# Motor control theories and their applications

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***Summary.*** *We describe several influential hypotheses in the field of motor control including the equilibrium-point (referent configuration) hypothesis, the uncontrolled manifold hypothesis, and the idea of synergies based on the principle of motor abundance. The equilibrium-point hypothesis is based on the idea of control with thresholds for activation of neuronal pools; it provides a framework for analysis of both voluntary and involuntary movements. In particular, control of a single muscle can be adequately described with changes in the threshold of motor unit recruitment during slow muscle stretch (threshold of the tonic stretch reflex). Unlike the ideas of internal models, the equilibrium-point hypothesis does not assume neural computations of mechanical variables. The uncontrolled manifold hypothesis is based on the dynamic system approach to movements; it offers a toolbox to analyze synergic changes within redundant sets of elements related to stabilization of potentially important performance variables. The referent configuration hypothesis and the principle of abundance can be naturally combined into a single coherent scheme of control of multi-element systems. A body of experimental data on healthy persons and patients with movement disorders are reviewed in support of the mentioned hypotheses. In particular, movement disorders associated with spasticity are considered as consequences of an impaired ability to shift threshold of the tonic stretch reflex within the whole normal range. Technical details and applications of the mentioned hypotheses to studies of motor learning are described. We view the mentioned hypotheses as the most promising ones in the field of motor control, based on a solid physical and neurophysiological foundation.*

## Introduction

Motor control is a relatively young field of research. It may be defined as an area of natural science exploring how the central nervous system (CNS) produces purposeful, coordinated movements in its interaction with the rest of the body and with the environment. Hence, the main goal of motor control research is to create a formal description, operating with exactly defined variables, of the physical and physiological processes that make such movements possible. Progress in motor control over the recent years has been slowed down by the lack of a broadly accepted and exactly defined set of notions that would be specific for typical problems of motor control, an adequate language for this area of research (1).

It is very hard to look for an adequate set of notions in an area that does not have them, but it is also very challenging and exciting. It is much more simple (and tempting) to borrow one of the developed approaches from another field that shares "key words" with motor control, for example classical mechanics, control theory, and engineering. One should keep in mind, however, that such approaches have strict limitations. They can provide tools that may help find answers to questions after the questions have been formulated. However, they cannot offer an adequate formulation of questions in a field that differs from the areas for which these approaches have been developed.

Biological objects belong to the physical world and they are alive. So, help with formulating questions may be expected to come from physics and biology (physiology), not from control theory and engineering developed to deal with objects in the inanimate world. Physics of the inanimate nature, while being a highly developed science, has troubles dealing with typical problems of motor control. First, in contrast to movements in the inanimate world, movements of biological objects are intentional and purposeful. These two notions cannot be easily incorporated into physics. Another problem is

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that the body is a very complex system, maybe too complex to be studied with the currently available physical tools, and many crucial variables are not directly measurable or even identifiable. Physics of living systems, unfortunately, does not exist so far, although one of the authors of this paper (M.L.L.) graduated some 30+ years ago from the Moscow Institute of Physics and Technology, and his major was indeed the nonexisting *Physics of Living Systems*.

Two aspects of motor control have been traditionally considered separately from each other. The first relates to the nature of physiological variables that are used by the brain to control muscles. The second relates to the problem of motor redundancy (2): How does the brain select particular solutions from infinite sets afforded by the redundant design of the neuromotor system at all levels of its analysis? Within this brief paper, we will review two theories that, to our opinion, are most promising in moving the field of motor control closer to physics of living systems.

The first of these theories is the equilibrium-point hypothesis (referent configuration hypothesis, 3–5), which is based on Galileo's principle of relativity and the fact that neurons are threshold elements. The second one is the uncontrolled manifold hypothesis (6, 7), which, in combination with the principle of abundance (1, 8), suggests a novel approach to the problem of motor redundancy. There have been several recent attempts to move towards combining the two approaches into a single theory of motor control (9, 10).

### Equilibrium-point theory: explanation of normal and disordered motor control

The equilibrium-point (EP) theory was first described by Feldman in a series of papers in the 1960s and 1970s. Over the past 50 years, the EP theory has been revised and refined from a hypothesis describing the control of a simple single-joint system to a theory addressing the production of complex movements, such as multi-joint movement and locomotion, and uniting the processes underlying movement production and perception.

Fundamental to the EP theory is the notion that *threshold position control* underlies intentional motor actions. To perform such actions, electrochemical influences descending from the brain in the presence of proprioceptive feedback to motoneurons are transformed into changes in the threshold muscle lengths or joint angles at which these motoneurons begin to be recruited, thus setting the spatial activation range in reference to the body geometry. This allows control levels of the CNS to specify *where*, in spatial coordinates, muscles are activated without being concerned about exact details on *when* and *how* they are activated. In the most advanced for-

mulation of the EP theory, activity of each muscle *emerges*, without any programming, depending on the difference between the actual configuration of the body and its threshold (referent) configuration, as well as on the rate of changes of this difference (11). A hallmark of the EP theory is that it describes motor control based on neurophysiological and physical principles.

In a series of experiments on the elbow joint in humans combining *involuntary movement* elicited by unloading of the preloaded arm (the unloading reflex), *voluntary changes* in the joint angle, and *full relaxation* of the elbow muscles while they were stretched, Asatryan and Feldman (12) identified invariant and modifiable neurophysiological variables involved in these motor actions.

