

1 **Flexible recruitments of fundamental muscle synergies in the trunk and lower limbs for highly**
2 **variable movements and postures**

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19 **Abstract**

20 The extent to which muscle synergies represent the neural control of human behavior remains unknown.
21 Here, we tested whether certain sets of muscle synergies that are fundamentally necessary across
22 behaviors exist. We measured the electromyographic activities of 26 muscles including bilateral trunk
23 and lower limb muscles during 24 locomotion, dynamic and static stability tasks, and extracted the
24 muscle synergies using non-negative matrix factorization. Our results showed that 13 muscle synergies
25 that may have unique functional roles accounted for almost all 24 tasks by combinations of single and/or
26 merging of synergies. Therefore, our results may support the notion of the low dimensionality in motor
27 outputs, in which the central nervous system flexibly recruits fundamental muscle synergies to execute
28 diverse human behaviors. Further studies using manipulations of the central nervous system and/or
29 neural recording are required the neural representation with such fundamental components of muscle
30 synergies.

31 Introduction

32 To execute human movements, the central nervous system (CNS) must control many degrees
33 of freedom from thousands of motor units within hundreds of skeletal muscles ¹. To simplify the
34 production of movements, the CNS may rely on a limited number of neural mechanisms ². Indeed, the
35 CNS exploits a reduced set of pre-shaped neural pathways, called muscle synergies, to achieve a large
36 variety of motor commands ^{3,4}. Muscle synergy theory assumes that the CNS combines a few sets of
37 activation to build muscle activation commands ⁵. Evidence of a limited set of muscle synergies has
38 been found in various human motor behaviors such as locomotion ⁶⁻⁹, reaching tasks ¹⁰, and sports
39 activities ¹¹⁻¹³.

40 It has been proposed that muscle synergies are shared across various motor tasks ^{5,14,15}.
41 Shared synergies facilitate the robustness of the neuromuscular system, which is thought to be
42 beneficial for stable postural control ^{15,16}, development ¹⁷, and expert motor skills ¹⁸. In contrast, studies
43 have also discovered the existence of task specific synergies to meet each biomechanical demand of
44 motor tasks ^{19,20}. An experimental study in frogs investigated muscle synergies during natural behaviors
45 such as walking, jumping, and swimming, indicating that each motor behavior is the consequence of a
46 combination of both synergies shared between behaviors and synergies specific to each or a few
47 behaviors ²¹. However, a substantial number of in-born and learned human movements and postures
48 that presents different behavioral contexts also exist ²². As such, it is possible that the sum of all shared
49 and task-specific synergies employed during a variety of human movements and postures may exceed
50 the number of relevant muscles ²³, violating the existence of a low dimensionality of human movement
51 controls based on muscle synergy theory ^{23,24}.

52 A previous study found that upper-limb hand exploration tasks for five sectors (frontal, right, left,
53 horizontal, and up) were modulated by seven muscle synergies (i.e., seven cluster centroids across
54 participants) with different functional roles ¹⁴. Furthermore, another study found that all three muscle
55 synergies of cycling can be well reconstructed by merging muscle synergies extracted from walking ²⁵.
56 Thus, the interpretation of existing literature suggests that the CNS may select the appropriate subsets
57 of muscle synergies, either independently or merged, from a large set that are established to execute
58 the substantial number of behavioral contexts and demands ^{14,25,26}. However, previous studies have not

59 recorded a large set of electromyographic (EMG) activities during a variety of human movements and
60 postural tasks with different biomechanical contexts to investigate the neural basis of muscle synergies.

61 We hypothesized the existence of fundamentally necessary muscle synergies that account for
62 a diverse range of human movements and postures. To investigate this possibility, we first extracted
63 muscle synergies from an EMG recording dataset made from 24 motor tasks of the trunk and lower
64 limb muscles to define the fundamental muscle synergies utilized across a highly variable context of
65 movements and postures. We then examined how these fundamental muscle synergies were used in
66 each motor task by comparing them to those extracted from the EMG datasets in each task.

67 **Methods**

68 *Experimental protocol*

69 Ten healthy volunteers (aged 21–35 years, all men) participated in the study. Each participant
70 provided written informed consent for participation in the study. The study was conducted in accordance
71 with the Declaration of Helsinki and was approved by the local ethics committee of the University of
72 Tokyo.

73 We focused on fundamental movement and postural tasks that serve as building blocks for the
74 efficient and effective execution of a variety of daily living activities and highly skilled actions such as
75 sports^{22,27,28}. Specifically, we used tasks that required movements through space (locomotion) and
76 controls against gravity (stability) in any plane²². Thus, all participants were asked to perform the 24
77 tasks described in Table 1. Supplementary Table S1 online presents the details of each movement and
78 postural task. The order of tasks was randomly assigned.

