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The case for and against muscle synergies

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A long standing goal in motor control is to determine the fundamental output controlled by the CNS: does the CNS control the activation of individual motor units, individual muscles, groups of muscles, kinematic or dynamic features of movement, or does it simply care about accomplishing a task? Of course, the output controlled by the CNS might not be exclusive but instead multiple outputs might be controlled in parallel or hierarchically. In this review we examine one particular hypothesized level of control: that the CNS produces movement through the flexible combination of groups of muscles, or muscle synergies. Several recent studies have examined this hypothesis, providing evidence both in support and in opposition to it. We discuss these results and the current state of the muscle synergy hypothesis.

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Introduction

Dating at least back to the work of Sherrington, several researchers have proposed that the CNS produces movement by combining small groups of muscles [1–13]. This hypothesis has been formulated in several different ways, but has been most recently expressed in terms of a group of muscles, also referred to as a muscle synergy, activated in a fixed balance (Figure 1). In this hypothesis, behavior results from the simple (usually linear in current formulations) combination of these synergies. In addition, these synergies come in a few different flavors [14]. In ‘synchronous synergies’, no temporal delay is allowed between different muscles — if a synergy is activated at a given time, all muscles within that synergy are active. In ‘time-varying synergies’, there is both a spatial component — the balance of activations across the muscles — and a temporal component. Each muscle in a time-varying

synergy has a fixed temporal profile which allows for delays between muscles within the same synergy.

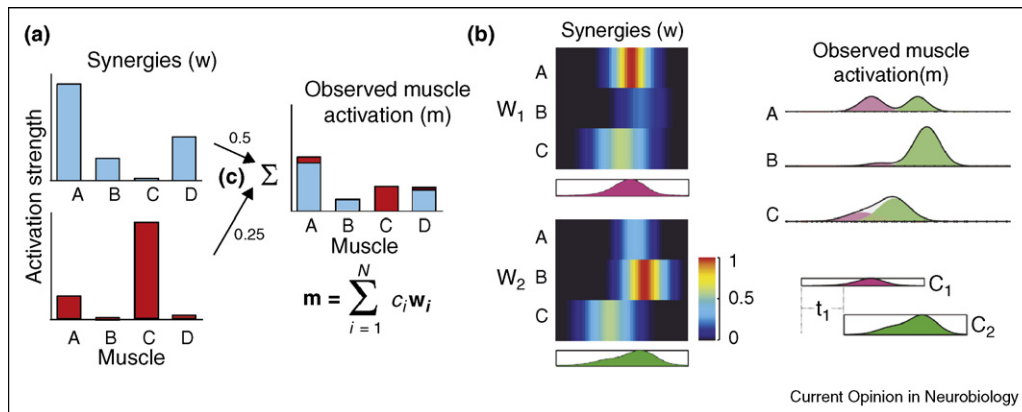
There are several usual motivations and interpretations given for this hypothesis. Commonly, muscle synergies are suggested as a solution to the degrees of freedom problem faced in motor control: instead of having to control many thousands of motor units or dozens of muscles, using muscle synergies the CNS can produce behavior by the control of a much smaller number of variables [15–17,11]. Related to this interpretation, others have suggested that muscle synergies provide a way for the CNS to bootstrap complex problems of optimal control; by identifying a task relevant subspace of control variables, the potentially difficult problems of optimization would be minimized [8,19–21]. Another interpretation of muscle synergies is that they provide a translation between task level goals (e.g. stabilizing the center of mass) and execution level commands (e.g. activation of individual muscles) that are necessary to accomplish those goals [4]. In this interpretation, synergies identify the relevant muscle groupings that, when activated together, allow for simplified control of particular biomechanical features of the limb (such as the global limb angle or orientation). This interpretation places muscle synergies as part of a hierarchical control strategy [22,23], providing a means of organizing both complex motor control variables and sensory feedback so that they can be controlled and interpreted in a task relevant manner. Finally, a different explanation for muscle synergies is that they reflect a relatively primitive solution to motor coordination implemented by phylogenetically ‘older’ neural systems, such as those in the spinal cord [8,24,10]. These solutions might be re-expressed when these systems are isolated (e.g. following stroke [25,26]) or when the behavioral demands faced by the intact CNS are directly addressed by these more primitive solutions. In other cases the CNS might work to suppress these more primitive solutions, breaking apart their coordinative structures or bypassing them in order to express more precisely adaptive behaviors [24,27,10].