*Involuntary behavior* was analyzed by unloading experiments in which the forearm was placed on a horizontal manipulandum and subjects resisted a specific load torque at a specific position with the elbow flexors. The elbow position, load torque and flexor and extensor electromyographic (EMG) activity were measured in this initial state, called the *equilibrium point* (EP) of the system (Fig. 1, filled circle *a*). The EP is thus comprised of both an equilibrium position and its associated equilibrium torque. In subsequent trials, from this initial EP, the elbow flexors were unloaded to varying amounts. Subjects were instructed *not to intervene voluntarily* when the unloading occurred. This means that they had to let the arm move to its natural new position after the unloading and not try to make a correction, to return the arm to the initial position or to relax completely.

After each time that the arm was partially unloaded, the arm naturally found a different final EP (open circles), depending on the amount of unloading that occurred. These final EPs were plotted on a torque-angle graph and together with the initial EP; they formed a smooth nonlinear torque-angle characteristic (upper left solid curve in Fig. 1).

After that, the subject was asked to *voluntarily change* the initial position against a load and the procedure was repeated from a new initial EP, yielding a new torque-angle characteristic (Fig. 1, right solid curve). In this way, a family of torque-angle characteristics was recorded. Finally, subjects were asked to *fully relax* their muscles while the elbow was extended by the manipulandum and a torque-angle characteristic of the subject's passive arm muscles was obtained (dashed curve in Fig. 1). The first two unloading characteristics (starting from points *a* and *b*) were similar: for each of them, the torque was nonlinearly related to the arm position, and EMG activity changed depending on the load. The characteristics were somewhat different in terms of shape, which may have resulted from dif-

ferences in the mechanical properties of muscles in different parts of the angular range, rather than from a voluntary action. Each unloading curve merged with the passive joint characteristic at a specific joint angle (R). At these points R, muscles became silent and ceased to generate active torque. These *thresh-old angles* were different for different characteristics (Fig. 1). From these experiments, Asatryan and Feldman (12) concluded that the threshold angle, R, at which muscles ceased to be active was invariant for a given initial set point or command. When the subject intentionally changed the initial arm posi-tion, a new R value was specified. The experiments also showed that to fully relax the arm muscles, the R had to be shifted beyond the upper biomechanical limit of the elbow joint (Fig. 1, R+) so that the mus-cles could remain silent in the entire biomechani-cal range of the elbow joint angle. In contrast, to fully activate the muscle, even at the shortest muscle



*Fig. 1.* Three experimental procedures leading to the notion that central shifts in the threshold position (R) underlie volun-tary motor actions

Procedures include: involuntary motor action – unloading re-flex – resulting from sudden unloading of the forearm to dif-ferent final equilibrium points (EPs, open circles) of pre-loaded elbow flexors from an initial EP (filled circle, a); voluntary mo-tor action when the subject changed the initial EP a to EP b; stretch of the fully relaxed elbow flexors (dashed curve). For each unloading characteristic (solid curves), the tonic EMG activity decreased with the decreasing residual torque (verti-cal lines) and became zero when the unloading characteristic reached the characteristic of the passive muscle at position R, called the threshold elbow position. For different unloading characteristics, threshold positions were different (ΔR). There-fore, the intentional motor action associated with the transition from EP a to EP b (or from one unloading characteristic to another), was accomplished by a change in the threshold angle R. Horizontal line at bottom of figure shows that the range of regulation of R (R− to R+) is greater than the biomechanical range of the joint.

length, the R had to be shifted beyond the lower limit of the biomechanical range (Fig. 1, R−). Thus, the CNS specifies R and its associated torque-angle characteristic and regulates the range of R within or beyond the biomechanical range of the joint. These empirical results underlie the EP theory.

It should be noted that for each torque-angle characteristic, neither the arm position, muscle torque, force, EMG, nor stiffness (the slope) was invariant. The EMG activity, for example, simply scaled with the magnitude of the load (Fig. 1, ver-tical segments near EPs), in accordance with the known EMG-force relationship (13). The invariant variable is the R.

Disorders in motor function following lesions to the CNS have been attributed to deficits in the range of regulation of R (14). Instead of using an un-loading procedure, R has been estimated in patients with stroke or cerebral palsy (CP) as the joint angle at which the *tonic stretch reflex threshold* (TSRT) is reached when the system is at rest (Fig. 2). Stretch-reflex thresholds depend on velocity *(dynamic stretch reflex threshold*; DSRT). One can determine DSRTs (asterisks in Fig. 2) from stretches at various veloci-ties and extrapolate these value to zero velocity to estimate the TSRT (15). In nondisabled individu-als, DSRTs can usually only be evoked in muscles at rest if the stretch is performed at a high veloc-ity (>300°/s; (15, 16); Fig. 2, dashed diagonal line). However, in adults with stroke and children with CP, muscles stretches at speeds as low as 8°/s, ap-plied to the elbow joint, can generate DSRTs (Fig. 2, solid diagonal line).

Previous studies in patients suggest that: 1) the TSRT lies within the physiological range of motion of the elbow (Fig. 2, TSRTs); 2) the TSRT is in-versely correlated with the degree of clinical spas-ticity (i.e. the lower the TSRT the higher the spas-ticity); 3) the TSRT is a better measure of spasticity than the gain of the stretch reflex (15, 17).