79 *Data collection*

80 EMG activity was recorded from the following 26 muscles distributed across the trunk and lower
81 limbs (13 bilateral muscles): tibialis anterior (TA), gastrocnemius medialis (MG), vastus medialis (VM),
82 rectus femoris (RF), biceps femoris (long head, BF), gluteus maximus (GM), gluteus medius (Gmed),
83 rectus abdominis (RA), oblique externus (OE), erector spinae at L2 (ESL2), erector spinae at Th9
84 (ESTh9), erector spinae at Th1 (ESTh1), and latissimus dorsi (LD). EMG activity was recorded using a
85 wireless EMG system (Trigno Wireless System; DELSYS, Boston, MA, USA). The EMG signals were

86 bandpass filtered (20–450 Hz), amplified (with a 300-gain preamplifier), and sampled at 1000 Hz.
87 Three-dimensional ground reaction force data were recorded at 1000 Hz from the force plates under
88 each belt of the treadmill.

89 *EMG processing*

90 The low-pass cut-off frequency influences the smoothing of EMG patterns and thus impacts the
91 number of extracted modules²⁹. To adequately compare EMG envelopes (i.e., EMG patterns with the
92 same smoothing) of movements performed for various tasks that had different features of dynamic
93 activities, the low-pass cut-off frequency must be adjusted for each task. Thus, an iterative adaptive
94 algorithm was used to extract the optimal EMG envelopes³⁰. This algorithm utilized information theory
95 to find a sample-by-sample optimal root-mean-square window for envelope estimation³⁰. This algorithm
96 allowed the filter to adequately follow fast changes in EMG activity while maintaining optimal extraction
97 when the EMG amplitude is changing slowly³⁰. A previous study used this algorithm and successfully
98 reconstructed muscle synergies during walking in individuals with and without transfemoral amputation
99³¹. The smoothed EMG envelopes were time-interpolated to generate 200 timepoints for each trial,
100 except for the right and left single-leg stance tasks.

101 We created the following two types of EMG matrices for each subject to examine the repertoire
102 of fundamentally necessary muscle synergies and how these synergies are used in each task. Similar
103 to previous studies^{14,32}, we pooled the EMG matrices of all 24 tasks to create an “all-task” EMG matrix
104 for each subject (i.e., the matrix was composed of the 26 muscles × the summation of timepoints of the
105 24 single-task EMG matrices) to extract fundamental muscle synergies across all tasks. We also
106 created a “single-task” EMG matrix composed of the 26 muscles × 1400 timepoints (seven strides or
107 repetitions × 200 timepoints for each task, except the right and left single-leg stances) for each of the
108 24 tasks to extract muscle synergies.

109 *Muscle synergy analysis*

110 In our analysis, we first identified the muscle synergies of each task for each subject using a
111 factorization algorithm of single-task EMG matrices, and then synergies of all tasks were extracted from
112 all-task EMG matrices using the same algorithm. We then proceeded to characterize representative

113 muscle synergies of individual tasks and all tasks across all participants using a hierarchical clustering
114 algorithm. Lastly, we analyzed the similarity between synergy cluster centroids of each individual task
115 and single or merged synergies of the all-task matrix to investigate how muscle synergies utilized by all
116 tasks contribute to the execution of each individual movement.

117 To explore muscle synergies, nonnegative matrix factorization (NMF) was used for each
118 subject from the single-task EMG matrices and the all-task EMG matrix. NMF has previously been
119 described as a linear decomposition technique^{33,34} according to equation (1):

120

$$121 \quad M = W \cdot C + e \quad (1)$$

122

123 where M ($m \times t$ matrix, where m is the number of muscles and t is the number of samples, i.e., the
124 spatiotemporal profiles of muscle activity) is a linear combination of muscle weighting components: W
125 ($m \times n$ matrix, where n is the number of muscle synergies) and C ($n \times t$ matrix, representing temporal
126 pattern components; and e is the residual error matrix. Each EMG vector in the matrix corresponding
127 to each muscle activity was normalized to the maximum amplitude across all tasks so that all muscle
128 scales ranged from 0 to 1. Prior to extracting muscle synergies, each muscle vector in the data matrix
129 was standardized to have unit variance, thus ensuring that the activity in all muscles was equally
130 weighted. However, after each synergy extraction, the unit variance scaling was removed from the data
131 so that each muscle variable ranged from 0 to 1 for data inspection and interpretation³⁵. To determine
132 the number of muscle synergies, NMF was applied to extract each possible n from 1 to 26 from each
133 dataset. The variance accounted for (VAF) by the reconstructed EMG (M) was calculated at each
134 iteration to extract the optimal number of muscle synergies. VAF was defined as a 100 \times square of the
135 uncentered Pearson's correlation coefficient^{36,37}. To prevent the extracted synergies from assuming a
136 suboptimal local minimum, each synergy extraction was repeated 100 times. Thus, the iteration with
137 the highest VAF was maintained⁸. We defined the optimal number n as the number fulfilling the
138 following two criteria: First, n was selected as the smallest number of modules that accounted for >90%
139 of the VAF³⁶. Second, n was the smallest number to which adding another module did not increase
140 VAF by >5%³⁸.