Evidence for and against muscle synergies

There has been a great deal of recent research examining this hypothesis, often based on using statistical analyses of EMGs during behavior. The basic approach in these experiments has been to firstly, measure EMGs from a large number of muscles during a complex behavior (or more than one behavior); secondly, use a computational analysis such as non-negative matrix factorization or independent components analysis to identify a set of synergies from the recorded EMGs; thirdly, evaluate

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Figure 1



Schematic representation describing the muscle synergy hypothesis. **(a)** A schematic representation for synchronous synergies. Two synergies (w) are scaled (c) and summed to produce the observed pattern of muscle activations (m). These synchronous synergies are fully described by the balance of activation across the muscles in each synergy: any temporal structure is specified by the scaling coefficients (c). **(b)** A schematic illustrating time-varying synergies. Two time-varying synergies (w) are shown. Each synergy specifies a weighting coefficient for one of the three muscles, indicated by the color of the bar and a temporal profile for these weightings. An observed pattern of muscle activations is created by scaling each synergy (c), temporally shifting them (t), then adding them together linearly, as indicated in the right of the figure. The purple and green waveforms indicate the contribution from each of the original synergies to the observed response. (b) is adapted by permission from Macmillan Publishers Ltd: Nature Neuroscience [17], copyright 2003.

whether the observed EMGs can be well described as the combination of these synergies; and fourthly, relate the identified muscle synergies to task relevant variables. Using such an approach, a wide range of motor behaviors have been suggested to be produced using muscle synergies [14–17,24,28–37]. Other studies have used a more direct examination of muscle activations to identify and analyze muscle synergies, thereby avoiding the more indirect statistical analyses [38,39].

Key to this approach is examining EMGs recorded under a rich enough range of behavioral conditions: the wider the range of behavioral conditions that can be explained by muscle synergies, the more support there is for such an explanation. In fact, one of the main critiques of experiments supporting the muscle synergy hypothesis is that they reflect task constraints rather than reflecting a neural control strategy [40,41,42]. In this critique, the ability of muscle synergies to explain a behavior reflects the fact that there are only a few ways that a task can be successfully performed, once all the task constraints are fully accounted for. For instance, if one considers stability requirements in addition to explicit task variables, the apparent redundancy of muscle activation patterns is reduced [43]. Similarly, if one considers additional potential demands placed on the CNS such as minimizing noise or other optimization criteria, then control of individual muscles could explain observed EMG patterns as well as muscle synergies [41]. Finally, if one assumes smooth recruitment of muscles across smooth changes in task variables (e.g. across different directions of reaches or forces), one would expect that muscle activations would

lie upon a low-dimensional, albeit nonlinear, manifold [42]. Thus, it can be difficult to predict how truly redundant a task is or how surprising it would be to find a low-dimensional solution to the task.

Recent experiments have attempted to address this critique by demonstrating that an impressive range of behaviors such as human reaching [44] and posture [45], primate grasping [46], and frog locomotion [47] and nocifensive reflexes [48] can be explained as combinations of muscle synergies. In the study examining human postural maintenance [45], it was shown that the long latency reflexes observed following phasic perturbations to the limb could be well explained by a few coordination patterns, or muscle synergies. Moreover, similar patterns were observed irrespective of whether working in a stiff or compliant environment. This was an unexpected result since previous work suggested that there should be an increased involvement of multiarticular muscles in the compliant environment. Another notable study examined the nocifensive reflexes in the spinalized frog [48]. This work was especially compelling since it did not rely on computational analyses but on more direct observations of muscle activations evoked in response to phasic stimulation of muscle afferents. The study demonstrated that such stimulation caused collective modulation of the amplitude and timing of muscles within a single putative muscle synergy, while leaving the muscles in other synergies unaffected. Importantly, this modulation did not alter the relative timings of the muscles within that synergy, suggesting that synergies produced by spinal circuitry in the frog were synchronous