Jobin and Levin (17) quantified the TSRT in the elbow flexors of children with CP and tested the stability of this measure as a possible estimate of spasticity. Fourteen children with CP and eight typically developed children participated in the trial. DSRTs were evaluated by performing eight sets of stretches at seven, randomly selected velocities be-tween 8 and 160°/s using a torque motor. The joint angle and velocity corresponding to the onset of the EMG in elbow flexors or extensors were recorded during each stretch. These points were the DSRTs for each stretch velocity. A linear regression line was computed through the DSRTs and the TSRT, or the SRT at 0°/s was extrapolated. For the *elbow flexors*, TSRTs expressed in angular coordinates occurred later (closer to full elbow extension) for slow veloci-ties of stretch compared to fast velocities of stretch.
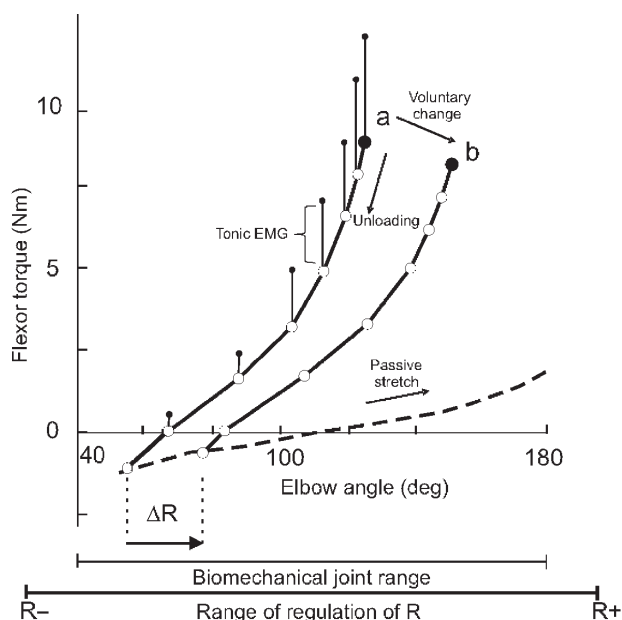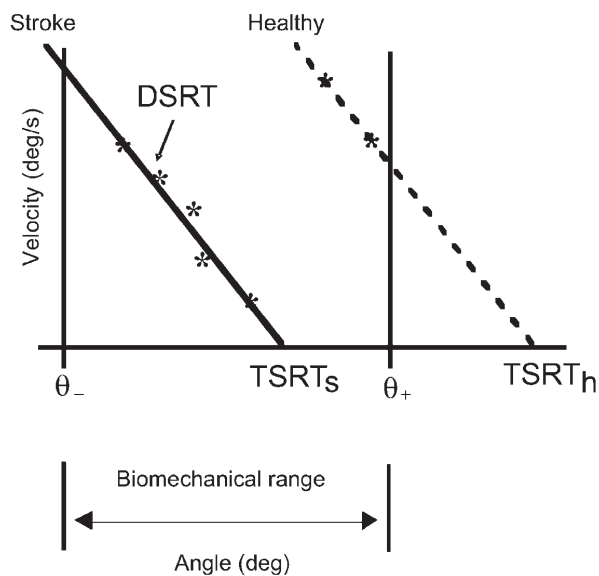
*Fig. 2.* Schematic illustration of tonic stretch reflex thresholds (TSRT) determined by extrapolation of a linear regression line through dynamic stretch reflex thresholds (DSRTs)
DSRTs are evoked by stretching elbow flexors at different velocities. In healthy subjects, DRSTs can only be evoked by high velocity stretches and the TSRT lies beyond the biomechanical range of the joint (TSRTh). In patients with spasticity, DSRTs occur earlier (at smaller joint angles), and the TSRTs lies within the biomechanical range of the joint.

The test–retest reliability of the computed TSRTs was estimated to be good (ICC=0.73, *P*<0.001). An important conclusion of this study was that the TSRT is a valid measure of spasticity, presently unavailable in clinical practice.

The use of this fundamental concept of the EP theory has led to a new and more in depth understanding of the mechanism underlying motor control deficits in patients with CNS lesions. Limitations in the ranges of regulation of the TSRT have been shown to correspond to the appearance of abnormal muscle activation patterns when patients attempt to make voluntary movements, such as excessive coactivation (18). In addition, ranges in which typical patterns of muscle activation can occur, such as reciprocal activation, have also been described using the TSRT approach. Using this basic notion of the EP theory, clinicians can identify specific deficits in motor control and work with patients to increase the range of regulation of TSRT in order to improve motor function.

**The concept of the uncontrolled manifold**

A general principle of movement generation in organisms is what Gelfand and Latash (1) have referred to as the *principle of abundance*: there are many more degrees-of-freedom available for any specific task than strictly needed. For instance, most tasks performed with our arms involve positioning, perhaps orienting the hand in space. That requires

between 3 and 6 degrees-of-freedom. Our arm has at least 10 degrees of freedom, however, and even more if we allow for movements of the upper body. Similarly, almost all joints are actuated by many more muscles than a pair of agonist and antagonist muscles that would be minimally required. When we grasp objects, our four fingers generate surface forces and moments, which could minimally be brought about by just two fingers that oppose the thumb.