141 *Clustering the modules across participants*

142 We identified the representative synergy vectors across participants using hierarchical
143 clustering analysis (Ward's method, Euclidian distance) of muscle synergies for each task and all tasks
144 ^{8,39}. The optimal number of clusters was determined using the gap statistic ⁴⁰. Subsequently, the muscle
145 synergies in each cluster were averaged across participants.

146 *Contributions of the muscle synergy of all tasks to the execution of each task*

147 To explore whether the muscle synergy defined by the all-task matrix contributes to executing
148 each task of movements and postures, the similarity between muscle synergies of single-task and all-
149 task matrices was quantified by the scalar product (SP) between these centroids of the synergy clusters
150 (normalized to unit vectors). For every comparison, each of the synergy cluster centroids of all-task was
151 matched to a synergy cluster centroid of each task by maximizing the total scalar product values.
152 Synergy clusters that could not be matched with $SP \geq 0.75$, were classified as unmatched ⁴¹.

153 *Contributions of merging muscle synergy of all tasks towards single-task execution*

154 We also expected that all-task muscle synergies can be merged to execute each single task of
155 movement and posture ⁴⁰. Thus, the merged synergies as a linear combination of the contributing
156 synergies were modeled by the following formula ^{18,41}:

157

$$158 \quad W_k \approx \sum_{i=0}^{N_b} D_i W_i, k = 1, \dots, n_b$$

159

160 where W_k is the k th muscle synergy vector from each individual task, W_i is the i th muscle synergy vector
161 derived from an all-task matrix, N_b is the number of synergies that contribute to the merging, and D_i is
162 a non-negative coefficient that scales the i th synergy in the merging. D_i was obtained from a non-
163 negative least-squares fit, implemented using MATLAB (function `lsqnonneg`). W_k and W_i were
164 normalized as unit vectors. Following criteria from previous studies ^{18,41}, the synergy merging was
165 identified when $N_b \geq 2$, $D_i \geq 0.2$ for all i , and the SP between $\sum_{i=0}^{N_b} D_i W_i$ and W_k was ≥ 0.75 .

166 To assess whether the synergies from each task can be explained as merging of synergies
167 from all tasks, we first identified the synergy cluster centroids of single-task and synergies of the all-

168 task (described above) and reconstructed each synergy cluster centroid of each individual task by
169 merging every possible combination of the synergy cluster centroids of all tasks.

170 **Results**

171 *Muscle synergies extracted from all-task EMG matrices*

172 Figure 1 presents 13 muscle synergies of an all-task matrix incorporating 24 trunk and lower
173 limb movement tasks (W1 to W13), which were grouped by cluster analysis across ten participants;
174 Table 2 summarizes the characteristics of the muscle synergies. Visual inspection revealed that muscle
175 synergies W1 to W5 were largely composed of the right-side muscles, while muscle synergies W6 to
176 W10 were mainly composed of the left-side muscles. Thus, we categorized W1 to W5 as muscle
177 synergies with right-side dominant patterns and W6 to W10 as muscle synergies with left-side dominant
178 patterns. The following pairs showed high similarity when the muscles in W6 to W10 were reordered so
179 that muscles on the left side of W6 to W10 corresponded to the same muscles on the right side of W1
180 to W5: W1 and W6 (SP = 0.93), W2 and W7 (SP = 0.97), W3 and W8 (SP = 0.97), W4 and W9 (SP =
181 0.85), W5, and W10 (SP = 0.93). Others such as W11, W12, and W13 were categorized as bilateral
182 patterns.

183 *Relationship between muscle synergies extracted from all-task EMG matrices and those extracted* 184 *from single-task matrices*

185 Table 3 presents the number of muscle synergies in each task, which were well explained (SP
186 > 0.75) by independent and merged muscle synergies from the all-task EMG matrices. Of note, all
187 synergies of each task except the one for the left single-leg stance could be explained by either single
188 or linear combination of multiple synergies from the all-task EMG matrices (SP > 0.75). The details of
189 the contributions of muscle synergies of all tasks to each task execution are presented in
190 Supplementary Table S2 online.

