De Coordinatione Motus Humani[1]: The Synergy Expansion Hypothesis

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Abstract

The search for an answer to Bernstein's degrees of freedom problem has propelled a large portion of research studies in human motor control over the past six decades. Different theories have been developed to explain how humans might use their incredibly complex neuro-musculo-skeletal system with astonishing ease. Among these theories, motor synergies appeared as one possible explanation. In this work, the authors investigate the nature and role of synergies and propose a new theoretical framework, namely the "expansion hypothesis", to answer Bernstein's problem. The expansion hypothesis is articulated in three propositions: mechanical, developmental, and behavioral. Each proposition addresses a different question on the nature of synergies: (i) How many synergies can humans have? (ii) How do we learn and develop synergies? (iii) How do we use synergies? An example numerical simulation is presented and analyzed to clarify the hypothesis propositions. The expansion hypothesis is contextualized with respect to the existing literature on motor synergies both in healthy and impaired individuals, as well as other prominent theories in human motor control. The expansion hypothesis provides a novel and testable framework to better comprehend and explain the nature, use and evolution of human motor skills.

Introduction

In 1899, Prof. Robert Woodworth questioned how humans could coordinate the actions of their incredibly numerous muscles and joints to perform most of their motor tasks with astonishing ease. Citing his own words: *"Even in comparatively unskilled movements it is remarkable how many groups of muscles must cooperate, and with what accuracy each must do just so much and no more."* (Woodworth, 1899).

Similarly, more than half a century later, Prof. Nikolai Bernstein published another milestone contribution trying to answer the same research question. Interestingly, his research started with a similar opening: "*The science of human movements and theories of motor co-ordination have until recently been one of the most obscure branches of human and comparative physiology; …*" (Bernstein, 1967). Bernstein later formulated what is known as the "degrees of freedom" problem. This concerns the astonishing redundancy (or abundance) of the human motor control system that fundamentally affords infinitely many solutions to the same motor problem. Therefore, the natural question that arises is: how do humans compute, find or select their specific solution for a given motor task?

Multiple hypotheses have been proposed through the years to answer this question. These hypotheses can be classified into four main categories – not always mutually exclusive: optimal control hypotheses (Kumar et al., 2016; Scott, 2004); equilibrium point hypotheses (Feldman, 1966, 1986); uncontrolled manifold hypotheses (Kang et al., 2004; Scholz & Schöner, 1999; Todorov, 2004); and motor synergy hypotheses (D'Avella & Bizzi, 2005; Latash et al., 2007; Santello et al., 1998).

Here we focus our attention on the theory of motor synergies. The term "synergy" – from the Greek word συνεργία i.e., 'working together' – was initially adopted to describe particularly repetitive and coordinated motor tasks such as locomotion. However, in more recent years the term has found an

[1] From Latin: "On the coordination of human motion".

increasing use in the motor control and medical literature in a broader sense and – often times – with different connotations.

Depending on the nature of the analyzed human behavior, we can talk of either neural (Cheung & Seki, 2021; Santello et al., 2013), muscular (Cheung et al., 2009; D'Avella & Bizzi, 2005; D'avella & Tresch, 2001; Weiss & Flanders, 2004), or kinematic synergies (Santello et al., 1998, 2016; Todorov & Ghahramani, 2004). In all these contexts, synergies are interpreted as a dimensionality reduction method that humans adopt to simplify control by fundamentally transforming a high-dimensional task to a lower-dimensional one. A common example can be found in the many studies of the kinematics of the human hand (Mason et al., 2001; Santello et al., 1998, 2013, 2016; Todorov & Ghahramani, 2004; Weiss & Flanders, 2004; West et al., 2023). By extracting synergies through dimensionality reduction techniques (e.g., Principal Component Analysis), a few synergies were able to account for most of the variance of different reaching and grasping hand motions. In a similar fashion, synergies were also extracted in studies of posture and movement of the lower limbs at the muscular level (Ting & McKay, 2007; Yang et al., 2019). An important question, rarely addressed in this prior work, is how these synergies emerge. This paper explores a possible answer.

Moreover, in all the aforementioned motor control studies, synergies assume a mostly-positive connotation. They represent a way to reduce control complexity by voluntarily reducing the dimensionality of the analyzed motor tasks. However, it is important to mention that synergies can also assume a negative connotation, such as in neuro-rehabilitation. In these cases, synergies or synergistic actions are interpreted as the unwanted, and typically uncontrolled, movements of patients' limbs in predetermined coordination patterns. For example, when discussing stroke survivors, synergy is often used to describe the result of undesired and involuntary motion of the paretic side (Avni et al., 2022; Barroso et al., 2017; Dipietro et al., 2009; Hadjiosif et al., 2022; Krakauer & Carmichael, 2017; Neckel et al., 2006; Roh et al., 2013; Yang et al., 2019).

This apparent contrast of positive and negative connotations of synergies often leads to confusion and disagreement between motor control and rehabilitation experts. In this work, to minimize confusion, we start by proposing a definition of motor synergy i.e., *the coordinated and simultaneous action of a group of features (neural, muscular, kinematic) to perform a specific motor task*. This definition is intended to remove any value judgement from the concept of synergy, thus leaving the reader free to consider it as negative or positive depending on the application context.

The current mathematical methods to extract synergies are based on matrix factorization techniques such as Principal Component Analysis (PCA), Factor Analysis (FA), Non-negative Matrix Factorization (NNMF), or Singular Value Decomposition (SVD) (D'avella & Tresch, 2001; Fazle Rabbi et al., 2020; Todorov & Ghahramani, 2004; Tresch et al., 2006; West et al., 2023). All of these methods are fundamentally designed to find lower-dimensional spaces within a given hyper-space of analyzed features. For example, when studying human hand kinematics, the feature space might account for ~20 hand joint angles. In this 20-dimensional hyper-space, the aforementioned techniques numerically extract directions (synergies) where most of the variance of the feature space lies.

These approaches intrinsically limit the number of possible synergies to no more than the number of analyzed features. However, this intrinsic limitation – dictated by the adopted mathematical approaches – precludes an answer to several interesting questions: How do synergies emerge in human behavior? How many synergies can humans have? Is there an upper or lower limit? The former question is sparsely investigated. If a synergy is a coordinated action of multiple features, how do we reach this coordination? Do we start from individual joint or muscle actions and learn to combine them? Or do we move from highly coordinated joint or muscle patterns and learn to refine them?

In this work, the authors propose a "synergy expansion hypothesis", to answer Bernstein's problem. This hypothesis aims to provide a comprehensive answer to the aforementioned questions by grounding the motor synergy hypothesis in the biomechanical structure and developmental history of human motor behavior. A numerical example is provided to facilitate an intuitive understanding of the hypothesis.

The Synergy Expansion Hypothesis

The synergy expansion hypothesis can be articulated as three propositions:

1. **Mechanical**: The number of synergies is not limited by the number of control features.
2. **Developmental**: Humans start from highly stereotyped and coordinated patterns (primordial synergies) and, through motor learning and development, learn new and more refined synergies.
3. **Behavioral**: Learned synergies are evoked upon need during a given motor task.

Mechanical Proposition

The human motor control system can be described in at least three major geometric hyper-spaces: task space, joint space and muscle space (Figure 1). The task (or work) space is the physical space in which we perform our motor actions. It can be described, considering a single end-effector, by up to $n_{ts} = 6$ independent variables. The most common (but not unique) choice is an orthogonal reference frame of three translations (surge, sway, heave i.e., x, y, z) and related axial rotations (roll, pitch, and yaw i.e., α, β, γ). These variables can be associated with a given "flow" i.e., task-space velocities ($\boldsymbol{v}$), and a given "effort" i.e., task-space generalized forces ($\boldsymbol{F}$) (Lagrange, 1788; Newton, 1687; Paynter, 1961). The joint (or configuration) space is the hyper-space defined by the human articulations/joints or, in other words, skeletal degrees of freedom. This hyper-space has as many dimensions as the number of human degrees of freedom. That number varies depending on the definition of "joint", ranging from $n_{js} \approx 200$ (Kandel et al., 2021) to about $n_{js} \approx 350$ (Cleveland Clinic, 2024; Healthline, 2024). The strictest criterion, for example, considers any two consecutive bones as a "joint". In the joint space, we can define a generalized coordinate (q) for each degree of freedom and this typically (but not exclusively) coincides with the joint angular configuration. Similarly to task-space, we can define a vector of joint-space velocities ($\dot{\boldsymbol{q}}$) and of joint-space generalized forces ($\boldsymbol{\tau}$) representing the "flow" and "effort" variables in the joint space (Lagrange, 1788; Newton, 1687; Paynter, 1961). Finally, we have the muscle hyper-space. This comprises a number of dimensions equal to the number of human muscles. This number is also subject to variation depending on the selection criterion, but it can be reasonably stated that there are $n_{ms} \approx 600+$ independently-addressable muscles in the human body (Kandel et al., 2021). The muscle hyper-space can be, therefore, characterized by a vector of muscle displacements ($\boldsymbol{x_m}$), muscle velocities ($\dot{\boldsymbol{x}}_{\boldsymbol{m}}$) and muscle forces ($\boldsymbol{F_m}$).

