European Journal of Applied Physiology (2021) 121:1009–1025
https://doi.org/10.1007/s00421-021-04604-9

INVITED REVIEW

How to improve the muscle synergy analysis methodology?

Nicolas A. Turpin[1] · **Stéphane Uriac**[1] · **Georges Dalleau**[1]

Received: 4 August 2020 / Accepted: 10 January 2021 / Published online: 26 January 2021

Abstract

Muscle synergy analysis is increasingly used in domains such as neurosciences, robotics, rehabilitation or sport sciences to analyze and better understand motor coordination. The analysis uses dimensionality reduction techniques to identify regularities in spatial, temporal or spatio-temporal patterns of multiple muscle activation. Recent studies have pointed out variability in outcomes associated with the different methodological options available and there was a need to clarify several aspects of the analysis methodology. While synergy analysis appears to be a robust technique, it remain a statistical tool and is, therefore, sensitive to the amount and quality of input data (EMGs). In particular, attention should be paid to EMG amplitude normalization, baseline noise removal or EMG filtering which may diminish or increase the signal-to-noise ratio of the EMG signal and could have major effects on synergy estimates. In order to robustly identify synergies, experiments should be performed so that the groups of muscles that would potentially form a synergy are activated with a sufficient level of activity, ensuring that the synergy subspace is fully explored. The concurrent use of various synergy formulations-spatial, temporal and spatio-temporal synergies- should be encouraged. The number of synergies represents either the dimension of the spatial structure or the number of independent temporal patterns, and we observed that these two aspects are often mixed in the analysis. To select a number, criteria based on noise estimates, reliability of analysis results, or functional outcomes of the synergies provide interesting substitutes to criteria solely based on variance thresholds.

Keywords Matrix factorization · Model selection · EMG processing · Motor module · Primitives

Abbreviations

EMG	Electromyography
ICA	Independent component analysis
iEMG	Integrated EMG
NNMF	Non-negative matrix factorization
PCA	Principal component analysis
pNMF	Projective non-negative matrix factorization
RMS	Root mean square
SNR	Signal to noise ratio
SSE	Sum of squared errors
SST	Total sum of square
SVD	Singular value decomposition
VAF	Variance accounted for

Introduction

Muscle synergy analysis is a tool used in various domains such as neurosciences, robotics, sport sciences or rehabilitation to gain insights about basic motor control science, motor coordination strategies or to quantify functional deficits in pathologies. The core of the method is to reduce the number of dimensions of the electromyographic (EMG) data, i.e., the number of muscles, to a limited set of meaningful variables, referred to as synergies. Synergy analysis and in particular muscle synergy analysis suffers from a critical lack of consensus throughout the many steps it requires (presented in Fig. 1). Several authors cautioned that their results are sensitive to methodological choices (Banks et al. 2017) and

Communicated by Michael Lindinger.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00421-021-04604-9.

✉ Nicolas A. Turpin
nicolas.turpin@univ.reunion.fr

Stéphane Uriac
stephane.uriac@univ.reunion.fr

Georges Dalleau
georges.dalleau@univ.reunion.fr

[1] IRISSE (EA 4075), UFR SHE-STAPS Department, University of La Réunion, 117 Rue du Général Ailleret, 97430 Le Tampon, France

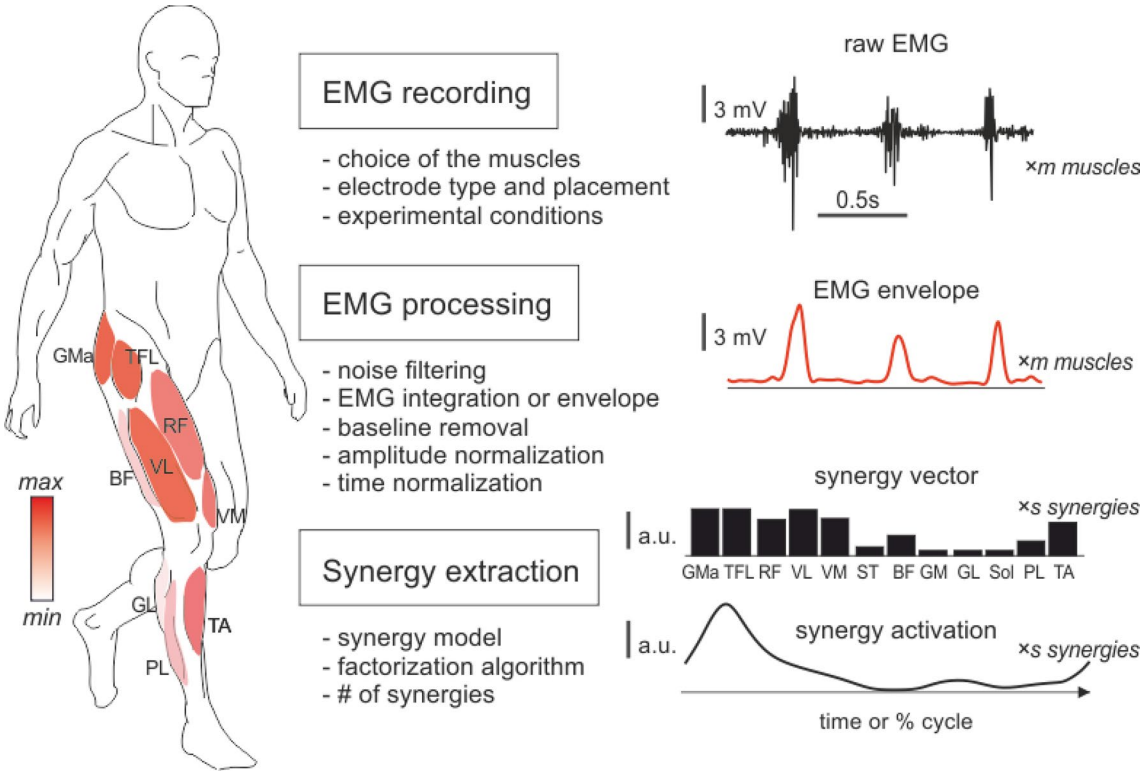

Fig. 1 Synergy analysis steps. Muscle synergy analysis consists of identifying the structure of muscle activations, either at the spatial level—represented by muscle synergy vectors—or at the temporal level—represented by muscle synergy activations. The analysis requires three main steps: EMG recording, EMG processing and synergy extraction. A lower limb synergy during walking is illustrated. Weightings of the different muscles in the synergy vector represent their relative contribution, and the synergy activation represents how the group of muscles is activated over time. The synergy vectors and synergy activations are unitless. However, multiplying the synergy vector by the synergy activation allows to recover the level of activity of the different muscles associated with a given synergy in the unit of the EMG envelopes (illustrated in color on the left of the image). *Gma* gluteus maximus, *TFL* tensor fasciae latae, *RF* rectus femoris, *VL* vastus lateralis, *VM* vastus medialis, *ST* semi-tendinosus, *BF* biceps femoris, *GM* gastrocnemius medialis, *GL* gastrocnemius lateralis, *Sol* soleus, *PL* peroneus longus, *TA* tibialis anterior

experimental conditions (Steele et al. 2015b). Some issues, of which model selection is the most prominent example, remain unresolved. We reviewed different aspects of synergy analysis to provide a better understanding of the effects of choosing one methodological approach over another and to provide recommendations whenever possible.

A systematic review of the literature was first performed to analyze the methodologies in use (see Supplementary Material). Only the conclusions are presented below. In this review the synergy extraction techniques are presented first as they are essential to understanding how characteristics of EMG signals affect the synergy analysis results.

Definition of the terms

A vast amount of literature demonstrated that motor actions and movements in both vertebrates and invertebrates can be decomposed into elemental coordinative structures often referred to as *synergies,* which etymologically means "work together". Other terms which have been used include mode, motor module, motor primitive, motor schemas, prototypes, or sub-movement (Latash 2020; Hogan and Sternad 2013; Mussa-Ivaldi and Solla 2004; Flash and Hochner 2005). These elemental structures have been evidenced at several levels of the motor hierarchy in the form of coordinated neural ensembles, joint angles, joint torque or muscle activations, for example (Gallego et al. 2017; Giszter 2015; Flash and Hochner 2005; Holdefer and Miller 2002). It is widely accepted that these basic elements represent building blocks of human movement patterns and that they could simplify the control of the numerous degrees of freedom of the body. These basic elements are also thought to be independent, meaning that they can be combined without interacting with each other—referred to as the principle of superposition (Flash and Hochner 2005; Bizzi and Cheung 2013).

Synergies have been particularly studied in relation to structured muscle activation patterns. This strategy appears reasonable given the high number of muscles that need to be controlled in general and given the fact that spinal motoneurons are considered to be the final common pathway of both

spinal and supraspinal motor influences. A simple definition of a muscle synergy given by Lee (1984) is "a set of muscles which act together to produce a desired effect". Drew and collaborators offered a definition free from the principle of superposition and defined a synergy as a group of muscles that are coextensive with respect to the onset and offset of the EMG activity (Drew et al. 2008; Krouchev et al. 2006). Bizzi et al. proposed that synergies are units of balanced muscle activations whose (linear) combinations give rise to complex muscle activity patterns (Bizzi and Cheung 2013; Tresch et al. 1999). This latter definition is consistent with observations made during both isometric or dynamic contractions showing that the activity of several muscles can be represented as the sum of activities of a small number of independent units which regroup multiple muscles, the synergies, and whose activity co-vary in magnitude (Davis and Vaughan 1993; Roh et al. 2012). Further studies provide evidence that the structure of these groups- i.e., relative activation level of the muscles within a synergy—is relatively conserved across different tasks and biomechanical conditions (Barosso et al. 2014; Hug et al. 2011; Torres-Oviedo and Ting 2010), suggesting that the synergies could form a repertoire from which more complex muscle activity patterns can emerge. Other formulations were proposed to take into account the fact that muscle activations during movements also possess a temporal structure, i.e., that they are organized into precise temporal sequences (e.g., Wong and Krakauer 2019; Overduin et al. 2015). The different synergy formulations found in the literature all have in common that the complexity of muscle activity patterns can be reduced to small sets of synergies due to their underlying structures. Therefore, dimensionality reduction techniques such as principal component analysis appeared particularly powerful for synergy identification (e.g., Davis and Vaughan 1993).

Muscle synergies can be conceptualized as vectors in the multidimensional muscle activation space (Fig. 2). This representation is useful for understanding analysis results and some of the behaviors associated, e.g., the necessity to have enough variations in muscle activity to properly identify the synergies ("Data acquisition and experimental conditions").