191 Figures 2 and 3 present examples of relationships between muscle synergies from the all-task
192 EMG matrices and those from the single-task EMG matrices: locomotion tasks including walking,
193 running, bilateral jump and sit-to-stand-to-sit (Fig. 2), and stability tasks including left lunge, cat-and-
194 dog, forward bend, and left rotation (Fig. 3). The relationships between muscle synergies from the all-

195 task EMG matrices and those from the other single-task EMG matrices are shown in Supplementary
196 Figs. S1 and S2 online.

197 **Discussion**

198 Several studies have investigated shared or merged muscle synergies across different tasks
199 such as walking and running^{8,42}, walking and cycling²⁵, various directions of reaching^{14,32} and stepping
200 and non-stepping postural controls³⁵. Their results indicated that different human behaviors use the
201 fundamental motor modules that reflect the functional control units as a neural constraint on motor
202 outputs. However, the extent to which representations of muscle synergies in the control of diverse
203 human behaviors have not been comprehensively investigated in previous studies. In our study, we
204 extracted muscle synergies from a large set of EMG (26 muscles) activities across bilateral locations of
205 the trunk and lower limbs during 24 locomotion and stability tasks that were fundamental for a variety
206 of physical activities. We found that 13 clusters of fundamental muscle synergies accounted for almost
207 all synergy clusters of each of the 24 tasks. When we compared the synergy clusters extracted from
208 individual tasks across participants, we found a high similarity ($SP > 0.75$) of a single or multiple linear
209 combinations from the 13 fundamental muscle synergy clusters extracted from all tasks across
210 participants. In the following sections, we discuss the possible neural mechanism underlying a diverse
211 set of human behaviors based on the assumptions that muscle synergies represent motor modules to
212 coordinate patterns utilized by the CNS²⁴.

213 *Characteristics of muscle synergies across 24 tasks*

214 We applied cluster analysis to the muscle synergies from the all-task EMG matrix across
215 participants, and identified 13 synergy clusters. As shown in Table 2, we broadly categorized muscle
216 synergies into three sets based on the major contributions of the muscles (i.e., right muscle patterns,
217 left muscle patterns, and bilateral muscle patterns). In the right and left muscle patterns, W1 and W6
218 were dominated by muscles around the ankle and knee joints (i.e., TA, RF, and VM). W2 and W7 were
219 mainly composed of muscles related to the knee and hip joints (i.e., RF, VM, Gmed, and GM), and W3
220 and W8 employed the ankle and hip joints (i.e., MG and Gmed). Furthermore, BF mainly contributed to
221 W4 and W9. While all four pairs were predominantly composed of extensor muscles that can move and
222 stabilize the body during locomotion and postural tasks, they may have a distinct functional feature

223 because the different tasks require different combinations of muscle synergies (Supplementary Table
224 S2 online). In contrast, the pairs of W5 and W10, W11, W12, and W13 were composed of back muscles
225 (i.e., ES, LD) and abdominal muscles (i.e., RAS and OE) either in unilateral or bilateral patterns (Table
226 2). Notably, they were widely observed across 24 tasks (Supplementary Table S2 online) and may be
227 used for bilateral trunk movements or stabilization of the body accompanied by W1 to W10 with
228 relatively low levels of trunk muscle activities when the lower limbs are moving⁴³. Although we still do
229 not know how muscle synergies in our study arise and whether they reflect neural structure for motor
230 outputs, 13 muscle synergies extracted from our study may form a repertoire of whole lower limb and
231 trunk muscle activation patterns, which can be shaped by biomechanical interactions and constrain the
232 environment through a lifetime^{18,44}.

233 *Hypothetical neural mechanisms underlying muscle-synergy controlling diverse behavior*

234 If we assume that the muscle synergy extracted from the whole-task EMG matrices in our data
235 may have a unique set of networks in which each synergy provides functionally necessary compositions
236 in muscle activities, then one can expect that any combinations of these synergies may provide stable
237 and predictable motor outputs in a diverse range of human behaviors⁴⁴. The strength of our finding is
238 that it indicates that there is a set of fundamental muscle synergies shared with different combinations
239 of these synergies in single and/or merging states to produce 24 locomotion and stability tasks.
240 Considering that several previous studies in animal and human experiments have confirmed that
241 muscle synergies observed in motor behaviors have cortical and subcortical neural underpinnings^{45–48},
242 it can be reasonably assumed that they are inherently robust and may be encoded in the CNS. Here,
243 we hypothesize the existence of neural mechanisms underlying the flexible recruitment of muscle
244 synergies in various combinations for executing a variety of movements and postures. For example, we
245 extracted four synergy clusters in locomotion tasks, including walking, running, and bilateral jumps.
246 Surprisingly, as shown in Fig. 2 and Supplementary Table S2 online, all synergies in the three tasks
247 used almost the same synergies of all tasks with different combinations to be merged ($SP > 0.8$).
248 Furthermore, even in the unique dynamic tasks such as cat-and-dog as well as simple axial tasks such
249 as forward bend and rotation, subsets of these 13 fundamental muscle synergies were used, either
250 independently or in a merging state (Fig. 3 and Supplementary Table S2 online).