as opposed to time-varying synergies (see Figure 1). Although the use of perturbation analyses in these studies diminishes concerns about task constraints by increasing the richness of behavioral conditions, such concerns are not entirely alleviated; it is not clear *a priori* at what point a task is 'complex enough' so that the muscle synergy based explanation is surprising enough to be confirmed.

Indeed, two recent studies [40^{**},42^{**}] have provided evidence arguing against the existence of muscle synergies. Both of these studies are based on analyses of variability in motor patterns. One recent trend in studies in motor control has been a re-examination of noise and variability in task performance [49–52]. Rather than treat this variability as reflecting 'errors' because of poor planning or control, these more recent studies consider this variability as reflecting efficient control, with the CNS only correcting for variability which prevents the accomplishment of task goals. Variability which does not affect the task can be allowed without penalty since attempts to correct such task irrelevant variability would be an unnecessary waste of effort. This hypothesis, referred to as the 'uncontrolled manifold' [51] or 'minimum intervention' hypothesis [42^{**}] and closely related to optimal feedback control [49], in some ways stands in contrast to the muscle synergy hypothesis. In the uncontrolled manifold hypothesis, the problem for the CNS is not in reducing the degrees of freedom, but in identifying those degrees of freedom which are task relevant and those which are not. Having excess degrees of freedom implies that the CNS is more likely to be able to use degrees of freedom which align well with the task demands than if the degrees of freedom were restricted: that is redundancy allows for flexibility. Although in many cases, research on the uncontrolled manifold hypothesis invokes structures which are identical to muscle synergies [53,54] (referred to as 'muscle-modes' or 'm-modes' in that work), these structures do not seem essential to their main hypothesis that the CNS controls only task relevant perturbations. Note also that in the uncontrolled manifold work, the term 'synergy' is used to refer to the flexible control of execution variables to regulate task relevant variability, rather the grouping of muscle activations as described in Figure 1 [50].

One recent study examined this minimum intervention hypothesis directly at the level of individual muscles and compared it to the muscle synergy hypothesis [42^{**}]. This study examined the structure of the within trial variability of finger motor control in humans during a force regulation task. The elegance of this study is that the experimenters were able to record from nearly every muscle which contributed to index finger force, thereby characterizing an accurate mapping between muscle activation and task performance. In support of the minimum intervention hypothesis, they demonstrated that people allowed for more variability in task irrelevant dimensions

than in task relevant dimensions, providing a clear demonstration of the minimum intervention principle at the level of physiological variables. Further, they demonstrated using either PCA or ICA that it was unlikely that the muscle coordination patterns could be well explained as muscle synergies. Although the authors allowed for a possible role for muscle synergies in planning versus in execution of movements, their results suggest that the CNS can control online individual degrees of freedom (i.e. muscles) as necessary in order to achieve task goals.

Another recent paper also examined the variability in human finger control during force production tasks [40^{**}]. Using a clever analysis, they effectively demonstrated that the patterns of variability observed during this task were best explained as reflecting the control of individual muscles, rather than muscle synergies. This was shown both experimentally and in computational analyses. Both of these studies provide strong challenges to the muscle synergy hypothesis as an explanation for the neural control of these tasks.

Muscle synergies for control

Another aspect of the muscle synergy hypothesis concerns its implications to the efficacy of control. As alluded to above, the best performance that the CNS can achieve is when it uses individual muscles: obviously, any movement using muscle synergies can be equally produced using individual muscles. Conversely, this also implies that the use of muscle synergies can potentially limit the efficacy of control by the CNS, since using muscle synergies restricts the range of muscle activation patterns. This issue of whether the potential simplification of control brought about by synergies comes at the expense of degraded control has remained central to this hypothesis.

