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Motor Control Strategies Revealed in the Structure of Motor Variability

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LATASH, M.L., J.P. SCHOLZ, and G. SCHÖNER. Motor control strategies revealed in the structure of motor variability. *Exerc. Sport Sci. Rev.*, Vol. 30, No. 1, pp 26–31, 2002. *We describe an uncontrolled manifold hypothesis, which suggests a particular solution for the notorious problem of motor redundancy. A body of recent experiments supports the uncontrolled manifold hypothesis and shows its ability to discover biological strategies of the coordination of apparently redundant motor systems. The hypothesis and associated computational apparatus have great potential for application in the areas of motor rehabilitation and motor skill acquisition.* **Keywords:** variablility, synergy, redundancy, finger, human

INTRODUCTION

One of the most commonly seen features in human movements is motor variability. Several attempts at the same task always lead to somewhat different patterns of performance, including the kinematics, kinetics, and patterns of muscle activation. Bernstein (1) used an expression "repetition without repetition" when he described consecutive attempts at solving a motor task. He meant that each repetition of an act involved unique, nonrepetitive neural and motor patterns. During the last half-century, motor variability has become an object of study in its own right, with review articles and monographs dedicated to this topic (8). Thus, most motor control researchers now view variability not as a nuisance that forces experimenters to record many trials of each motor task but rather as a window into the central organization of the system that produces voluntary movements.

One of the obvious origins of motor variability is motor redundancy. At each level of analysis of the system for the production of voluntary movements, there are many more elements contributing to performance than are absolutely necessary to solve a motor task. In other words, a motor task does not prescribe a single, particular motor pattern such that the CNS is confronted with a problem of choice: how to select a particular way of solving each particular problem. Examples of such problems in motor control literature include the problem of inverse kinematics and the problem of inverse dynamics. Problems of this type belong to the ill-posed class; they have been termed problems of motor redundancy or Bernstein's problems (5,14). Bernstein himself viewed the problem of "elimination of redundant degrees of freedom" (DOFs) as the central issue of motor control (1).

There have been many attempts to address the problem of motor redundancy in its original formulation. These involved, in particular, application of optimization principles based on certain mechanical, engineering, psychological, or complex cost functions. However, we suggest that the problem itself has been inadequately formulated.

SYNERGIES AND STRUCTURAL UNITS

In the 1960s, Gelfand and Tsetlin (4) formulated a set of axioms for the organization of groups of elements united by a common goal (structural units). They considered movements to be controlled in a hierarchical but not prescriptive manner. The controller organizes relations among elements at an hierarchically lower level, and these relations assure stability of motor performance with respect to a particular motor task. