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Brief History of the Uncontrolled Manifold Hypothesis and Its Role in Motor Control

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HIGHLIGHTS

- The concept of uncontrolled manifold is readily compatible with the principle of abundance
- The UCM concept can be applied to different effectors from a muscle to the whole body
- The UCM concept offers insightful applications to movement disorders
- This concept requires generalization to spaces of neural control variables

ABBREVIATIONS

ASAs	Anticipatory synergy adjustments
ASA_{SS}	Steady-State ASA
ASA_{TR}	Transient ASA
C-	Coactivation command
E_1	Elemental variable 1
E_2	Elemental variable 2
Fx	Effector producing force
J	Jacobian matrix
k	Apparent stiffness
ME	Motor equivalent
ORT	Orthogonal
PD	Parkinson's disease
R-	Reciprocal command
RC	Reference Coordinates
UCM	Uncontrolled manifold
VF	Virtual finger
V_{UCM}	Inter-trial variance components along the UCM
V_{ORT}	Inter-trial variance components along the ORT
X	Spatial coordinate
ΔV	Synergy index

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BACKGROUND: The apparent problem of motor redundancy was replaced by the principle of abundance and turned into a theoretical framework and associated toolbox for exploration of performance-stabilizing synergies.
AIM and METHOD: We review briefly the development of the main methods within the UCM framework and some of the main findings, both basic and clinical. The UCM framework is naturally merged with the theory of hierarchical movement control with spatial referent coordinates.
RESULTS: The UCM framework has established itself as a productive framework for the analysis of movement control, in particular as related to stability of salient performance variables. It led to the discovery of novel phenomena such as trade-offs within hierarchical systems, anticipatory synergy adjustments, synergies within systems of different complexity from single muscles to the whole body. It has also led to promising results offering sensitive biomarkers to various neurological disorders. Recent experiments suggest the existence of three main levels of organization of performance-stabilizing synergies tentatively associated with cortical, subcortical, and spinal circuitry.
CONCLUSION: Currently, this approach is in its adulthood. Further progress may be expected in focusing on spaces of neural control variables, developing the method for analysis across species, and expanding the range and depth of clinical studies.

KEYWORDS: Abundance | Stability | Synergy | Referent coordinate | Hierarchy

"To the memory of John P. Scholz – A friend, a gentleman, and a scientist"

LIFE BEFORE UCM

It is hard to believe that a quarter of a century has passed since the seminal publication by John Scholz and Gregor Schöner in 1999 [1] inaugurating the uncontrolled manifold (UCM) hypothesis. The origins of this hypothesis can be traced back to the classical study of Nikolai Bernstein [2] of professional blacksmiths who performed their labor movement – hitting the chisel with the hammer – multiple times. Bernstein quantified the trajectories of the tip of the hammer and of individual arm joints and claimed that the former showed the smallest inter-trial variability. Since, clearly, the brain could only send signals to muscles crossing the joints, not to the hammer, the result implied that the joints compensated for each other errors (deviations from the mean trajectories) across trials to keep the hammer trajectory relatively consistent. In 1994, we discussed with Gregor Schöner how Bernstein could compare variability of the tip of the hammer measured in spatial Euclidian coordinates with variability in the joint space measured in angular units. Clearly, some kind of mapping between these two spaces was necessary to reach the main Bernstein conclusion. The necessity of such mapping was explicitly formulated by Gregor Schöner in a paper published in 1995 [3].

The general idea of *error compensation* among effectors had been expressed in several studies preceding the introduction of the UCM concept. Such studies involved either external perturbations applied to one or a few of the effectors or self-generated actions perturbing the salient task-specific variable, or simply repetitive movements without any explicit perturbations. They explored a range of actions including speech [4], precision grip [5], multi-joint pointing [6], and multi-finger accurate force production [7]. All the mentioned studies have shown that task-specific performance variables could show relatively small deviations in the presence of relatively large changes in the contributions of elements (digits, joints, articulators, etc.).

For many years, general theoretical conceptualization of the phenomena of error compensation has been elusive. One of the problems can be traced back to another important contribution by Bernstein, his formulation of the problem of motor redundancy. In any action, multiple elements are involved at different levels of analysis (joints, digits, muscles, articulators, etc.), producing a large number of elemental variables, more than the number of task constraints. In any given realization, a specific combination of the elemental variables is observed. How does the brain select those specific combinations from the infinite number of solutions? Bernstein viewed this as a central problem of motor control and saw the solution in the *elimination of redundant degrees-of-freedom* [8] (see also [9]). This view dominated the field for decades leading to the development and application of the concept of optimization to voluntary movements (reviewed in [10-12]).

At closer examination, the problem of motor redundancy seems to be ill-formulated (reviewed in [13-15]). It is not inherent to the neural control of movement but reflects specific levels of analysis selected by individual researchers. For example, the problem of pressing with a finger and producing a certain force level is non-redundant at the finger level (in contrast, for example, to the same task performed while pressing with four fingers). The same problem is redundant at the level of muscle involvement. Another example: Muscle co-contraction has been viewed as a means of alleviating the problem of motor redundancy at the joint configuration level by “freezing” joints (cf. [16]), while it obviously leads to making this problem worse at the level of muscle activation. Assuming that this problem is inherent to brain processes involved in the neural control of movement requires committing to a motor control theory. We will return to this issue based on the theory of control with spatial referent coordinates (reviewed in [17]), a development of the equilibrium-point hypothesis [18,19].