Formally, the EMG activity of m muscles at a given time t (noted $\mathbf{e}(t)$) is obtained by the linear combination of s

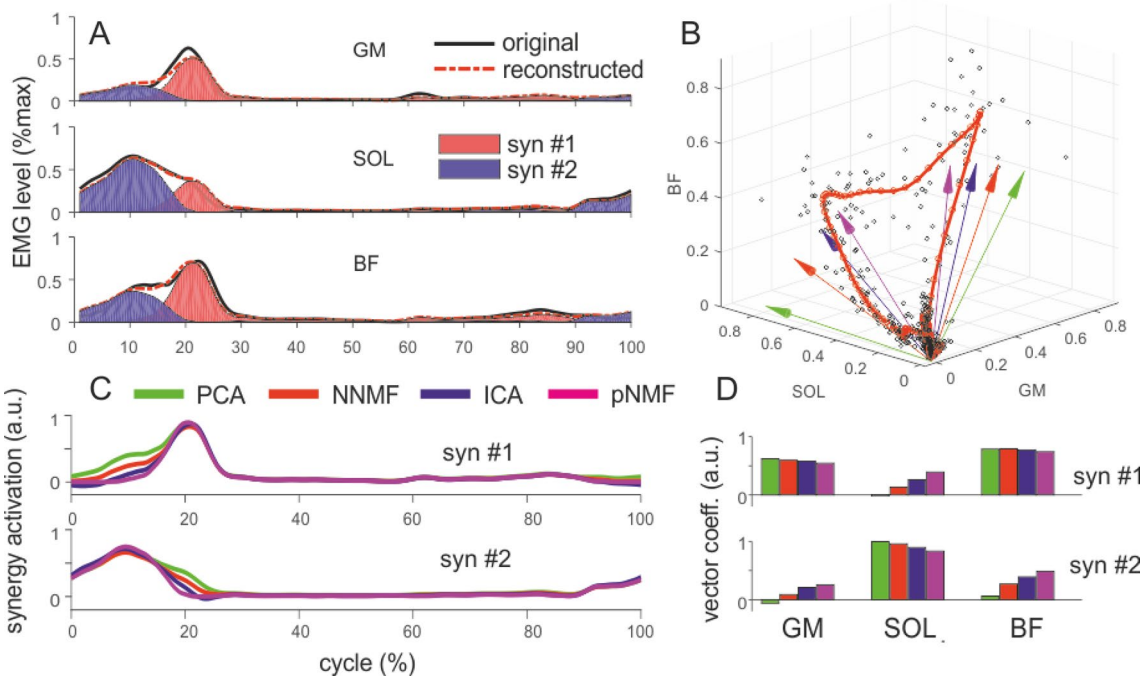

Fig. 2 Representation in the muscle activation space. **a** Muscle activations (solid black line) and their reconstruction by the synergy model (dashed red line). The contributions of each synergy are colored in red and blue (projective non-negative matrix factorization method–pNMF). **b** 3D representation of muscle activations. The red line is the trajectory of the average muscle activations. A sample of 100 pts are plotted as black circles. Unit vectors in green, red, blue and magenta were obtained using principal component analysis (PCA + varimax rotation), non-negative matrix factorization (*NNMF* Lee and Seung algorithm), independent component analysis (*ICA* Infomax), and pNMF, respectively. VAF was 97.3% for ICA, NNMF and PCA and 96.0% for pNMF. Data were from a rowing task (Turpin et al. 2011). **c**, **d** Synergy activations and synergy vector coefficients obtained from the different methods. The data cloud seems to evolve in some privileged directions (close to the ICA and pNMF vectors here) but all vectors define roughly the same subspace. The degree of overlapping of synergy activation coefficients varies with vector orientation, which depends on the algorithm. *GM* gastrocnemius medialis, *SOL* soleus, *BF* biceps femoris

synergy vectors noted $\mathbf{w}_j$ (of dimension $1 \times m$) and scaled in amplitude by a time- (or condition-) varying synergy activation coefficient, noted $c_j(t)$ (Ting and Chvatal 2010):

$$\mathbf{e}(t) = \sum_{j=1}^{s} c_j(t)\mathbf{w}_j + \text{residual},$$

where $s \leq m$ is the number of synergies, j the synergy index going from 1 to s. This equation is rewritten in matrix form as:

$$\mathbf{E} = \mathbf{W} \times \mathbf{C} + \mathbf{residual}, \quad (1)$$

with **E**, **W**, **C** and **residual**, matrices of dimensions, $m \times T$, $m \times s$, $s \times T$ and $m \times T$, respectively. T being the number of time samples.

This representation allows to separate the spatial (**W**) and temporal (**C**) components of EMG data and to define their dimensionality—a notion that appeared very useful when studying pathological movement patterns (Steele et al. 2015a; Clark et al. 2010). The spatial structure of EMG patterns refers to the subspace in which most of the EMG data lie and is defined using the synergy vectors in **W**. The weightings define the direction of the vectors and represent how much each muscle increases its activation when a synergy is activated. The dimensionality of the EMG data can be defined as the minimal number of vectors necessary to explain most of the data variance (variance accounted for or VAF > 80–95%). The temporal structure refers to how the activation coefficients are sequenced in time relative to each other.

Synergy extraction

The question of the algorithm

Given Eq. (1) the common method of synergy identification is matrix factorization applied to the EMG data matrix. The goal of matrix factorization as a dimensionality reduction technique is to form a reduced set of vectors in the muscle activation space whose linear combination can explain most of the data variance (Fig. 2b). In other words, the method regroups muscles that co-vary with each other to form synergies, which are the vectors delineating the subspace. However, these vectors can be oriented in an infinite number of ways. This means that the relative weighting of each muscle within a synergy can also vary in an infinite number of ways (Fig. 2b), questioning the physiological meaning of the extracted synergy vectors. Therefore, some constraints are used to generate a unique set of vectors, such as non-negativity, sparseness or mutual orthogonality of the vectors, or statistical independence of the time-varying activation. As a consequence, a large variety of algorithms was proposed to satisfy one or several of these constraints (Choi et al. 2005; Singh et al. 2018).

The issue of algorithm selection for synergy extraction has been investigated in numerous papers, including the seminal paper of Tresch and collaborators (Tresch et al. 2006). They tested several algorithms such as factor analysis, principal component analysis (PCA), non-negative matrix factorization (NNMF) and independent component analysis (ICA), and showed that the diverse factorization techniques provide similar results in terms of synergy vectors and synergy activation. This suggests that extracted vectors are not artifacts of the algorithms, but reflect basic aspects of the organization of muscle activation patterns (Tresch et al. 2006). However, and as exemplified in Fig. 2, some differences can be found between the outcomes of the different algorithms. During relatively similar experiments, previous results concluded that muscle synergies were either robust (using NNMF) or variable (using PCA) across experimental conditions, such as in postural control (e.g., Krishnamoorthy et al. 2004; Torres-Oviedo and Ting 2010), or pedaling (Wakeling and Horn 2009; Hug et al. 2011). Based on real and simulated data, Tresch et al. (2006) recommended the use of ICA applied to the subspace defined by PCA. However, most previous studies preferred the use of NNMF algorithms (Rabbi et al. 2020). Minimization of the residuals coupled with non-negativity constraints appear to give NNMF interesting properties such as generalizability and interpretability (Lambert-Shirzad and Van der Loos 2017; Lee and Seung 1999). Generalizability refers to the ability of a set of synergies identified in a given condition to explain EMG variations in another condition. Interpretability is made easier, because the NNMF algorithm allows only additive combinations of the synergies, and the synergies found are often sparse, each representing/activating only a few number of muscles. For example, when comparing synergy vectors, previous studies found large similarities between different tasks or different conditions of the same task using NNMF (Hug et al. 2011; Scano et al. 2019). Further studies tested and compared NNMF to other techniques such as PCA, ICA or factor analysis and concluded that it is superior when fixed and positive synergy vectors are assumed (Lambert-Shirzad and Van der Loos 2017; Steele et al. 2015b; Ebied et al. 2018).

However, the other above-mentioned techniques should not be discarded as they provide insightful results regarding the structure of motor output at both spatial and temporal levels (Yang et al. 2019; Kargo and Nitz 2003). Most factorization techniques actually appear similar in terms of subspace representation, and they are all able to fit data to similar degrees of accuracy (Fig. 2). The major distinction between the different algorithms lies in the vector orientation rather than in the subspace that they define. Given that vector comparisons (correlations) and subspace comparisons

(cross-validations) might provide different results (Oliveira et al. 2014), the choice of algorithm may, therefore, have an effect at this level. In our opinion, a seldom recognized consequence of these direction changes is that they introduce variations in the degree of overlapping of synergy activations, which appear more or less correlated with each other for the same dataset (Fig. 2c). Therefore, the choice of algorithm may have an impact on the study of the temporal structure. In the example provided in Fig. 2, vectors from the ICA and projective non-negative matrix factorization (pNMF) algorithms provide the least amount of overlapping between activation coefficients. This is consistent with their objective-functions, i.e., ICA maximizes the independence of activation profiles and pNMF, their orthogonality (Bell and Sejnowski 1995; Yang and Oja 2010). Limiting overlapping between synergy activations would be consistent with the supposed sequential nature of the motor command, as observed at the cortical level for example (Drew et al. 2008), but further studies are needed to clarify this point.

Solutions to the factorizations are associated with ambiguities in the scaling of the two components, **W** and **C**, and in the order of vectors in each component (permutation ambiguity). Scaling ambiguity implies that the information about EMG amplitude is lost, making it difficult to compare the components in terms of magnitude and to interpret the activation levels of the synergies. To allow for comparisons, previous studies forced vectors to have unit l_2-norm, or each synergy vector was normalized with respect to the greatest weighting coefficient in that synergy (Muceli et al. 2014). Note that to preserve the equality in Eq. (1), if **D** is the diagonal matrix used to normalize **W**, i.e., $\mathbf{W} \times \mathbf{D}$, then **C** should be pre-multiplied by $\mathbf{D}^{-1}$. As for the permutation, this only becomes a problem when the synergies need to be compared with those extracted from other conditions or other subjects (Cappellini et al. 2016). The way the components should be compared between subjects and conditions deserves further studies.

A greater problem is that several **W** and **C** can satisfy $\mathbf{E} = \mathbf{W} \times \mathbf{C}$ with similar residuals (Rickard and Cichocki 2008). Figure 2 illustrates this fact using different algorithms. However, solutions are generally not unique, even for a given algorithm, because of the presence of local minima, a common problem when one wants to optimize a function. To avoid local minima, previous studies ran the algorithm several times and then took the solution with the lowest cost. In the literature reviewed, the number of runs ranged between 10 and 100 (Cappellini et al. 2016; Cheung et al. 2012; Hug et al. 2011), although there is no consensus about the ideal number of runs, and a lack of evidence to indicate whether or not diverse local minima are associated with great differences in terms of solutions. It is worth noting that we also observed a global minimum attained with even a single run using PCA initialization (Turpin et al. 2020).

The existence of several minima is exacerbated when synergy activation coefficients are correlated with each other (Tresch et al. 2006; Soomro et al. 2018; Steele et al. 2015b). The phenomenon is illustrated in Fig. 3, where two groups of muscles (synergy #2 and synergy #3) are activated simultaneously without being coupled in amplitude.

This configuration can prove problematic as the "true" synergies become difficult to identify. A simulation study previously indicated that sparse initialization can improve the identification of correlated synergies (Soomro et al. 2018). Using PCA solutions, which were close to the input vectors in our example in Fig. 3, it was actually possible to recover the input synergy vectors. Initialization using SVD or PCA solutions also has the advantage of hastening the convergence of the algorithm (Zheng et al. 2007; Boutsidis and Gallopoulos 2008). The influence of this phenomenon on real EMG data is difficult to evaluate. During a pedaling task, Soomro et al. (2018) compared the results of a synergy analysis using either random or sparse initializations and found very little differences in the synergies extracted, suggesting an absence of correlated synergies in this task. However, such a conclusion might not be generalizable to other tasks.

The different synergy models

In various tasks such as walking (Barroso et al. 2014), cycling (Hug et al. 2011) or postural responses (Torres-Oviedo and Ting 2010), previous studies found evidence that muscles within a synergy could be activated in a relatively fixed balance despite changing biomechanical contexts, meaning that synergy vectors possess very similar directions in the muscle activation space in these various contexts. The identification of synergies as fixed vectors corresponds to the model in Eq. (1) and is often referred to as the *synchronous* or *spatial synergy model.* This model assumes that the activations of synergies (**C**) can vary across time or conditions while the spatial structure, **W**, remains fixed. In this case the **E** matrix is organized as follow:

$$\mathbf{E} = \left[\mathbf{E}_1 \middle| \mathbf{E}_2 \middle| \ldots \mathbf{E}_n\right] \cong \mathbf{W} \times \left[\mathbf{C}_1 \middle| \mathbf{C}_2 \middle| \ldots \mathbf{C}_n\right],$$

with $\mathbf{E}_k$ and $\mathbf{C}_k$, the **E** (muscle × time) and **C** (synergy# × time) matrices for condition k ($k = 1 \ldots n$), concatenated in line. Time is not necessarily normalized in this model, as the focus is put on identifying the muscle weighting coefficients (**W**). It is also possible to fix the activation coefficients while allowing **W** to vary across time or conditions (the *temporal synergy model*), and in this case the $\mathbf{E}_k$ should be concatenated in column (Delis et al. 2014):

$$\mathbf{E} = \left[\mathbf{E}_1; \mathbf{E}_2 \ldots; \mathbf{E}_n\right] \cong \left[\mathbf{W}_1; \mathbf{W}_{2;} \ldots \mathbf{W}_n\right] \times \mathbf{C}.$$

An important point is that, contrary to the previous formulation, each column of $\mathbf{E}_k$ should possess a certain