The principle of abundance or task-relative redundancy gives rise to the question of how the many degrees-of-freedom are harnessed to achieve a given task. This question has been known for a long time as the degree-of-freedom problem (2) and is central to much research in motor control. Researchers have asked, for instance, which variables the CNS "uses" to plan, time, and control movement.

There is consensus now that movement planning is best characterized in external, task-relevant coordinates, such as the direction of movement of the end-effector in external space. Response times, for instance, are functions of spatial task parameters. Knowing end-effector movement direction beforehand leads to a stronger reduction of response time than knowing movement extent (19). Although such dependences do not preclude that movement preparation may also reflect effector-level processes, a coherent and comprehensive account of movement preparation can be provided at the level of end-effector variables (20). This is also consistent with the neurophysiology of motor and premotor cortex. The majority of cells in these areas display relatively uniform tuning curves to such spatial movement parameters as the direction in space of end-effector motion or the direction in space of forces that act on the end-effector (21, 22). These tuning curves may depend also on joint configuration (23), but largely retain their uniform shape, again suggesting an account in terms of this spatial parameter.

Many different mechanisms seem to be involved in controlling the timing of movements, from spinal pattern generators, cerebellar estimators, to cortical mechanisms (24). The abstract functional description of timing as a form of neuronal oscillation accounts for coordination among multiple timed movements through the coupling among such oscillators (25). Such coupling establishes stable patterns of relative timing. Stability, the capacity to restore the pattern following stochastic or external perturbations, is constitutive for such patterns of coordination. This is best seen when stability is lost. Generically, the pattern in which homologous limbs alternate ("antiphase") becomes unstable for higher movement frequencies, leading to a switch to the inphase pattern. Although it is tempting to think of the mechanisms that establish stable patterns of coordination as re-

siding at a level close to the neural control of the effectors (26), it turns out that this is not appropriate. In a series of elegant experiments, Mechsner and colleagues (27) exploited the instability of antiphase to establish whether antiphase is defined anatomically (homologous muscles alternating) or spatially (movement of two end-effectors toward each other). It turned out, that it is the spatially defined antiphase pattern that becomes unstable at higher frequencies, even though it is anatomically close to the stable in-phase pattern.

The control of limb movement cannot be achieved entirely at a level of task-relevant spatial variables. At some point, muscles must be activated, forces must be generated, and joints must be moved. Even so, since Nikolai Bernstein's studies of movements in skilled workers, the notion has been around that the control of limb movements gives priority to the spatial shape of the movement over the trajectories of the individual joints (see account in Zatsiorky (28)). For many years, research efforts were aimed at establishing which variables the CNS *controls* when it generates a movement trajectory. Two candidates were spatial end-effector variables or joint-level variables. One way to ask the question was by looking for invariance, that is, finding out if movement trajectories are simpler and depend less on task parameters when represented in end-effector vs. in joint coordinates (29). Although spatial representations of movement seem to capture more of the simplicity and invariance (30), overall no clear pattern emerged. Moreover, most of this work used tasks in which the effector did not have abundant degrees-of-freedom, so in principle, spatial and joint-level trajectories were strictly transformable into each other. This weakened the case for identifying any one of the variables as being "more controlled" than any other.

Today there is consensus that the appropriate operational definition of a variable being "controlled" is that it is stabilized against perturbations (31). The variability across trials is then a possible measure of stability: highly stable states resist stochastic perturbations more than less stable states. Even variance, however, cannot help to decide which variable is the preferred one in human motor control when a non-abundant task setting is used: it is true also at the level of variance that a one-to-one mapping between joint angles and spatial end-effector coordinates precludes any decision about a control priority.

In a task-effector system that has abundant solutions, or is redundant in more conventional parlance, such a decision can be made, however. When the CNS has the "choice" among an ensemble of joint-level realizations of the same spatial movement of the end-effector, we may investigate if it stabilizes these choices at the joint level as much as it stabilizes the end-effector motion. Indeed, Bernstein had partly argued on this basis, postulating that the end-effector paths were less variable than the joint level trajectories. That comparison is, alas, difficult to make. End-effector variance is measured in centimeters (squared), joint variance in radians or degrees (squared). Therefore, a direct comparison is meaningless. What is needed is a shared space in which all variables can be embedded and a shared metric enables comparisons.

This is what the concept of the *uncontrolled manifold* achieves (6, 7, 32). The idea is to use joint space as the embedding space in which all variance is measured. The structure of the variance in joint space is now interpreted relative to spatial task variables. This is done by defining a subset, the *uncontrolled manifold* (UCM), that contains all those combinations of joint angles that are consistent with one particular end-effector position. There is such an UCM for any position of the end-effector. The hypothesis is then that, at any given point during the movement, joint configurations vary primarily within that subset rather than outside of it.

An operational formulation linearizes the UCM, which is typically possible given the limited range of joint variance. Trials in the same task setting are aligned in time based on movement initiation and termination. Time is recoded as percent of the mean movement time. At any given moment of this warped time, the variability in joint space is analyzed by decomposing it into a component that lies within the UCM and a component that lies orthogonal to it. The component within the UCM is consistent with no variance at the level of the spatial task variable. The component orthogonal to the UCM is consistent with a variable spatial task variable. The UCM hypothesis about the structure of variance is thus that there is more variance within the UCM than orthogonal to it. In other words, the CNS preferentially stabilizes those combinations of joint angles that matter for the stabilization of the spatial task variable than those combinations of joint angles that do not.