An alternative view on the apparent excess of elemental variables was suggested as the *principle of abundance* [13,20]. According to this principle, the numerous elemental variables (at all levels) are not sources of computational problems for the brain but important parts of mechanisms that allow to provide desired degree of dynamical stability for salient task-specific performance variables. This idea was implied in the formulation of the UCM hypothesis: No degrees-of-freedom are ever eliminated, they are all used to provide dynamical stability of performance. Note that both features, addressing the problem of motor redundancy and ensuring dynamical stability of performance, have been discussed by Bernstein as originating at the same level of movement construction, the *Level of Synergies*. This term comes from a Greek word combination meaning “work together”, and it has been used for ages in numerous fields from theology to motor control. Further, we will use the term synergy to address both aspects, grouping of elements at the selected level of analysis and covariation of elemental variables contributing to stability of performance (reviewed in [8,15]).

THE UCM-BASED TOOLBOX

Formal analysis of synergies, within the UCM framework, starts with defining mapping between the spaces of elemental variables (those produced by elements at the selected level of analysis) and a potentially important performance variable, which can be multi-dimensional. In a linear approximation, this has been done using the matrix of partial derivatives of the selected performance variable with respect to the elemental variables, i.e., the Jacobian matrix (**J**). It is assumed that the average across repetitive trials value (time series) of the performance variable represents its desired value (time series), and that deviations from this value are reflections of its imperfect stability under the action of unpredictable factors, both extrinsic and intrinsic. It is also assumed that the average point (time series) in the multi-dimensional space of elemental variables represents a preferred solution for the problem of producing the performance variable. Further, for any given value of the performance variable, a solution subspace (the UCM) is approximated as the null-space of the **J**, i.e., a subspace where small deviations of elemental variables have no effect on the performance variable.

Figure 1 illustrates a simple task of producing a desired value of the sum of two elemental variables (E_1 and E_2). The **J** matrix for this task is [1 1], and its null-space is shown as the slanted line corresponding to the equation $E_1 + E_2 = C$. An average across multiple trials solution is shown as the black point. The thin lines show potential fields along the UCM and along the orthogonal to the UCM subspace (ORT) illustrating that the ORT direction shows higher stability as compared to the UCM.

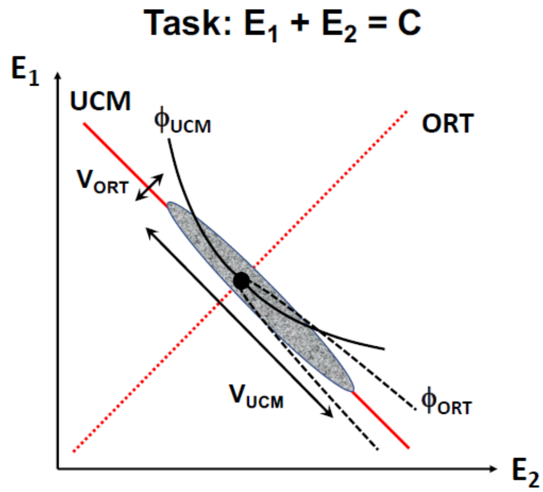

Figure 1. A schematic illustration of a task of producing a constant value of the sum of two elemental variables (E1 + E2 = C). The solutions space is shown as the solid slanted line. An average across multiple trials solutions is shown as the black point. The curved lines show potential fields along the UCM and along the orthogonal to the UCM subspace (ORT), ΦUCM and ΦORT. Note that variance along the UCM is larger than along the ORT ($V_{UCM} > V_{ORT}$).

The most commonly used method of analysis has compared inter-trial variance components along the UCM and along ORT, V_{UCM} and V_{ORT}, normalized per dimension in each subspace. It has been assumed that, if the selected performance variable is stabilized by some neural mechanisms, V_{UCM} is expected to be larger than V_{ORT}, i.e., the unavoidable inter-trial variance is channeled into the space where deviations of elemental variables have no effect on the performance variable. Commonly, the two metrics, V_{UCM} and V_{ORT}, have been combined into a single metric, a synergy index (ΔV) reflecting the relative amounts of the two variance components in the total amount of variance in the space of elemental variables. V_{UCM} has been addressed informally as “good variance” because large amounts of V_{UCM} both reflect stability of the salient performance variable and allow performing secondary tasks with the same set of elemental variables without detrimental effects on that salient performance variable.

Another method quantified and compared deviations within UCM and ORT following a brief action or a quick response to an external perturbation. Deviations within the UCM are motor equivalent (ME) in a sense that they, by definition, lead to no change in the salient performance variable. In other words, these deviations are wasteful if the task is to change the performance variable quickly and efficiently, for example with minimal expenditure of metabolic energy – a common currency within the body (cf. [21]) and a commonly used cost function within optimization approaches [11,22,23]. A number of studies have shown that quick corrections of actions in response to unexpected perturbations have very large ME components as compared to the non-ME components, which are required to produce corrections [24-26]. These apparently wasteful components of actions have been interpreted as consequences of much lower stability along the UCM.

The two pairs of outcome variables, {V_{UCM}; V_{ORT}} and {ME; non-ME}, are expected to correlate if the data are sampled from a single distribution (cf. [27]). Such correlations have indeed been shown in experiments [28], although not without exceptions [29], The exceptions have been interpreted as consequences of intentional corrections by the subjects resulting in sampling from different distributions. The relative usefulness of the two pairs of metrics remains to be explored in detail. In particular, the number of trials to reach a criterion of statistical robustness is smaller for {ME; non-ME} as compared to {V_{UCM}; V_{ORT}} [30] making quantification of motor equivalence attractive in clinical studies when participants may not be able to perform multiple trials per conditions to allow estimation of the variance indices.