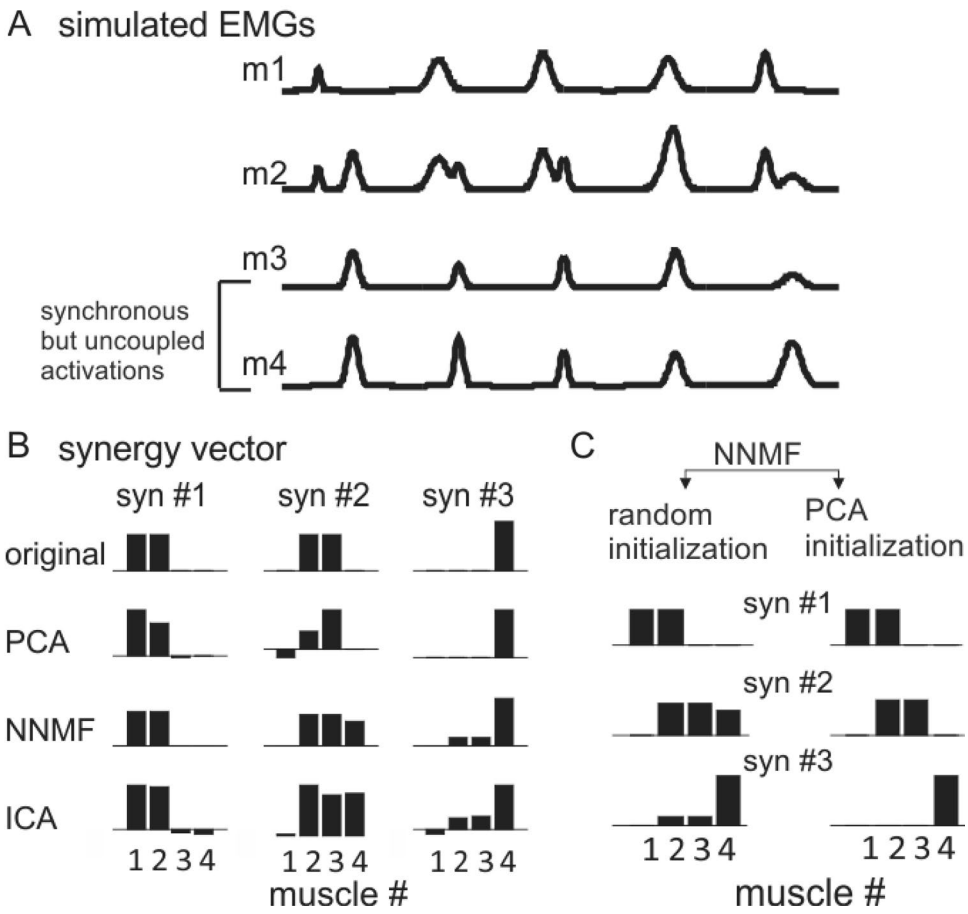

Fig. 3 The case of synchronous but uncoupled muscle activations. **a** Here we used a simple simulation to obtain muscle-like waveforms (m1…m4) that show synchronous but uncoupled activations, i.e., in m3 and m4. Activation coefficients were modeled as Gaussians scaled differently in amplitude. Original synergy vectors used in the simulation are shown in **b**. The co-variation between m3 and m4 are captured by non-null coefficients in syn #2 and syn #3 for both NNMF and ICA methods, but not for PCA. **c** Initializing the NNMF algorithm using PCA results instead of random values in this case resulted in a better identification of the input synergy vectors. VAF explained by different algorithms and initializations was 100% (no noise added), demonstrating the presence of several solutions to the equation $\mathbf{E} = \mathbf{W} \times \mathbf{C}$

congruence over the different *k*, e.g., correspond to similar percentages of time, for example. It is assumed in this model that activations of the synergies are sequenced similarly across cycles or tasks and that the weightings of muscle synergies can vary. Such a model is widely used to analyze activity of the so-called central pattern generators, which are supposed to organize the rhythmic activity of both upper and lower limbs during locomotion (Ivanenko et al. 2005). Therefore, matrix factorization is able to specifically extract spatial or temporal structures of muscle activations depending on the organization of the matrices. Even so, mainly the first form—**W** fixed—was used for analyzing both spatial and temporal structures of motor output (Ivanenko et al. 2005; Kargo and Giszter 2008).

During dynamic movements the temporal structure of muscle activation often takes the form of sequenced, Gaussian-like impulses called basic patterns, unit bursts or primitives (Lacquaniti et al. 2012; Giszter et al. 2007; Sartori et al. 2013). A priori, the numbers of synergy vectors and basic patterns are different. For example, during simple reaching movements of the arm, 4 or 5 muscle synergies are necessary to reconstruct the muscle activations in various directions (Cheung et al. 2009; Muceli et al. 2010; Roh et al. 2013) though each single movement is composed of only 2 or 3 basic patterns (the so-called tri-phasic pattern). Delis and colleagues proposed a space-by-time decomposition in which both components explicitly appear, i.e., each module $\mathbf{C}_{i,\cdot}$ and each synergy vector $\mathbf{W}_{\cdot,j}$ can be independently combined to produce complex muscle activation patterns (Delis et al. 2014). This decomposition is performed by a tri-factorization algorithm which essentially use the Lee and Seung (2001) to first find (fixed) **C** and (fixed) **W** from the $\mathbf{E}_k$ concatenated in line or in column, respectively, and then find the association matrices $\mathbf{A}_k$ for each condition separately, such that

$$\mathbf{E}_k \cong \mathbf{W} \times \mathbf{A}_k \times \mathbf{C}.$$

The decomposition clearly separates temporal and spatial structures in a single analysis.

Another proposed formulation in which spatial and temporal structures are linked together is the *spatio-temporal* or *time-varying synergy* model (d'Avella and Tresch 2006; d'Avella et al. 2003, 2006; Chiovetto et al. 2016). In this formulation each synergy is viewed as a temporal sequence of multiple muscle activations, each of which can be shifted in time and scaled in amplitude, depending on the conditions. This model reflects the idea that

complex movements are generated by learning sequences of sub-movements, in which the overall organization might eventually constitute modules recruited as independent units (Shmuelof et al. 2012; Klein Breteler et al. 2007; Viviani and Laissard 1991). Although it is debatable whether the temporal sequence of motor actions can be encoded together with muscle synergy vectors (Wong and Krakauer 2019; Kargo and Giszter 2008), the analysis certainly provides valuable information about the spatio-temporal organization of the motor output (Berger et al. 2020). A simple way to extract spatio-temporal synergies is to use the formulation proposed in Klein Breteler et al. (2007):

$$\mathbf{E} = \left[\mathrm{vec}\left(\mathbf{E}_1\right);\mathrm{vec}\left(\mathbf{E}_2\right);\mathrm{vec}\left(\mathbf{E}_k\right) \ldots \mathrm{vec}\left(\mathbf{E}_n\right)\right] \cong \mathbf{W} \times \mathbf{C}.$$

With vec ($\mathbf{E}_k$) indicating the vectorized matrix $\mathbf{E}_k$, where the lines of the matrix are placed end to end to form a single line vector. Similar to the temporal synergy model, columns of each $\mathbf{E}_k$ should be congruent, e.g., time-normalized data. The vec ($\mathbf{E}_k$) from different trials or conditions are then concatenated in column. **W** contains the spatio-temporal vectors (in line) and **C** contains the coefficients modulating the activation amplitude of the synergies. Notice that the formulation proposed by d'Avella et al. (2003) is more refined, because the synergy onset times can also be modulated. Although the *time-varying synergy* model has been less frequently used than the synchronous synergy model, it is comparable in its ability to explain EMG data, and it also provides additional information about the relation between spatial and temporal components (Esmaeili and Maleki 2020; d'Avella et al. 2006).

While each of these models—spatial, temporal, and spatio-temporal—provide different information about the structure of motor output, a recent study has provided evidence that they can complement each other in synergy analysis (Berger et al. 2020). Such an approach, using different synergy formulations, should be encouraged in future studies.

EMG signal acquisition and processing

Synergy analysis is based on the examination of the amplitude of EMG signals, using either averaged activity or different measures of its envelope (Ting and Macpherson 2005; Valero-Cuevas et al. 2009; Zandvoort et al. 2019). EMG amplitude reflects the output of spinal motoneurons but their relation is not simple (Milner-Brown and Stein 1975; Martinez-Valdes et al. 2018). Therefore, the technique used to obtain and process EMG signals is of fundamental importance.

EMG envelope

Synergy analysis inherits every EMG drawback, such as amplitude cancellation or cross-talk (Farina et al. 2014). Basic recommendations for acquiring and processing this signal are generally well-followed and have been largely documented (De Luca et al. 2010)—see also the guidelines of Surface Electromyography for the Non-Invasive Assessment of Muscles–SENIAM–http://www.seniam.org/.

In the synergy literature, however, there appears to be no consensus of the best method used to validate EMG envelopes (Shuman et al. 2017). The most commonly accepted method to obtain the envelope is to low-pass filter the rectified EMG (using a zero-lag, Butterworth filter in most cases): the EMG envelope is obtained by smoothing the EMG signal after rectification, i.e., taking its absolute value or using Hilbert transformation (Zandvoort et al. 2019). Other filtering methods include those similar to moving average (iEMG, RMS, etc. Yang et al. 2019; Turpin et al. 2017) or intensity analysis using wavelet transform (Frere 2017). Although not thoroughly investigated, the differences between these various methods are likely to be small.

There is evidence that the degree of smoothing of EMG envelope affects spatial and temporal structures of synergies and the determination of the number of synergies (Shuman et al. 2017; Hug et al. 2012; d'Avella and Tresch 2006). Large variations in cut-off frequencies are found in the literature when using low-pass filters, ranging from 1 (Muceli et al. 2014) to 40 Hz (Kim et al. 2018a). Decreasing this cut-off frequency "widens" the EMG profiles, thereby increasing their degree of overlapping, which naturally affects synergy vectors (Shuman et al. 2017; Santuz et al. 2017; Kieliba et al. 2018). Zandvoort et al. (2019) performed a synergy analysis on the modulus of the Hilbert transform of the EMG signals to preserve their higher spectral contents (without low-pass filtering the data) and found similar synergy vectors compared to a more commonly-used filter (second order, low-pass Butterworth, cut-off = 9 Hz). Therefore, using very smooth EMG patterns doesn't seem to be justified when the spatial structure is investigated. Based on previous studies we suggest that a cut-off frequency of approximately 9–12 Hz may preserve subject-specific information while reducing the amount of noise (Hug et al. 2019; Shiavi et al. 1998).

In addition, other processing techniques such as demeaning the raw signal or removing the baseline (minimal value) from the envelope were sometimes used (Roh et al. 2013) to correct a possible bias in the amplifier and to remove baseline noise or constant tonic activity in the muscles (Law et al. 2011; d'Avella et al. 2006). Baseline correction is not commonly used in the synergy literature, but may improve the signal-to-noise ratio (SNR) of the EMG signal (Law et al. 2011), which is known to strongly influence synergy

analysis results (d'Avella and Tresch 2006; Steele et al. 2013). Therefore, it deserves further investigations.

