separate synergies were highly similar to the merging among global synergies, there is a possibility that setting of VAF threshold (global VAF > 90% and muscle VAF > 80%) could lead to the merging of separate synergies, as determining the $N_{\text{syn}}$, which reconstructed the original EMG dataset well. The setting of the VAF threshold was critical for examining muscle synergies, and several researchers cared about the criteria based on VAF curve to determine the number of synergies (Cheung et al. 2005, 2009; Torres-Oviedo et al. 2006; Tresch et al. 2006). The previous study suggested that more numbers of synergies should be required for task achievement than the good reconstruction of EMG activities based on the VAF threshold (de Rugy et al. 2013). In this study, we set several patterns of the VAF threshold, for example, global VAF > 95% and muscle VAF > 85%; however, the merged structures of synergies were basically preserved (unpublished observation), indicating that the original EMG data were well reconstructed, and the merging of synergies was observed, even if we raise the precision of the VAF threshold. However, there is the other possibility that the merging of muscle synergies was caused by the overestimation of global synergies compared with that of separate synergies. Hence, to justify the fact, we compared the goodness of data reconstruction between task VAF in the global synergy extraction and global VAF in the separate synergy extraction. Because the datasets across joint angle patterns in the global synergy extraction corre-
sponded to the datasets in the separate synergy extraction, the task VAF was comparable to the global VAF in the separate synergy extraction. In a representative subject (ID1), the mean task VAF in the defined number of synergies was 93.563 ± 2.401, whereas the global VAF averaged for six joint angle patterns in each defined number of synergies was 92.197 ± 0.939, and there were no significant difference between them. Therefore, we did not overestimate the number of synergies in the global synergy extraction, and the greater number of synergies in the global synergies than that in the separate synergies arose from the influence that the global synergies must account for the datasets of the other joint angle patterns. Thus the number of global synergies was not caused by an overestimation, but was inevitably required to explain global datasets. Therefore, the merging structure was not artifactual composition affected by the setting of VAF threshold, but was suggested to be actual spatial organization.

Selective recruitment of muscle synergies is joint pattern specific. In the present study, we substantially altered the joint angles to change the physiological parameters and found that the activation levels of muscle synergies were changed across joint angles. For example, the first global synergy W1 shown in Fig. 5, which was mainly composed of biarticular muscle (RF), was activated in a relatively low level when the knee joint angle was 50°/180° (knee/hip) in which the RF was most stretched, suggesting that this synergy may be specifically modulated based on the knee joint angle. The activations of the second synergy W2, which predominantly contained the monoarticular knee extensors (vasti muscles), indicated lower peak values as knee joint was extended. Furthermore, the activation levels were affected by not only knee joint, but also hip joint, angles, i.e., the activation in 130°/90° pattern were higher than in 130°/180° (knee/hip), indicating that the activations of muscle synergies also depend on the neighboring irrelevant joints, which was previously reported in muscle levels (Nozaki et al. 2005).

Interestingly, not only the activations levels but also the direction indicating the peak of each global muscle synergy were modulated, depending on the force directions and joint angles (Fig. 5). It is reported that individual muscles were recruited based on the preferred force direction, i.e., the preferred combination of the relevant joint torques, and the activation profiles on the torque plane indicated cosine-like behavior (cosine tuning) (Hoffman and Strick 1999). In the muscle synergy space, the activations were directionally tuned around the preferred force direction, indicating peak activations in this study. As changing joint angles, moreover, the preferred directions were shifted. One possibility is the changes of the directions generating net joint torque as a function of joint angles. As second possibility, in the previous study, different motoneurons were recruited, depending on the forearm positions (Kakei et al. 1999). In addition to the architectural factor, therefore, it is suggested that the CNS should also determine the preferred directions of individual muscle synergies based on the joint angles.

Muscle synergies in neural circuitry. The resulting structures of muscle synergy weightings were affected by the selection of relevant muscles (Steele et al. 2013) or criteria for data reconstruction (de Rugy et al. 2013), and the extractions of the essential structure have still been discussed. The merged synergies observed in the present study might provide not only evidence for the recruitment patterns of muscle synergies, but also the significance of task setting in experiments, which could lead to extract unessential structure of muscle synergies. In our suggestion, the merging indicated that the structure was not due to the spatial configuration of muscle synergy, but rather to descending commands through the common neural input (discussed above). Therefore, this merging may not represent the essential structure, or minimum unit, of muscle synergies in the neural circuitry. As limiting our experimental conditions to the joint pattern of 50°/180° (knee/hip), about four synergies, including the merging, were estimated (Fig. 6). Therefore, the constraints of task setting may frequently lead to misinterpretation when the main purpose of a study is not to examine the low dimensional structure of muscle activities in a given task space, but to clarify the essential structure of muscle synergy in neural circuitry. Thus, to examine the essential structure of muscle synergy, further studies that focus on various changes in neurophysiological parameters are needed.

In summary, we found the merging or decomposing of lower limb muscle synergies, which were selectively recruited, depending on the required force-generating capability as a function of the joint angles. These results led us to conclude that the CNS controls the activations of muscle synergies based on the joint angle during multidirectional isometric force generation.


Steele KM, Tresh CM, Perreault EJ. The number of choice of muscles impact the results of muscle synergy analyses. *Front Comput Neurosci* 7: 1–9, 2013.