APPLICATIONS TO SPACES OF MECHANICAL AND ELECTROPHYSIOLOGICAL VARIABLES

Early studies applied the analysis of variance within the UCM framework to spaces of kinematic [1,31] and kinetic [32,33] elemental variables. These applications were relatively straightforward since the **J** matrix could be computed from the configuration of the effector. There were, however, hidden problems. Drawing conclusion relevant to the neural control of movement based on results of such studies assumes that, in the absence of a special control process, the data distributions are expected to be spherical. This is far from being obvious. For example, the presence of biarticular and multi-articular muscles and inter-joint reflexes makes joint rotations coupled. So, analysis in a joint configuration space may be expected to produce non-spherical data distributions in the absence of any specific synergies. By chance, such distributions can be elongated along the UCM computed for a performance variable or orthogonal to it leading to spurious conclusions. How practically important are these factors? In particular, can humans move one joint at a time? There are no data answering these questions. The situation is even more complicated for analysis in spaces of segmental angles because, obviously, moving a single proximal joint alone leads to changes in the segmental angles of all the more distal segments. These built-in covariations may also lead to spurious conclusions. It is better to avoid analysis in spaces where unavoidable covariation of elemental variables is produced by peripheral, including biomechanical, factors.

The situation becomes even more complicated in the analysis of multi-digit actions because of the phenomenon of enslaving [34], which makes digit forces non-independent. Originally, to account for finger enslaving, finger forces were transformed into *modes*, hypothetical central variables that could be manipulated by the brain one at a time [32,35]. Such analyses implied that enslaving was a robust phenomenon and, after being defined on a set of tasks, it could be applied to other tasks. Recent studies have shown, however, that enslaving tends to drift (increase) with time during constant finger force production tasks [36,37]. Whether using finger modes should be preferred as compared to analysis in finger force spaces remains an open issue.

Application of the UCM framework to spaces of electrophysiological variables, such as EMG indices, led to the emergence of an auxiliary toolbox. It would be naïve to assume that the brain manipulates a set of neural variables directed at individual muscles. So, the first step in those studies has been defining muscle groups that show parallel changes in the activation levels of individual muscles. This has been done with the help of various matrix factorization methods, in particular the principal component analysis, which leads to a set of orthogonal eigenvectors – an advantage for further normalization of the variance indices. Such groups have been addressed with various terms such as factors, primitives, modes, and synergies. Further, since the mapping between indices of EMG (such as mV or mVs) and mechanical variables directly relevant to the task is typically unknown, the only practical approach has been to discover the **J** matrix using experimental data, commonly with the help of multiple linear regression techniques [38,39]. Relatively recently, the UCM-based analysis has been applied to studies of performance-stabilizing synergies in spaces of firing frequencies of individual motor units within a muscle and across agonist-antagonist muscle pairs [40] (reviewed in [41]). Both features of synergies were demonstrated: Grouping motor units into a small number of groups (MU-modes) and stabilization of the task-specific performance variable organized in the spaces of MU-modes, i.e., $V_{UCM} > V_{ORT}$.

APPLICATIONS TO SPACES OF HYPOTHETICAL CONTROL VARIABLES

All the aforementioned studies analyzed inter-trial variance and/or motor equivalence in spaces of peripheral elemental variables. This has always been a potential weakness of the approach because peripheral mechanical and muscle activation variables cannot in principle be prescribed by the brain as emphasized by many researchers starting with Bernstein [8]. In particular, the discovered patterns could be consequences of correlated changes in the reflex contributions to muscle activation levels. To extend the method to spaces of control variables, one had to commit to a theory of motor control, which specifies such variables explicitly. This has been done within the framework of the theory of control with spatial referent coordinates (RCs, linear or angular; reviewed in [17,42]). Within this framework, the control of any effector can be described with two basic commands, the reciprocal command (*R*-command) and coactivation command (*C*-command). The *R*-command defines spatial coordinate where the net force by the agonist and antagonist muscles is zero, i.e., its RC. The *C*-command defines the range where both agonist and antagonist muscles are active simultaneously. This is illustrated in Figure 2 for an effector producing force F_X along a spatial coordinate X. Note that, at the level of mechanics, changing the *C*-command leads to changes in the shape of the resultant $F_X(X)$ characteristic or, in a linear approximation, the apparent stiffness (k) of the effector (cf. [43]).

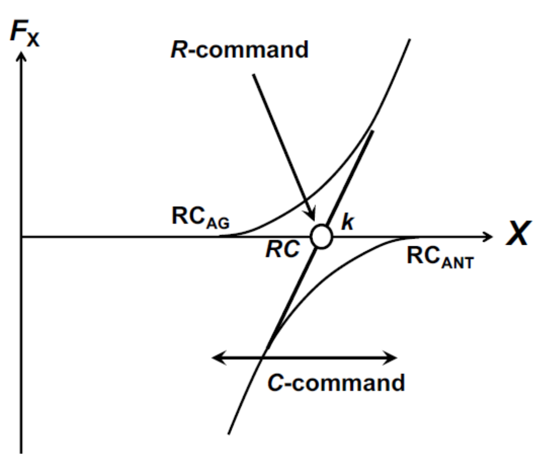

Figure 2. An effector produces force F_X along a spatial coordinate X. The thin curves show force-coordinate characteristics for two opposing muscles, agonist (positive force values) and antagonist (negative force values). They were addressed as “invariant characteristics” in the original publications [18,19]. The agonist and antagonist muscle groups are controlled by setting referent coordinates, RC_{AG} and RC_{ANT}. At the level of mechanics, changing the *R*-command leads to shifts in the RC for the effector. Changes in the *C*-command leads, in a linear approximation, to changes in the apparent stiffness (k) of the effector.

