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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.

Keywords

Motor control; equilibrium-point hypothesis; synergy; uncontrolled manifold hypothesis; motor disorders

1. 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 (see Gelfand & Latash 1998).

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. But 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 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 (MLL) graduated some 30+ years ago from the Moscow Institute of Physics and Technology, and his major was indeed the non-existing *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 (Bernstein 1967): 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, Feldman 1966, 1986, 2007), 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 (Schöner 1995; Scholz & Schöner 1999), which, in combination with the principle of abundance (Gelfand & Latash 1998, 2002), suggest 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 (Martin et al. 2009; Latash et al. 2010).

2. 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 1960’s and 70’s. 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 formulation 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 (Feldman, in press). 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 pre-loaded arm (the unloading reflex), *voluntary changes* in the joint angle, and *full relaxation* of the elbow muscles while they were stretched, Asatryan and Feldman (1965) identified invariant and modifiable neurophysiological variables involved in these motor actions.

Involuntary behaviour 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 non-linear 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 non-linearly 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 differences 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 *threshold angles* were different for different characteristics (Fig. 1). From these experiments, Asatryan and Feldman (1965) 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 position, 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

muscles could remain silent in the entire biomechanical range of the elbow joint angle. In contrast, to fully activate the muscle, even at the shortest muscle 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, vertical segments near EPs), in accordance with the known EMG-force relationship (Bigland & Lippold 1954). 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 (Levin and Feldman 1994). Instead of using an unloading 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 velocities and extrapolate these value to zero velocity to estimate the TSRT (Levin 2000). In non-disabled individuals, DSRTs can usually only be evoked in muscles at rest if the stretch is performed at a high velocity ($> 300^\circ/\text{s}$; Levin 2000; Thilmann et al. 1991; Fig. 2, dashed diagonal line). However, in adults with stroke and children with CP, muscles stretches at speeds as low as $8^\circ/\text{s}$, applied 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 inversely correlated with the degree of clinical spasticity (i.e. the lower the TSRT the higher the spasticity); 3) the TSRT is a better measure of spasticity than the gain of the stretch reflex (Levin 2000; Jobin & Levin 2000).

Jobin and Levin (2000) 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 between 8 and $160^\circ/\text{s}$ 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 $0^\circ/\text{s}$ was extrapolated. For the *elbow flexors*, TSRTs expressed in angular coordinates occurred later (closer to full elbow extension) for slow velocities of stretch compared to fast velocities of stretch. The test-retest reliability of the computed TSRTs was estimated to be good ($\text{ICC}=0.73$, $p<0.001$). 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 co-activation (Levin et al. 2000). Also, 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.

3. The concept of the uncontrolled manifold

A general principle of movement generation in organisms is what Gelfand and Latash (1998) 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 (Bernstein 1967) 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 (Rosenbaum 1980). 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 (Erlhagen & Schöner 2002). 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 (Georgopolous et al. 1982, 1992). These tuning curves may depend also on joint configuration (Scott & Kalaska 1995), but largely retain their uniform shape, again suggesting an account in terms of this spatial parameter.

Many different mechanism seem to be involved in controlling the timing of movements, from spinal pattern generators, cerebellar estimators, to cortical mechanisms (Ivry et al. 2004). 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 (Schöner & Kelso 1988). 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 ("anti-phase") becomes unstable for higher movement frequencies, leading to a switch to the in-phase pattern. Although it is tempting to think of the mechanisms that establish stable patterns of coordination as residing at a level close to the neural control of the effectors (Grossberg et al. 1997), it turns out that this is not appropriate. In a series of elegant experiments, Mechsner and colleagues (2001) exploited the instability of anti-phase to establish whether anti-phase 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 anti-

phase 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 Zatsiorsky 1998). 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 (Morasso 1981). Although spatial representations of movement seem to capture more of the simplicity and invariance (Lacquaniti 1989), 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 (Won & Hogan 1995). 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). So 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 (Schöner 1995; Scholz & Schöner 1999; Latash et al. 2007). 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 (e.g., Scholz et al. 2000; Tseng et al. 2002). The ideas have been generalized to the control of isometrical force generation by the fingers of the hand (e.g., Latash et al., 2002) as well as to the control of muscular activation to achieve particular location of the center of pressure by a standing person (Krishnamoorthy et al., 2003). 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 mechanically? A theoretical model (Martin et al. 2009; see also Goodman & Latash, 2006 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.