This conception has been operationalized and applied to a large set of movement systems and movement tasks (33, 34). The ideas have been generalized to the control of isometric force generation by the fingers of the hand (35) as well as to the control of muscular activation to achieve particular location of the center of pressure by a standing person (36). In all cases, strong structure of variance was observed at the level of the elemental variables (joint angles, individual finger forces, or muscle activations) that was consistent with the preferred stabilization of spatial task variables (end-effector position, spatial pointing directions, spatial force vector, or center of pressure coordinate).

Thus, the CNS controls all elemental degrees-of-freedom, including joint angles, digit forces, and muscle activations. But it does so in a way that reflects the spatial task constraints by preferentially stabilizing task-relevant directions in joint (or finger or muscle) space. What does this mean mechanistically? A theoretical model ((9, 37) for a related model) proposes that the neuronal command signals sent to all joints are selectively coupled to the descending motor commands. Only those combinations of joint angles that affect a spatial task variable are driven by the descending movement and timing plan while combinations of joint angles orthogonal to these combinations are free to vary, to accommodate other task constraints, or to receive back-coupling from the sensed effector position. The model makes use of the conception of an equilibrium point for every joint-muscle system, which accounts for how initial and terminal joint configuration differ.

## Practical applications of the uncontrolled manifold theory

The UCM approach (7) has proven to be a powerful tool to investigate the flexibility/stability aspect of synergies (32). This has been performed in a variety of contexts, including reaching (34, 38, 39), finger force production (35, 40–44), and postural control (33, 36, 45–49) among other tasks. Most studies to date have used the approach to investigate motor abundance, analyzing the variance of motor elements across repetitions of a task, or across time in tasks with during relatively steady-state performance. This section addresses a number of important practical issues that should be considered to apply and interpret properly the results of this analysis.

### Number of data points required

When applying the UCM approach to analyze variance in the space of a set of motor elements, the number of data points used in the analysis is an important consideration. As discussed below, for tasks where the configuration of the elements changes substantially throughout the movement (e.g., joint motion when reaching to a target), analysis needs to be performed across trials at comparable points in the movement time. Ideally, the more data points or number of trials in this reaching example, the better. Depending on the nature and complexity of the experimental conditions, however, the number of trials may be limited by the ability of subjects to perform a large number of trials per condition. This is particularly an issue for studies of patients who may be limited in their ability to perform many trials because of fatigue (50). We have performed informal tests of how the variance structure changes with the number of trials included when analyzing a reaching task. Figure 3 illustrates the results of one

such test where 50 trials of reaching were performed by a subject with mild hemiparesis resulting from a stroke. Depending on the portion of the reach examined, UCM analysis performed on different blocks of 10 randomly selected trials could result in significant quantitative differences in the variance components within the UCM and orthogonal to the UCM ($V_{UCM}$ and $V_{ORT}$), although the relative magnitudes of $V_{UCM}$ and $V_{ORT}$ did not differ much across blocks. The quantitative differences diminished with the number of trials included in each block. This is illustrated in Fig. 3.1, which shows the standard deviation of the variance components across the trial blocks of a given number of trials. The standard deviation stabilizes somewhat with 20 or more trials included. One might expect the standard deviation to approach zero, but trial-to-trial variability in performance is not unusual, especially in stroke survivors. This is certainly not a definitive test, but it suggests loosely that one should include at least 20 trials for UCM analysis to increase the chance of having a stable estimate of the variance components. As noted, this is not always possible if multiple conditions are studied and the experiments involve patients. With fewer trials, however, caution should be used in interpreting the data across conditions. Fortunately, this is not an issue when the analysis can be performed across time during the performance of relatively steady-state tasks such as postural control, where a large number of data points can be included in the analysis (46).

### Relating task space to the space of motor elements

The UCM approach requires being able to relate changes in a hypothesized task variable to changes in the space of the motor elements (7). This requires a formal model relating how variability of the motor elements affects the task variable. This is usually not a problem for kinematic studies, where a formal geometric model linking typically can be written down. For example, changes in the hand's position can be related directly to small changes in the current joint configuration through a model of link lengths and trigonometric functions of the joint angles (39). This allows computing the Jacobian of the system that allows representing task-specific variables in the space of elemental variables (joint angles).

This may not be as trivial for studies involving analysis of the relationship between changes in muscle activation patterns, as estimated by EMG activity, to a task-relevant variable such as the center of pressure (CoP) coordinate (37, 47, 48). Although a formal model relating EMG signals to such task variables is theoretically possible, available models are extremely complicated, involve a large number of parameter estimates that are themselves a potential
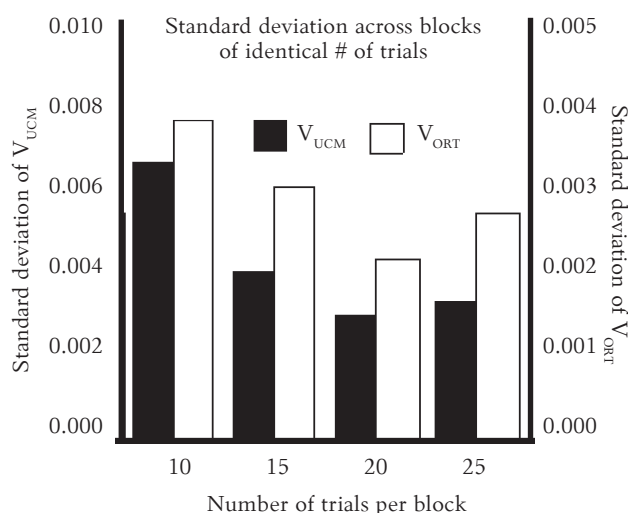
*Fig. 3.* Standard deviation of variance components, $V_{UCM}$ and $V_{ORT}$ across five blocks of 10, 15, 20, or 25 trials Variance is computed as rad² per dimension of each subspace. Trials were randomly selected from a group of 50 trials collected for this subject. The largest reduction in standard deviation occurs between 10 and 15 trials.