Knowing the skeletal and muscular geometry of the human body, it is possible to define a mapping between the effort and flow variables of the task, joint, and muscle spaces. Specifically, the joint space coordinates ($\boldsymbol{q}$) allow the unique definition of both the task and muscle space coordinates. The differential form of these two mappings is provided by two different Jacobian matrices: the task-space Jacobian ($J(\boldsymbol{q})$) and the muscle-space Jacobian ($J_m(\boldsymbol{q})$). For a detailed presentation of Jacobian matrices, the authors recommend the work by Murray et al. (Murray et al., 1994).

The task-space Jacobian is a $n_{ts} \times n_{js}$ matrix ($J(\boldsymbol{q}) \in \mathbb{R}^{n_{ts} \times n_{js}}$) that uniquely maps the joint-space velocities ($\dot{\boldsymbol{q}}$) to task-space ($\boldsymbol{v}$):

$$\boldsymbol{v} = J(\boldsymbol{q}) \cdot \dot{\boldsymbol{q}} \qquad (1)$$

The muscle-space Jacobian is a $n_{ms} \times n_{js}$ matrix ($J_m(\boldsymbol{q}) \in \mathbb{R}^{n_{ms} \times n_{js}}$) that uniquely maps the joint-space velocities ($\dot{\boldsymbol{q}}$) to muscle-space ($\dot{\boldsymbol{x}}$):

$$\dot{\boldsymbol{x}}_{\boldsymbol{m}} = J_m(\boldsymbol{q}) \cdot \dot{\boldsymbol{q}} \qquad (2)$$

These mappings focus on the "flow" variables of the three considered spaces. However, the three spaces are also physically coupled and, as consequence, obey the law of power continuity. The mechanical power at the task-space ($P_t = \boldsymbol{F} \cdot \boldsymbol{v}$), joint-space ($P_j = \boldsymbol{\tau} \cdot \dot{\boldsymbol{q}}$), and muscle-space ($P_m = \boldsymbol{F_m} \cdot \dot{\boldsymbol{x}}_{\boldsymbol{m}}$) must be the same:

$$P = P_t = P_j = P_m \quad (3)$$

Substituting Eqs. 1 and 2 into Eq. 3, it is possible to obtain the mapping between the "effort" variables of the considered hyper-spaces:

$$\boldsymbol{\tau} = J(\boldsymbol{q})^T \cdot \boldsymbol{F} \qquad (4)$$

$$\boldsymbol{\tau} = J_m(\boldsymbol{q})^T \cdot \boldsymbol{F_m} \quad (5)$$

As can be observed from Eqs. 4-5, the transpose of the task and muscle Jacobians provides a unique mapping between the task-space and muscle-space forces to the joint torques. Figure 1 shows a graphical representation of these relations.

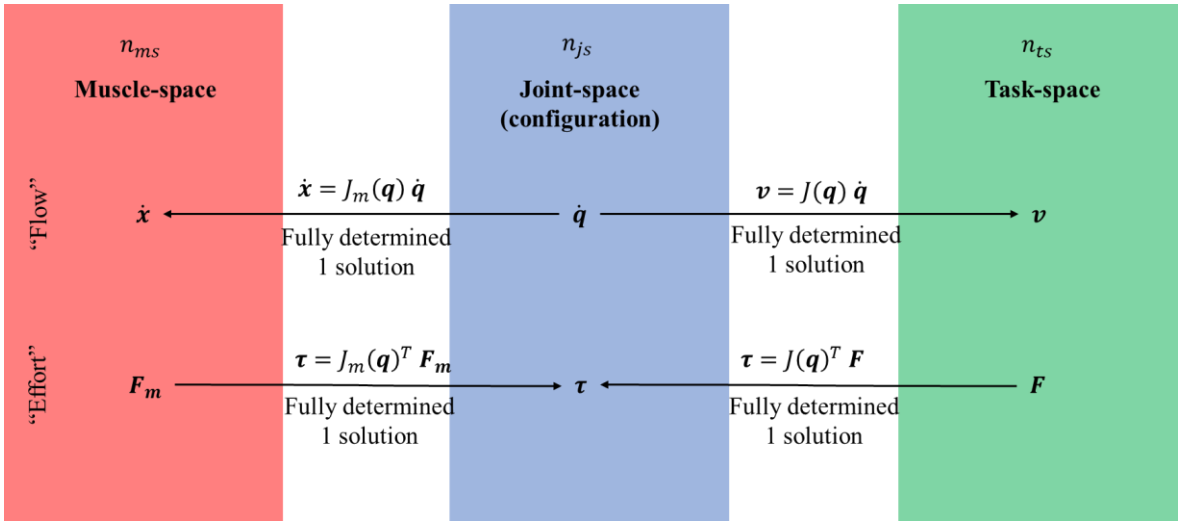

Figure 1 – The relationship between some of the different spaces of human motor control. These spaces are characterized by n_{ms}, n_{js}, n_{ts} dimensions respectively for the muscle, joint and task space. It is important to underline that $n_{ms} > n_{js} > n_{ts}$. The arrows describe the direction of fully determined transformations. Interestingly, the joint-space coordinates (q) allow for a full description of both the muscle and task space variables.

These unique mappings fundamentally provide a one-to-one relation between the different hyper-spaces of human motor action. However, such mappings are non-consecutive i.e., you can't directly map from task-space to muscle-space – either in terms of "flow" or "effort" variables – with a unique transformation.

For example, if we try to identify the muscle velocities ($\dot{\boldsymbol{x}}_{\boldsymbol{m}}$) required to perform a desired task-space motion ($\boldsymbol{v}$), we need to combine Eqs. 1 and 2, obtaining:

$$\dot{\boldsymbol{x}}_{\boldsymbol{m}} = J_m(\boldsymbol{q}) \cdot J(\boldsymbol{q})^{-1} \cdot \boldsymbol{v} \qquad (6)$$

This requires the matrix inversion of the task-space Jacobian. However, because $n_{js} > n_{ts}$, the resulting system of equations is under-determined, and therefore, there is no unique inverse i.e., solution, but infinitely many of them. Specifically, there exist infinitely many solutions whose dimensionality is equal to the size of the null-space of the task-space Jacobian ($Null\big(J(\boldsymbol{q})\big)$), where the null-space is the linear subspace that describes a mapping to a zero vector.

Similarly, if we try to identify the muscle force vector ($\boldsymbol{F_m}$) required to generate a desired task-space force ($\boldsymbol{F}$), we need to combine Eqs. 4 and 5, obtaining:

$$\boldsymbol{F_m} = J_m(\boldsymbol{q})^{-T} \cdot J(\boldsymbol{q})^T \cdot \boldsymbol{F} \qquad (7)$$

In this case, the inversion of the muscle-space Jacobian transpose also leads to an under-determined system of equations with infinitely many solutions (with dimensionality determined by the null-space of the muscle-space Jacobian $Null\big(J_m(\boldsymbol{q})\big)$) since $n_{ms} > n_{js}$.

From a human motor control perspective, we can imagine these non-unique solutions as the spaces where kinematic and muscular synergies may usefully be defined. Independently of the neural basis of the synergies, to generate a desired task-space force or motion, a specific trajectory in the null-space must be selected in agreement with Equations 6 and 7. The selected trajectories in the null-space represent our selectable synergies. In fact, a synergy can be imagined as one of the possible solutions of the Jacobian inverse in the "flow" domain or transposed Jacobian inverse in the "effort" domain. Specifically, kinematic synergies can be identified in the inversion of the task-space Jacobian, $J(\boldsymbol{q})$, when going from task-space velocities to joint-space velocities ($\dot{\boldsymbol{q}} = J(\boldsymbol{q})^{-1} \cdot \boldsymbol{v}$), while muscular synergies may be identified when

mapping joint-space torques to muscle-space forces ($\boldsymbol{F_m} = J_m(\boldsymbol{q})^{-T} \cdot \boldsymbol{\tau}$). These coordination patterns can be considered as **selectable synergies** in the sense that individuals can choose between (infinitely) many of them and select the one they prefer. Figure 2 shows a graphical description of the emergence of selectable kinematic and muscular synergies from the matrix inversions of the Jacobians.

