Postural Synergies

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Synonyms

Muscle synergies; functional muscle synergies; motor primitives; M-modes

Definition

A ►postural synergy is a preferred pattern of muscle co-activation that is used by the nervous system to maintain standing balance. Each postural synergy specifies a pattern of muscle activation across many muscles. Through flexible combinations of postural synergies, a repertoire of postural behaviors is produced. By eliminating the need to control each muscle independently, postural synergies are thought to simplify the neural control task of selecting and coordinating multiple muscles across the body. A postural strategy defines the overall goals involved in the maintenance of balance; these can vary depending on the particular postural task, the context in which the task is performed and the postural configuration. Postural synergies define the muscle activation patterns that are used by the nervous system to implement various postural strategies.

Description of the Theory

Introduction

The theory of postural synergies address the basic question of whether the nervous system activates each muscle independently when it performs a task or whether the multiple muscles are activated together, thus reducing the total number of neural command signals necessary. Currently, postural synergies are thought to represent neural "building blocks" for generating a wide range of postural behaviors. Each postural synergy specifies a pattern of muscle activation across many muscles and is purportedly controlled by one neural command signal. By combining muscle synergies in various proportions, a continuum of muscle activation patterns for postural control can be generated using just a few neural command signals.

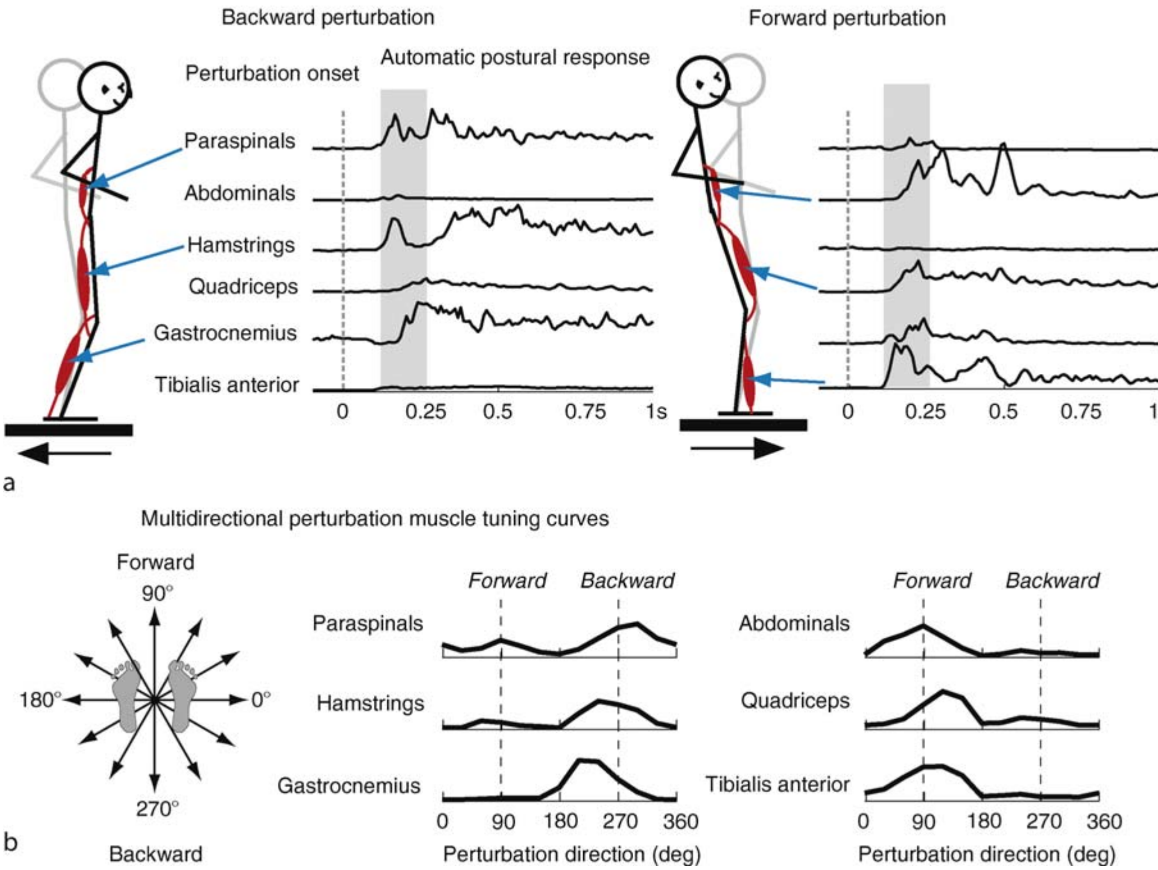
The long-standing debate within the general motor control field over the concept of muscle synergies is exemplified by the specific debate over the existence of postural synergies. Nashner first described "fixed" postural synergies in subjects standing on a moving perturbation platform [1]. Distinct patterns of muscle activation across the ankle, knee, hip and trunk were reliably observed when the platform was moved either forwards or backwards (Fig. 1a) and were thought to represent two different postural synergies [2]. Originally, it was thought that postural synergies were activated in a mutually exclusive fashion and that each muscle was activated by only one postural synergy (Fig. 2a).