source of error, and are generally limited to a few degrees-of-freedom. One way to circumvent this problem has been to use regression methods to estimate an analog of the Jacobian that relates changes of the task variable to small changes in the elemental variables. Successful application of such methods has been performed in studying postural reactions in a variety of contexts (36, 47). The comparability of this experimental approach for estimating the Jacobian to one based on a formal geometric model has been verified recently in two separate studies of kinematic redundancy (51, 52), although future confirmation in a paradigm relating muscle activation to a task-relevant variable would be useful.

A related issue is the determination of the elemental variables. In studies relating EMG activity to kinetic variables such as the CoP, it is typically not possible to record activity from every muscle involved in the task. It has also been accepted that the brain does not specify activation levels of each muscle separately. Hence, such studies typically assume that muscles are grouped and the brain uses a few variables to modify in parallel the activation levels within each group. Nonetheless, conclusions based on such studies require caution and the more of the motor elements that can be included, the better.

In addition, including motor elements that have little or no effect on the task being studied will artificially inflate the variance estimates, especially $V_{UCM}$. For example, depending on the context and experimental question, spurious conclusions could result by including rotational degrees-of-freedom about the long axes of the humerus and forearm in a study of planar reaching. Consider, for exam-

ple, reaching with the hand, from an initial position where the forearm rests on a table, elbow flexed to 90⁰, and hand pointing forward, to a target located at a fixed distance immediately above the hand. These rotational degrees-of-freedom have little or no effect on the vertical position of the hand along its path to the target. Therefore, any variation in these angles will contribute only to $V_{UCM}$, although this additional variance may have no relationship to the task. Caution should be used, therefore, when determining what degrees-of-freedom to included. At the very least, this issue should be considered when interpreting the experimental results.

### *Identification of task variables*

UCM analysis is related to other methods such as principal component analysis (PCA), where the structure of variance among a combination of motor elements is analyzed. PCA may be considered an objective approach because it is performed without direct connection to a hypothesis about what task variable might be generating the observed structure in the space of the motor elements. In contrast, for UCM analysis, the structure of variance in the motor element space is always related to a hypothesized task variable through a formal model linking the two spaces. The decision about what task variables to investigate certainly has a subjective element. Including the analysis of a number of relevant task variables may be important if one is investigating questions about what the nervous system "cares" most about in a given task.

Thus, application of the UCM method of analysis is useful only if one has an explicit experimental question to address related to the structure of variance of the elemental variables in relation to changes in a task variable and/or when performing a task under different constraints. For a given task, one has to hypothesize what task-level variables are "most important" for the nervous system. Indeed, by analyzing how the variance of the elemental variables is structured relative to different task variables, it is possible to differentiate among the relative importance of such variables for the task being investigated. In some cases, it may even be useful to differentiate among different dimensions of the same task variable. For example, in studies of the sit-to-stand action under different task constraints, it was shown that joint variance was structured mostly to stabilize the horizontal position of the center of mass (CoM) in contrast to the vertical CoM position (7). Stability of the vertical CoM position through the use of flexible combinations of joint postures was more evident, however, when sitting down, where vision of the seat was limited (53).

An additional caution is required when interpreting differences in the variance components after

UCM analysis among different task variables if the model relating task space to elemental space is very different in the two cases. For example, in kinematic studies, the geometry of the system will influence the degree to which variance in joint space affects variance of a task variable. Because the models relating different task variables to joint variance may be quite different, it would be important to examine the extent to which $V_{ORT}$ actually affects the task variable in both cases. That is, the same amount of $V_{ORT}$ may affect one variable more than the other. This relationship can be identified by examining the singular values of the Jacobian in each case, as demonstrated by Freitas et al. (52).

### *Indices of the strength of a synergy*

Different methods of combining the two variance components obtained from UCM analysis, i.e. $V_{UCM}$ and $V_{ORT}$, have been used in previous studies to provide an index of the strength of a synergy stabilizing the task variable for which the analysis was run. Initially this involved examining the ratio of the two components. More recent investigations have used the relative difference between the components (54, 55), in part because the ratio has a floor effect and is not normally distributed. The idea is that a larger value of this measure indicates a stronger synergy. Concluding that one person or task exhibits a stronger synergy than another may be valid depending on the values of the individual variance components. Thus, the interpretation of such a measure requires caution.

