# Motor control revisited: A novel view

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## ABSTRACT

When the central nervous system (CNS) generates voluntary movement, many muscles, each comprising thousands of motor units, are simultaneously activated and coordinated. Computationally, this is a daunting task, and investigators have strived to understand whether and how the CNS's burden is reduced to a much smaller set of variables. In the last few years, my collaborators and I have searched for physiological evidence of simplifying strategies by exploring whether the motor system makes use of motor modules, to construct a large set of movements. The core argument for the neural origin of motor modules rests on studies of the spinal cord in several vertebral species, conducted using a variety of techniques. With these approaches, we were able to provide the experimental basis for a modular organization of the spinal cord circuitry in vertebrates. A spinal module is a functional unit of spinal interneurons that generates a specific motor output by imposing a specific pattern of muscle activation (muscle synergy). Muscle synergies are neural coordinative structures that function to alleviate the computational burden associated with the control of movement and posture. In this mini review I will address two critical questions: 1) Are the muscle synergies explicitly encoded in the nervous system? and, 2) How do muscle synergies simplify movement production? I will argue that shared and task-specific muscle synergies are neurophysiological entities whose combination, orchestrated by the

motor cortical areas and the afferent systems, facilitates motor control and motor learning.

## INTRODUCTION

Anatomists, physiologists and neurologists have known for quite some time that the number and the variety of cells in the human brain is an impressive 82 billion. Surprisingly, knowledge of this impressive number has not raised a great deal of interest, and it has rarely been the focus of speculation on how the brain can possibly handle and coordinate such a large number of cells. With respect to the motor system, presumably a third or a quarter of the 82 billion are devoted to motor functions, but neuroscientists, until recently, had no way to guess how the CNS deals with such redundancy nor could they point out any biological mechanism in charge of coordinating the billions of "motor" cells to generate movements that are so effective and precise.

In this mini review, I will summarize the experimental work that in the last twenty years has provided a novel perspective on identifying anatomo-physiological structures that coordinate and control the enormously redundant neuronal space.

This novel perspective is based on the experimental demonstration of a modular organization of the spinal cord [1, 2, 3]. A number of results and especially the recent work of Levine *et al.* [3] established that the spinal cord modules are key anatomo-physiological structures found in vertebrates.

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Anatomically, the modules are made up of groups of spinal interneurons, whose efferent fibers make contact with distinct sets of motorneurons. It follows that whenever these interneurons are activated by descending cortico-spinal impulses and/or reflex pathways from the periphery, a distinct set of muscles becomes active. This process leads to the formation of muscle "synergies" which represent a kind of functional building block whose combination leads to the "construction" of voluntary movements.

To clarify this concept I will describe the way in which we have identified the muscle synergies and how the muscle synergies combine to "construct" voluntary movements [4]. The first step involved the simultaneous recording of electromyographic activity (EMG) from a large number of limb muscles during a variety of motor behaviors. In figure 1 which is presented here as an example,

we started by recording from 13 leg muscles in a frog during 3 distinct motor behaviors: jumping, walking and swimming. We then pooled the EMG records of 13 leg muscles and then proceeded to identify muscle synergies by using a factorization algorithm-- the non-negative matrix (NMF) -- on the pooled set of muscles. The factorization procedure essentially performs a dimensionality reduction by grouping the muscles that tend to co-vary in the data set into individual synergies. The extracted synergies must be viewed as a compact representation of the most salient features embedded in the variability present in the EMG data.