Three recent studies [55^{*},56^{**},57^{*}] have addressed the efficacy of motor control based on muscle synergies. These studies used biomechanical models to demonstrate that complex behaviors could be produced effectively using combinations of muscle synergies. The first study [56^{**}] initially identified muscle synergies from humans during normal locomotion using the statistical methods described previously, and then used these synergies to activate the muscles in a complex biomechanical model of human walking. They demonstrated that these experimentally identified synergies were able to produce realistic locomotion in their biomechanical model, suggesting that synergies could be used effectively for control. A similar conclusion was reached in another recent study [55^{*}]. This study postulated that muscle synergies should be chosen as those that are most effective at controlling the significant task relevant dynamics of the limb. Using this principle, a set of muscle synergies was identified and it was found that these synergies could then be used to produce effective motor control, albeit for

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a relatively simple task. Finally, a study in frogs [57^{*}] demonstrated that a relatively simple modulation of three synergies could accomplish the range of trajectories observed during natural frog hindlimb wiping behaviors and proposed a simple scheme of their regulation. Each of these studies provides evidence that a control scheme based on muscle synergies might be an effective way for the CNS to produce movement, similar to previous studies [58,19,20].

However, one could look at these studies from a different perspective. As has been suggested by others, when techniques of optimal control are used to solve a motor control task, a low-dimensional control space is naturally identified, reflecting the task relevant dynamics of the limb [18,19,49]. This control space, although in general a nonlinear subspace, might nonetheless be approximately spanned by a low-dimensional basis set, such as provided by muscle synergies. The results described above showing that synergies can be used for effective control therefore could be interpreted as using alternative ways (i.e. examination of actual EMG patterns, identifying synergies for controlling limb dynamics) to identify the low-dimensional task relevant control space that optimal control would have identified on its own. However, in the case of the frog wiping study, considerable evidence for the use of the same muscle synergies has come from previous studies [38,48^{**},24].

Implementations of muscle synergies

There has been relatively little work directly examining the muscle synergy hypothesis in terms of their neural implementations and there are many possible ways they might be implemented. For instance, the divergence of individual corticospinal neurons across several different motor pools might be interpreted in this context [4] and such an explanation has been offered for corrective movements during locomotion in cats [27] and reaching in primates [59]. Similarly, the divergent projection patterns of some spinal interneuronal systems [60,61] could be interpreted as coordinating groups of muscles into muscle synergies. Conversely, at the level of spinal interneurons, muscle fields defined by spike triggered averaging in awake behaving monkeys tend to consist of only one or two muscles, which is smaller than might be expected for the muscle synergy hypothesis [62]. One might consider that cortical systems encode a large number of muscle synergies, choosing to activate only those synergies which were most appropriate for a particular task [4,27]. This would result in a very sparse code for movement, in which only those neurons coding the synergies appropriate for a particular task would be activated. Note that in this case, muscle synergies would not solve the problem of redundancy at the neural level, since there are likely to be many more neurally coded muscle combinations than there are muscles. Such a possibility would resemble the overcomplete basis sets, which have been

used in the analysis of sensory systems [63–65]. It is clear that additional experiments are necessary to evaluate the potential neural implementations of these muscle synergies, which would provide support or criticisms to the muscle synergy hypothesis.

Future directions and perspectives

As evidenced by the experiments of the past few years, evaluations of this muscle synergy hypothesis remain ongoing. Although there is considerable evidence supporting this hypothesis, it is clear that much of this evidence remains circumstantial and the recent experiments contradicting it are challenges to it. There is therefore a need for experiments which are able to more critically evaluate this hypothesis.