These conclusions were challenged by later studies that showed flexibility in patterns of muscle activation in response to a backward perturbation. Depending on the perturbation amplitude and prior experience of the subject, two types of responses were observed, the "ankle strategy" and the "hip strategy," so named for the major joint motions involved. Each strategy elicits a very different pattern of muscle activation, demonstrating that postural synergies to a particular direction of perturbation are not fixed. Moreover, when perturbations were given in many directions in the horizontal plane, even more complex patterns of muscle activation emerged in both humans and cats [2]. Each different perturbation direction elicited a unique pattern of muscle activation (Fig. 1b), suggesting that muscles must be controlled independently to perform multidirectional balance control. It was for this reason that the notion of muscle synergies was then rejected as being too constraining and inflexible for the production of natural movements [3].

Recently, new computational techniques have helped to demonstrate that a motor control architecture based on muscle synergies can both simplify neural control as well as provide flexibility in motor output. In the new framework, more than one muscle synergy can be activated during a postural response and each muscle can also be activated by more than one synergy. By varying the magnitude of the neural command signals to just a few muscle synergies, many different muscle activation patterns can be generated (Fig. 2b), including the responses to multidirectional postural responses describe above [4]. The neural substrates of muscle synergies for postural control remain unknown. Where muscle synergies are encoded within the neural control hierarchy is a complex topic and may also be task dependent. It is hypothesized that postural synergies are formed in the brainstem, based on observations of postural control following neural impairment.