The presence of the two basic commands makes the control of any effector abundant with a possibility of performance-stabilizing synergies. However, the two commands are not directly measurable, and so far, studies of synergies at the level of control have been limited to using mechanical proxies of the two commands, the intercept and slope of the $F_X(X)$ characteristic. Such studies have been informative showing performance-stabilizing synergies for different effectors, from single fingers to the whole body [44,45]. The UCM in the {RC; *k*} space stabilizing force by an effector is typically hyperbolic and does not allow linearization. This has been another problem preventing researchers from using analysis of inter-trial variance. Instead, hyperbolic regression and randomization methods (cf. [46]) have been used to quantify synergies in the {RC; *k* } space.

The concept of control with spatial RCs can be applied to different effectors, from the whole body to individual muscles and motor units (reviewed in [14,42]). Figure 3 illustrates a hypothetical hierarchy involved in the control of a multi-joint effector. Note that the dimensionality of control increases from the task level down to the levels of specific effectors, joints, digits, muscles, and motor units. These few-to-many transformations afford the possibility of organizing synergies stabilizing higher-level control variables by co-varied involvement of lower-level variables. This can potentially be based on feedback loops from peripheral sensory endings as well as those within the central nervous system shown by arrows. The scheme in Figure 3 has to be taken with a big grain of salt. It is motivated by the anatomy of the human body, and some of the levels may be apparent, not real. For example, a study of spino-cerebellar pathways in cats has shown modulation of those signals not with joint angles, which have dedicated sensors, but with higher-order variables such as "leg length" and "leg orientation", which do not have dedicated sensors [47].

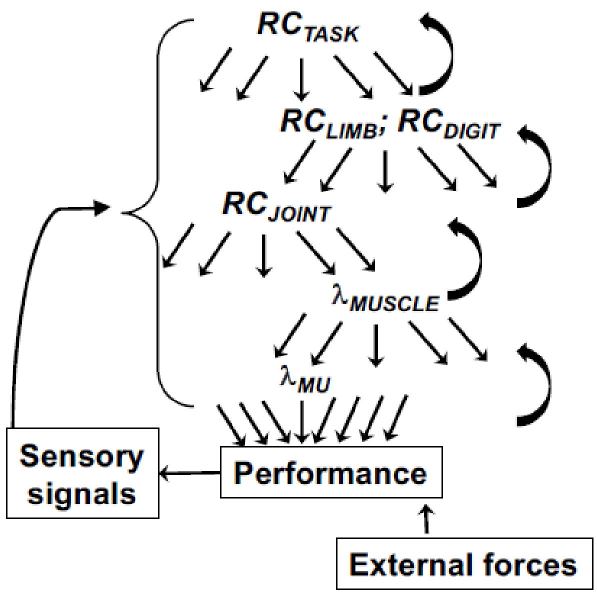

Figure 3. A schematic illustration of the control in a hierarchy involved in the control of an effector. Note that the dimensionality of control (referent coordinates, RC) increases from the task level down to the levels of specific joints, digits, muscles, and motor units. Back-coupling loops stabilizing behavior from peripheral sensory endings and within the central nervous system are shown with arrows.

The relations between the theory of control with RCs and the UCM-based concept of synergy are non-trivial. On the one hand, within the hierarchical scheme in Figure 3, synergies stabilizing performance variables desired by the actor and indirectly encoded in the low-dimensional task-level RC time functions can be organized using feedback loops both within the central nervous system, from abundant sets of lower-level RC time functions, and from peripheral sensory endings. On the other hand, what matters for the actor is stability of salient performance variable, not necessarily its source. So, it is possible that peripheral factors, including anatomical and biomechanical ones, may drive covariations of elemental variables stabilizing performance with minimal contribution from the neural control levels. In most cited studies, it has been assumed that action stability is primarily a function of the neural control, i.e., of the RC hierarchy, but the role of peripheral factors remains relatively underexplored.

The organization of synergic control in a hierarchical system is non-trivial. Indeed, consider only two levels of a hierarchy (Figure 4). To have a synergy stabilizing performance at the upper level, V_{UCM} has to be relatively large, which requires relatively large inter-trial variance of the elements. At the lower level, variance of each of the elements is, by definition, V_{ORT}. This large V_{ORT} requires very large V_{UCM} to ensure synergic control. This may be problematic, although not impossible. A study of two-hand, multi-finger pressing tasks showed that, indeed, in such tasks no synergies were seen stabilizing the contribution of each individual hand, while there were strong synergies at the two-hand level [48]. During prehensile tasks performed using the prismatic grip – the thumb opposing the four fingers – the control is commonly viewed as hierarchical. At the top level, the task is shared between the thumb and "virtual finger" (VF, an imagined digit with the force/moment vector equal to the summed vectors of the individual fingers, [49]). At the lower level, the VF action is shared among the four actual fingers. A study of synergies stabilizing force and moment components has shown that some of them were stabilized at one level only, while others – at both levels [50]. Such studies may be useful as windows into the salient control levels, which may differ from the apparent anatomy-based levels shown in Figure 4.

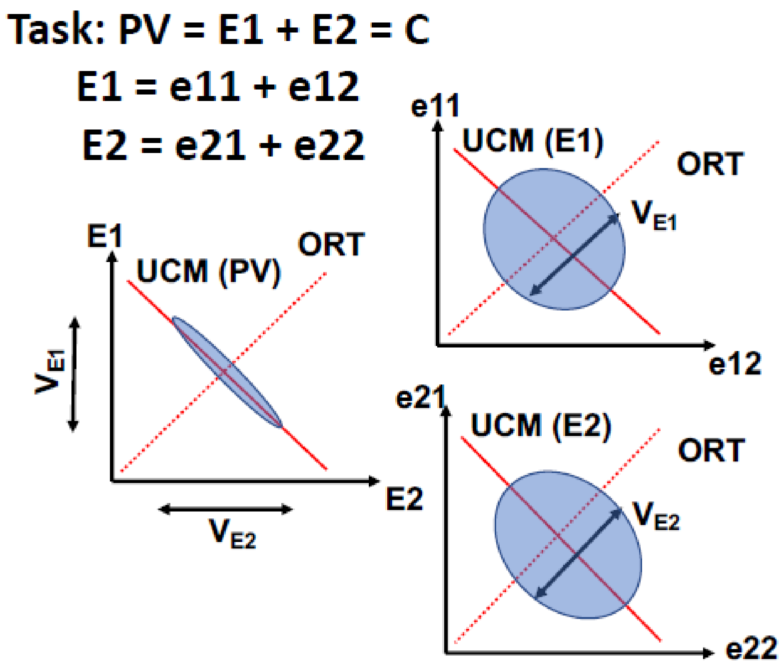

Figure 4. Consider the task of keeping constant the sum of two effectors (E1 and E2), when the output of each effector is the sum of two lower-level effectors, e11 + e12 and e21 + e22. A synergy stabilizing performance implies large VUCM, which requires large inter-trial variance of the elements, V_{E1} and V_{E2}. At the lower level, variance of each of the elements is, by definition, VORT. This creates a problem for arranging synergies at both levels.

ANTICIPATORY CHANGES IN ACTION STABILITY

The UCM-based method of analysis of stability has led to several discoveries. Some of them have already been mentioned. Here we address a group of phenomena related to anticipation in motor behavior. High stability of salient variables may be functionally important during steady-state or slow actions. If one wants to change a performance variable quickly, strong synergies stabilizing this variable become counter-productive. This has been discussed in detail as a stability-agility trade-off (reviewed in [51]). Evolutionary success required controlled stability of action, and a number of studies have shown that humans can adjust action stability independently of other action characteristics, as seen, for example, in average across trials performance. These phenomena have been addressed as anticipatory synergy adjustments (ASAs, reviewed in [14,15]).

There are two types of ASAs. The first is associated with a drop in the index of performance-stabilizing synergy seen in young healthy persons 300±100 ms prior to a self-initiated quick action or reaction to a predictable perturbation [52,53]. The second type represents a drop in the synergy index (the normalized difference between V_{UCM} and V_{ORT}) during steady-state performance under conditions that a quick action or a change in the ongoing action may be required at an unpredictable time in future or in only some of the trials [54-56]. These have been labeled as transient ASAs (ASA_{TR}) and steady-state ASAs (ASA_{SS}), respectively. They are illustrated in Figure 5 using the earlier example of two elements contributing to a common task. Panel A shows the task of producing a constant output with a possibility of unexpected changes in the output magnitude followed by a self-initiation quick change in (E_1 + E_2). Panel B shows cartoon inter-trial distributions of the data points for a steady-state action in the absence of any changes in performance, during steady-state when an unexpected target could emerge, and prior to the self-initiated quick change in (E_1 + E_2). Panel C illustrates the same data assuming that stability of action reflects depth of a potential field.