In this specific case, the outcome of the factorization resulted in the identification of five muscle synergies. Note in figure 1 that each synergy (W1 to W5) represents the time course of 13 leg muscles and the color code indicates the degree of activation of individual muscles. In synergy W1
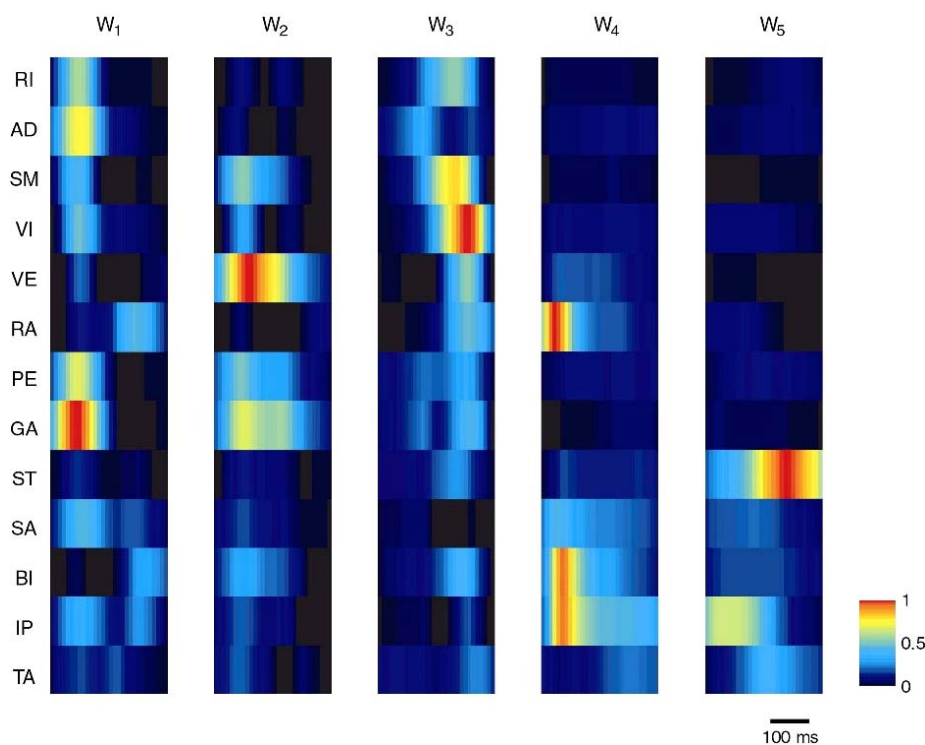


**Figure 1.** Time-varying muscle synergies extracted from jumping, swimming, and walking muscle patterns in three frogs. Each synergy (columns $W_1$ to $W_5$) represents the activation time-course (in color code) of 13 muscles over 30 samples (300 ms total duration) normalized to the maximum sample of each muscle. (RI = rectus internus, AD = adductor magnus, SM = semimembranosus, VI = the knee extensor vastus internus, VE = vastus externus, RA = rectus anterior, PE = the ankle extensors peroneus, GA = gastrocnemius, ST = mainly semitendinosus, SA = semitendinosus, BI = biceps, IP = ilio-psoas, TA = tibialis anterior).

the most active muscles are rectus internus (RI), adductor magnus (AD), the semimembranosus (SM), vastus internus (VI), peroneus (PE) and gastrocnemius (GA). It is also relevant that each synergy can contain both flexor and extensor muscles, and that in many instances the same muscle may be represented in more than one synergy. In addition to identifying the muscle components of the synergies, the algorithm also provides a weighting coefficient of activation for each synergy.

The simple inspection of figure 1 raises an important question -- how confident can we be that the muscle synergies have biological meaning and are not a mathematical construct? In answer to this query, Tresch *et al.* [5] showed that most of the currently used factorization algorithms perform comparably. These results indicate that the extracted muscle synergies are not mathematical artifacts, but rather reflect muscle activation.

### Examples of reconstruction of EMG patterns as a combination of the muscle synergies

The upper part of figure 2 shows EMG records of a frog that is engaged in 3 motor behaviors: jumping, walking and swimming. Figure 2 shows the names of the thirteen muscles and the shaded gray areas represent the rectified, filtered and integrated EMGs during a single instance of the 3 motor behaviors. Most importantly, the black line contouring the gray areas represents a reconstruction based on combining the muscle synergies extracted by the factorization process.

The lower section of figure 2 shows the weighting coefficient of the 5 synergies found by the computational procedure. The coefficient is illustrated *via* rectangular boxes whose height represents amplitude, while their position indicates onset delay and box width the synergy duration.

Three important points emerge from inspection of figure 2: 1) the same synergy may be utilized in different motor behavior (see W1 and W3 in both jumping and walking); 2) what makes the difference between these behaviors is that the coefficients are different in amplitude and timing; 3) different behaviors may be constructed by linearly combining the same synergies with different timing and scaling factors. Such an organization

might help to simplify the production of movements by reducing the degrees of freedom that need to be specified [6, 4].

### Do muscle synergies simplify movements by decreasing the number of degrees of freedom?

In the last few years many investigators have examined motor behaviors in animals and humans with the just-described procedure. The results show that combining a small set of muscle synergies appears to be a general strategy that the CNS utilizes for simplifying the control of limb movement and posture [7, 8, 9, 10, 4]. Taken together, these results indicate that for each single task there is a simplification in the control of movement because, as shown in figure 2 for the jumping task, there is a reduction in the number of controlling factors - just 3-4 synergies – relative to the number of active muscles (~13). Hence, one could argue that the implementation of a synergy control scheme may be an advantage. However, given that the muscle synergies required in some movements are a mixture of shared and task-specific synergies, the issue of simplification cannot be determined at this time mainly because we do not yet know how many motor behaviors make use of task-specific synergies [11, 6].