Consider as an example emergency responders pressing with the index and middle fingers to generate chest compressions in an infant having cardiac arrest. In such an incident, one needs to produce a stable force that is large enough to restore the heartbeat while minimizing injury to the infant. This could be achieved, in principle, by pressing with a fixed amount of force by each finger on successive repetitions. However, biological systems are variable and it is difficult to generate the identical amount of force by each finger on each compression. If one were to plot the two finger forces against each other across all repetitions (Figure 4A), then this independent control strategy would yield a circular cloud of points, the diameter of which would indicate how successful the strategy was in stabilizing the total force. Notice, however, that, because the forces act independently of each other, the total force may frequently fall below the desired compressive force level, or even injure the infant's chest because the total force is too high. A more desirable solution would be to co-vary the finger forces through a synergy that links their output to the task requirements. Plotting the results of such a control strategy would result in a cigar shaped cloud of points with a negative slope, indicating that when one finger's force increases too much, the other finger's force is reduced by a comparable amount and vice versa to preserve the total force. Coupling the natural variability of the fingers' forces in this way may reflect the fact that the nervous system has available to it flexible ways to combine the motor elements when needed. Perfect compensation between the fingers would result in all data points falling along the diagonal line in Figure 4B. If this compensation is not perfect, as likely is the case, the cloud of points will become fatter and more cigar-shaped. This fattening of the diagonal cloud of finger forces indicates greater $V_{ORT}$ when performing UCM analysis. Comparing results across two such emergency responders, if the repetitive force structure was fatter for one of them with no comparable difference in the diagonal length of the two clouds of finger forces, i. e. no difference in $V_{UCM}$, then one certainly could conclude that one responder exhibits a stronger finger force synergy than the other.

It is problematic to make such a conclusion without examining the magnitude of the individual components, however. Consider the difference in the two clouds of points in Fig. 4B. Although the cloud of points in the right panel of this figure (responder #2) is fatter than in the left panel (responder #1) (i.e. responder #2 has larger $V_{ORT}$), the force variance also extends substantially further along the diagonal representing the UCM for responder #2 (much larger $V_{UCM}$). The typically used synergy index in this case may indicate a stronger synergy for responder #2. However, only $V_{ORT}$ affects the task variable's variance. Therefore, responder #1's performance would be associated with less task variability. It would be odd to conclude that this individual exhibits a weaker synergy if the notion of a functional synergy is associated with successful task performance. A similar result was reported by Reisman and Scholz (38) in a study comparing reaching between healthy control subjects and persons with mild hemiparesis who had suffered a stroke. The latter individuals had significantly greater overall joint variance that was distributed across both subspaces of joint space compared to the control subjects. Thus, a similar synergy index would have suggested an equally strong synergy in these individuals as the controls despite having significantly higher $V_{ORT}$ and much greater task error.

### *Effects of practice and motor disorders studied with the UCM method*

Several studies have demonstrated that the method of the UCM hypothesis can be used to explore changes in motor coordination that accompany movement disorders, atypical development, aging, and practice. In particular, the mentioned
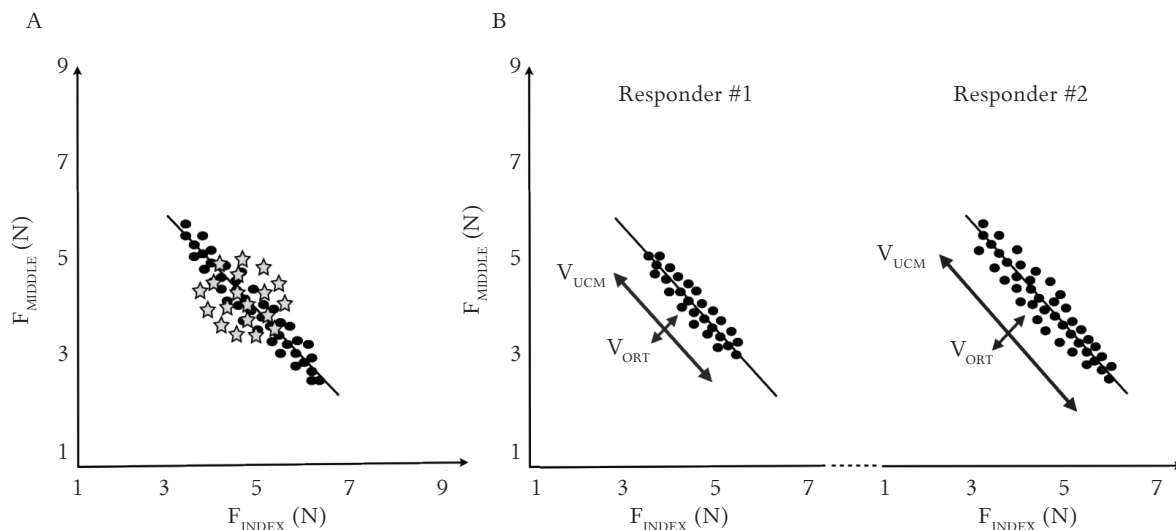
*Fig. 4.* In a two-finger force production task, independent control of each finger leads to uncorrelated variance across
epetitions (forming a circle, stars)
Negative covariation of finger forces decreases the total force variance. B. Comparison of the $V_{UCM}$ and $V_{ORT}$ components of variance
in two hypothetical first responders performing infant CPR. The often used synergy index (e.g., $[V_{UCM} - V_{ORT}] / [(V_{UCM} + V_{ORT})/2]$)
would result in a larger value for responder #2 than responder #1, despite the fact that $V_{ORT}$, the only variance component that can
lead to task level variance, is smaller for responder #1. The comparison emphasizes the need to examine each component of vari-
ance as well as any combined index when making conclusions about the usefulness of a synergy.

study of Reisman and Scholz (38) of hemiparetic
subjects after stroke documented similar indices of
multi-joint synergy (the relative amounts of $V_{UCM}$
and $V_{ORT}$ in the total joint configuration variance)
stabilizing the endpoint trajectory during reaching
movements by the affected arm (contralateral to
the stroke site) of the patients and similar move-
ments performed by healthy subjects. This unex-
pected result underscored the importance of ex-
ploring both variance indices, $V_{UCM}$ and $V_{ORT}$, in
clinical studies.