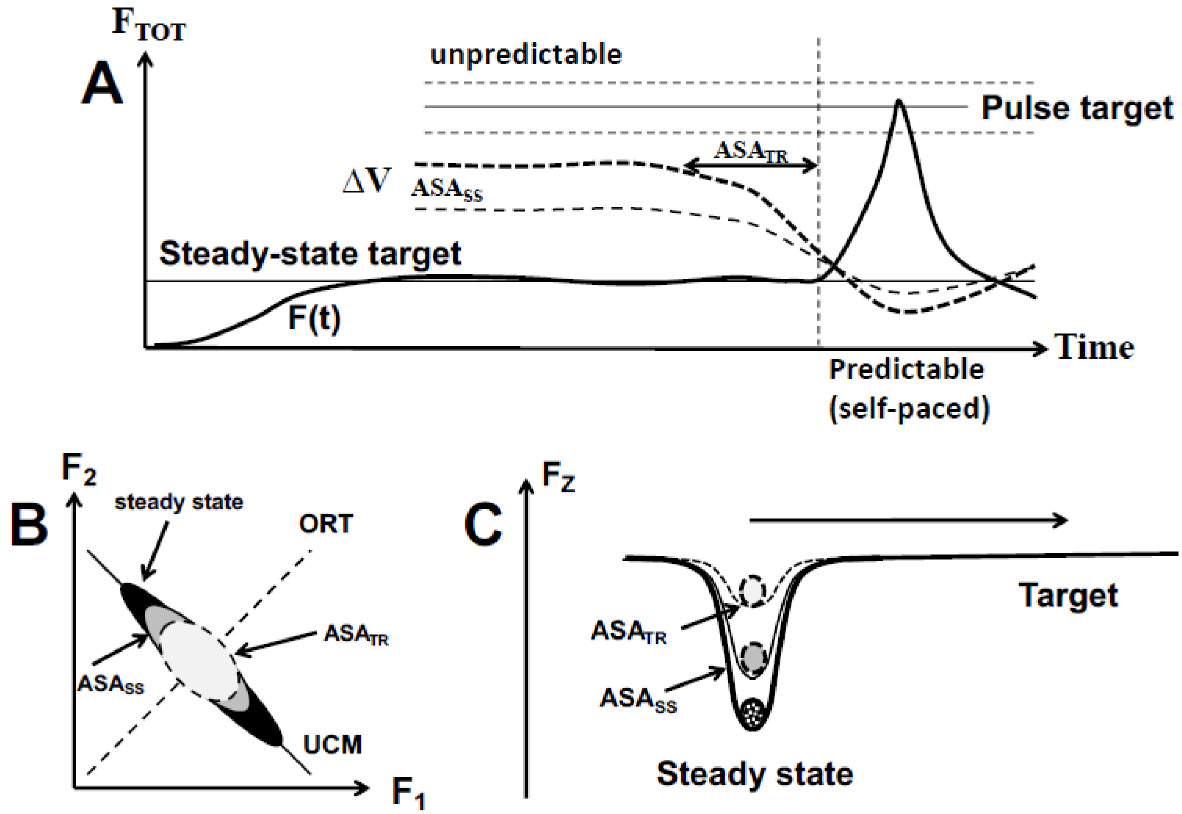

Figure 5. A: The task of producing a constant output of two elements (E1 + E2 = C) with a possibility of unexpected changes in the output magnitude followed by a self-initiation quick change in (E_1 + E_2). B: Inter-trial distributions of the data points for a steady-state action in the absence of any changes in performance (the dark ellipse), when an unexpected target could emerge (the lighter ellipse), and prior to the self-initiated quick action (the very light ellipse). C: An illustration of the same data assuming that stability of action reflects depth of a potential field, Φ.

ASA_{SS} can be seen with the naked eye in some athletic competitions. For example, a tennis player getting ready for a powerful serve and a goalkeeper preparing for a penalty shot both show visibly increased postural sway reflecting a decrease in postural stability. This facilitates the initiation of a fast action independently of its direction. Relative invariance of ASA_{TR} to action direction has also been shown experimentally [57].

Theoretically, a drop in the synergy index may be due to an increase in V_{ORT} and/or a drop in V_{UCM}; both scenarios have been documented in the mentioned papers. Recently, sensitivity of both ASA_{TR} and ASA_{SS} to speed of a future action has been documented [58]: Both types of ASAs become smaller and may even disappear when the planned upcoming action is slower as compared to very fast actions used in most of the earlier studies. This is potentially an important finding for clinical applications when control participants typically are able to perform faster actions as compared to groups of patients with impaired neural control of movements. We will return to clinical applications of ASA indices a bit later.

WHERE DOES THE UCM COME FROM?

While the UCM concept and associated methods of analysis involve computational steps, these computations have not been assumed to happen within the central nervous system, only in the minds of the researchers. Just like equations in classical physics involve computations, these are never assumed to reside in the objects to which they apply. From the very beginning, the controlled stability of actions has been assumed to reflect physical (including physiological) processes within the body. The most developed accounts for the UCM concept have been developed by the group of Gregor Schöner [59,60], which also incorporate the ideas of control with spatial RCs. While the mapping between the assumed processes and neurophysiological structures remains speculative, the basic ideas of back-coupling and the role of feedback circuits within the central nervous system and from peripheral receptors are important for conceptualization of the UCM.

In particular, an important role of short-latency feedback circuits in ensuring stability of actions has been suggested nearly twenty years ago [61]. Recent studies of intra-muscle synergies corroborate this idea and suggest that intra-spinal and reflex-based circuits contribute to movement stability across tasks and effectors (reviewed in [51]) in addition to supraspinal synergic mechanisms, which are more task-specific and sensitive to conditions of movement execution, in particular to the presence of visual feedback on salient variables. Recent studies of intra-muscle and multi-effector (multi-muscle) synergies have strongly suggested the existence of at least two classes of performance-stabilizing synergies. Intra-muscle synergies stabilize reflex-induced changes in performance, show no effects of hemispheric dominance, and are robust independently of the availability of visual feedback [62-64]. In contrast, multi-effector synergies show no stabilization of reflex-based changes in performance, show strong effects of dominance (compatible with the dynamic dominance hypothesis, [65]), and are highly sensitive to visual feedback. For example, turning off the visual feedback on the force produced by the four fingers of a hand leads to unintentional force drifts (cf. [66,67]) accompanied by the disappearance of multi-finger force-stabilizing synergies with no effects on intra-muscle synergies [64].

It seems feasible that the two classes of synergies reflect different levels of back-coupling hypothesized within the scheme by Martin and colleagues [60], those targeting spinal levels of control and those updating the RC functions at higher levels. As far as supraspinal mechanisms of synergies are concerned, a number of studies have shown high sensitivity of synergies to disorders of subcortical circuitry in such conditions as Parkinson's disease, multi-system atrophy, and multiple sclerosis (reviewed in [68]). In contrast, effects of cortical stroke have been variable ranging from no effects on synergy indices to weakening of the synergies [69-72] (reviewed in [68,73]).