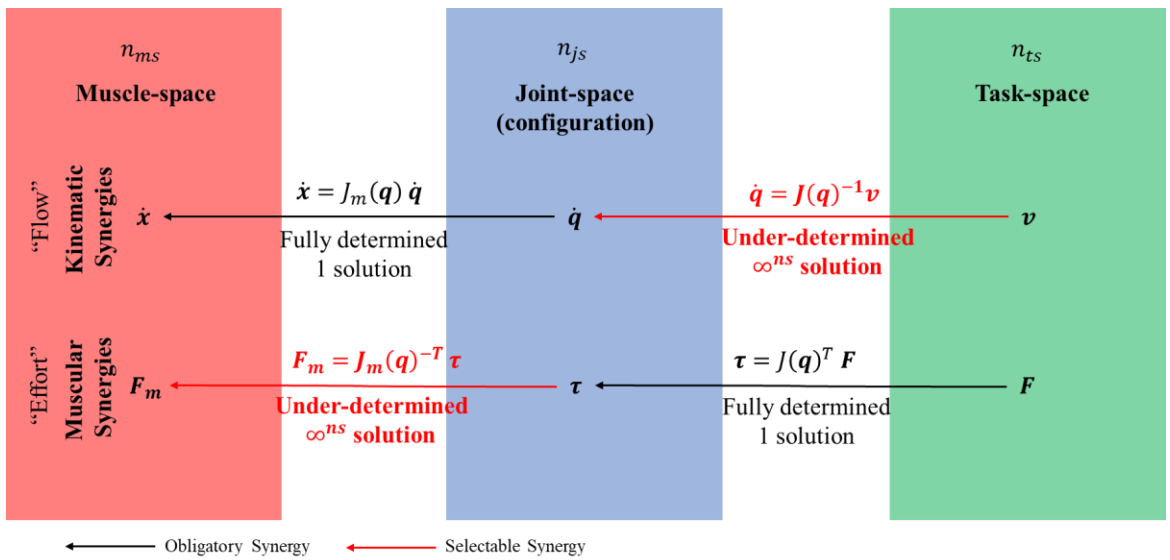

Figure 2 – The mechanical framework describing the emergence of motor control synergies. Synergies emerge from the mapping of task-space variables into joint, and subsequently, muscle space quantities. Synergies can be categorized as obligatory or selectable, depending on the determination of the related transformation i.e., a fully-determined transformation will lead to an **obligatory** synergy, while an under-determined transformation will lead to a **selectable** synergy.

It is interesting to observe that, when moving from task-space to muscle space, there are still some uniquely defined mappings (Fig. 2). For example, joint-space torques are uniquely defined by task-space forces ($\boldsymbol{\tau} = J(\boldsymbol{q}) \cdot \boldsymbol{F}$); muscle-space velocities are uniquely defined by joint-space velocities ($\dot{\boldsymbol{x}}_{\boldsymbol{m}} = J_m(\boldsymbol{q}) \cdot \dot{\boldsymbol{q}}$). These uniquely-defined transformations are dictated by geometry and configuration, and can be interpreted as **obligatory or mandatory synergies**. In simpler words, if I want – for example – to generate a certain end-effector force with my arm given a certain configuration, I will have to generate a uniquely defined set of joint torques with no option for other solutions.

A limitation – worth emphasizing – of the mechanical proposition is that the proposed framework in Figure 2 does not consider that the lever arms of the muscle forces are not always constant, and are functions of the exerted force. While this would influence the relation between force and torque, it does not change the fact that an under-determined mapping exists between muscle forces and joint torques. Therefore, considerations of the first proposition of the expansion hypothesis are still valid.

Another consideration can be made on the dimension of the task space. Above we argued that the task space could have up to $n_{ts} = 6$ degrees of freedom. However, our human body can interact with the external environment at multiple locations i.e., we can use different parts of our body to perform motor tasks. For example, we can use one of our hands to manipulate chopsticks, while using the other hand to hold or move a cup of coffee. In this case, the dimensionality of the task space is larger than 6. A growing dimension of the task-space will shrink the null-space of selectable synergies, thus limiting the hyper-space that is typically available. The limit case is when the task-space dimension reaches the joint-space dimension, thus leading to the absence of a null-space. In other words, the selectable synergies will shrink to only one obligatory synergy. As an example readers may imagine the game of "Twister", where participants are invited to place their hands and feet in particular configurations, up to a limit where they will find it impossible to complete task (Foley & Aftorney, 1966).

Given the proposed mechanical framework for describing motor synergies, we can conclude that the number of synergies is determined by the size of the null-space, not the number of features (muscles, joints, or task-space variables), consistent with the first proposition of the expansion hypothesis. Moreover, a numerical simulation (refer to the Numerical Example Section) further suggests that different subjects may exhibit different synergies for the same motor tasks.

Developmental Proposition

If we look at the development of motor skills during infancy and childhood, we discover that healthy individuals follow a highly-stereotyped sequence. Seefeldt and Gallahue's early works provide a good introduction to the different phases of motor development (Gallahue, 1982; Seefeldt, 1980, 1986). At least three main phases can typically be distinguished. The first phase is dominated by reflexes and it characterizes the neonatal and sometimes prenatal period. Examples are palmar grasp, walking or parachute reflexes to cite some (Anekar & Bordoni, 2022; Cupute et al., 1984; McGraw, 1932). These reflexes involve the coordinated and 'hard-wired' motion of multiple muscles and joints. The immediately succeeding phase consists of the inhibition of such reflexes to build what are known as fundamental or rudimentary motor skills. Common examples are crawling, pulling, pushing, throwing, or walking. This phase starts around the first year of age and continues through all of early childhood (1 to 7 years old approximately). In the fundamental motor skill learning phase, children learn to perform voluntary coordinated motor actions necessary to navigate the surrounding environment. The last stage is the so called specific or specialized phase during which children learn more advanced motor skills linked to task-specific actions. Typical examples are sport, dance or motor skills dedicated to musical instruments.

The stages of motor development highlight an intriguing aspect: humans consistently progress from highly coordinated and unspecialized motor actions to highly individuated and specialized actions.

An example of this coordination-to-individuation behavior can be observed in the literature on development of prehension. Starting from the pioneering work of Halverson (Halverson, 1931), and followed by the improvements of Hohlstein and Butterworth (Butterworth et al., 1997; Hohlstein, 1982); the literature agrees that prehension follows 3 fundamental steps after the inhibition of the palmar grasp reflex (Anekar & Bordoni, 2022; Niezgoda & Beers, 2017). The first step is characterized by the use of the whole hand in an unspecialized manner. This is followed by a second stage during which children use parts of the hand while some specialization begins to develop. The last phase is reached when infants start using the pads of the distal phalanges, the tips of the fingers, in a specialized manner. In other words, humans proceed from highly coordinated power grasps to finger-specific precision grasps.

This trend, that coordination is progressively fragmented, or developed, in more individuated control is observed not only during childhood, but also in adults when learning more advanced motor skills. An example can be found in piano playing. In the work by Furuya et al., the authors observed how musically naïve subjects acquired individuated finger control after practicing some elementary piano exercises (Furuya et al., 2014).

From the perspective of the synergy expansion hypothesis, humans might start with a predefined set of motor synergies such as grasping, pulling, pushing, walking, etc. These **preliminary or primordial synergies** are later refined, fragmented and/or combined to acquire new and more advanced motor skills such as playing a musical instrument, dancing, or practicing a sport. While individuals might start from the same set of primordial synergies, no constraints are placed on how different subjects converge to a given motor action. This is in line with a recent experiment presented by Garcia et al. where they showed how long-term learning in rodents can be systematically represented by multiple transitions through hierarchical saddle points (Garcia et al., 2023). The Numerical Example Section provides a possible mathematical description of how multiple subjects, despite starting from the same initial condition, might converge to substantially different synergies.

This does not preclude the use or existence of individual muscle, joint or motor actions. Those are possible and trivially achieved in any healthy unimpaired adult human being. However, these individual

actions appear more plausibly as a consequence of the refinement of a previously highly coordinated movement. To state it in a different way, **highly individuated muscle or joint movements can be interpreted as the most refined motor synergies** where the coordinated action involves only a small subset (as few as one element) of muscles or joints. However, the human musculoskeletal system presents physical constraints (e.g., tendons and ligaments) that do not allow a perfect uncoupling of every muscle and every joint. This provides a biomechanical limit to the level of individuation that a motor synergy can reach. Todorov and Ghahramani highlighted this in their study on kinematic synergies of the hand showing that synergistic i.e., coordinated, behavior emerged even when subjects where tasked to perform highly individuated joint motions (Todorov & Ghahramani, 2004). Moreover, synergistic behavior might also emerge from the intrinsic constraints of a particular motor task forcing the individual to move certain muscles or joints with a certain configuration e.g., when trying to grasp an object in a cluttered space you adapt arm configuration to avoid obstacles.