### Some investigators have argued that muscle synergies may have a non-neural origin

Recently, Kutch and Valero-Cuevas [12] have proposed that the muscle synergies extracted by using a factorization procedure arise from limb biomechanics. Through modeling and experiments with cadavers these investigators have emphasized the importance of non-neural constraints and suggested ways that biomechanics could produce coupling among muscles. To gain a perspective on the points raised by Kutch and Valero-Cuevas [12], I would like to mention a developmental study published by Domenici *et al.* in Science [13]. Domenici and colleagues [13] demonstrated that, in toddlers, the development of muscle synergies is the result of the addition of new synergies to a few basic patterns present at birth. Over the years, as the individual grows, there is a progressive addition and fine tuning of these synergies. While the role of genetics, sensory feedback, descending cortico-spinal signal and
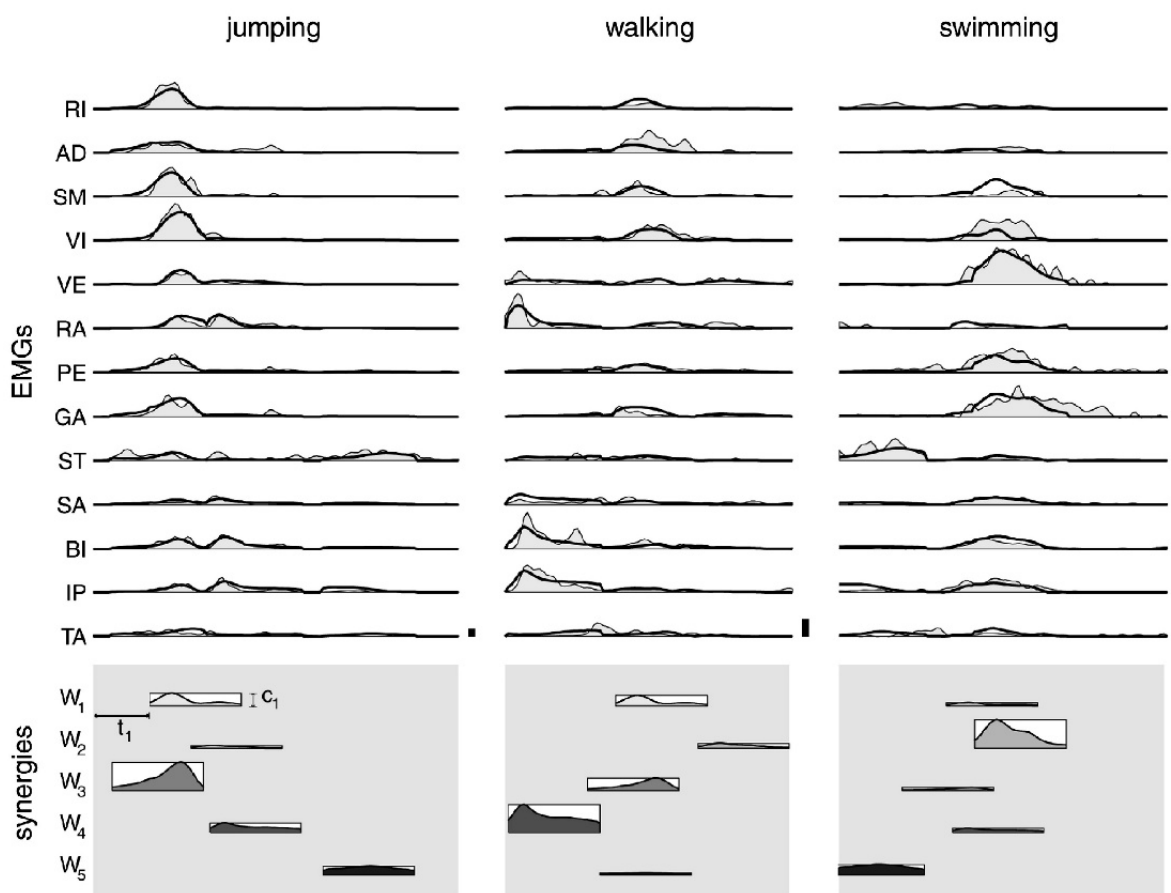
**Figure 2.** Examples of reconstruction of EMG patterns as combinations of time-varying muscle synergies. The three columns are examples of a jump, a walking cycle, and a swimming cycle. Upper section (EMGs): the thick line shows the reconstruction of muscle patterns and the shaded area represents the rectified, filtered and integrated EMGs. Lower section (synergies): the coefficients of the five synergies as the horizontal position (onset delay, $t_i$) and the height (amplitude, $c_i$) of a rectangle whose width corresponds to the synergy duration. The shaded profile in each rectangle illustrates the averaged time-course of the muscle activation waveforms of the corresponding synergy. Note the different amplitude scaling used in the three columns.

especially biomechanics remains to be understood, it is likely that these factors contribute to the shaping of spinal cord interneuronal circuitry. Thus, it is reasonable to assume that at the termination of the developmental process the biomechanical properties of the limbs are fully integrated into the architecture of the spinal modules.