Amplitude normalization

EMG envelope amplitudes are often normalized by a reference value before extracting the synergies. Normalization allows to redistribute the variance equally among the muscles and to regularize the amplitude of the different synergy vector coefficients, making them more interpretable. Although EMG envelopes are generally normalized by the maximum value, the mean value or the standard deviation computed over the entire dataset (Shuman et al. 2017; Banks et al. 2017; Turpin et al. 2017), muscle synergies were extracted without any normalization in a few studies (Muceli et al. 2014; Yang et al. 2019; Cappellini et al. 2016). As indicated by Muceli et al. (2014), normalizing by the maximum value amplifies noise as well as signal, which could have negative effects on synergy identification. It can be shown that synergy vectors and residuals are directly influenced by normalization. Normalizing EMGs corresponds to the pre-multiplication of the non-normalized version of Eq. (1) by a diagonal matrix **D**, composed of the inverses of the normalization values:

$$\mathbf{E} = \mathbf{D} \times \mathbf{E}_{\mathbf{un-norm}} \times = \mathbf{D} \times \mathbf{W}_{\mathbf{un-norm}} \times \mathbf{C} + \mathbf{D} \times \mathbf{residual}_{\mathbf{un-norm}},$$

with the subscript *un-norm* denoting the un-normalized versions of the matrices. Therefore, it is not surprising that normalization can affect the similarities between synergy vectors (Banks et al. 2017) and the determination of the number of synergies, as this determination is mainly based on the study of the residuals (Kieliba et al. 2018). It appears that the effect on VAF is significant (Kieliba et al. 2018), although, the effects on synergy vectors are not always clear. Generally speaking, and as demonstrated in Fig. 4, the absence of task-independent normalization is a strong limitation when comparing different subjects. In particular, this should be taken into account when comparing healthy and pathological subjects for whom the signal-to-noise ratio of the recorded EMG channels are often very different. Still, Cappellini et al. (2016) compared different subject populations using both normalized and non-normalized EMG and did not report divergent conclusions. Kieliba et al. (2018) normalized EMG envelopes by either the maximum over

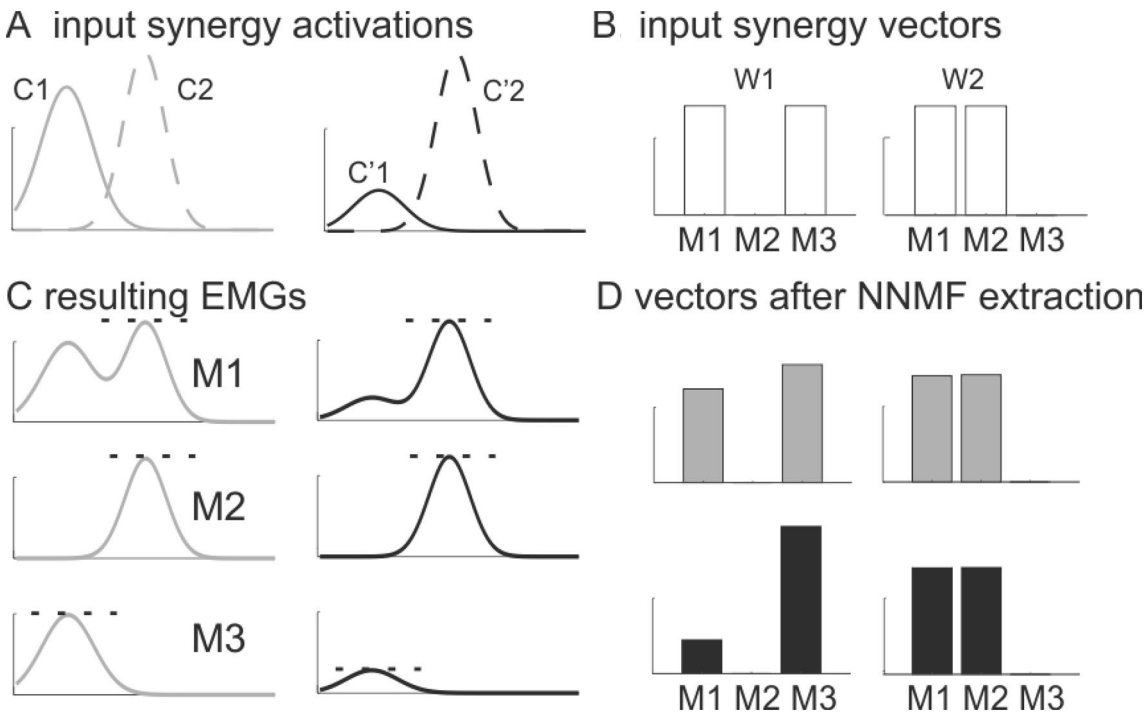

Fig. 4 Illustration of the normalization effects. We simulated the activity of 3 muscles (M1, M2 and M3) as the combination of two synergy activations (solid and dashed lines in **a**) and two synergy vectors (W1 and W2 in **b**) in two conditions (gray and black). No noise was added in these simulations. The difference between these two conditions is that the activation coefficient of the first synergy is higher in the gray condition (i.e., C1 > C′1). Here C1 and C′1 activate W1, while C2 and C′2 activate W2. In **c**, the dashed horizontal lines indicate the maximum of each muscle. **d** The NNMF algorithm was applied after normalization of the EMGs relative to their respective maxima. The presence of M1 in two different synergies make its amplitude relative to the other muscles depending on how the different synergies are activated during the task. Original synergy vectors could not be identified in either case

all data or by the maximum obtained during maximal voluntary contractions (MVC), and found no significant effects on synergy vectors. Normalization by the maximum value obtained during isometric MVCs was sometimes performed (Manickaraj et al. 2017; Kieliba et al. 2018; Israely et al. 2017), but it is difficult to obtain a true maximum for all muscles that are generally recorded (> 5) during such a test and might be exhausting or even impossible for populations with pathologies, pain or unaccustomed to the task (Lindstroem et al. 2012). However, such normalization would enable suitable comparison between subjects and studies. Alternative methods have not been considered in the synergy literature (Sousa and Tavares 2012; Yang and Winter 1984; Besomi et al. 2020).

Data acquisition and experimental conditions

Intra-muscular recordings were sometimes performed in humans in addition to surface EMGs (Valero-Cuevas et al. 2009; Heales et al. 2016; Ajiboye and Weir 2009; Saito et al. 2018; Ivanenko et al. 2004; Turpin et al. 2020). In these studies, deep muscles did not produce specific synergies. Although these muscle recordings did not likely have much impact on the number of synergies, they clearly provide a more refined analysis of the spatial structure (Heales et al. 2016).

Inter-electrode distance affects the selectivity of recordings, that is, the volume detection of muscle fiber activity, i.e., large inter-electrode distance allows to record a greater volume of muscle fibers (Fuglevand et al. 1992), but, at the same time, it is associated with greater probability of cross-talk (Farina et al. 2014; Campanini et al. 2007). Cross-talk might exaggerate positive correlations between adjacent muscle recordings, and therefore, it would affect the spatial structure rather than the temporal structure of synergies (Ivanenko et al. 2004). In the literature reviewed, inter-electrode distances were not always reported; in those studies that did report it, the distances appear variable, i.e., from 10 to 22 mm (Zandvoort et al. 2019; Muceli et al. 2014). However, the influence of cross-talk on synergy analysis results is difficult to estimate (Farina et al. 2014).

The number of recorded muscles varies widely across studies, ranging between 5 and 32 (van der Krogt et al. 2016; Van Criekinge et al. 2019). We found no recommendation about any "optimal" set of muscles to study for a given task. A common-sense rationale for choosing the set of muscles is that they should all participate in the task, but the recording of all muscles participating in one given task is feasible only in a few cases (Valero-Cuevas et al. 2009). There is evidence suggesting that some synergies might be composed of muscles spanning more than one joint (Drew et al. 2008; Levine et al. 2014), and that at a functional level, even upper and lower limb muscles can be coordinated in a synergistic fashion (Ivanenko et al. 2005). Still, it is difficult to identify a priori all muscles or muscle groups that would create independent components, and in our opinion exploratory studies are required before a new task can be fully investigated.

The specific set of muscles chosen and grouped together may affect the number of synergies and their structure. For example, Gizzi et al. (2011) and Chia-Bejarano et al. (2017) compared their results during walking using different sets of muscles (7 vs. 16 and 8 vs. 13, respectively) and found similar but not identical synergy vectors. The relative magnitude of the synergy vector coefficients differed slightly between results obtained from the two sets of muscles that were used, suggesting that the algorithm (NNMF in both) is sensitive to the variance of the different muscles included in the analysis. The results of Steele et al. (2013) on simulated data confirmed such a behavior for the NNMF algorithm, and these authors suggested to ensure that the selected set of muscles contains the muscle with the highest coefficient or with the highest isometric force to improve the similarity between synergy vectors.

This creates the problem of missing EMG channels which is frequent in clinical evaluations and certainly affects analysis outcomes. Previous studies used a weighted version of the NNMF algorithm to cope with missing muscle channels (Shuman et al. 2019) but this problem has not yet been addressed thoroughly.

The amount of data used to extract synergies also varies substantially across studies. For example, during walking, the number of cycles used to extract synergies can range between 1 and 40 (Oliveira et al. 2014; Hinnekens et al. 2020). Oliveira et al. (2014) compared synergies obtained with averaged EMG data or with concatenated EMG matrices and suggested a minimum of 20 cycles to obtain synergy vectors that would be generalizable. Other studies showed that the correct identification of synergy vectors actually requires the presence of substantial data variability in terms of activation amplitude (Oliveira et al. 2014; Steele et al. 2015b; Ranganathan and Krishnan 2012), notably during biomechanically constrained tasks (Burkholder and van Antwerp 2013; Steele et al. 2015b). The magnitude of EMG variation may have a direct influence on synergy analysis results, in particular on the orientation of synergy vectors and their ability to explain other datasets. In Fig. 5 we show how the absence of a proper exploration of the synergy subspace can adversely influence the synergy analysis outcomes. In the data in Fig. 3, for example, if averaged patterns were used instead of the entire data, the muscles that co-vary without being coupled in amplitude would have belonged to the same synergy and two synergies instead of three would have accounted for 100% of the variance. However, the temporal structure, composed of two sequential

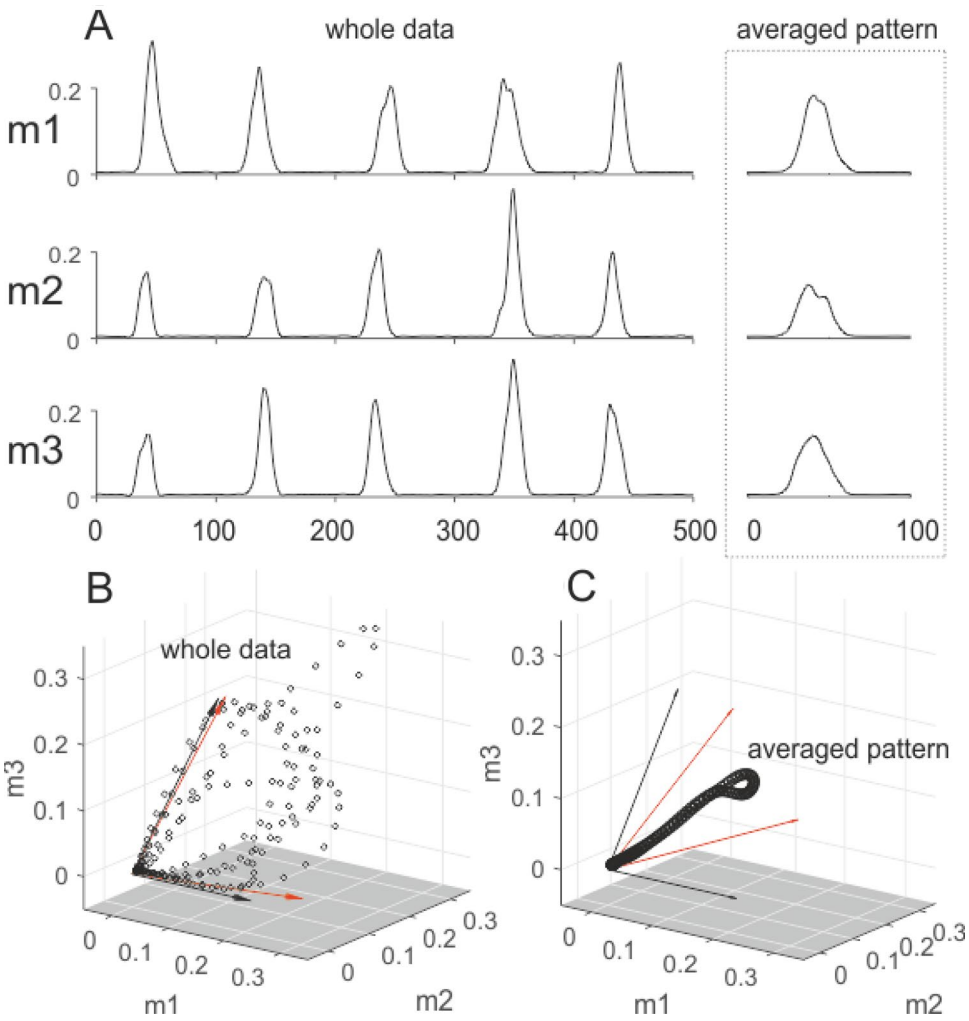

Fig. 5 Data range affects NNMF results. Non-negativity constraints coupled with the optimization of both **W** and **C** (in $\mathbf{E} = \mathbf{W} \times \mathbf{C}$ + residuals) implies that the vectors are "outside"—at the edges—of the data cloud, i.e., they form a simplicial cone. This outside area may be large if the range of data variation is small, which may be the case when averaging the data. Therefore, this range may have an effect on NNMF results. The waveforms in **a** (m1, m2 and m3) were generated by activation coefficients (**C**) consisting in Gaussians with varied amplitudes and using the bases $\mathbf{w}_1 = [0, 0.6, 0.8]^T$ and $\mathbf{w}_2 = [1, 0, 0]^T$ (black vectors in **b** and **c**). The resulting **E** matrix ($\mathbf{E} = \mathbf{W} \times \mathbf{C}$) was corrupted with white noise (amplitude = 0.01) and then low-pass filtered (cut-off = 9 Hz). In **b** and **c**, the vectors in red were obtained using NNMF applied on **E** (random initialization) and the average patterns of **E**, respectively. Using cross-validation (Lee and Seung updates), the red vectors in **b** explained 99.8% of data variation in **c** (vs. 99.8% using the original vectors), while the red vectors in **c** explained only 97.3% of data variation in **b** (vs. 99.3%)

bursts, could still be identified by the algorithm. This indicates that averaging across cycles or repetitions can lead to mixed or merged synergies. Therefore, matrix factorization might be able to identify the temporal structure of EMG data from averaged data (Maclellan et al. 2014; Zelik et al. 2014; Ivanenko et al. 2005), but some information about the spatial structure may be lost.