Indeed, one of the main difficulties with this hypothesis is that it is difficult to falsify. It is clear that neural circuitry does allow for the possible activation of single muscles, single motor units, or individual neurons and that, with training, the CNS can learn to control even these individuated degrees of freedom [66]. Recent work demonstrating operant conditioning of motor cortical neuron populations for BMI applications makes this point especially clear [67,68]. So even if synergies contributed to movement, their effects might be obscured by other pathways controlling individual muscles. Further, one could also say that the lack of synergy structure found in the recent studies examining finger control reflects the high degree of specialization and flexibility inherent in this system (even though synergies have been used to explain hand movements [12,46,69]). In this way, it is always possible to claim that any deviations from the muscle synergy hypothesis reflect these differences and therefore do not necessarily falsify this hypothesis.

We see at least three directions of future experiments which might provide more direct evidence either supporting or falsifying the muscle synergy hypothesis. First, analyses such as that performed by Valero-Cuevas *et al.* [42^{**}] and Kutch *et al.* [40^{**}] should be done across many different behaviors and a wider range of behavioral conditions to evaluate whether the structure in the variability of muscle activation patterns is consistent with the muscle synergy hypothesis. Although the analyses used in those experiments exploit some ideal features of finger control, similar experiments should be possible in other behaviors and would help address concerns about synergies arising from task constraints. Second, it should be possible to use synergies to explain suboptimal performance of the CNS [70]. If the CNS has access to a limited set of synergies at a particular time based on the tasks that it currently is able to accomplish, this should suggest that some new tasks should be easier to perform than others [44^{*}]: if the muscle activation patterns required by the new task lay within the space defined by existing muscle synergies, learning the new task should be relatively easy.

In contrast, if the required activations lay outside that space, then the learning should be more difficult and initial performance should be suboptimal. Designing such tasks requires an accurate musculoskeletal model along with knowledge of the existing muscle synergies which would make it possible to predict which tasks would be easy and which would be difficult to learn. Third, experiments examining the properties of neurons in the spinal cord or elsewhere can be done to evaluate their relationship to synergy structures observed during behaviors. If neurons' activity patterns and/or effective connectivity to the musculature were directly relatable to muscle synergy structures, it would suggest strongly that the CNS does encode and control movement using this control strategy.

Finally, we wish to propose an alternate interpretation of muscle synergies that is related to previous proposals [4,20,71]. Rather than considering muscle synergies as reflecting a strategy for the simplification of control, we suggest that synergies might be considered in the larger context of the intimate interactions between the properties of the musculoskeletal system and neural control strategies. In this context, muscle synergies could be considered as reflecting the statistics of the external world, acknowledging the fact that the external world also consists of the musculoskeletal system itself [72**]. In the same way that properties of natural scenes might influence the structure of the visual system [63], we suggest that statistics of the musculoskeletal system and external world might influence the structure of motor systems. The large number of neurons in motor cortex and their many different patterns of influences on muscles could be considered as providing an overcomplete representation that captures the rich statistics of the limb and environment. In this context, regular patterns of muscle coordination might be analogous to the Gestalt principles of vision, reflecting heuristic strategies employed by the nervous system to control the limb [4]. In the same way that the statistics of the visual scene imply that visual images near one another might belong to the same object, one might argue that muscles which produce a complementary action to one another or which are commonly activated (e.g. by stretches [73]) might also be expected to be activated together. Such 'expectations' would not fundamentally limit the control exerted by the CNS: although nearby visual patches with similar characteristics are often part of the same object, we are still able to perceive them as separate if necessary. But these expectations might guide control, providing a useful default behavior which, based on regular properties in the periphery and environment, can be expected to be adaptive more times than not. In this context, it becomes important to try to predict situations where these expected regularities lead to errors in motor control, analogous to the 'illusions' observed in vision and which would be related to the motor learning predictions described previously. This broader issue of how the

statistics of the musculoskeletal system influence neural representations and control strategies is a potentially interesting focus in motor control research which has received attention in recent years [72**]. Note also that considering these issues for motor control is highly integrative, emphasizing the nature of both the motor and the sensory statistics, because of the tight connections between estimation and control when producing a task. It will be interesting to explore the potential role of muscle synergies in considering these issues.

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