251 Interestingly, we found that muscle synergies in 24 locomotion and stability tasks were
252 predominantly reconstructed by merging various combinations of fundamental muscle synergies (Table
253 3). A study reported that muscle synergies of cycling can result from merging synergies of walking ²⁵.
254 Another recent study showed the merging of original muscle synergies during running through running
255 training ¹⁸. It is suggested that merged synergies were the result of the co-recruitment of multiple muscle
256 synergies by neural networks driving the muscle synergies represented as C in equation 1 ^{24,44}. Based
257 on previous studies, we speculate that the upstream driving layer (e.g., C_{task} in Fig.4) may flexibly recruit
258 the fundamental muscle synergies (e.g., W' in Fig. 4) located at different levels from the driving layers
259 in the motor hierarchy to execute highly variable tasks (the schematic structure in Fig. 4). Our
260 hypothesis is possibly equivalent to a generalized two-level CPG model for the control of locomotor
261 muscle activity ⁴⁹. The model consists of two distinct neural network layers: 1) a pattern formation (PF)
262 network layer that defines groups of synergistic and antagonistic motoneuron pools and 2) a rhythm
263 generation layer that controls the activity of PF networks. However, it should be noted that the exact
264 neural substrates encoding muscle synergies and their driving networks in humans remain largely
265 unknown.

266 Since we propose that upstream driver C presents synchronous recruitments of the
267 fundamental muscle synergies that have distinct functional roles in organizing muscle synergies for the
268 24 locomotion and stability tasks, it is possible that the CNS may also coordinate other simple or
269 complex human behaviors using certain combinations of these synergies. Thus, muscle synergies
270 during human behaviors found in previous extensive research may reflect layered structures composed
271 of the fundamental muscle synergies extracted from our study. The advantage of these hypothetical
272 mechanisms is that it prevents the sum of all muscle synergies from exceeding the number of relevant
273 muscles utilized during diverse human behaviors, supporting the premise of compendium in
274 coordinative patterns to execute several movements under different biomechanical conditions ²³.
275 Further research is needed to investigate the muscle synergies identified by factorization algorithms
276 coupled with CNS manipulations and/or neural recordings (e.g., CNS stimulations, spinalization, and
277 electroencephalogram) to validate the neural representation of the fundamental muscle synergies
278 observed in our study ²⁴.

279 *Clinical implications*

280 The results of this study may have several clinical implications. First, several studies have
281 investigated muscle synergies in individuals with different characteristics, such as musculoskeletal and
282 neurological disorders ⁵⁰⁻⁵² as well as athletes ^{8,18,53}. Since we identified the fundamental muscle
283 synergies that may underlie diverse human behaviors in healthy individuals, investigating the changes
284 in muscle synergies such as the number of synergies as well as their compositions in a population of
285 interest may facilitate the understanding of distinct features in motor controls that are associated with
286 severity of symptoms ^{50,54} or that profile myriad skills and performance in athletes ^{27,28}. Second, recent
287 studies have shown the efficacy of muscle synergy-based interventions using functional electrical
288 stimulations (FES) on motor performance in stroke survivors ^{55,56}. Since our study found that each
289 synergy may have functionally plausible patterns that play an important role in executing diverse human
290 movements and postures, it may provide a rationale for designing interventions that use FES to focus
291 on these functional sets of muscle synergies to improve motor performance. Lastly, we found that
292 different tasks with various biomechanical demands and constraints may largely share the same muscle
293 synergies with different combinations of synergies to be merged. Thus, clinicians may choose to
294 intensively train a particular task to transfer the effectiveness to other tasks ⁵⁷, given that the transfer of
295 motor learning effects among tasks will be high when muscle synergies involved in different motor tasks
296 are shared ⁵⁸.