Besides its variability, the actual level of muscle activation is of importance in the detection of synergies. Muscle synergies must be activated above noise level to be identified. For example, during standing cycling, a synergy linked to knee flexors is barely activated below ~ 250 W (Turpin et al. 2017) and cannot be robustly identified in any of the subjects at low exercise intensity. Similarly, in pathology, neural input to the muscles is often diminished (Klein et al. 2010), and this may influence the recruitment of synergies. In this respect, Kim et al. (2018b) suggested that children with cerebral palsy may have similar synergies compared to typically developing children during walking, but that these synergies appear to be recruited less frequently and with more variability across the walking strides. Although previous studies have suggested to remove the small and inconsistent muscle activations to increase the consistency of the analysis (Ghislieri et al. 2020), these small activations may have significant functional effects and be clinically relevant (Kim et al. 2018b; Barradas et al. 2020). These problems are difficult to eliminate and should be taken into account when designing and performing experiments.

The number of synergies

The VAF vs. number-of-synergies curve

An important measure in synergy analysis is the VAF by the model, which is taken as a measure of goodness of fit. VAF (un-centered) is typically computed as:

$$\mathrm{VAF} = 1 - \mathrm{SSE}/\mathrm{SST},$$

with SSE the sum of squared errors and SST the total sum of square (the sum of all elements in **E**, after they have been

squared; *cf*. Equation (1). In some studies VAF (centered) was computed with the term SST replaced by the trace of the covariance matrix of **E** (d'Avella et al. 2006; Hinnekens et al. 2020). Other measures of goodness of fit such as log-likelihood ratio or Pearson's R^2 can be found in the synergy literature (Tresch et al. 2006; Togo and Imamizu 2017). These different VAF computations provide different values for a given decomposition (Togo and Imamizu 2017). Using different normalizations of EMGs, different numbers of muscles or different factorization algorithms, the values or the allure of the VAF curve may change drastically (Tresch et al. 2006; Kieliba et al. 2018; Castellini and van der Smagt 2013) (Fig. 5b). VAF is also strongly influenced by level of noise or unstructured EMG and by data filtering (Hug et al. 2012; d'Avella and Tresch 2006). Therefore, measures of goodness of fit and VAF appear difficult to compare between studies.

Both cross-validation and bootstrapping procedures have been used in previous studies to yield better estimates of true VAF values. Cross-validation is a procedure in which VAF is measured in parts of the dataset not used to extract synergies, thereby ensuring that the values truly estimate the amount of errors—as VAF is maximized by the optimization process (Hirashima and Oya 2016; d'Avella et al. 2003; Muceli et al. 2010). Bootstrapping allows estimating both mean and confidence intervals by computing VAF from different and randomly sampled parts of the dataset (Allen et al. 2017). However, the advantage of using these methods have not been confirmed.

Selecting an appropriate number of synergies

A sticking point in synergy analysis is the determination of the number of synergies. This is a historic problem (Jackson 1993) and is significant since the number of synergies influences comparisons between subjects or conditions (Kim et al. 2018b).

Several methods used to defined the number of synergies rely on identifying a knee point—a sharp inflexion- and the straight line that should follow it on the VAF vs. number-of-synergies curve (Tresch et al. 2006). This straight line is generally taken as evidence that only unstructured data or noise are captured by the components that follow. The knee point can be determined by visual inspection in some cases (Catell's scree test in factor analysis) but can be impossible if the VAF curve is too smooth (Fig. 6).

Fixed VAF thresholds are a commonly used criteria for defining the number of synergies, i.e., VAF > 80–95% associated with the constraint that VAF per muscle > 75–85% or that further increase in VAF is less than 2–7% (Kaiser criterion in factor analysis) (Sawers et al. 2015; Chia Bejarano et al. 2017; Hug et al. 2011; Maclellan et al. 2014). These thresholds are often determined heuristically based on the specificity of each dataset to ensure that most of the variance is accounted for when choosing the first *N* dimensions. The comparisons with VAF increase for unstructured data is also very common (Cheung et al. 2005; Takei et al. 2017) (Horn's parallel analysis in factor analysis—Fig. 6c). In particular, this method proved to be robust with regards to the degree of EMG smoothing (Hug et al. 2012). There are other methods relying on information criteria such as Akaike or Bayesian information criteria (Tresch et al. 2006; Chiovetto et al. 2014). However, all these methods showed only limited performances (Severini and De Marchis 2018; Tresch et al. 2006). Despite the great amount of work on this subject, defining the number of synergies without ambiguity continues to be difficult.

As a consequence, the criterion VAF > 0.9 might appear to be conservative as it ensures a "sufficient" representation of the data. Still, this also is debated (Kim et al. 2016; Barradas et al. 2020). First, VAF is sensitive to several factors, including the level of noise (Shuman et al. 2017), which indicates that this criterion may give different results depending on the quality of the EMG signal or processing techniques. Second, the residuals—which account for 5–20% of total variation—are not merely noise (Valero-Cuevas et al. 2009; Barradas et al. 2020). They may actually represent small synergies (Kim et al. 2018b) or results from a certain degree of flexibility or non-linearity of the spatial structure that is not captured by the linear model (Barradas et al. 2020).

Alternatively, some authors suggested to determine the number of synergies based on either their ability to discriminate between different motor tasks or their functional outcomes (Delis et al. 2013, 2018). Kim et al. (2016) proposed a form of stability-based criterion consisting of an analysis of the synergies extracted from several cycles (during walking). Because of their observation that at a certain (optimal) number the synergy structure became stable across cycles, they recommended to select the number of synergies according to which inter-cycle similarity is the highest. These methods are promising for solving the model selection problem and should be further investigated.

Previous studies also extracted the same number of synergies for all subjects based on results at the population level (Turpin et al. 2017; Maclellan et al. 2014; Gizzi et al. 2011; Lunardini et al. 2017). Knee points were often more clearly visible when the VAF curves were averaged across subjects (Gizzi et al. 2011; Hug et al. 2011). Additionally, there is evidence suggesting that the distribution of the number of synergies at the population level—notably when using the criterion VAF > 90%—resembles a normal distribution with a clear mode (Roh et al. 2013; Shuman et al. 2019). These observations may justify using the same number for all participants. However, possible inter-individual differences would be lost.

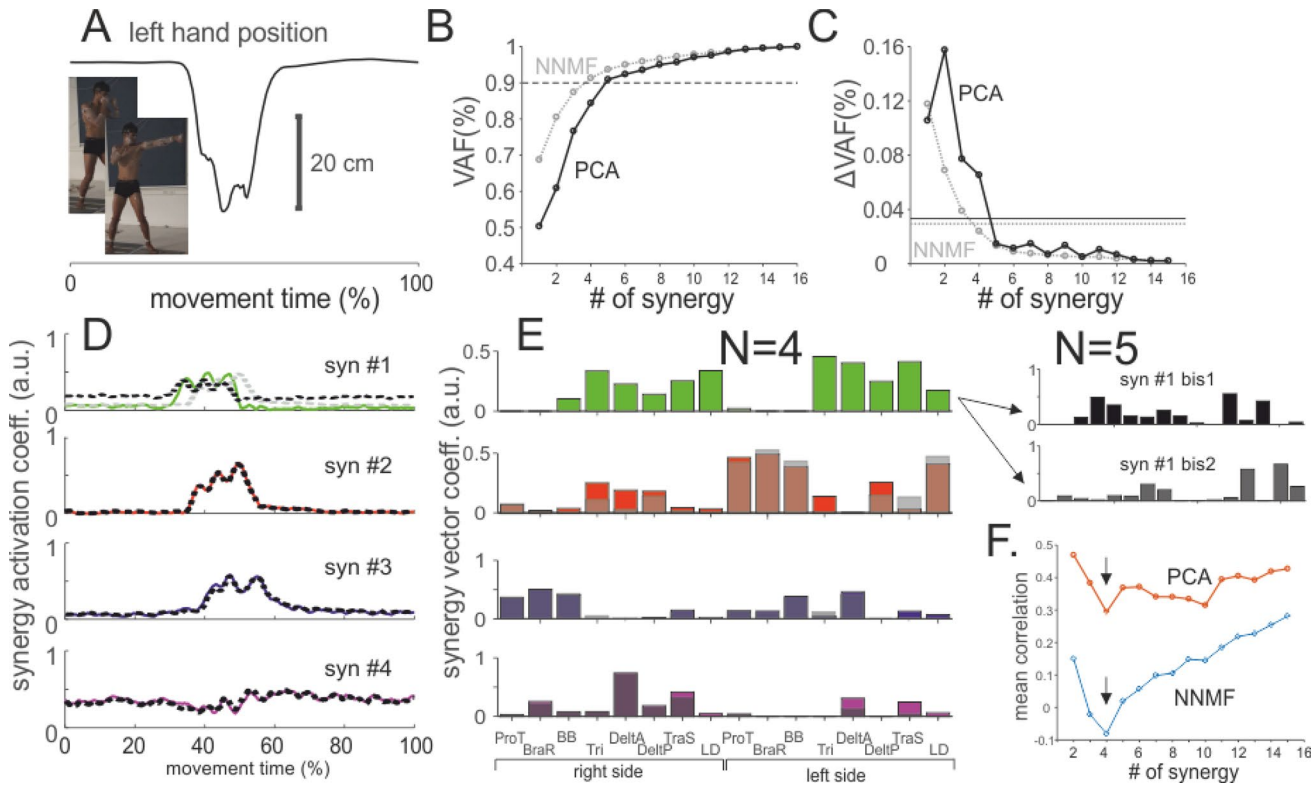

Fig. 6 Behavior when increasing the number of synergies. **a** Antero-posterior position of the left hand. The task consisted of punching toward a target with the left hand and to come back to the initial position (unpublished data). A set of 16 muscles from the right and left sides of the body were recorded over 10 repetitions of the task (see method in Supplemental Data). **b** VAF as a function of the number of synergies in the model for NNMF (in gray) and PCA (in black). A defined knee point is visible for PCA at $N=5$. VAF reached 90% at $N=4$ for NMF and $N=5$ for PCA. **c** VAF-slopes (ΔVAF). The slopes were computed as VAF $(N+1)$ − VAF (N). The horizontal lines represent 75% of the slope for shuffled data (Cheung et al. 2005), which is an almost constant value. ΔVAF was lower than the threshold at $N=4$ for NMF and $N=5$ for PCA. **d**, **e** Synergy activation (**d**) and synergy vectors (**e**) at $N=4$ (colored data) and $N=5$ (gray and black data) extracted with NNMF. Because of their similarity, the synergy vectors at $N=5$ and $N=4$ were superimposed for syn #2, #3 and #4 (in shaded gray). Increasing the number of synergies from 4 to 5, synergy #1 was further dissociated into syn #1 bis1 and syn #1 bis2. **f** Minimum correlation criterion. Mean correlations between the column of C (temporal component of EMG data, cf. Eq. 1) were plotted as a function of the number of synergies extracted for PCA and NMF. Arrows indicate the minima, which suggest the presence of only 4 distinct temporal components. *ProT* pronator terres, *BraR* bracoradialis, *BB* biceps brachii, *Tri* triceps brachii, *DeltA* deltoid, anterior part, *DeltP* deltoid, posterior part, *TraS* trapezius, superior part, *LD* latissimus dorsi

While the reviewed literature can be divided into studies focusing on temporal modules (Zelik et al. 2014) and those focusing on synergy vectors (Cheung et al. 2012; Ting and Macpherson 2005), the synergy extraction algorithms and methods used for model selection were often the same. In the following paragraph we show how ambiguity in the determination of the number of synergies might also result from an indifferentiation between the numbers of independent temporal patterns and synergy vectors.