Another theory against the idea of a neural origin for muscle synergies sees the possibility that muscle synergies reflect regularities in reflexes, especially those originating from the muscle spindles. The way in which reflexes affect the spinal interneurons and synergy composition was

investigated by Cheung [14]. His experiments involved recording of muscle synergies before and after deafferentation (by sectioning the dorsal roots) and demonstrated that most of the synergies were found to be shared between intact and deafferented data sets. It follows that most of the synergies involved in motor behaviors are centrally organized, but their activity might be modulated by sensory feedback so that the final motor output is adapted to the external environment. In conclusion, the available experimental evidence recognizes the role of biomechanics and of reflexes as factors that shape the CNS mechanisms leading to the formation of muscle synergies.

## Cortical control of synergies

There are numerous cortical areas that are concerned with generating signals for voluntary movements. Among these are the dorsal and ventral premotor, the supplementary motor area, the primary motor cortex, and parietal areas. These highly interconnected regions receive a diverse modality of inputs from a variety of sources including external sensory information, internal sensory information from the proprioceptive system, the executive attentional system and inputs from major subcortical areas such as the cerebellum and the basal ganglia. There are of course a variety of output pathways that connect premotor and primary motor cortical areas with different classes of spinal neurons. While these cortical regions play a central role in generating motor behavior, there is a lack of consensus on how neural processing in these areas contributes to voluntary movements.

Given the anatomical complexies and our poor understanding of cortical functions, it is difficult to draw conclusions from the few experiments that have attempted to establish a cortical role for the control of muscle synergies. Among the investigators that have searched to connect muscle synergies with cortical processing, [15, 7] the studies of Overduin [7] demonstrated that intra cortical microstimulation in monkeys elicited EMG patterns that could be decomposed into muscle synergies. Importantly, these EMG patterns were found to be similar to those evoked during the same animal's voluntary movements. It is possible that electrical stimulation may have activated a set of cortical neurons that happened to have the correct connections to the spinal cord interneurons. Whether this finding indicates that the cortex "encodes" synergies remains to be determined. As discussed above it is the architecture of the spinal cord that is the main factor in the expression of muscle synergies-- the supraspinal regions may just provide signals for the interneurons.

## Motor cortical damage and muscle synergies

Recently, we and others began studying stroke patients by asking the following questions: 1) Can factorization procedures and the resulting muscle synergy changes tell us something about the central nervous system processes that follow stroke? 2) Are there a variety of muscle synergy patterns that specifically follow motor cortical strokes? 3) Can these novel patterns change the way in which rehabilitation is practiced?

To provide answers to these questions we recorded EMGs from the muscles of patients affected by unilateral strokes [16, 17].

We found that in patients with mild to moderate impairment, the synergies in the affected and unaffected arms were similar even though the electromyographic patterns of the affected arm showed evidence of differential modulation. In patients with severe impairments we observed a different pattern of muscle synergies. In the affected arm of some patients, multiple synergies appeared to merge, while in other patients the synergies of the stroke-affected arm appeared to have gone through a process of fractionation.

While at this point we cannot advance any hypothesis on the origin of fractionation and merger of synergies, these results are nonetheless important because they provide markers that may shed some light on the diverse processes that follow cortical and subcortical injuries of the CNS.

## CONCLUSION

In this review I have outlined a new view on the generation of voluntary movements. All in all we have gained a good understanding on the role that the spinal cord and muscles are having in shaping the modules that have been described. In contrast, our knowledge of the supraspinal machinery involved in synergy activation is inadequate--we need to know how the signals that are sent to the spinal cord are generated at cortical and subcortical levels. But, there are reasons for optimism – the recent spectacular development of new technologies are making it possible to record simultaneously from hundreds of cortical neurons. The utilization of these imaging techniques in combination with the power of optogenetics will undoubtedly achieve the hoped-for progress in elucidating the role of supraspinal structures in muscle synergy genesis in the not-too-distant future.

## CONFLICT OF INTEREST STATEMENT

Author, Emilio Bizzi, certifies that he has no affiliations with or involvement in any organization or entity with any financial interest in the subject matter or materials discussed in this manuscript.

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