297 *Limitations*

298 Our study had several limitations. First, it has been reported that the number of recording
299 muscles may affect the amount and structure of muscle synergies ⁵⁹. Although EMG recordings in our
300 study were relatively large (i.e., 26 EMG channels), we limited the recording of EMGs from only the
301 major muscles in the trunk and lower limbs. Similarly, we were also limited to 24 fundamental tasks that
302 involved only locomotion and postural tasks. As such, tasks that accompany coordination between the
303 upper limbs, trunk, and lower limbs were not considered ⁵. Thus, it is conceivable that some relevant
304 muscle synergies may have been missed in our study. Second, because we used a larger set of EMG
305 recordings and tasks, our time constraint during experiments precluded the measurement of kinematic
306 data such as joint angles as well as velocities, and allowed variability of movements in each task, which
307 may impact muscle synergy extractions. The lack of availability of kinematic data ceases to separates
308 the movement phase and thus unable to investigate the contributions of the fundamental muscle

309 synergies for each phase of each task⁴⁴. Lastly, although we extract the fundamental muscle synergies
310 using NMF that may present neural mechanisms for diverse human behaviors, whether the
311 factorization-derived synergies reflect neural organization to coordinate human behaviors remains
312 questionable²⁴. This can be due to the possibility that extracted muscle synergies represent
313 biomechanical constraints of tasks rather than neural constraints⁶⁰ and the nonlinearity in magnitude
314 summations of the EMG or force vectors^{61,62}.

315 **Conclusion**

316 In this paper, we extracted a repertoire of fundamental muscle synergies from the EMGs during
317 a variety of human behaviors that involve trunk and lower limb movements in healthy individuals. We
318 found that the flexible recruitment of the fundamental muscle synergies in either the independent or
319 merging state can account for almost all 24 behaviors, including locomotion and stability tasks. Our
320 findings may support the notion that low dimensional motor modules are required in a diverse range of
321 human behaviors with different biomechanical contexts.

322 **Data availability**

323 All data are available upon reasonable request.

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460

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463 **Author contributions**

464 Conception and design of the work H.S., H.Y. and A.S.; data acquisition H.S., A.S., and T.K.; data
465 analysis H.S. and H.Y.; data interpretation H.S., H.Y., A.S., T.K. and K.N.; drafted the manuscript
466 H.S., H.Y., A.S., T.K. and K.N. All authors approved the final version of the manuscript and agree to
467 be accountable for the content of the work.

468 **Additional Information**

469 The authors declare no competing interests.

470

471 **Figure legends**

472 **Figure 1. Muscle synergies of all tasks. (a)** Centroids of the hierarchical clustering performed on the
473 muscle synergies of all tasks across ten participants. **(b)** Dendrograms represent the results of cluster
474 analysis (Ward's method, Euclidian distance) where optimal number of clusters were determined based
475 on the gap statistics.

476

477 **Figure 2. The relationship between muscle synergies of all tasks and muscle synergies of**
478 **locomotion tasks including (a) walk, (b) run, (c) bilateral jump and (d) sit-to-stand-to-sit.** The
479 figures show the synergy cluster centroids of these tasks that could be explained by either a single or
480 linearly combined multiple synergy cluster centroids of all tasks (synergies in blue) matched by
481 maximizing scalar product > 0.75 . Observed muscle synergies extracted from the single-task EMG
482 (orange) and their reconstructions by merging their respective W_1 - combinations (dark orange) are
483 further presented.

484

485 **Figure 3. The relationship between muscle synergies of all tasks and muscle synergies of**
486 **stability tasks including (a) left lunge, (b) cat-and-dog, (c) forward bend and (d) left rotation.** The
487 figures show the synergy cluster centroids of these task that could be explained by either a single or
488 linearly combined multiple synergy cluster centroids of all tasks (synergies in blue) matched by
489 maximizing scalar product > 0.75 . Observed muscle synergies extracted from the single-task EMG
490 (orange) and their reconstructions by merging their respective W_1 - combinations (dark orange) were
491 further presented.

492

493 **Figure 4. A hypothetical neural mechanism of merged fundamental muscle synergies with its**
494 **temporal patterns in a diverse range of human behaviors.** This model shows that the CNS flexibly
495 recruits multiple synergies for different tasks. For example, $C_{task1-1}$ with W_1 and W_2 and $C_{task1-2}$ with W_2
496 and W_3 turn on while $C_{task2-1}$ and $C_{task2-2}$ turn off to execute task 1. Similarly, $C_{task1-1}$ with W_1 , W_2 , and W_3
497 and $C_{task1-2}$ with W_2 , W_3 , and W_4 turn on, ceasing to be active in $C_{task1-1}$ and $C_{task1-2}$ for task 2.

498 **Table legends**

499 **Table 1. Movement and postural tasks.** Shown are the order of 24 locomotion and stability task.
500 Stability tasks are divided into three subcategories: static postures, dynamic postures and axial. Rt:
501 right; Lt: left.