An interesting connection could be drawn between the coordination to individuation of motor synergies and the emergence of the unwanted synergies in neurally impaired subjects. For example, post-stroke survivors often show the emergence of these undesired coupled movements that won't allow them to individually move their limbs e.g., the shoulder abduction – elbow flexion synergy (Twitchell, 1951). Could it be that neural damage, and in particular stroke, forces subjects to regress towards the primordial synergies we learned as children, and that motor recovery is a form of re-wiring and re-learning of the more refined synergies of adulthood? Another example might come from the study of posture in stroke-survivors. Boehm et al. showed how stroke survivors tend to change the orientation of their ground reaction force towards a more leaning forward posture (Boehm & Gruben, 2016), which might be associated to the forward-oriented upright posture of infants.

Behavioral Proposition

The last aspect of the synergy expansion hypothesis concerns the storing and use of the acquired motor synergies. The authors propose that the learned synergies are stored in memory and recruited upon need. This requires the capability of humans to store specific groups of coordinated actions and re-evoke them. If this is true, we should expect minimal computational effort to perform a learned motor action, since the human motor controller should 'simply' perform a *select-and-shoot strategy* of the necessary synergy required for the task (Figure 3).

We can imagine synergies stored as two different elements: the synergy composition ($w_i(\boldsymbol{f})$) and the synergy evolution ($u_i(t)$). The synergy composition is a vector containing the contribution of each controlled feature (f) to the considered synergy such that $w_i(\boldsymbol{f}) = [f_1 \dots f_m]$, where "m" is the number of features controlled by that synergy and "i" is the specific synergy. As highlighted by the mechanical proposition of the expansion hypothesis, the number of stored synergy compositions $W = [w_1(\boldsymbol{f}) \dots w_N(\boldsymbol{f})]$ can be greater than the number of controlled features i.e., $N \gg m$. The synergy evolution is a scalar function specifying how a selected synergy composition will evolve over time. Analogously to the synergy composition, no theoretical limits are imposed to the number of temporal evolutions i.e., $U = [u_1(t_1) \dots u_N(t_N)]$ with $N > 0$, and $0 \leq t_i \leq t$.

This subdivision of synergies into compositions and temporal evolutions is in line with the recent work proposed by Cheung and Seki, where they proposed a similar topology for the neural basis of motor synergies (Cheung & Seki, 2021).

When an individual is asked to perform a certain motor task, a "selector" will pick-up from the stored synergies a certain subset N_s of synergy compositions and temporal evolutions with $N_s \leq N$. Once selected, the composition and temporal evolutions will be combined to generate the desired feature commands:

$$\alpha(\boldsymbol{f}, t) = \sum_{i=1}^{N_s} w_i(\boldsymbol{f}) \cdot u_i(t_i) \quad (8)$$

Depending on the type of controlled feature, the resulting commands will have to obey either Equation 6 for kinematic synergies or Equation 7 for muscular synergies.

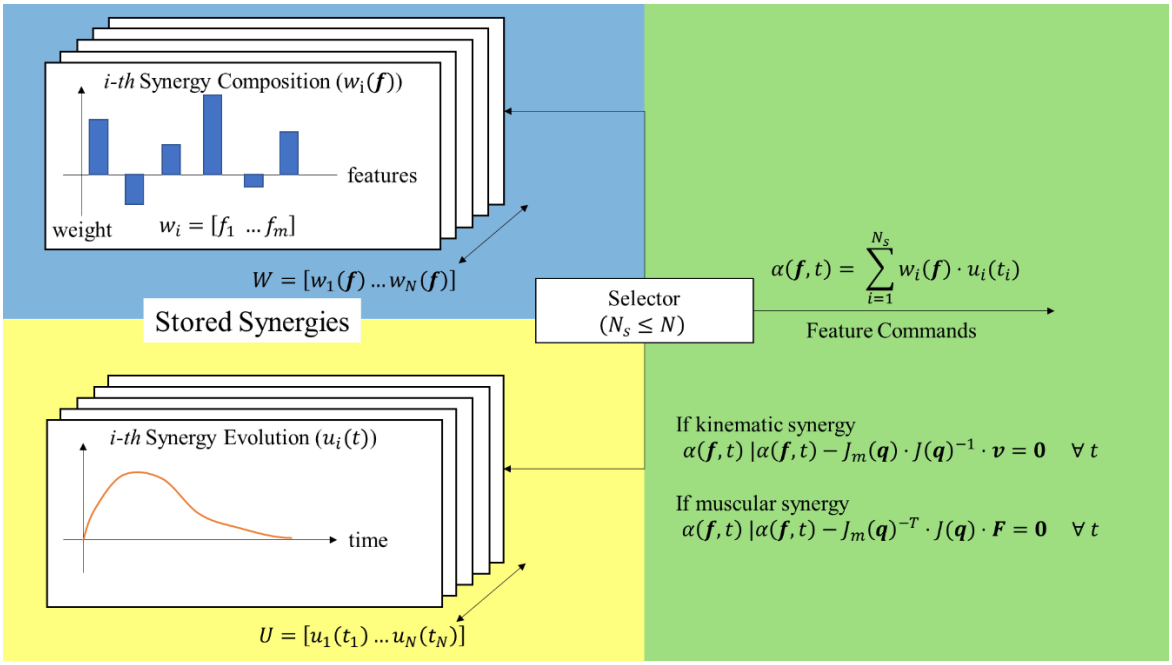

Figure 3 - Diagram showing the 'select-and-shoot' strategy to generate the feature commands to perform a given motor action.

No particular constraints are placed on the mathematical properties of the synergy composition vector $w_i(\boldsymbol{f})$. Nonetheless, an interesting question is whether the vector components are constant or time-varying. This would not affect the 'select-and-shoot' strategy, but it would definitely change the role of the synergy evolution component $u_i(t)$. In other words, if the elements of $w_i(\boldsymbol{f})$ can change sufficiently rapidly over time, the temporal evolution terms can be directly included within the synergy composition. The literature on synergy extraction mostly focused on synergy compositions with constant components. However, D'avella and Tresch showed the possibility to decompose muscle patterns also using time-varying synergies (D'avella & Tresch, 2001). Another interesting possibility is that the synergy composition vector can be updated over longer time scales to account for motor learning.

In literature, the synergy evolution patterns $u_i(t_i)$ are typically extracted by means of dimensionality reduction, thus reflecting the observed trajectories in the sampled motor tasks. When moving from analysis to synthesis of synergies, no guidelines are available on how to shape such time paths. However, multiple studies on human unconstrained motions highlighted the tendency of humans to move following smooth and continuous trajectories, characterized by bell-shaped velocity profiles (Flash & Hogan, 1985; Hogan, 1985; Morasso, 1981; Mussa-Ivaldi et al., 1985). An interesting study, still not fully explored, would be the investigation of the properties of the synergy evolution function $u_i(t)$, to validate the extension of previous motor control studies to control with motor synergies.

The 'select-and-shoot' strategy aligns with the idea of feed-forward predictive motor commands. This is in line with the work by Yeo et al. in which they showed that feed-forward motor commands are necessary to deal with the presence of substantial feedback delay (Yeo et al., 2016). Nonetheless, this does not preclude the presence of feedback control. The literature has widely investigated this possibility, showing how such feedback control models can competently describe many aspects of human motor behavior (Diedrichsen et al., 2010; Kumar et al., 2016; Scott, 2004; Todorov, 2004, 2005; Van Wouwe et al., 2022). In the proposed behavioral proposition, feedback can play a role in adapting – e.g., by means of a sensory driven gain – the magnitude of the synergy composition ($w_i(\boldsymbol{f})$) or the synergy evolution ($u_i(t)$). For example, imagine a case in which a subject is tasked to grasp an object. According to the 'select-and-shoot'

strategy, the subject will recruit the 'most adequate' synergy composition and evolution to perform the task and send out that command (the feed-forward part). However, it is a common tendency of humans to superimpose corrective actions near the end of a reach to a target (Woodworth, 1899). This will require some sort of feedback, that could be achieved either by turning off the 'magnitude' of the previously shot synergy, or by 'shooting' a compensating synergy to augment the previous one.