Degrees of Freedom Problem

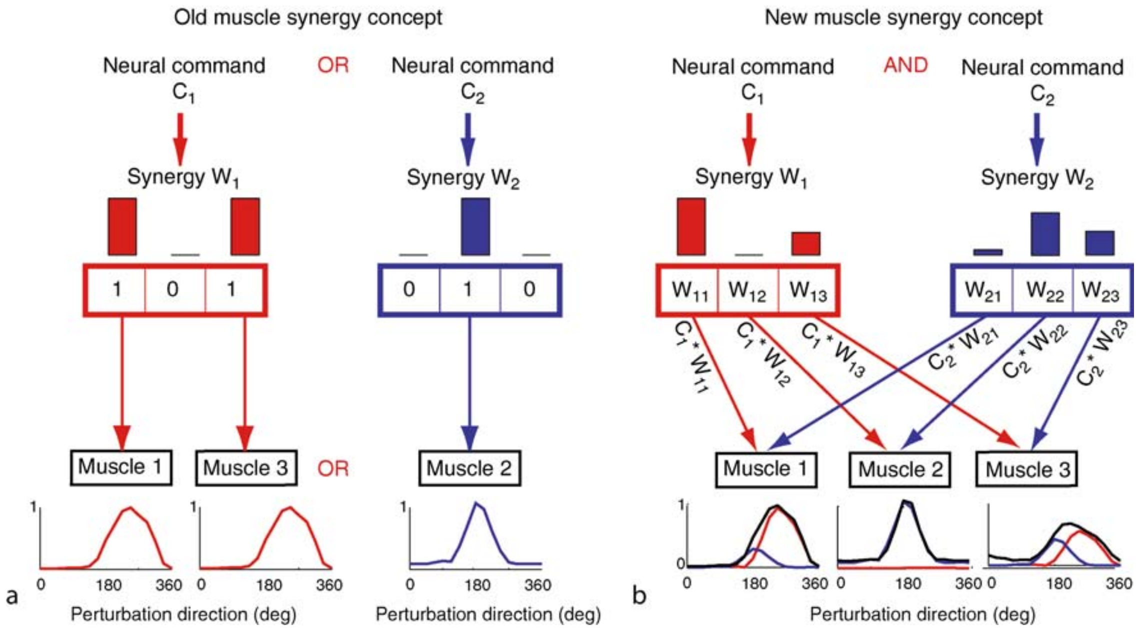
To maintain standing balance, the nervous system must confront the classic "degrees of freedom" problem posed by Nikolai Bernstein [5], where many different solutions are available due to the large number of elements or degrees of freedom involved. In postural control, a large number of muscles and joints across the limbs, trunk and neck must be coordinated to maintain the body's ►center of mass (CoM) over the base of support, typically formed by the feet. The large



Postural Synergies. Figure 1 Muscle activity evoked following perturbations to the support-surface. (a) Backward perturbations elicit activity in muscles on the posterior side of the body. (b) Forward perturbations elicit activity in muscles on the anterior side of the body. The gray area represents the initial muscular response to perturbation, called the automatic postural response (APR). (c) The magnitude of the response during the APR varies as a function of direction and can be plotted as a tuning curve. Each muscle has a unique tuning curve, suggesting that each muscle is activated by a separate neural command signal.

number of degrees of freedom afforded by the multiple joints and muscles in the body thus allow for many solutions that can accomplish the task goals equally well. This multiplicity or redundancy of solutions allows flexibility in performing the postural task; it also poses the problem that the nervous system must choose from a large set of possible solutions. In contrast, if the body were a simple rigid stick balanced on one end, then the angle of the stick in space would completely determine the location of the center of mass with respect to the base of support. Moreover, if only one muscle is available, there is no ambiguity as to how to activate the muscle in order to move the center of mass. Thus, the "degrees of freedom problem" occurs only when overall task requirements are not sufficient to specify multiple output variables controlled by the nervous system.

Bernstein proposed the existence of synergies as a neural strategy for simplifying the control of multiple degrees of freedom by coupling or grouping output variables [5]. This scheme was based on experimental observations that many joint angles appear to be controlled together rather than independently during motor tasks. For example, during locomotor tasks such as running, the hip, knee and ankle joints all flex and extend at the same time, suggesting that they are not controlled independently. However, such observations only identify correlations between the joint motions. A variety of muscle activation patterns can produce similar joint movements. Therefore, joint angle changes do not necessarily have a direct relationship to neural command signals activating muscles. Since muscle activation is directly caused by motoneuron firing, correlations between muscle activation patterns can be more plausibly derived from a single neural command that is distributed across the various motoneuron pools. Thus, muscle synergies may represent a mechanism by which the nervous system can achieve repeatable multijoint coordination.



Postural Synergies. Figure 2 Illustrations of two different muscle synergy concepts. (a) In the original muscle synergy concept, only one muscle synergy was elicited at a time, and muscles could only be activated by one synergy. Therefore, all muscles activated by the same synergy would have the same directional tuning curve, determined by the neural command c that activated it. (b) In the new concept, more than one synergy can be activated at a time. Further, muscles can participate in multiple synergies, and have different weightings in each synergy. Therefore, each muscle's tuning curve is a weighted average of the two tuning curves of each muscle synergy.