502

503 **Table 2. Characteristics of muscle synergy clusters of all tasks.** The following pairs showed high
504 similarity when the muscles in W6 to W10 were reordered so that muscles on the left side of W6 to
505 W10 corresponded to the same muscles on the right side of W1 to W5: W1 and W6 (SP = 0.93), W2
506 and W7 (SP = 0.97), W3 and W8 (SP = 0.97), W4 and W9 (SP = 0.85), W5, and W10 (SP = 0.93).
507 We categorized W1 to W5 as muscle synergies with right-side dominant patterns and W6 to W10 as
508 muscle synergies with left-side dominant patterns. W11, W12, and W13 were categorized as bilateral
509 patterns. Muscles that account for > 0.5 of activation levels are classified as major muscles and
510 between 0.1 to 0.5 were as minor muscles. isp: ipsilateral, con: contralateral, bil: bilateral.

511

512 **Table 3. The relationship between synergy clusters of each task and synergy clusters of all**
513 **tasks.** The number of synergy clusters for each task and the number of a single or merged synergy
514 cluster centroids of all tasks that were well matched (scalar product > 0.75) or unmatched to a
515 synergy cluster centroid of each task. Bil: bilateral; Rt: right; Lt left; JP: jump; SJP: single leg jump;
516 STS: sit-to-stand-to-sit; SLS: single leg stance; DS: deep squat; SS: single leg squat; LG: lunge; RB:
517 rocking backward; RF: rocking forward; CE: cross extension; CD: cat-and-dog; FB; forward bend; SB:
518 side bend; BB: backward bend; RT: rotation.

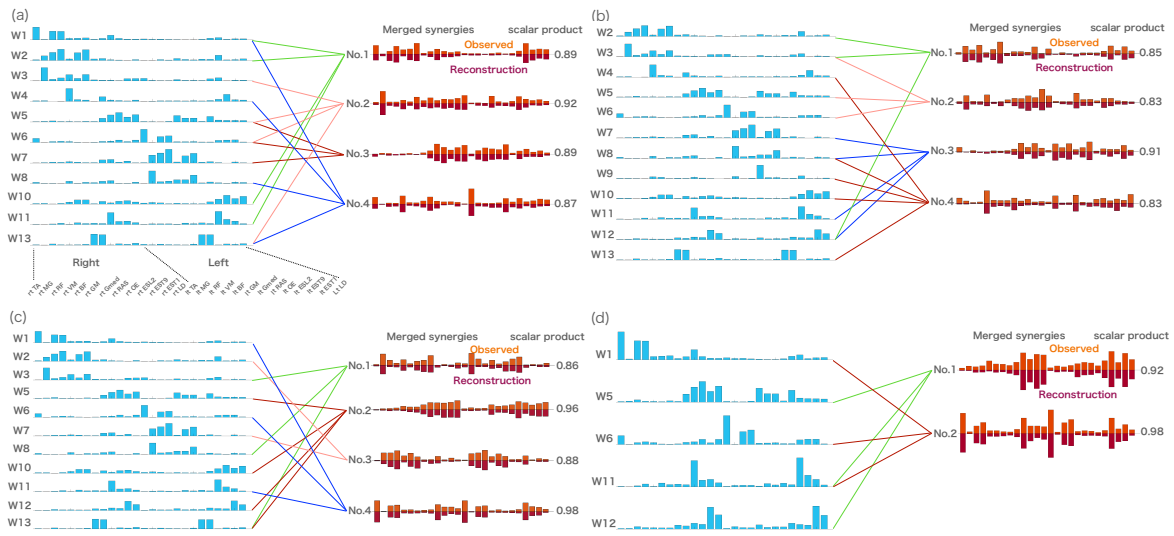
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520 Figure 1:



521

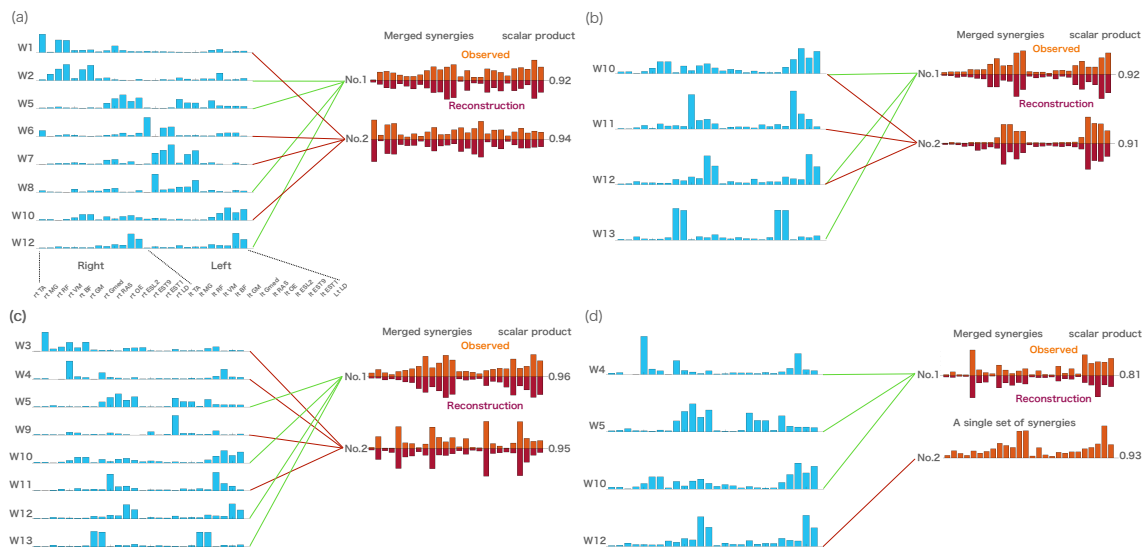
522 Figure 2:



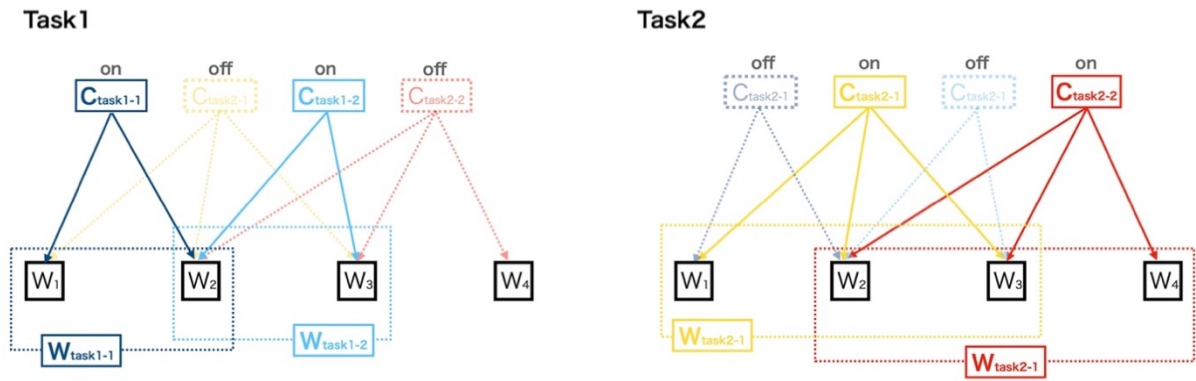
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525 Figure 3:



528 Figure 4:



529

530 Table 1:

Locomotion		1	Walk (1.5 m/s)	531
		2	Run (2.7 m/s)	532
		3	Bilateral jump	533
		4	Rt single leg jump	534
		5	Lt single leg jump	535
		6	Sit to stand to sit	536
Stability	Static postures	7	Rt single leg stance	537
		8	Lt single leg stance	538
	Dynamic postures	9	Deep squat	539
		10	Rt single leg squat	540
		11	Lt single leg squat	541
		12	Rt lunge	542
		13	Lt lunge	543
		14	Rocking backward	544
		15	Rocking forward	545
		16	Rt cross extension	546
		17	Lt cross extension	547
		18	Cat-and-dog	548
	Axial	19	Forward bend	549
		20	Rt side bend	550
		21	Lt side bend	551
		22	Backward bend	552
		23	Rt rotation	553
		24	Lt rotation	554
			555	

556 Table 2:

Unilateral patterns		Major muscles	Minor muscles
Right patterns	Left patterns		
W1	W6	ispTA, ispRF, ispVM	(ispESL2, ispEST9, ispEST1, conTA, conESL2, conEST9, conLD)
W2	W7	ispVM, ispRF, ispGM, ispGmed	(ispMG, ispOE, conBF, conOE, conESL2)
W3	W8	ispMG, ispGmed	(ispRF, ispVM, ispBF, ispGM, ispEST1, ispLD, conTA, conBF, contOE, conESL2)
W4	W9	ispBF	(ispMG, ispGM, ispOE, ispESL2, conESL2, conEST9)
W5	W10	ispEST9, ispLD	(ispOE, ispESL2, ispEST1, conBF, conGM, conGmed, conOE, conESL2, conEST9, conEST1, conLD)
Bilateral patterns			
M11		bilESL2	(bilEST9, bilEST1)
M12		bilEST1	(bilLD)
M13		bilRAS, bilOE	

557