The selection of the appropriate synergy compositions and evolutions for a given motor task is an interesting question, though outside of the scope of this work. A possible approach can be found in the recent work by Heald et al. in which they propose contextual inference as a way to learn motor repertoires (Heald et al., 2021). Related works that could help in answering the selection process fall within the family of research interested in the processes of 'motor learning' and 'motor adaptation' widely investigated in multiple neuroscientific works (Brashers-Krug et al., 1996; Heald et al., 2021; Oh & Schweighofer, 2019; Stefan et al., 2005).

A Numerical Example

An example of how synergies can emerge from the "mechanical proposition" of the expansion hypothesis can be obtained considering a 3-bar linkage model representing planar motion of the upper-limb as presented in Figure 4.

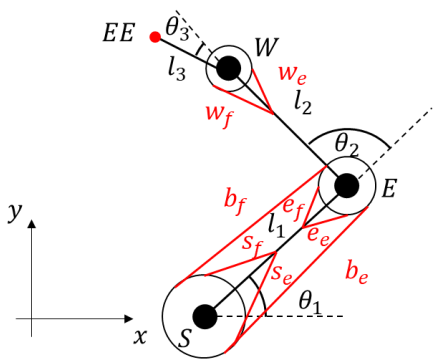

Figure 4 - Three bar link model representing the planar motion of the upper-limb. 'S' represents the shoulder joint, 'E' the elbow, 'W' the wrist, and 'EE' the end-effector. The solid black lines (l_1, l_2, l_3) represent respectively the upper-arm, fore-arm, and hand. The angles $(\theta_1, \theta_2, \theta_3)$ are respectively the shoulder, elbow, and wrist joint angles. The solid red lines represent the line of action of 8 muscles: two shoulder mono-articular flexors (s_f, s_e), two elbow mono-articular flexors (e_f, e_e), two wrist mono-articular flexors (w_f, w_e), and two bi-articular shoulder-elbow flexors (b_f, b_e).

Considering the joint relative angle coordinates $(\theta_1, \theta_2, \theta_3)$ as configuration variables, the end-effector (EE) task-space kinematics can be described as:

$$\begin{cases} x_{EE} = l_1 c_1 + l_2 c_{12} + l_3 c_{123} \\ y_{EE} = l_1 s_1 + l_2 s_{12} + l_3 s_{123} \end{cases} \quad (9)$$

Where c_i, s_i are notations respectively for the cosine and sine functions e.g., $c_{12} = \cos(\theta_1 + \theta_2)$; while l_i are the lengths of the rigid links representing respectively the upper-arm, fore-arm, and hand.

The task-space Jacobian is obtained from the task-space kinematics through partial differentiation of Eqs. (9):

$$J(\boldsymbol{\theta}) = \begin{bmatrix} -l_1 c_1 - l_2 c_{12} - l_3 c_{123} & -l_2 c_{12} - l_3 c_{123} & -l_3 c_{123} \\ l_1 s_1 + l_2 s_{12} + l_3 s_{123} & +l_2 s_{12} + l_3 s_{123} & +l_3 s_{123} \end{bmatrix} \quad (10)$$

Similarly, the joint relative angle coordinates can be used as configuration variables to describe muscle shortening. In the considered case, we focused on an 8-muscle system composed of: 2 mono-articular shoulder flexor-extensors of length (s_f, s_e), 2 mono-articular elbow flexor-extensors of length (e_f, e_e), 2 mono-articular wrist flexor-extensors of length (w_f, w_e), and 2 bi-articular shoulder-elbow flexor-extensors of length (b_f, b_e). The relation mapping joint angles to muscle contractions is uniquely defined by geometry:

$$[s_f \quad s_e \quad b_f \quad b_e \quad e_f \quad e_e \quad w_f \quad w_e]^T = \boldsymbol{M}(\theta_1, \theta_2, \theta_3) \quad (11)$$

where $\boldsymbol{M}$ is a vectorial function $\boldsymbol{M} = [M_1 \dots M_8]$, with $M_i: \mathbb{R}^3 \rightarrow \mathbb{R}^8$, that maps the joint angular trajectories to the muscle elongations. By means of partial differentiation of $\boldsymbol{M}$ with respect to θ_i, the muscle Jacobian can be computed as:

$$J_m(\boldsymbol{\theta})_{i,j} = \frac{\partial M_i}{\partial \theta_j} \qquad (12)$$

Two Jacobian (J, J_m) matrices can be used to move, respectively, from the two-dimensional task space (x, y) to the three-dimensional joint space $(\theta_1, \theta_2, \theta_3)$, and from that joint space to the eight-dimensional muscle space $(s_f, s_e, b_f, b_e, e_f, e_e, w_f, w_e)$.

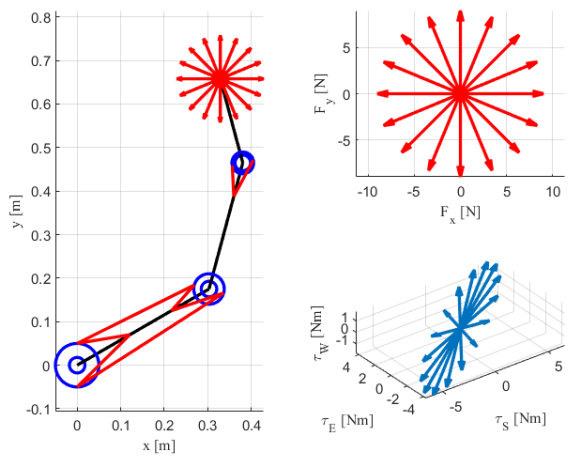

Figure 5 – Example of the generation of obligatory synergies in the joint-space. The left panel shows the arm model in the cartesian space with a series of end-effector forces represented with red arrows. The right top panel shows the amplitude and direction of such forces in the task-space. The right bottom panel presents the mapping of such forces in the torque-space.

Consider now the case in which we are tasked to generate a series of planar forces (F_x, F_y) at the end-effector – i.e., the hand – of our arm model in a given arm configuration $(\theta_1, \theta_2, \theta_3)$. In order to generate such forces, the shoulder, elbow and wrist joints will have to generate – according to Equation (4) – a set of uniquely defined torques, namely an obligatory synergy:

$$[\tau_s \; \tau_e \; \tau_w]^T = J(\boldsymbol{\theta})^{\boldsymbol{T}} \cdot \left[F_x \; F_y\right]^T \qquad (13)$$

Figure 5 provides a graphical example of the generation of such obligatory synergies by means of Equation 13. Specifically, you can observe that for every end-effector force vector $\left[F_x \; F_y\right]^T$, a uniquely defined torque vector $[\tau_s \; \tau_e \; \tau_w]^T$ is obtained.

When moving from joint-space to muscle-space, in order to generate the desired torque coordination (τ_s, τ_e, τ_w), the subject will have to generate a combination of muscle forces in agreement with the inverse of Equation (5):

$$\left[F_{s_f} \; F_{s_e} \; F_{b_f} \; F_{b_e} \; F_{e_f} \; F_{e_e} \; F_{w_f} \; F_{w_e}\right]^T = J_m(\boldsymbol{\theta})^{-T} \cdot [\tau_s \; \tau_e \; \tau_w]^T \qquad (14)$$

However, as explained in the Mechanical Proposition section, the inversion of $J_m(\boldsymbol{\theta})^T$ is not uniquely defined i.e., the system of equations is under-determined. This leaves space for infinitely many combinations of muscle forces to generate the same torque coordination. These are what we defined as **selectable** synergies. In this specific case, the infinitely many combinations will lie in the null-space of $J_m(\boldsymbol{\theta})^T$ which will have a dimensionality equal to $n_{ns} \leq n_m - n_\tau$, where n_{ns} is the size of the null-space, n_m is the number of muscles and n_τ the number of torques.

A numerical simulation was implemented to show how the same task could be completed using different i.e., **selectable**, synergies. Assume a group of subjects is tasked to learn how to generate a certain arm end-effector force $\boldsymbol{F}$ in a planar configuration (refer to Figure 6). The previously presented arm model is adopted. For example, consider the generation of 10 N of force in the positive 'x' direction.