In the data provided in Fig. 6 we found that 4 synergies were necessary to achieve a VAF > 90% using NNMF, whereas the VAF curve crossed this threshold at $N=5$ while using PCA. Using the thresholds determined by the evolution of VAF for unstructured data (Fig. 6c), these numbers were confirmed for each algorithm. Extracting 5 synergies instead of 4 led to the split of synergy #1 (panel E). The resulting synergies possessed very similar activation profiles (panel D). We measured the mean correlations between the columns of **C** and plotted them as a function of the number of synergies. A clear minimum appeared at $N=4$, suggesting that only 4 distinct synergy activations underlain these data. However, the well-defined knee point on the VAF curve for PCA (Fig. 6b) also suggested that the data were composed of 5 synergies. PCA was obtained by an Eigen-decomposition of the covariance matrix of EMG data and, as in Fig. 3, this algorithm may be more efficient than NNMF for capturing correlations in the EMG amplitudes. This suggests that synergy #1 could actually be constituted of (at least) two (correlated) synergies. The point of this example is that the number of "minimally-correlated" activation coefficients is in principle less than the number of synergy vectors, as several synergies might be activated simultaneously (Fig. 3).

The first number is rather linked to the temporal structure, and the second to the spatial structure of the motor output. Previous studies used a notion of *fundamental synergies*—defined as synergies activated with a single peak during gait stride (Santuz et al. 2017)—to define the number of synergies. This approach may provide a less ambiguous way to define the number of components but, as explained above, the number of chosen components may depend on which aspect—spatial or temporal—the study is focusing on.

Other identification methods

In this review we focused on techniques that analyze the amplitude of surface EMGs to identify regularities in spatial, temporal or spatio-temporal patterns of multiple muscle activation, with the basic assumption that the activations of muscles within a synergy co-vary in amplitude. In this context, matrix factorization became a standard technique, but other techniques can also be used to identify muscle synergies. For example, Drew et al. (2008) used a cluster analysis applied on the onsets and offsets of muscle activations to identify the groups of muscles that are activated together. Their identification technique was consistent with the phasic and sequential activity observed in pyramidal tract neurones recorded in cats during locomotion. Interestingly, the composition of synergies was quite close to what could be extracted using matrix factorization (Krouchev et al. 2006). However, this technique does not provide information about amplitude modulation of muscle activations within a synergy. Cross-correlation, mutual information or coherence analysis can also be used to identify information shared in the activity of pairs of muscles to regroup them into functional synergies (Del Vecchio et al. 2019; Kerkman et al. 2018; Holdefer and Miller 2002). Boonstra et al. (2015) presented an interesting work in which after they identified what they called a functional muscle network by analyzing the coherence between different pairs of muscles, they found that even right and left side muscles can belong to the same functional group (Kerkman et al. 2018). Coherence and spectral analysis is becoming more and more popular to identify muscle synergies, and researchers have suggested that these methods may separate purely functional synergies—in which muscles would simply show some correlated activities—from synergies in which muscles would genuinely share common inputs (Frere 2017; Bruton and O'Dwyer 2018; Del Vecchio et al. 2019). Coherence analysis seeks to identify how synaptic inputs to the motor neuron pools are shared between different muscles (Laine and Valero-Cuevas 2017; De Marchis et al. 2015; Charissou et al. 2017). Identification of these common inputs appears difficult using conventional surface electrodes, notably during movements (Farina et al. 2014), and although they can be regrouped a posteriori, the analysis in itself is limited to the study of pairs of muscles. However, advances in technology, notably the use of matrix of electrodes (Farina et al. 2016), may facilitate such analysis in the future and provide new insights about the formation of muscle synergies.

Conclusions

The goal of this review was to clarify selected aspects of the muscle synergy analysis methodology that may create potential confusions. Note that some results of this review are presented as supplemental material. The key points of this review can be summarized as follows.

In terms of algorithm, most matrix factorization algorithms that were used in the literature provided insightful results about the motor output structure and the omnipresence of the non-negative matrix factorization technique in the literature (> 60% of publications—Rabbi et al. 2020) might not be fully justified. PCA for example is efficient in describing the subspace in which the data lie (see Supplemental Material), but vector orientation is not robust across datasets. NNMF provides generalizable and interpretable (sparse and positive) components. However, NNMF is sensitive to the number of muscles included in the analysis as well as to the data range, and it generally possesses multiple solutions. We suggest that other algorithms besides NNMF might be better suited to study the temporal structure (e.g., ICA). The different models of synergy structure (spatial, temporal and spatio-temporal) provide different information and are also complementary with each other. The concurrent use of these different formulations should be encouraged in future studies. In terms of data analysis and acquisition, we showed that amplitude normalization has a major influence on synergy analysis outcomes. Previous studies showed that (1) strong smoothing of EMG envelopes is detrimental to the study of spatial structure, (2) experimental conditions should induce sufficient variability in the EMG amplitudes to properly explore the synergy subspace and robustly identify the spatial structure and (3) identification of the number of synergies should not be based solely on VAF-thresholds. The number of synergy vectors and the number of basic patterns (also called unit bursts or temporal primitives) are often combined in the analysis but may deserve separate determinations and descriptions. We suggest that the separation of these aspects in the analysis might make it less ambiguous to select the appropriate number of synergies.

Acknowledgements The authors thank Benjie BARTOS for the English corrections. We also thank Tieme LARAQUE for his valuable comments on the manuscript.

Author contributions All authors contributed equally to this work.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Ajiboye AB, Weir RF (2009) Muscle synergies as a predictive framework for the EMG patterns of new hand postures. J Neural Eng 6(3):036004. https://doi.org/10.1088/1741-2560/6/3/036004

Allen JL, McKay JL, Sawers A, Hackney ME, Ting LH (2017) Increased neuromuscular consistency in gait and balance after partnered, dance-based rehabilitation in Parkinson's disease. J Neurophysiol 118(1):363–373. https://doi.org/10.1152/jn.00813.2016

Banks CL, Pai MM, McGuirk TE, Fregly BJ, Patten C (2017) Methodological choices in muscle synergy analysis impact differentiation of physiological characteristics following stroke. Front Comput Neurosci 11:78

Barradas VR, Kutch JJ, Kawase T, Koike Y, Schweighofer N (2020) When 90% of the variance is not enough: residual EMG from muscle synergy extraction influences task performance. J Neurophysiol. https://doi.org/10.1152/jn.00472.2019

Barroso FO, Torricelli D, Moreno JC, Taylor J, Gomez-Soriano J, Bravo-Esteban E, Piazza S, Santos C, Pons JL (2014) Shared muscle synergies in human walking and cycling. J Neurophysiol 112(8):1984–1998. https://doi.org/10.1152/jn.00220.2014

Bell AJ, Sejnowski TJ (1995) Blind separation and blind deconvolution: an information-theoretic approach. In: 1995 International conference on acoustics, speech, and signal processing, 1995. IEEE, pp 3415–3418

Berger DJ, Masciullo M, Molinari M, Lacquaniti F, d'Avella A (2020) Does the cerebellum shape the spatiotemporal organization of muscle patterns? J Neurophysiol, Insights from subjects with cerebellar ataxias. https://doi.org/10.1152/jn.00657.2018

Besomi M, Hodges PW, Clancy EA, Van Dieën J, Hug F, Lowery M, Merletti R, Søgaard K, Wrigley T, Besier T, Carson RG, Disselhorst-Klug C, Enoka RM, Falla D, Farina D, Gandevia S, Holobar A, Kiernan MC, McGill K, Perreault E, Rothwell JC, Tucker K (2020) Consensus for experimental design in electromyography (CEDE) project: amplitude normalization matrix. J Electromyogr Kinesiol 53:102438. https://doi.org/10.1016/j.jelekin.2020.102438

Bizzi E, Cheung VC (2013) The neural origin of muscle synergies. Front Comput Neurosci 7:51

Boonstra TW, Danna-Dos-Santos A, Xie HB, Roerdink M, Stins JF, Breakspear M (2015) Muscle networks: connectivity analysis of EMG activity during postural control. Sci Rep 5:17830. https://doi.org/10.1038/srep17830

Boutsidis C, Gallopoulos E (2008) SVD based initialization: a head start for nonnegative matrix factorization. Pattern Recogn 41(4):1350–1362

Bruton M, O'Dwyer N (2018) Synergies in coordination: a comprehensive overview of neural, computational, and behavioral approaches. J Neurophysiol 120(6):2761–2774. https://doi.org/10.1152/jn.00052.2018

Burkholder TJ, van Antwerp KW (2013) Practical limits on muscle synergy identification by non-negative matrix factorization in systems with mechanical constraints. Med Biol Eng Comput 51(1–2):187–196. https://doi.org/10.1007/s11517-012-0983-8

Campanini I, Merlo A, Degola P, Merletti R, Vezzosi G, Farina D (2007) Effect of electrode location on EMG signal envelope in leg muscles during gait. J Electromyogr Kinesiol 17(4):515–526. https://doi.org/10.1016/j.jelekin.2006.06.001

Cappellini G, Ivanenko YP, Martino G, MacLellan MJ, Sacco A, Morelli D, Lacquaniti F (2016) Immature spinal locomotor output in children with cerebral palsy. Front Physiol 7:478. https://doi.org/10.3389/fphys.2016.00478

Castellini C, van der Smagt P (2013) Evidence of muscle synergies during human grasping. Biol Cybern 107(2):233–245. https://doi.org/10.1007/s00422-013-0548-4

Charissou C, Amarantini D, Baurès R, Berton E, Vigouroux L (2017) Effects of hand configuration on muscle force coordination, co-contraction and concomitant intermuscular coupling during maximal isometric flexion of the fingers. Eur J Appl Physiol 117(11):2309–2320

Cheung VC, d'Avella A, Tresch MC, Bizzi E (2005) Central and sensory contributions to the activation and organization of muscle synergies during natural motor behaviors. J Neurosci 25(27):6419–6434. https://doi.org/10.1523/jneurosci.4904-04.2005

Cheung VC, Piron L, Agostini M, Silvoni S, Turolla A, Bizzi E (2009) Stability of muscle synergies for voluntary actions after cortical stroke in humans. Proc Natl Acad Sci USA 106(46):19563–19568. https://doi.org/10.1073/pnas.0910114106

Cheung VC, Turolla A, Agostini M, Silvoni S, Bennis C, Kasi P, Paganoni S, Bonato P, Bizzi E (2012) Muscle synergy patterns as physiological markers of motor cortical damage. Proc Natl Acad Sci USA 109(36):14652–14656. https://doi.org/10.1073/pnas.1212056109

Chia Bejarano N, Pedrocchi A, Nardone A, Schieppati M, Baccinelli W, Monticone M, Ferrigno G, Ferrante S (2017) Tuning of muscle synergies during walking along rectilinear and curvilinear trajectories in humans. Ann Biomed Eng 45(5):1204–1218. https://doi.org/10.1007/s10439-017-1802-z

Chiovetto E, Endres D, d'Avella A, Giese M (2014) Model selection for the extraction of EMG synergies. dim 2:1

Chiovetto E, d'Avella A, Giese M (2016) A unifying framework for the identification of motor primitives. arXiv preprint arXiv:1603006879