Computational Methods for Identifying Postural Synergies

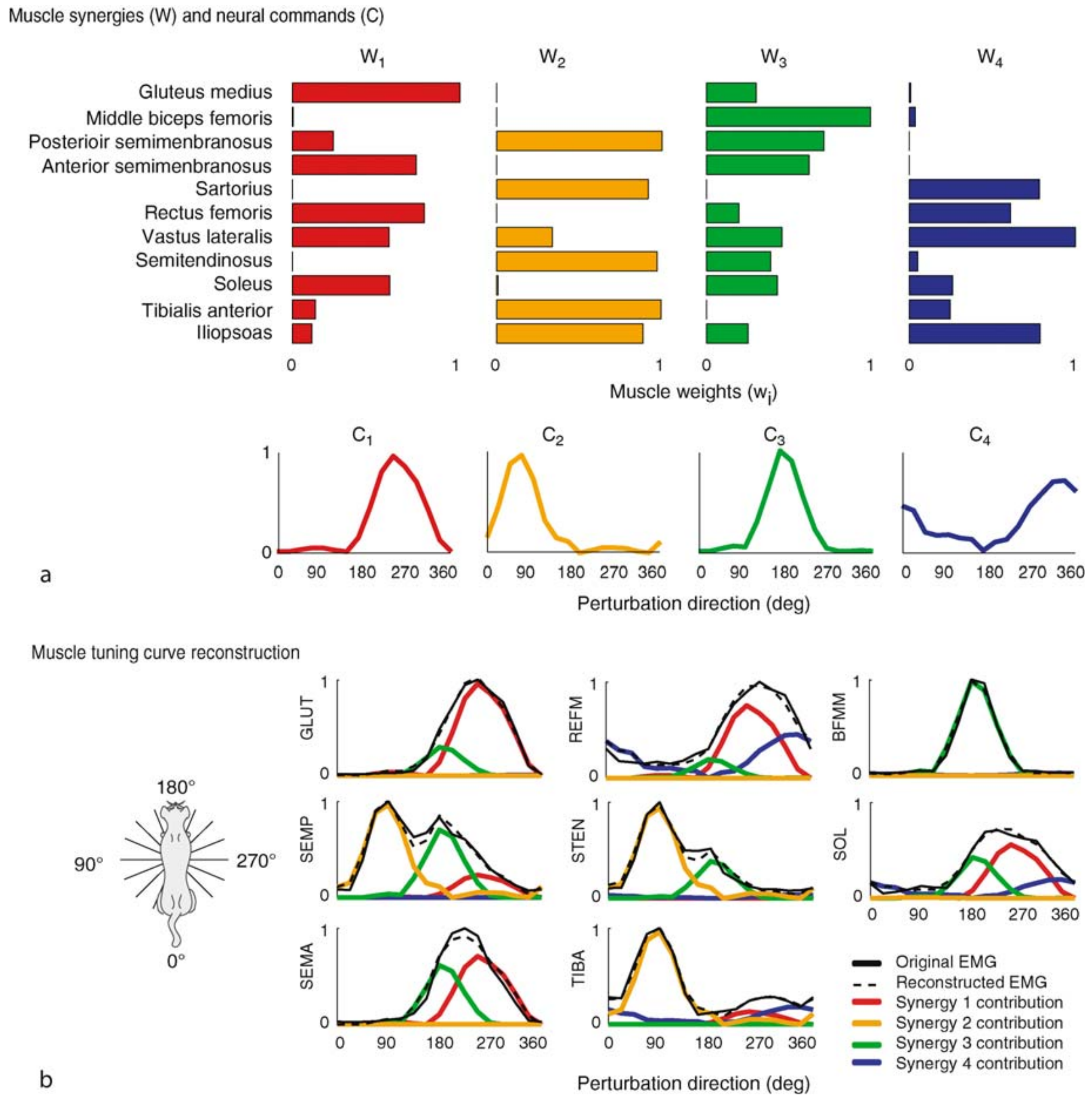
Recent computational techniques have redefined the working hypothesis of how muscle synergies can allow for flexible motor coordination while also simplifying the degrees of freedom problem. In this new formulation, a single synergy specifies a fixed muscle activation pattern that is modulated by a single neural command signal, but multiple muscle synergies can be activated at one time [4,6,7]. Mathematically, each muscle activation pattern is thus composed of a linear combination of a few (n) muscle synergies $\mathbf{W}_i$, each activated by one neural command c_i. The net muscle activation pattern vector **M** is therefore hypothesized to take the form:

$$\mathbf{M} = c_1\mathbf{W_1} + c_2\mathbf{W_2} + \ldots. + c_n\mathbf{W}_n$$

M is a vector where each element is the resulting level of activation in each muscle (Fig. 3a). $\mathbf{W}_i$ is a vector that specifies the pattern of muscle activity defined by that muscle synergy. Each element of $\mathbf{W}_i$ takes a value between 0 and 1, representing the relative contribution of each muscle to that muscle synergy. Each muscle synergy is then activated by a single, scalar neural command signal c_i, which determines the relative contribution of the muscle synergy $\mathbf{W_i}$ to the overall muscle activation pattern, **M**.

The above formulation allows for flexible "mixing" of a set of muscle synergies to produce the final output muscle activation pattern. Therefore, if two muscle synergies are present, rather than defining just two output muscle activation patterns, as in previous definitions (Fig. 2a), an entire continuum of output muscle activation patterns can be generated by varying the commands c_1 and c_2. Within this continuum, individual muscle activations are not strictly correlated to each other because most muscles belong to more than one muscle synergy and are thus activated independently by two different neural commands (Fig. 2b).

Linear decomposition techniques can be used to identify muscle synergies from experimentally measured muscle activation patterns. Because the number of muscle synergies is smaller than the number of muscles for any given task, the spectrum of muscle activation patterns that can be generated using muscle synergies is more limited than the case where muscles are controlled independently. However over the entire behavioral repertoire the number of muscle synergies could exceed the number of muscles. This dimensional reduction, which simplifies the degrees of freedom problem, can be identified using several mathematical analysis techniques such as principal components analysis (PCA), independent components analysis (ICA) and factor analysis (FA) [6]. Another such technique, non-negative matrix factorization (NMF),



Postural Synergies. Figure 3 Muscle synergies and neural commands used to generate muscle tuning curves during postural responses in cats. (a) Each muscle can participate in each muscle synergy with a different weight, indicated by the bars. (b) Neural commands to each muscle synergy can also be illustrated as tuning curves. Each muscle synergy therefore has preferred direction of activation. (c) EMG tuning curves can be reconstructed using muscle synergies. Each muscle's tuning curve is found by summing the product of each tuning curve, c_i and the weighting of each muscle within the synergy W_i. All muscle tuning curves are thus constrained to be weighted averages of the synergy tuning curves. Therefore, the muscle tuning curves have more varied and complex shapes than the synergy tuning curves.

allows complex data sets to be more successfully partitioned into meaningful parts [4,6,8]. NMF is particularly useful for data that are inherently positive valued, such as neural spike trains or muscle activations. The extracted elements are based on the components forming the data set rather than on more holistic features. For example, when applied to images of faces, a non-negative extraction routine generates vectors representing noses, ears and eyes, whereas PCA generates components that all tend to look roughly like an entire face [8].