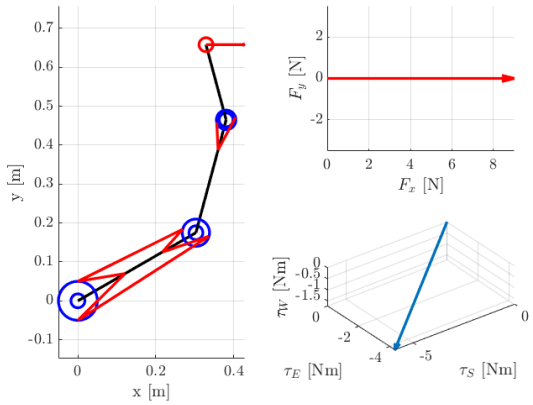

Figure 6 - Three body rigid arm model generating a horizontal arm force. The left panel shows the arm configuration and desired force direction (red arrow). The top right panel show the desired end-effector force, while the bottom right panel show the obligatory torque coordination to generate such end-effector force.

Assume also that each subject starts from a rest condition for which $\boldsymbol{F_{m_0}} = \mathbf{0} \in \mathbb{R}^8$. In such a scenario, we can imagine subjects to learn this task by iteratively varying their muscle force vector $\boldsymbol{F_m}$ to satisfy the following equality:

$$\Delta\boldsymbol{\tau} = J_m^T \boldsymbol{F_m} - J^T \boldsymbol{F} = \mathbf{0} \quad (15)$$

Algorithmically, this may be modeled as a stochastic gradient descent learning problem, where subjects are trying to minimize an error that can be defined – for example – as:

$$e = \sum_{k=1}^{3} (\Delta\tau_k)^2 \quad (16)$$

We do not claim that is exactly how humans learn a new behavior. However, it is a plausible theory.

At each new iteration 'i', a series of 5 new possible force vectors $\boldsymbol{F_{m_i}}$ are generated by adding a random increment ΔF to each element of $\boldsymbol{F_{m_i}}$. For each of these 5 new possible force vectors, the algorithm selects the one minimizing the error function (Eq. 16). This is done to simulate the exploration of different directions in the muscle force hyper-space. The force vector at the next iteration will be equal to:

$$\boldsymbol{F_{m_{i+1}}} = \arg min\, e \quad (17)$$

The learning continues until the error goes below an arbitrary threshold i.e., $e \leq e_{th}$. In the considered simulation, our increment ΔF was a pseudo-random uniformly distributed value of range $\pm 25\ N$. However, since muscles can only pull ($F > 0$), if the resulting muscle force would be lower than zero, the algorithm would force it to zero. A threshold of $e_{th} = 1 \cdot 10^{-2} N^2 m^2$ was chosen. The error function e used the sum of squares in order to avoid cancellation due to sign changes. Alternatively, the absolute value function could also have been used.

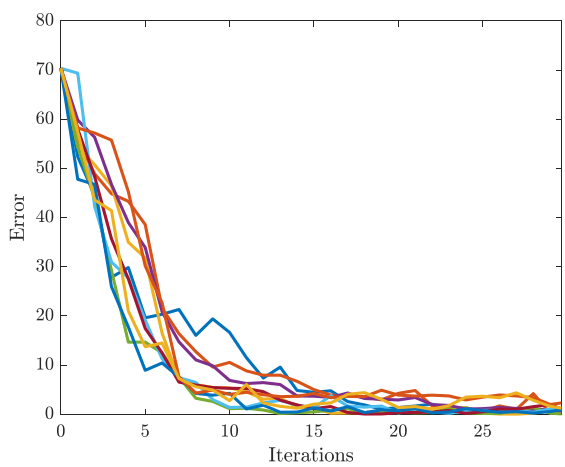

Figure 7 – Trend of the error function with respect to the number of iterations for the stochastic gradient descent learning algorithm of selectable muscle force synergies. Each colored line represents a different run of the algorithm.

Figure 7 presents the error function trend of 15 different runs of the proposed learning algorithm, all starting from the same initial zero muscle force vector $\boldsymbol{F_m}$. All the runs converged below the imposed threshold – notably at different iterations. This confirms that each of the 15 generated muscle force synergies $\boldsymbol{F_m}$ is capable of producing the required output force $\boldsymbol{F}$.

In addition to the 15 generated selectable muscle synergies, the least-square solution was added as an additional comparison factor. This was computed solving Equation 14 with a constrained Moore-Penrose inverse (Moore, 1920; Penrose, 1955). The constrained approach was chosen to enforce only positive forces. Figure 8 provides a graphical representation of all the resulting muscle synergies.

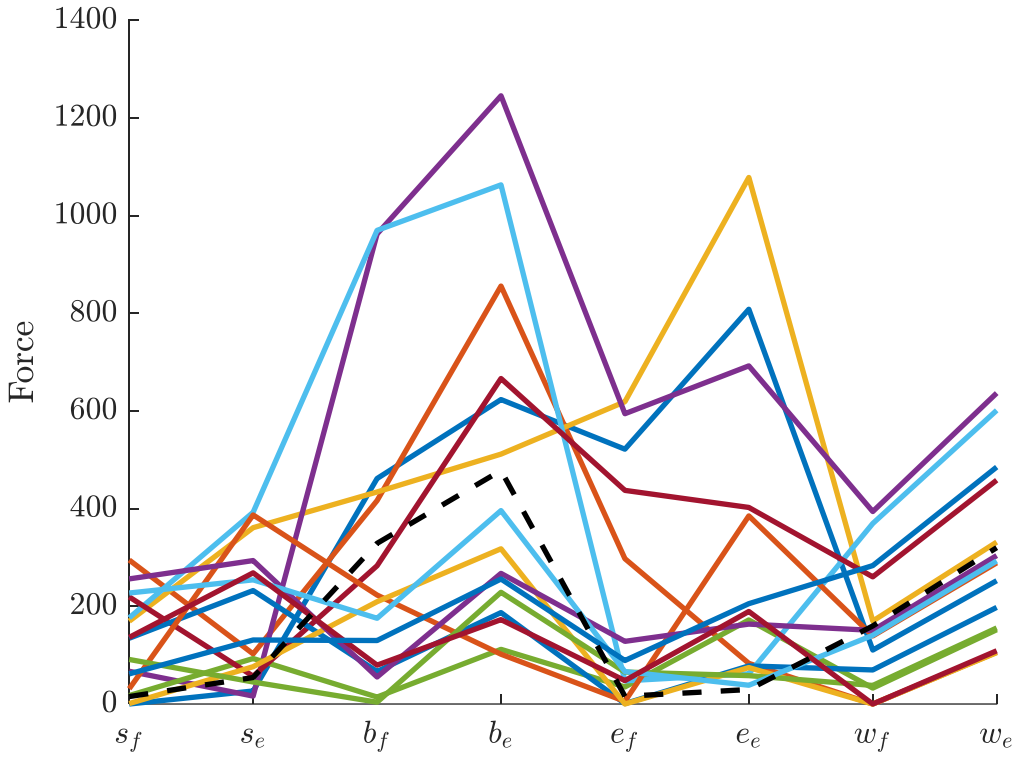

Figure 8 –Line chart representing the muscle forces of each of the 15+1 iterations. The first 15 selectable synergies are presented as continuous colored lines, the constrained least-square solution (16th) is presented as a dashed black line. The x-axis labels represent the shoulder flexor (s_f), shoulder extensor (s_e), biarticular shoulder-elbow flexor (b_f), biarticular shoulder-elbow extensor (b_e), elbow flexor (e_f), elbow extensor (e_e), wrist flexor (w_f), wrist extensor (w_e).

Despite all the runs starting from the same initial condition i.e., resting muscle force, the algorithm converged to very diverse solutions. The wide variability of possible selectable synergies of muscles forces can be observed from Figure 8, where we can appreciate that every muscle assumed different values across equally successful synergies.

The same numerical analysis has been performed also for three other end-effector force directions: negative ‘x’, positive ‘y’, and negative ‘y’. Similar results were found for all the analyzed cases. The Supplementary Material contains the complete results of such simulations.

If we imagine every separate run as a different subject during his/her learning of the force generation task, this result confirms that it could be possible to reach different solutions to the same motor task, despite starting from the exact same initial condition i.e., **primordial** motor synergy. This is in line with both the Mechanical and Developmental propositions of the expansion hypothesis.

This numerical example – focused on the generation of end-effector forces in a constant planar arm configuration – showed the emergence of multiple **selectable** muscle synergies to deliver the same end-effector force. However, the validity of this approach can be generalized to kinematic synergies, as explained in the Mechanical Proposition section.

Discussion & Conclusion

In this work we proposed a new framework for the synthesis and use of motor synergies to answer Bernstein's coordination problem. The key idea is that motor synergies are the building blocks of human motor control that emerge as a natural consequence of the motor 'abundance' of our musculoskeletal system (Mechanical proposition). These synergies are the result of motor development as it appears that humans learn motor skills starting from highly coordinated patterns – such as infantile reflexes – to highly specialized and individuated actions (Developmental proposition). Learned synergies are stored/memorized and evoked upon need following the theories of 'motor learning' and 'adaptation' (Behavioral proposition).