Choi S, Cichocki A, Park H-M, Lee S-Y (2005) Blind source separation and independent component analysis: a review. Neural Inf Process Lett Rev 6(1):1–57

Clark DJ, Ting LH, Zajac FE, Neptune RR, Kautz SA (2010) Merging of healthy motor modules predicts reduced locomotor performance and muscle coordination complexity post-stroke. J Neurophysiol 103(2):844–857

d'Avella A, Tresch M (2006) Muscle synergies for motor control. In Handbook of neural engineering. Wiley, New York, pp 449–465

d'Avella A, Saltiel P, Bizzi E (2003) Combinations of muscle synergies in the construction of a natural motor behavior. Nat Neurosci 6(3):300–308. https://doi.org/10.1038/nn1010

d'Avella A, Portone A, Fernandez L, Lacquaniti F (2006) Control of fast-reaching movements by muscle synergy combinations. J Neurosci 26(30):7791–7810. https://doi.org/10.1523/jneurosci.0830-06.2006

Davis BL, Vaughan CL (1993) Phasic behavior of EMG signals during gait: use of multivariate statistics. J Electromyogr Kinesiol 3(1):51–60. https://doi.org/10.1016/1050-6411(93)90023-p

De Luca CJ, Gilmore LD, Kuznetsov M, Roy SH (2010) Filtering the surface EMG signal: movement artifact and baseline noise contamination. J Biomech 43(8):1573–1579. https://doi.org/10.1016/j.jbiomech.2010.01.027

De Marchis C, Severini G, Castronovo AM, Schmid M, Conforto S (2015) Intermuscular coherence contributions in synergistic muscles during pedaling. Exp Brain Res 233(6):1907–1919. https://doi.org/10.1007/s00221-015-4262-4

Del Vecchio A, Germer CM, Elias LA, Fu Q, Fine J, Santello M, Farina D (2019) The human central nervous system transmits common synaptic inputs to distinct motor neuron pools during non-synergistic digit actions. J Physiol 597(24):5935–5948. https://doi.org/10.1113/jp278623

Delis I, Berret B, Pozzo T, Panzeri S (2013) A methodology for assessing the effect of correlations among muscle synergy activations on task-discriminating information. Front Comput Neurosci 7:54. https://doi.org/10.3389/fncom.2013.00054

Delis I, Panzeri S, Pozzo T, Berret B (2014) A unifying model of concurrent spatial and temporal modularity in muscle activity. J Neurophysiol 111(3):675–693. https://doi.org/10.1152/jn.00245.2013

Delis I, Hilt P, Pozzo T, Panzeri S, Berret B (2018) Characterization of whole-body muscle activity during reaching movements using space-by-time modularity and functional similarity analysis. In: Proceedings of the 10th hellenic conference on artificial intelligence, 2018. pp 1–7

Drew T, Kalaska J, Krouchev N (2008) Muscle synergies during locomotion in the cat: a model for motor cortex control. J Physiol 586(5):1239–1245. https://doi.org/10.1113/jphysiol.2007.146605

Ebied A, Kinney-Lang E, Spyrou L, Escudero J (2018) Evaluation of matrix factorisation approaches for muscle synergy extraction. Med Eng Phys 57:51–60. https://doi.org/10.1016/j.medengphy.2018.04.003

Esmaeili J, Maleki A (2020) Muscle coordination analysis by time-varying muscle synergy extraction during cycling across various mechanical conditions. Biocybern Biomed Eng 40(1):90–99

Farina D, Merletti R, Enoka RM (2014) The extraction of neural strategies from the surface EMG: an update. J Appl Physiol (1985) 117(11):1215–1230. https://doi.org/10.1152/japplphysiol.00162.2014

Farina D, Negro F, Muceli S, Enoka RM (2016) Principles of motor unit physiology evolve with advances in technology. Physiology (Bethesda) 31(2):83–94. https://doi.org/10.1152/physiol.00040.2015

Flash T, Hochner B (2005) Motor primitives in vertebrates and invertebrates. Curr Opin Neurobiol 15(6):660–666

Frere J (2017) Spectral properties of multiple myoelectric signals: new insights into the neural origin of muscle synergies. Neuroscience 355:22–35. https://doi.org/10.1016/j.neuroscience.2017.04.039

Fuglevand AJ, Winter DA, Patla AE, Stashuk D (1992) Detection of motor unit action potentials with surface electrodes: influence of electrode size and spacing. Biol Cybern 67(2):143–153. https://doi.org/10.1007/bf00201021

Gallego JA, Perich MG, Miller LE, Solla SA (2017) Neural manifolds for the control of movement. Neuron 94(5):978–984

Ghislieri M, Agostini V, Knaflitz M (2020) Muscle synergies extracted using principal activations: improvement of robustness and interpretability. IEEE Trans Neural Syst Rehabil Eng 28(2):453–460. https://doi.org/10.1109/tnsre.2020.2965179

Giszter SF (2015) Motor primitives—new data and future questions. Curr Opin Neurobiol 33:156–165

Giszter S, Patil V, Hart C (2007) Primitives, premotor drives, and pattern generation: a combined computational and neuroethological perspective. Prog Brain Res 165:323–346

Gizzi L, Nielsen JF, Felici F, Ivanenko YP, Farina D (2011) Impulses of activation but not motor modules are preserved in the locomotion of subacute stroke patients. J Neurophysiol 106(1):202–210. https://doi.org/10.1152/jn.00727.2010

Heales LJ, Hug F, MacDonald DA, Vicenzino B, Hodges PW (2016) Is synergistic organisation of muscle coordination altered in people with lateral epicondylalgia? A case–control study. Clin Biomech (Bristol, Avon) 35:124–131. https://doi.org/10.1016/j.clinbiomech.2016.04.017

Hinnekens E, Berret B, Do MC, Teulier C (2020) Modularity underlying the performance of unusual locomotor tasks inspired by developmental milestones. J Neurophysiol 123(2):496–510. https://doi.org/10.1152/jn.00662.2019

Hirashima M, Oya T (2016) How does the brain solve muscle redundancy? Filling the gap between optimization and muscle synergy hypotheses. Neurosci Res 104:80–87

Hogan N, Sternad D (2013) Dynamic primitives in the control of locomotion. Front Comput Neurosci 7:71

Holdefer R, Miller L (2002) Primary motor cortical neurons encode functional muscle synergies. Exp Brain Res 146(2):233–243

Hug F, Turpin NA, Couturier A, Dorel S (2011) Consistency of muscle synergies during pedaling across different mechanical constraints. J Neurophysiol 106(1):91–103. https://doi.org/10.1152/jn.01096.2010

Hug F, Turpin NA, Dorel S, Guevel A (2012) Smoothing of electromyographic signals can influence the number of extracted muscle synergies. Clin Neurophysiol 123(9):1895–1896. https://doi.org/10.1016/j.clinph.2012.01.015

Hug F, Vogel C, Tucker K, Dorel S, Deschamps T, Le Carpentier E, Lacourpaille L (2019) Individuals have unique muscle activation signatures as revealed during gait and pedaling. J Appl Physiol (1985) 127(4):1165–1174. https://doi.org/10.1152/japplphysiol.01101.2018

Israely S, Leisman G, Machluf C, Shnitzer T, Carmeli E (2017) Direction modulation of muscle synergies in a hand-reaching task. IEEE Trans Neural Syst Rehabil Eng 25(12):2427–2440. https://doi.org/10.1109/tnsre.2017.2769659

Ivanenko YP, Poppele RE, Lacquaniti F (2004) Five basic muscle activation patterns account for muscle activity during human locomotion. J Physiol 556(Pt 1):267–282. https://doi.org/10.1113/jphysiol.2003.057174

Ivanenko YP, Cappellini G, Dominici N, Poppele RE, Lacquaniti F (2005) Coordination of locomotion with voluntary movements in humans. J Neurosci 25(31):7238–7253. https://doi.org/10.1523/jneurosci.1327-05.2005

Jackson DA (1993) Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. Ecology 74(8):2204–2214

Kargo WJ, Giszter SF (2008) Individual premotor drive pulses, not time-varying synergies, are the units of adjustment for limb trajectories constructed in spinal cord. J Neurosci 28(10):2409–2425. https://doi.org/10.1523/jneurosci.3229-07.2008

Kargo WJ, Nitz DA (2003) Early skill learning is expressed through selection and tuning of cortically represented muscle synergies. J Neurosci 23(35):11255–11269

Kerkman JN, Daffertshofer A, Gollo LL, Breakspear M, Boonstra TW (2018) Network structure of the human musculoskeletal system shapes neural interactions on multiple time scales. Sci Adv. https://doi.org/10.1126/sciadv.aat0497

Kieliba P, Tropea P, Pirondini E, Coscia M, Micera S, Artoni F (2018) How are muscle synergies affected by electromyography preprocessing? IEEE Trans Neural Syst Rehabil Eng 26(4):882–893. https://doi.org/10.1109/tnsre.2018.2810859

Kim Y, Bulea TC, Damiano DL (2016) Novel methods to enhance precision and reliability in muscle synergy identification during