4. Practical applications of the uncontrolled manifold theory

The UCM approach (Scholz & Schöner 1999) has proven to be a powerful tool to investigate the flexibility/stability aspect of synergies (Latash et al. 2007). This has been performed in a variety of contexts, including reaching (Reisman & Scholz 2003; Tseng & Scholz 2005; Tseng et al. 2002), finger force production (Latash et al 2001, 2002; Li et al 1998; Olafsdottir et al. 2007; Shim et al. 2003; Zhang et al. 2008), and postural control (Freitas et al. 2006; Hsu et al. 2007; Krishnamoorthy et al. 2003, 2004, 2007; Reisman et al 2002a; Scholz et al. 2001) 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 (Reisman & Scholz 2006). 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 Figure 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 (Hsu et al. 2007).

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 (Scholz & Schöner 1999). 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 (Tseng & Scholz 2005). This allows computing the Jacobian of the system that allows to represent 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 (Krishnamoorthy et al. 2003, 2004, 2007). 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 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 (Krishnamoorthy et al. 2003, 2004). 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 (Freitas & Scholz 2010; Freitas et al. 2010), 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 example, reaching with the hand, from an initial position where the forearm rests on a table, elbow flexed to 90° , 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 include. 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 (Scholz & Schöner 1999). 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 (Reisman et al. 2002b).

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. (2010).

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 (Gorniak et al. 2007, 2009b), 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 heart beat 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 Figure 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 (2003) 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 study of Reisman and Scholz (2003) 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 movements performed by healthy subjects. This unexpected result underscored the importance of exploring both variance indices, V_{UCM} and V_{ORT} , in clinical studies.

Persons with Down syndrome show low indices of multi-finger synergy in multi-finger accurate force production tasks (Latash et al. 2002b; Scholz et al. 2003). 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 performance 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 coordination of the fingers reflected in lower indices of synergies stabilizing total force and total moment of force produced by the fingers (Shinohara et al. 2004; Olafsdottir et al. 2007). A six-week strength training protocol resulted in improved accuracy of performance in force production tasks which correlated with an increase in the synergy index (Olafsdottir et al. 2008). So, this study has shown that synergy index may be a predictive factor of accurate performance.

Several studies of the effects of practice on synergy indices in young, healthy persons (Latash et al. 2003; Kang et al. 2004; reviewed in Latash 2010) have suggested a two-stage process of performance improvement with practice. These stages correspond to (1) discovery and strengthening of motor synergies stabilizing salient performance variable(s); and (2) their weakening when other aspects of motor performance are optimized. Within the equilibrium-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) synergies 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 performance variable (V_{UCM}). Adjusting control to other aspects of performance during the second stage (for example, esthetics, energy expenditure, time, fatigue, etc.) may lead to a drop in V_{UCM} .

5. Concluding Comments

A few recent studies attempted to link the equilibrium-point hypothesis, the principle of abundance, and the uncontrolled manifold hypothesis into a single, coherent scheme on how natural voluntary movements are produced. These involved a theoretical study by Martin et al. (2009) and two experimental studies (Gorniak et al. 2009b; Latash et al. 2010). 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.

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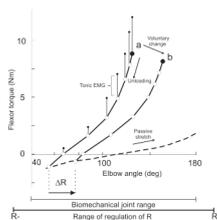


Figure 1.

Three experimental procedures leading to the notion that central shifts in the threshold position (R) underlie voluntary motor actions. Procedures include: involuntary motor action – unloading reflex – resulting from sudden unloading of the forearm to different final equilibrium points (EPs, open circles) of pre-loaded elbow flexors from an initial EP (filled circle, a); voluntary motor 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 (vertical 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). Therefore, 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.