Persons with Down syndrome show low indi-
ces of multi-finger synergy in multi-finger accurate
force production tasks (56, 57). Then tend to show
positive co-variation of individual finger forces as if
they used the hand as a fork turned upside down
and scaled efforts of individual fingers in parallel.
However, a relatively brief training session led to a
significant improvement in accuracy of their per-
formance accompanied by an increase in the synergy
index and more flexible use of individual fingers of
the hand.

Elderly persons are known to show a decline in
the hand function over a range of everyday tasks.
This decline is accompanied by an impaired coor-
dination of the fingers reflected in lower indices of
synergies stabilizing total force and total moment of
force produced by the fingers (42, 58). A six-week
strength training protocol resulted in improved ac-
curacy of performance in force production tasks,
which correlated with an increase in the synergy in-
dex (59). Therefore, this study has shown that syn-

ergy index may be a predictive factor of accurate
performance.

Several studies of the effects of practice on syn-
ergy indices in young, healthy persons (60–62) have
suggested a two-stage process of performance im-
provement with practice. These stages correspond
to (1) discovery and strengthening of motor syner-
gies stabilizing salient performance variable(s); and
(2) their weakening when other aspects of motor
performance are optimized. Within the equilibri-
um-point hypothesis, the first stage may be viewed
as consisting of two steps, the elaboration of an
adequate referent configuration trajectory and the
elaboration of multi-joint (multi-muscle) syner-
gies stabilizing the referent configuration trajectory.
Both steps are expected to lead to more variance in
the space of elemental variables that is compatible
with a desired time profile of the salient perform-
ance variable ($V_{UCM}$). Adjusting control to other as-
pects of performance during the second stage (for
example, esthetics, energy expenditure, time, fa-
tigue, etc.) may lead to a drop in $V_{UCM}$.

**Concluding comments**

A few recent studies attempted to link the equi-
librium-point hypothesis, the principle of abun-
dance, and the uncontrolled manifold hypothesis
into a single, coherent scheme on how natural vol-
untary movements are produced. These involved a
theoretical study by Martin et al. (9) and two ex-
perimental studies (10, 55). These first attempts
show that creating such a coherent scheme based on

the reviewed hypothesis is feasible. Moreover, this seems to be the only currently available direction of research that promises success in achieving the main goal of motor control as stated in the Introduction: to create a formal description, operating with exactly defined variables, of the physical and physiological processes that make coordinated voluntary movements possible.

# Raumenų valdymo teorija bei jos pritaikymas

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**Raktažodžiai**: raumenų valdymas, pusiausvyrinio taško hipotezė, sinergija, nevaldomos įvairovės hipotezė, motorikos sutrikimai.

**Santrauka**. Straipsnyje analizuojama keletas hipotezių, turinčių įtakos raumenų valdymui, apimant pusiausvyros taško (atskaitinė konfiguracija) hipotezę, nekontroliuojamos įvairovės hipotezę bei sinergijos idėją, grindžiamą raumenų gausa.

Pusiausvyrinio taško hipotezė grindžiama neuroninių baseinų aktyvacijos slenksčio valdymo teorija, kuri sudaro galimybę tirti tiek valingus, tiek nevalingus judesius. Atskiro raumens valdymas gali būti aprašomas raumens aktyvacijos slenksčio pokyčiais lėto raumens ilgėjimo metu (toninio ištempimo reflekso slenkstis). Kitaip nei vidiniai modeliai pusiausvyrinio taško hipotezė neapima nervų funkcijos vertinimų, apskaičiuojamų mechaninių kintamųjų.

Nevaldomos įvairovės hipotezė grindžiama dinaminių sistemų pritaikymu judėjimui. Ji siūlo rinkinį įrankių, galinčių analizuoti sinerginius pokyčius perteklinių elementų tinkle, susijusių su stabilizacija potencialiai svarbių judesio atlikimo kintamųjų. Atskaitinės konfiguracijos hipotezę ir perteklinis principas natūraliai gali būti sujungti į paprastą koherentišką schemą, valdančią daugiaelementines sistemas. Gauti eksperimentiniai sveikų asmenų ir pacientų, turinčių judėjimo sistemos sutrikimų, duomenys apžvelgiami siekiant pagrįsti minėtas hipotezes. Pastebima, jog judėjimo sutrikimai, susiję su raumenų spazmais, įvardijami kaip pasekmė ribotų galimybių pakeisti toninės įtampos reflekso slenkstį normaliu dydžiu. Aprašomos techninės detalės ir minėtų hipotezių pritaikymas tiriant judesių mokymo fenomenus. Apžvelgėme hipotezes kaip daugiausia turinčias įtakos raumenų valdymui, pagrįstas motyvuotais fizikiniais ir neurofiziologiniais pagrindais.

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