Muscle Synergies in Postural Control

During postural responses to perturbations in different directions, multiple muscles across the body are activated and for each different direction of the perturbation, a different pattern of muscle activation is elicited (Fig. 1b). In both humans and in cats, a stereotyped, directionally specific pattern of muscle activity called ►automatic postural response (APR) is evoked after perturbations to the support surface. The muscle activation occurs after the platform motion begins, but before the center of mass moves appreciably, with a latency of around 50 ms in the cat and 100 ms in humans. In both cases, this latency is about twice the ►stretch reflex latency for distal muscles and evokes a much larger response than the stretch reflex [2]. Each muscle's activation level can be expressed in terms of a muscle tuning curve, which shows the variation of the muscle activation with perturbation direction (Fig. 1b – human, Fig. 3b – cat). Thus, for some directions, a muscle may have high activation and for others it may not be active at all. These muscle tuning curves define the complex patterns of muscle activation evoked across many perturbation directions [2,4,9].

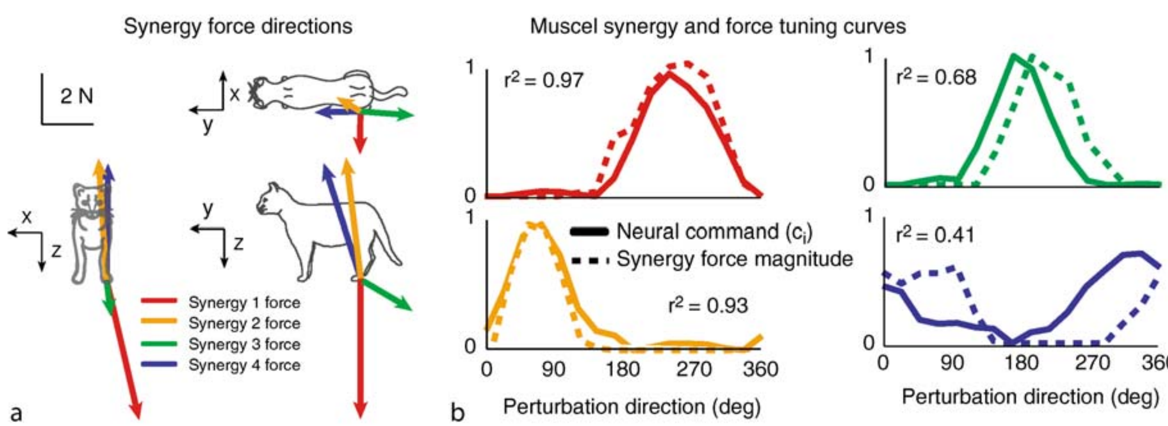
Although each direction of perturbation evokes a slightly different pattern of muscle activation over all muscles, these variations can be explained by a combination of just a few muscle synergies in the cat [4]. Over 95% of the variability in as many as fourteen muscle tuning curves can be explained by combining just four muscle synergies (Fig. 3b). Instead of activating each muscle independently for each perturbation direction, only four neural commands, each activating a synergy $\mathbf{W_i}$, need to be specified with amplitude $\mathbf{c}_i$ for any perturbation direction. The net muscle activation pattern is thus found by adding up the contributions of each muscle synergy to each muscle's activation level.

Muscle synergies may coordinate the limb to produce a specific biomechanical function for stabilizing the body. In the cat, it has been suggested that each muscle synergy allows the leg to produce a force in a particular direction in order to stabilize the leg (Fig. 4a). Variations in the components of active force generated by each leg are correlated to the variations in the neural commands of each muscle synergy (Fig. 4b). Each muscle synergy can generate a specific direction of force; the forces are distributed so that upward, downward, anterior, posterior and lateral force direction can be produced. Thus, muscle synergies may be organized to produce specific task-level biomechanical functions [4].