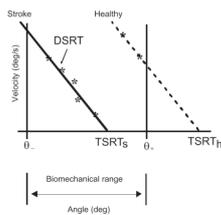


Figure 2. Schematic illustration of tonic stretch reflex thresholds (TSRT) determined by extrapolation of a linear regression line through dynamic stretch reflex thresholds (DSRTs). DSRTs are evoked by stretching elbow flexors at different velocities. In healthy subjects, DRSTs can only be evoked by high velocity stretches and the TSRT lies beyond the biomechanical range of the joint (TSRT_h). In patients with spasticity, DSRTs occur earlier (at smaller joint angles), and the TSRTs lies within the biomechanical range of the joint.

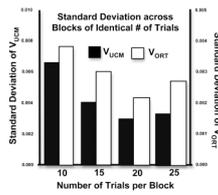


Figure 3. Standard deviation of variance components, V_{UCM} and V_{ORT} across five blocks of 10, 15, 20, or 25 trials. Variance is computed as rad^2 per dimension of each subspace. Trials were randomly selected from a group of 50 trials collected for this subject. The largest reduction in standard deviation occurs between 10 and 15 trials.

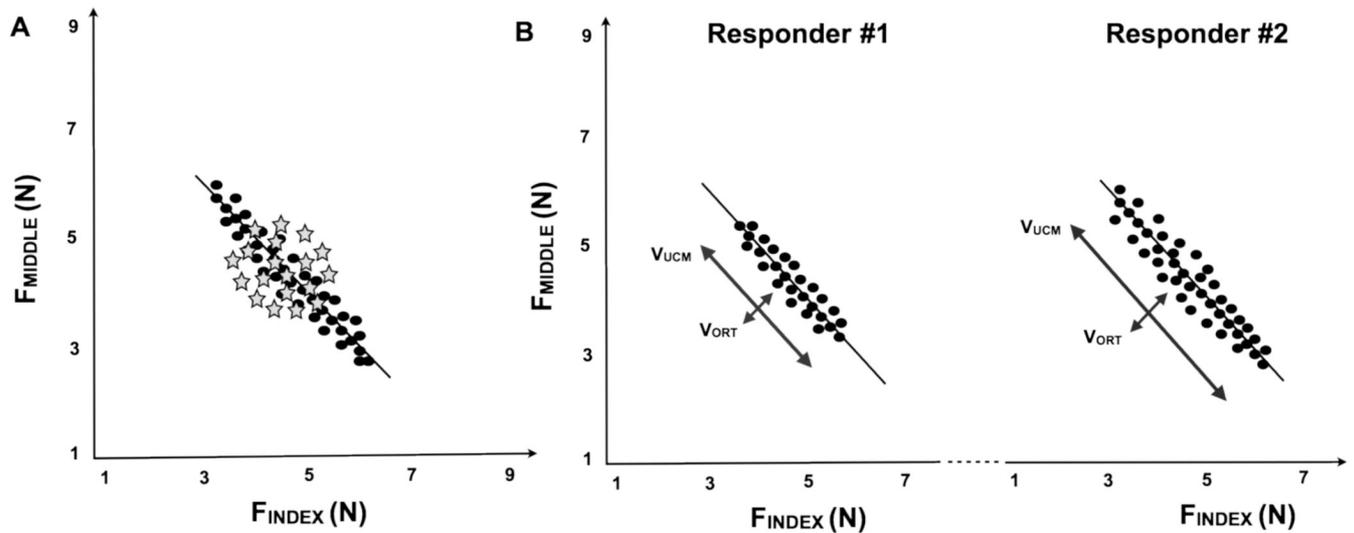


Figure 4.

In a two-finger force production task, independent control of each finger leads to uncorrelated variance across repetitions (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 variance as well as any combined index when making conclusions about the usefulness of a synergy.