As of today, motor synergies have been considered to be an approach to control simplification that humans might employ to manage their highly complex musculoskeletal system. This is consistent with the proposed definition of a synergy – *the coordinated and simultaneous action of a group of features (neural, muscular, kinematic) to perform a specific motor task*. The expansion framework fully agrees with this vision. The fact that we can have infinitely many synergies, many more than the number of controlled features, simply highlights that there is no upper limit to the number of synergies that may exist. However, it does not contradict the dimensionality reduction purpose of some synergies.

The expansion hypothesis focused on the mechanical operational spaces (muscle, joint and task) of humans where a mapping between the different domains can be drawn based on geometry and configuration. However, when we move from muscle space to neural space – whether it is spinal or cortical – there is not (to the best of the authors' knowledge) a clear way to build a continuous mapping between the impressive dimensionality of neural space and muscle space. While the challenge to find such a mapping remains open, several works demonstrated the possibility to decode multiple motor actions from the central nervous system of humans, rodents and primates (Inoue et al., 2018; Kennedy & Schwartz, 2019a, 2019b; Keshavarzi et al., 2022; Moran & Schwartz, 1999; Rodman & Albright, 1987; Schwartz, 1993). Nonetheless, the large disparity between the size of the neural space and the muscle space suggests the presence of a dimensionally large redundant space within which individuals can find multiple pathways to the same solution. This is further stressed in the recent review by Cheung and Seki in which they tried to tackle the neural basis of motor synergies. Their work highlighted the important role of several factors such as the motor cortex, the brain stem and spinal cord in the coordination, temporal activation and tuning of muscle synergies (Cheung & Seki, 2021). They also present a hypothetical hierarchical structure to organize the activation and driving of motor synergies with two distinct neural mechanisms. Their idea – in agreement with previous work on muscle and kinematic synergies (Cheung et al., 2009; D'Avella & Bizzi, 2005; D'avella & Tresch, 2001; Mason et al., 2001; Santello et al., 1998, 2016) – is that motor synergies are characterized by two different mechanisms: a synergy organization component that accounts for the contribution of each feature to the considered synergy, and a temporal activation component that informs the temporal evolution of the synergy itself (Giszter & Hart, 2013; Hart & Giszter, 2013). This aligns with what we proposed in the 'behavioral' proposition of the expansion hypothesis i.e., the 'select-and-shoot' strategy.

The extreme redundancy of the human motor control system was also approached by the theory of dimensional 'bliss' and motor abundance introduced by Latash (Latash, 2012). He suggested that human redundancy allows the central nervous system to generate multiple solutions to the same task – aligning with Bernstein's classical observation of "repetition without repetition" (Bernstein, 1967). The expansion hypothesis agrees with these observations, suggesting that – at least at the muscular and joint level – the availability of these multiple solutions is ensured by mechanics.

Experiments should be developed to test and validate the expansion hypothesis, with a particular emphasis on: (i) the availability of more synergies than number of controlled features (mechanical), (ii) the

refinement of synergies from coordination to individuation (developmental), and (iii) the possibility to recruit and activate synergies to perform motor tasks (behavioral). The authors recommend especially two experiments. A first one, to test the 'Mechanical' proposition, should look at the differences between subjects in performing the same set of motor actions. How similar or different are the observed synergies? Is it possible to find more synergies than the number of controlled features? A second experiment, to test the 'Developmental' proposition, should look at the number of synergies (either muscular or kinematic) during childhood development or during motor learning in specific tasks in adults. Can we observe a growing number of synergies with age or with increased skill? Do the synergies share common features with the primordial ones? This paper motivates this interesting topic of future research.

In conclusion, the synergy expansion hypothesis establishes a foundation for future research in the field of human neuromotor control with the aim to provide new answers to Bernstein's – still open – problem.

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Supplementary Material

The numerical analysis on the generation of different selectable muscle synergies presented in the main manuscript for a given end-effector force direction (positive ‘x’) was replicated in three additional end-effector force directions: negative ‘x’, positive ‘y’, negative ‘y’. The same force magnitude of 10 N was maintained across conditions. 15+1 muscles synergies were generated for each case following the method presented in the Numerical Example Section.

Negative ‘x’ Direction

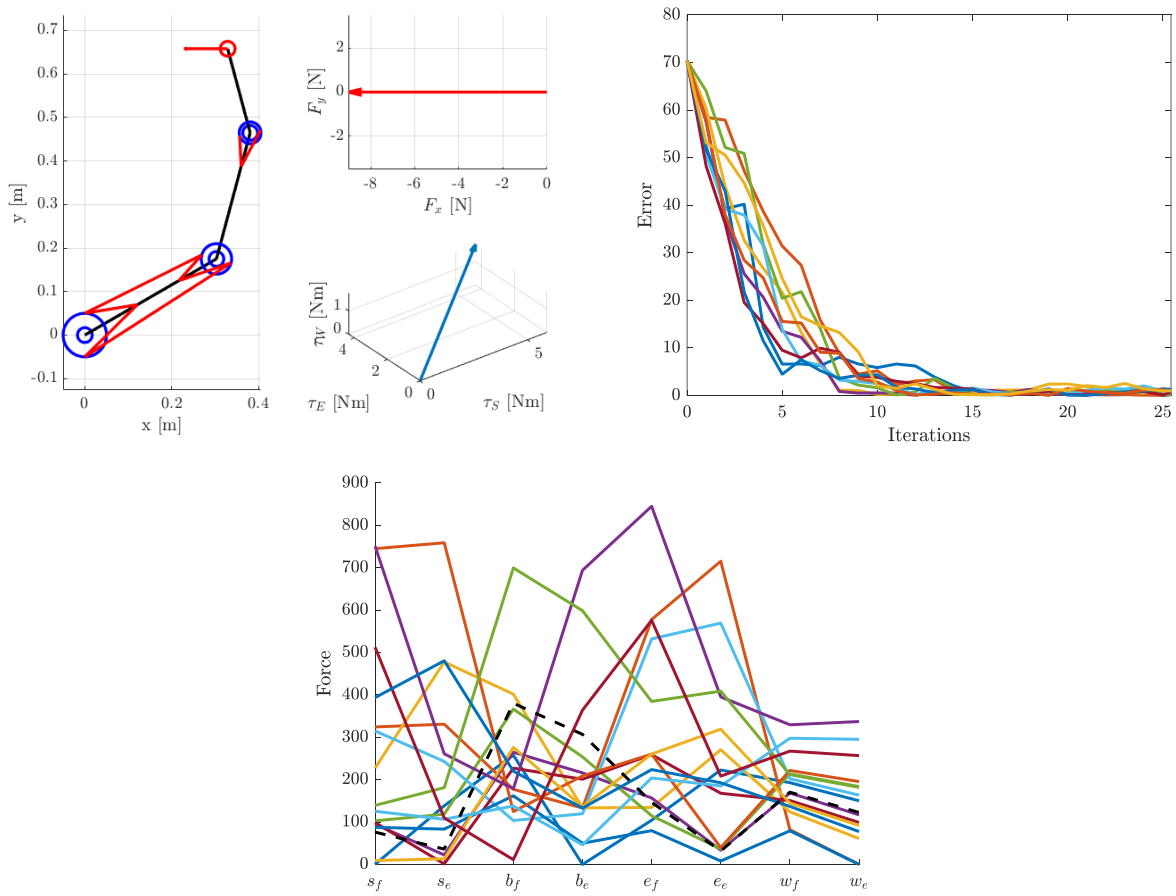

Figure 9 – **Top Left**: Three body rigid arm model generating a horizontal arm force. The left panel shows the arm configuration and desired force direction (red arrow). The top right panel show the desired end-effector force, while the bottom right panel show the obligatory torque coordination to generate such end-effector force. **Top Right**: Trend of the error function with respect to the number of iterations for the stochastic gradient descent learning algorithm of selectable muscle force synergies. Each colored line represents a different run of the algorithm. **Bottom**: Line chart representing the muscle forces of each of the 15+1 iterations. The first 15 selectable synergies are presented as continuous colored lines, the constrained least-square solution (16th) is presented as a dashed black line. The x-axis labels represent the shoulder flexor (s_f), shoulder extensor (s_e), biarticular shoulder-elbow flexor (b_f), biarticular shoulder-elbow extensor (b_e), elbow flexor (e_f), elbow extensor (e_e), wrist flexor (w_f), wrist extensor (w_e).