A recent study explored the indices of synergies at three levels during multi-finger accurate force production tasks [74]. In addition to analysis of intra-muscle and multi-finger force-stabilizing synergies, this study quantified the synergies at the {RC; *k*} level reflecting the hypothetical *R*- and *C*-commands. Force-stabilizing synergies were found at all three levels of analysis. However, no correlations were found across the synergy indices quantified at the three levels suggesting their independent origins. A hypothetical scheme reflecting these findings is illustrated in Figure 6. It seems feasible that the {RC; *k*} synergies are hierarchically the highest, possibly involving pre-M1 cortical levels, followed by the multi-finger synergies based on subcortical circuitry, and by intra-muscle synergies based on spinal circuitry. The presence of multiple parallel mechanisms contributing to dynamical stability of movements ensures that no major disruption happens when one of these mechanisms stops contributing to action for some reason. For example, as mentioned earlier, turning visual feedback off during accurate force production tasks leads to loss of force stability reflected in its drifts. On the other hand, the drifts are not erratic but relatively consistent in their patterns and limited in magnitude suggesting that stability is not completely lost but rather attenuated.

Cortical, pre-M1: $$\mathbf{F_{TOT}} \approx -RC(R)\bullet k(C)$$

Subcortical loops: $$\mathbf{F_{TOT} = F_I + F_M + F_R + F_L}$$

Spinal cord: $$\mathbf{F_{TOT}} \approx \sum \mathbf{k_i \bullet MU\text{-}mode_i}$$

Figure 6. Three hypothetical levels of ensuring stability of action by an effector and the hypothetical neurophysiological substrates. Force by an effector (e.g., a hand) may be stabilized at the level of R- and C-commands, at the level of sharing it across the fingers (I – index, M – middle, R – ring, and L – little), and at the level of involvement of the motor unit groups (MU-modes).

SUBCLINICAL AND CLINICAL APPLICATIONS

Many conditions, from natural aging to neurological disorders, are associated with problems related to movement stability. Examples range from mishandling hand-held objects to ataxic limb movements, and to problems with postural stability. Less obviously, problems with movement initiation may also be related to impaired control of stability, the most obvious example may be episodes of freezing in Parkinson's disease. In this case, however, they are related to impaired ability to attenuate stability of salient performance variables and make it difficult to initiate properly timed quick changes in the performance variables (see the earlier example of ASAs). The two aspects of the impaired control of movement stability have been addressed as impaired stability and impaired agility (reviewed in [68]).

Indices of stability quantified within the UCM framework show high sensitivity to relatively mild changes in the control of movements, e.g., those seen under atypical development, under fatigue, with healthy aging, and in populations at high risk for neurological disorders (reviewed in [15]). In particular, persons with Down syndrome show reduced indices of multi-finger synergies during accurate force production [75], muscle fatigue can lead to increased multi-effector synergy indices and reduced intra-muscle synergies [76,77], older persons show reduced synergy indices during steady-state tasks and reduced ASAs in preparation to quick actions [78,79], and professional welders who are predisposed to basal ganglia disorders due to the accumulation of manganese and iron in the brain show smaller synergy indices [80].

The high sensitivity of synergy indices to Parkinson's disease (PD) has been shown in studies, which demonstrated significantly changed indices of both performance-stabilizing synergies and ASAs in effectors and tasks apparently unaffected by the disease (according to the clinical examination) [81,82] and in *de novo* PD patients [83,84]. These indices are also differentially sensitive to both dopamine-replacement treatment and deep brain stimulation in PD [85-87]. Overall, even though clinical studies using the UCM-based methods are still relatively few, they promise important practical impact as behavioral biomarkers at early stages of neurological disorders and as predictors of both treatment and disease progression, e.g., predicting episodes of freezing in PD [73,88].

It remains mostly unknown if training can lead to improved control of the action stability. So far, various studies have shown that at early stages of practicing an unusual task, synergies stabilizing performance variables strengthen, primarily due to the drop in V_{ORT}, and at later stages they can weaken, primarily due to a disproportionate drop in V_{UCM} [89-91]. In conditions challenging stability, an increase in V_{UCM} can accompany a drop in V_{ORT} [92,93] (cf. [94]). This is encouraging given that a number of clinical studies have documented reduced amounts of V_{UCM} leading to low synergy indices [82,95]. So, designing studies to encourage higher V_{UCM} seems a promising strategy. Unfortunately, so far, transfer of the effects of practice to more functional tasks has been limited (reviewed in [96]).

THE FUTURE OF THE UCM

One of the most difficult aspects of understanding and exploring the UCM concept is separating underlying hypotheses from the associated toolbox. The primary hypothesis is that the central nervous system uses abundant sets of elemental variables to ensure task-specific dynamical stability of salient performance variables. Secondary hypotheses have emerged based on experimental explorations of the primary hypothesis. They relate, in particular, to ability of the brain to modulate stability of action depending on plans and expectations (as reflected in ASAs), changes in the ability to ensure proper stability properties of movements with subclinical (fatigue and aging) and clinical states, the role of timing and spatial errors in the dynamical stability [97,98], and a few others. So far, the toolbox to explore these hypotheses has most frequently included the analysis of the structure of inter-trial variance and of motor equivalence. Clearly, it is unproductive to try to disprove the toolbox, although delineating its limits of application and reliability of the outcome variables is important. In contrast, trying to disprove specific hypotheses is potentially very valuable and can lead to their refinement or even falsification and replacement by a different theoretical framework.