walking. Front Hum Neurosci 10:455. https://doi.org/10.3389/fnhum.2016.00455
Kim M, Kim Y, Kim H, Yoon B (2018a) Specific muscle synergies in national elite female ice hockey players in response to unexpected external perturbation. J Sports Sci 36(3):319–325. https://doi.org/10.1080/02640414.2017.1306090
Kim Y, Bulea TC, Damiano DL (2018b) Children with cerebral palsy have greater stride-to-stride variability of muscle synergies during gait than typically developing children: implications for motor control complexity. Neurorehabil Neural Repair 32(9):834–844. https://doi.org/10.1177/1545968318796333
Klein CS, Brooks D, Richardson D, McIlroy WE, Bayley MT (2010) Voluntary activation failure contributes more to plantar flexor weakness than antagonist coactivation and muscle atrophy in chronic stroke survivors. J Appl Physiol (1985) 109(5):1337–1346. https://doi.org/10.1152/japplphysiol.00804.2009
Klein Breteler MD, Simura KJ, Flanders M (2007) Timing of muscle activation in a hand movement sequence. Cereb Cortex 17(4):803–815. https://doi.org/10.1093/cercor/bhk033
Krishnamoorthy V, Latash ML, Scholz JP, Zatsiorsky VM (2004) Muscle modes during shifts of the center of pressure by standing persons: effect of instability and additional support. Exp Brain Res 157(1):18–31. https://doi.org/10.1007/s00221-003-1812-y
Krouchev N, Kalaska JF, Drew T (2006) Sequential activation of muscle synergies during locomotion in the intact cat as revealed by cluster analysis and direct decomposition. J Neurophysiol 96(4):1991–2010. https://doi.org/10.1152/jn.00241.2006
Lacquaniti F, Ivanenko YP, Zago M (2012) Patterned control of human locomotion. J Physiol 590(10):2189–2199
Laine CM, Valero-Cuevas FJ (2017) Intermuscular coherence reflects functional coordination. J Neurophysiol 118(3):1775–1783. https://doi.org/10.1152/jn.00204.2017
Lambert-Shirzad N, Van der Loos HM (2017) On identifying kinematic and muscle synergies: a comparison of matrix factorization methods using experimental data from the healthy population. J Neurophysiol 117(1):290–302
Latash ML (2020) On primitives in motor control. Mot Control 24(2):318–346
Law LF, Krishnan C, Avin K (2011) Modeling nonlinear errors in surface electromyography due to baseline noise: a new methodology. J Biomech 44(1):202–205. https://doi.org/10.1016/j.jbiomech.2010.09.008
Lee WA (1984) Neuromotor synergies as a basis for coordinated intentional action. J Mot Behav 16(2):135–170
Lee DD, Seung HS (1999) Learning the parts of objects by non-negative matrix factorization. Nature 401(6755):788–791. https://doi.org/10.1038/44565
Lee DD, Seung HS (2001) Algorithms for non-negative matrix factorization. In Advances in neural information processing systems. Springer, New York, pp 556–562
Levine AJ, Hinckley CA, Hilde KL, Driscoll SP, Poon TH, Montgomery JM, Pfaff SL (2014) Identification of a cellular node for motor control pathways. Nat Neurosci 17(4):586–593. https://doi.org/10.1038/nn.3675
Lindstroem R, Graven-Nielsen T, Falla D (2012) Current pain and fear of pain contribute to reduced maximum voluntary contraction of neck muscles in patients with chronic neck pain. Arch Phys Med Rehabil 93(11):2042–2048. https://doi.org/10.1016/j.apmr.2012.04.014
Lunardini F, Casellato C, Bertucco M, Sanger TD, Pedrocchi A (2017) Children with and without dystonia share common muscle synergies while performing writing tasks. Ann Biomed Eng 45(8):1949–1962. https://doi.org/10.1007/s10439-017-1838-0
Maclellan MJ, Ivanenko YP, Massaad F, Bruijn SM, Duysens J, Lacquaniti F (2014) Muscle activation patterns are bilaterally linked during split-belt treadmill walking in humans. J Neurophysiol 111(8):1541–1552. https://doi.org/10.1152/jn.00437.2013
Manickaraj N, Bisset LM, Devanaboyina V, Kavanagh JJ (2017) Chronic pain alters spatiotemporal activation patterns of forearm muscle synergies during the development of grip force. J Neurophysiol 118(4):2132–2141. https://doi.org/10.1152/jn.00210.2017
Martinez-Valdes E, Negro F, Falla D, De Nunzio AM, Farina D (2018) Surface electromyographic amplitude does not identify differences in neural drive to synergistic muscles. J Appl Physiol (1985) 124(4):1071–1079. https://doi.org/10.1152/japplphysiol.01115.2017
Milner-Brown HS, Stein RB (1975) The relation between the surface electromyogram and muscular force. J Physiol 246(3):549–569. https://doi.org/10.1113/jphysiol.1975.sp010904
Muceli S, Boye AT, d'Avella A, Farina D (2010) Identifying representative synergy matrices for describing muscular activation patterns during multidirectional reaching in the horizontal plane. J Neurophysiol 103(3):1532–1542. https://doi.org/10.1152/jn.00559.2009
Muceli S, Falla D, Farina D (2014) Reorganization of muscle synergies during multidirectional reaching in the horizontal plane with experimental muscle pain. J Neurophysiol 111(8):1615–1630. https://doi.org/10.1152/jn.00147.2013
Mussa-Ivaldi FA, Solla SA (2004) Neural primitives for motion control. IEEE J Ocean Eng 29(3):640–650
Oliveira AS, Gizzi L, Farina D, Kersting UG (2014) Motor modules of human locomotion: influence of EMG averaging, concatenation, and number of step cycles. Front Hum Neurosci 8:335. https://doi.org/10.3389/fnhum.2014.00335
Overduin SA, d'Avella A, Roh J, Carmena JM, Bizzi E (2015) Representation of muscle synergies in the primate brain. J Neurosci 35(37):12615–12624. https://doi.org/10.1523/jneurosci.4302-14.2015
Rabbi MF, Pizzolato C, Lloyd DG, Carty CP, Devaprakash D, Diamond LE (2020) Non-negative matrix factorisation is the most appropriate method for extraction of muscle synergies in walking and running. Sci Rep 10(1):8266. https://doi.org/10.1038/s41598-020-65257-w
Ranganathan R, Krishnan C (2012) Extracting synergies in gait: using EMG variability to evaluate control strategies. J Neurophysiol 108(5):1537–1544
Rickard S, Cichocki A (2008) When is non-negative matrix decomposition unique? In: 2008 42nd Annual conference on information sciences and systems, 2008. IEEE, pp 1091–1092
Roh J, Rymer WZ, Beer RF (2012) Robustness of muscle synergies underlying three-dimensional force generation at the hand in healthy humans. J Neurophysiol 107(8):2123–2142. https://doi.org/10.1152/jn.00173.2011
Roh J, Rymer WZ, Perreault EJ, Yoo SB, Beer RF (2013) Alterations in upper limb muscle synergy structure in chronic stroke survivors. J Neurophysiol 109(3):768–781. https://doi.org/10.1152/jn.00670.2012
Saito A, Tomita A, Ando R, Watanabe K, Akima H (2018) Similarity of muscle synergies extracted from the lower limb including the deep muscles between level and uphill treadmill walking. Gait Posture 59:134–139. https://doi.org/10.1016/j.gaitpost.2017.10.007
Santuz A, Ekizos A, Janshen L, Baltzopoulos V, Arampatzis A (2017) On the methodological implications of extracting muscle synergies from human locomotion. Int J Neural Syst 27(5):1750007. https://doi.org/10.1142/s0129065717500071
Sartori M, Gizzi L, Lloyd DG, Farina D (2013) A musculoskeletal model of human locomotion driven by a low dimensional set of impulsive excitation primitives. Front Comput Neurosci 7:79. https://doi.org/10.3389/fncom.2013.00079

Sawers A, Allen JL, Ting LH (2015) Long-term training modifies the modular structure and organization of walking balance control. J Neurophysiol 114(6):3359–3373. https://doi.org/10.1152/jn.00758.2015

Scano A, Dardari L, Molteni F, Giberti H, Tosatti LM, d'Avella A (2019) A comprehensive spatial mapping of muscle synergies in highly variable upper-limb movements of healthy subjects. Front Physiol 10:1231. https://doi.org/10.3389/fphys.2019.01231

Severini G, De Marchis C (2018) Effect of SNR normalization on the estimation of muscle synergies from EMG datasets. In: 2018 IEEE international symposium on medical measurements and applications (MeMeA), 2018. IEEE, pp 1–5

Shiavi R, Frigo C, Pedotti A (1998) Electromyographic signals during gait: criteria for envelope filtering and number of strides. Med Biol Eng Comput 36(2):171–178. https://doi.org/10.1007/bf02510739

Shmuelof L, Krakauer JW, Mazzoni P (2012) How is a motor skill learned? Change and invariance at the levels of task success and trajectory control. J Neurophysiol 108(2):578–594. https://doi.org/10.1152/jn.00856.2011

Shuman BR, Schwartz MH, Steele KM (2017) Electromyography data processing impacts muscle synergies during gait for unimpaired children and children with cerebral palsy. Front Comput Neurosci 11:50. https://doi.org/10.3389/fncom.2017.00050

Shuman BR, Goudriaan M, Desloovere K, Schwartz MH, Steele KM (2019) Muscle synergies demonstrate only minimal changes after treatment in cerebral palsy. J Neuroeng Rehabil 16(1):46. https://doi.org/10.1186/s12984-019-0502-3

Singh RE, Iqbal K, White G, Hutchinson TE (2018) A systematic review on muscle synergies: from building blocks of motor behavior to a neurorehabilitation tool. Appl Bionics Biomech. https://doi.org/10.1155/2018/3615368

Soomro MH, Conforto S, Giunta G, Ranaldi S, De Marchis C (2018) Comparison of initialization techniques for the accurate extraction of muscle synergies from myoelectric signals via nonnegative matrix factorization. Appl Bionics Biomech

Sousa AS, Tavares JMR (2012) Surface electromyographic amplitude normalization methods: a review. Electromyogr New Dev Proced Appl

Steele KM, Tresch MC, Perreault EJ (2013) The number and choice of muscles impact the results of muscle synergy analyses. Front Comput Neurosci 7:105. https://doi.org/10.3389/fncom.2013.00105

Steele KM, Rozumalski A, Schwartz MH (2015a) Muscle synergies and complexity of neuromuscular control during gait in cerebral palsy. Dev Med Child Neurol 57(12):1176–1182

Steele KM, Tresch MC, Perreault EJ (2015b) Consequences of biomechanically constrained tasks in the design and interpretation of synergy analyses. J Neurophysiol 113(7):2102–2113

Takei T, Confais J, Tomatsu S, Oya T, Seki K (2017) Neural basis for hand muscle synergies in the primate spinal cord. Proc Natl Acad Sci USA 114(32):8643–8648. https://doi.org/10.1073/pnas.1704328114

Ting LH, Chvatal SA (2010) Decomposing muscle activity in motor tasks: methods and interpretation. In: Danion F, Latash M (eds) Motor control:theories, experiments, and applications. Oxford University Press, Oxford, pp 102–138

Ting LH, Macpherson JM (2005) A limited set of muscle synergies for force control during a postural task. J Neurophysiol 93(1):609–613. https://doi.org/10.1152/jn.00681.2004

Togo S, Imamizu H (2017) Empirical evaluation of voluntarily activatable muscle synergies. Front Comput Neurosci 11:82. https://doi.org/10.3389/fncom.2017.00082

Torres-Oviedo G, Ting LH (2010) Subject-specific muscle synergies in human balance control are consistent across different biomechanical contexts. J Neurophysiol 103(6):3084–3098. https://doi.org/10.1152/jn.00960.2009

Tresch MC, Saltiel P, Bizzi E (1999) The construction of movement by the spinal cord. Nat Neurosci 2:162–167

Tresch MC, Cheung VCK, d'Avella A (2006) Matrix factorization algorithms for the identification of muscle synergies: evaluation on simulated and experimental data sets. J Neurophysiol 95(4):2199–2212. https://doi.org/10.1152/jn.00222.2005

Turpin NA, Guevel A, Durand S, Hug F (2011) No evidence of expertise-related changes in muscle synergies during rowing. J Electromyogr Kinesiol 21(6):1030–1040. https://doi.org/10.1016/j.jelekin.2011.07.013

Turpin NA, Costes A, Moretto P, Watier B (2017) Can muscle coordination explain the advantage of using the standing position during intense cycling? J Sci Med Sport 20(6):611–616. https://doi.org/10.1016/j.jsams.2016.10.019

Turpin NA, Martinez R, Begon M (2020) Shoulder muscle activation strategies differ when lifting or lowering a load. Eur J Appl Physiol 120(11):2417–2429. https://doi.org/10.1007/s00421-020-04464-9

Valero-Cuevas FJ, Venkadesan M, Todorov E (2009) Structured variability of muscle activations supports the minimal intervention principle of motor control. J Neurophysiol 102(1):59–68. https://doi.org/10.1152/jn.90324.2008

Van Criekinge T, Vermeulen J, Wagemans K, Schroder J, Embrechts E, Truijen S, Hallemans A, Saeys W (2019) Lower limb muscle synergies during walking after stroke: a systematic review. Disabil Rehabil. https://doi.org/10.1080/09638288.2019.1578421

van der Krogt MM, Oudenhoven L, Buizer AI, Dallmeijer A, Dominici N, Harlaar J (2016) The effect of EMG processing choices on muscle synergies before and after BoNT-A treatment in cerebral palsy

Viviani P, Laissard G (1991) Timing control in motor sequences. In: Fagard J, Wolff PH (eds) Advances in Psychology, vol 81. North-Holland, Amsterdam, pp 1–36. doi: https://doi.org/10.1016/S0166-4115(08)60758-X

Wakeling JM, Horn T (2009) Neuromechanics of muscle synergies during cycling. J Neurophysiol 101(2):843–854. https://doi.org/10.1152/jn.90679.2008

Wong AL, Krakauer JW (2019) Why are sequence representations in primary motor cortex so elusive? Neuron 103(6):956–958. https://doi.org/10.1016/j.neuron.2019.09.011

Yang Z, Oja E (2010) Linear and nonlinear projective nonnegative matrix factorization. IEEE Trans Neural Netw 21(5):734–749

Yang JF, Winter DA (1984) Electromyographic amplitude normalization methods: improving their sensitivity as diagnostic tools in gait analysis. Arch Phys Med Rehabil 65(9):517–521

Yang Q, Logan D, Giszter SF (2019) Motor primitives are determined in early development and are then robustly conserved into adulthood. Proc Natl Acad Sci USA 116(24):12025–12034. https://doi.org/10.1073/pnas.1821455116

Zandvoort CS, van Dieen JH, Dominici N, Daffertshofer A (2019) The human sensorimotor cortex fosters muscle synergies through cortico-synergy coherence. Neuroimage 199:30–37. https://doi.org/10.1016/j.neuroimage.2019.05.041

Zelik KE, La Scaleia V, Ivanenko YP, Lacquaniti F (2014) Can modular strategies simplify neural control of multidirectional human locomotion? J Neurophysiol 111(8):1686–1702. https://doi.org/10.1152/jn.00776.2013

Zheng Z, Yang J, Zhu Y (2007) Initialization enhancer for non-negative matrix factorization. Eng Appl Artif Intell 20(1):101–110