Positive ‘y’ Direction

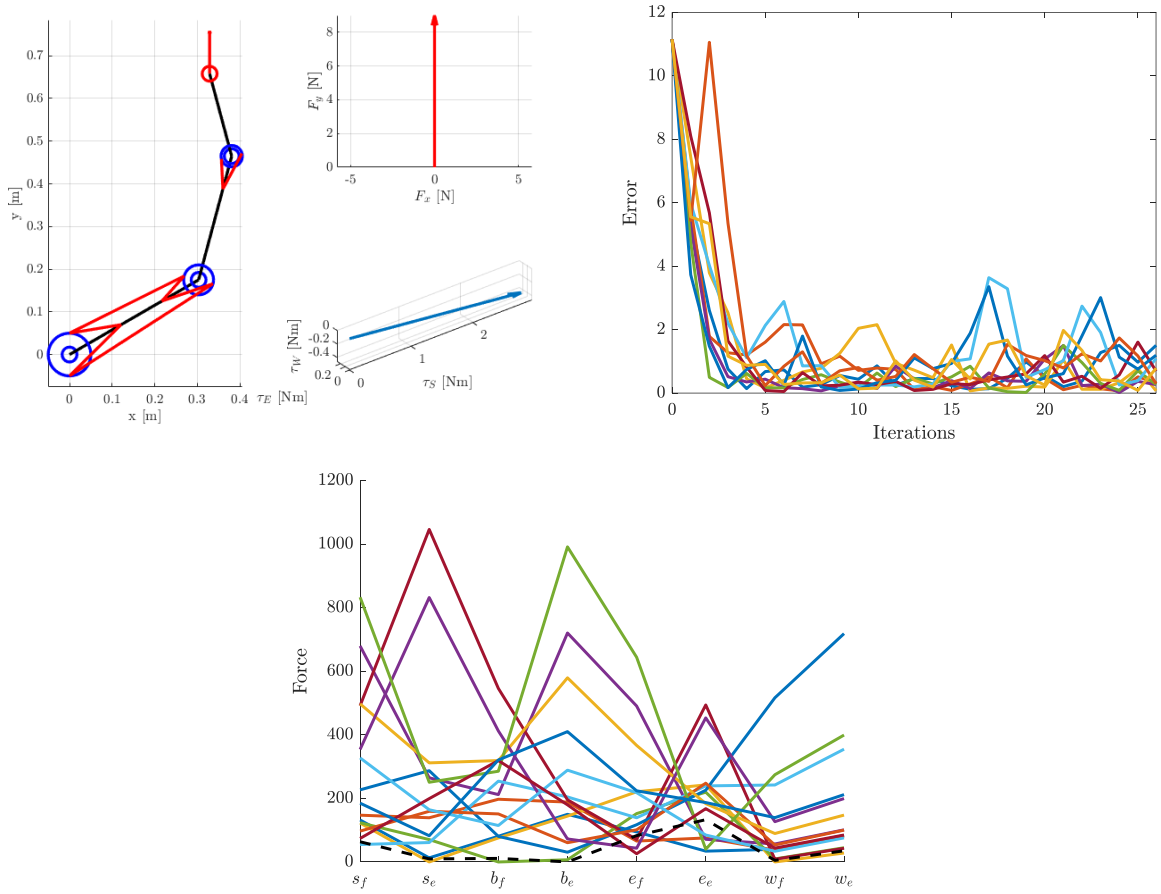

Figure 10 – **Top Left**: Three body rigid arm model generating a horizontal arm force. The left panel shows the arm configuration and desired force direction (red arrow). The top right panel show the desired end-effector force, while the bottom right panel show the obligatory torque coordination to generate such end-effector force. **Top Right**: Trend of the error function with respect to the number of iterations for the stochastic gradient descent learning algorithm of selectable muscle force synergies. Each colored line represents a different run of the algorithm. **Bottom**: Line chart representing the muscle forces of each of the 15+1 iterations. The first 15 selectable synergies are presented as continuous colored lines, the constrained least-square solution (16th) is presented as a dashed black line. The x-axis labels represent the shoulder flexor (s_f), shoulder extensor (s_e), biarticular shoulder-elbow flexor (b_f), biarticular shoulder-elbow extensor (b_e), elbow flexor (e_f), elbow extensor (e_e), wrist flexor (w_f), wrist extensor (w_e).

Negative ‘y’ Direction

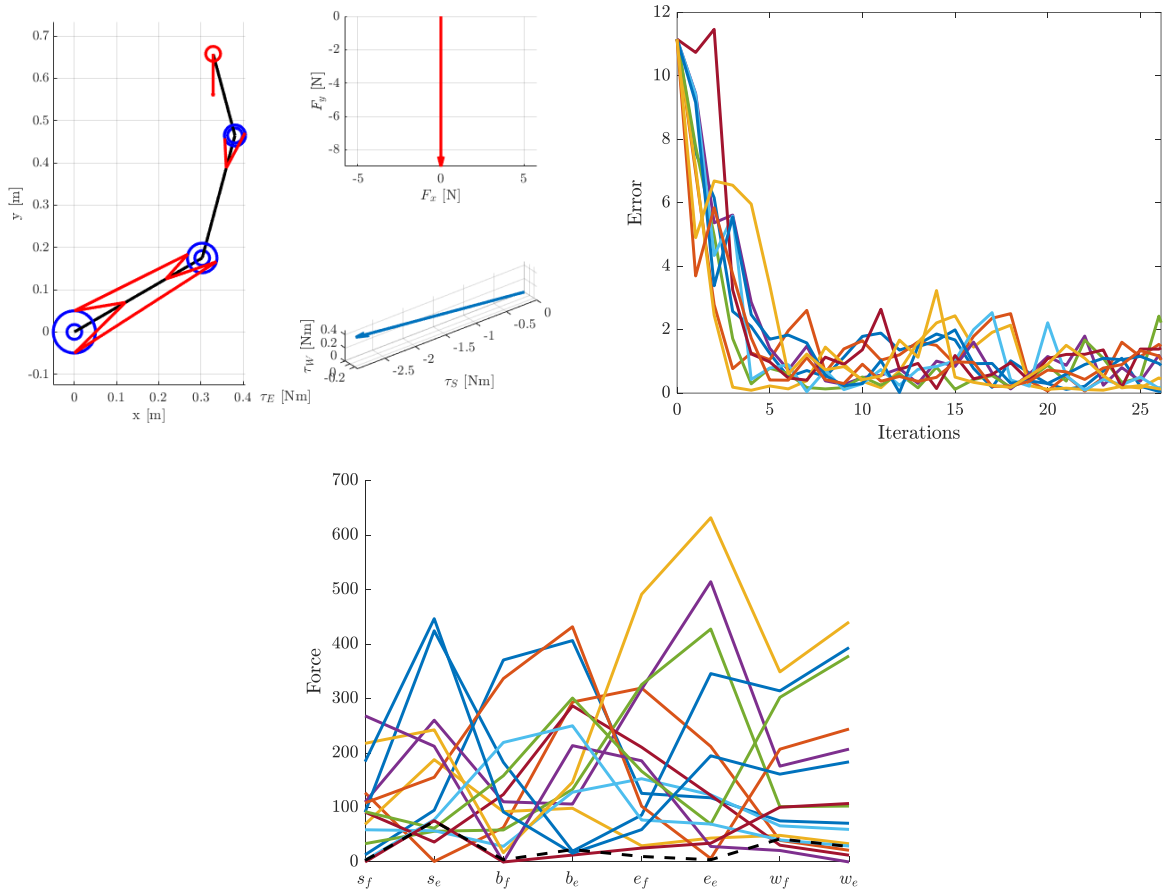

Figure 11 – **Top Left**: Three body rigid arm model generating a horizontal arm force. The left panel shows the arm configuration and desired force direction (red arrow). The top right panel show the desired end-effector force, while the bottom right panel show the obligatory torque coordination to generate such end-effector force. **Top Right**: Trend of the error function with respect to the number of iterations for the stochastic gradient descent learning algorithm of selectable muscle force synergies. Each colored line represents a different run of the algorithm. **Bottom**: Line chart representing the muscle forces of each of the 15+1 iterations. The first 15 selectable synergies are presented as continuous colored lines, the constrained least-square solution (16th) is presented as a dashed black line. The x-axis labels represent the shoulder flexor (s_f), shoulder extensor (s_e), biarticular shoulder-elbow flexor (b_f), biarticular shoulder-elbow extensor (b_e), elbow flexor (e_f), elbow extensor (e_e), wrist flexor (w_f), wrist extensor (w_e).