As of now, the process account of the UCM-associated stability of movements [60] provides the most useful framework and guidelines for future analysis. The most obvious gap in our knowledge is related to only speculative links of the assumed processes to neurophysiological substrate. The current guesses are based primarily on a handful of studies using the UCM-based analysis in patient populations. Very few studies have applied this method to studies of movement stability in animals (e.g., [99,100]). Potentially, animal studies can provide more direct information on the underlying neurophysiological circuitry given the possibility of performing invasive procedures and more direct recordings.

One of the challenges in analysis of synergies is shifting from sets of elemental variables at the level of performance (which are typically selected subjectively, commonly based on the available equipment) to sets of theory-based control variables such as RCs. The first described attempts have provided promising results but the available tools for recording control variables (λs, RCs, *R*-command, and *C*-command) and their changes in real time are currently limited and based on a number of assumptions and simplifications. So far, mechanical and EMG-based proxies of those variables have been used. Maybe, combining analysis of both mechanical and electrophysiological variables could lead to progress in this field.

The idea of hierarchical control with RCs (see Figure 4) raises a problem related to the described trade-offs between synergies at different levels of a hierarchy. Recent studies have suggested the existence of three levels at which synergies are organized, the task level of the *R*- and *C*-commands, the level of sharing the task across effectors (such as limbs and digits), and the level of stabilizing action of individual muscles [64,74]. The presence of multiple circuits stabilizing action is not surprising given the obvious importance of action stability in the process of evolution. Other levels, e.g., those involved in stabilizing movement in individual joints, may be apparent, not real, unless single-joint movement represents a salient task component. A related issue is the unintentional drifts in performance that have been reported during isometric force production tasks (reviewed in [15]). So far, studies of such drifts within the UCM-framework have reported disappearance of synergies at the level of effector involvement, dramatic reduction of synergies at the level of the *R*- and *C*-commands, and no effects on motor unit-based synergies [64,101]. These studies have to be reproduced using a variety of tasks. The differential sensitivity of circuits involved in action stability may be an important factor defining specific features of movement disorders, but such studies have not been performed yet.

So far, most UCM-based studies have explored indices of the relative amounts of inter-trial variance or displacement within the UCM and ORT. Less attention has been paid to analysis of data within the UCM (cf. [102]), although the importance of reduced V_{UCM} has been emphasized in several clinical studies [86,95]. It seems that excessive stability along the UCM (as reflected in low V_{UCM}), i.e., preferring stereotypical solutions, is highly important in its effects on stability of everyday movements. A related underexplored issue is the structure of variance within the UCM. It is possible that some directions within the UCM are stabilized more than others reflecting importance of other variables in addition to the variables for which the UCM was computed. Note that the UCM-based analysis is always subjective: It starts with selecting a performance variable that is seen by the researcher as salient for the task. A number of early studies have shown, however, that the brain can reformulate the task based on its past experience and other criteria and stabilize a variable that has not been mentioned in the task formulation [32,33]. Maybe combining the UCM-based toolbox with more objective analysis of the structure of variance, e.g., the principal component analysis, can help discover hidden salient variables.

An aspect of synergic control that has not been explored in detail is the apparent trade-off among three properties of movements, their stability (as reflected in the structure of variance, $V_{UCM} > V_{ORT}$), optimality (sticking to a criterion that defines average across trials sharing of the salient variable across elemental variables), and agility (ability to change a salient variable quickly) (reviewed in [51]). Such trade-offs have been invoked, in particular, in studies of ASAs and synergy indices in the dominant and non-dominant extremities [103,104] and in studies of individual digits of the human hand [105]. Can such inherent trade-offs be avoided? Can a person be both optimal, agile, and stable? We do not know answers to these questions, which are obviously relevant for such diverse fields as athletics and motor rehabilitation.

There are plenty of unsolved methodological issues related to analysis within the UCM framework. Some of them, such as reliability of the main outcome indices, the number of trials required to reach a criterion of statistical robustness, and a few others have been addressed recently [30,106,107]. A number of issues, however, remain acknowledged but not analyzed in sufficient detail. These include the linearization using the null-space of the **J** matrix in most studies, assumptions that the **J** matrix does not change significantly within the selected time (or phase) window of analysis, potential interdependence among elemental variables unrelated to the task, etc.

Applied studies performed within the UCM-based framework are still few and fragmented despite the obvious functional importance of the proper control of action stability. Very little is known about changes in the neural control of movement stability with typical and atypical development. In contrast, this method has been applied at the other end of the spectrum, to studies of aging demonstrating impairment in indices of both movement stability and its adjustments in preparation to quick actions (ASAs). Studies of neurological patients have demonstrated the sensitivity of the indices quantified within the UCM framework to a variety of disorders. However, changes in these indices with disease progression, pharmacological therapy, brain stimulation, and rehabilitation are next to unknown with only a handful of exceptions. This field is waiting to be adequately developed.

Very little is known about changes in indices of stability with athletic training and motor rehabilitation although, obviously, developing better stability of actions and better agility could be very beneficial in various sports and in recovery of functional everyday movements. In laboratory conditions, practice has been shown to lead to major changes in the indices of synergies, in particular on V_{UCM}. In contrast, no studies have explored potential effects of practice on ASAs.

Overall, the UCM-based approach seems to be at a stage of maturity. It is considered seriously by most researchers as both a viable theoretical framework and useful toolbox to analyze the neural control of movement stability. It is up to next generation of researchers to address the missing pieces of the puzzle and to develop this approach and its applications. This would require deep understanding of the main aspects of the approach and the associated fields such as linear algebra, statistics, and neurophysiology: Challenging but not impossible.

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