Even for postural perturbations of the same direction, multiple muscle synergies may exist. In backward perturbations of the support surface in humans, two types of responses can be elicited. One is called the "ankle strategy" where the body remains upright and most of the motion occurs around the ankle joint. The other is called the "hip strategy," where the trunk tilts forwards and the hip angle motion is most predominant. Each strategy can be defined by a specific pattern of joint torques. Because joint torques directly relate to the force generation of the musculature, this suggests that there are muscle synergies underlying these two strategies. While these two strategies were initially thought to be mutually exclusive, they in fact represent two different postural synergies that can be combined to produce a whole continuum of intermediate responses [2,11]. Therefore, rather than having a simple repertoire of just two response patterns, the flexible combination of these postural synergies allows the APR to be tuned and varied with perturbation amplitude, prior experience and anticipation.

Encoding of Muscle Synergies in the CNS

If muscle synergies reflect neural control mechanisms, then what are the neural substrates that generate muscle synergies? It is now understood that postural synergies



Postural Synergies. Figure 4 Forces produced during the automatic postural response correlate with muscle synergy activations. (a) Forces produced during postural responses can be decomposed into four force vectors. (b) During postural response, the magnitude of each force vector required to reproduce the total force varies as a function of direction and can be illustrated as a tuning curve. The tuning curves of force magnitude are highly correlated with the tuning curves of the neural commands c_i activated the muscle synergies. Thus, each force vector may represent the functional output of the muscle synergy.

cannot be explained just by reflexes acting in response to muscle stretch. In both humans and cats, it has been shown that perturbations that stretch the muscles differently can activate the same muscle synergies. For example, Nashner originally demonstrated that for a backward translation of the support surface, the calf muscle is stretched as the subject falls forward and that the same muscle is subsequently activated to maintain balance, consistent with a stretch reflex. In contrast, if a toes up rotation of the support surface is given, the calf muscle is stretched but the subject falls backwards, so that the antagonist muscle is activated to restore balance, in direct opposition to the stretch reflex [1]. This same principle has been demonstrated in multidirectional perturbations in both cats and humans [9]. Moreover, the loss of a single sensory modality, such as proprioceptive, vestibular or visual loss, does not appear to significantly affect muscle activation patterns, only their activation levels. Therefore muscle synergies are not a direct response to local sensory input, but appear to be related to more global variables, such as the direction of CoM displacement caused by the perturbation, that require multisensory integration [2,9].

How postural synergies are encoded in the nervous system is not known. For locomotor tasks, the encoding of muscle synergies appear to be located within the neural circuitry of the spinal cord [7], as animals can produce locomotor activity from a spinal cord that is isolated from the brain following spinal cord transection. These same animals can support their own weight while standing, but direction specific responses to postural perturbations are lost. This suggests that postural synergies are generated within the spinal cord [10]. It is known that the brainstem is essential to the maintenance of postural orientation and equilibrium and it is possible that neural mechanisms producing postural synergies reside there. Moreover, postural synergies appear intact in patients with postural impairments due to lesions in higher brain centers. For example, Parkinson's disease is characterized by pathology of the basal ganglia, which project to brainstem areas that are important for postural control. Individuals with Parkinson's disease have the aility to generate postural synergies that are similar to control subjects, but have difficulty changing the muscle synergy that is activated when perturbation conditions change. Similarly, in individuals with cerebellar dysfunction, postural synergies are similar to control subjects, but their activation levels do not decrease with repeated perturbations as in control subjects. Therefore, the muscle synergy structure appears intact, but the ability to correctly activate the neural commands to those muscle synergies is compromised, which impairs the postural stability in these individuals [2]. The theory of postural synergies therefore contributes to our understanding of the role of various nervous system structures in postural control and can guide experimental investigations that may further the validity of the theory.

►Postural Strategies

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Postural Tone

Definition

Background tension developed by the antigravity muscles. It represents a prerequisite for the maintenance of posture. The postural tone is regulated by intrinsic properties of spinal motoneurons, by the tonic activity of the corresponding muscle spindle afferents and by signals arising from brainstem systems projecting to the spinal cord, including the vestibular nuclei and the reticular formation.

►Postural Synergies
►Vestibulo-Spinal Reflexes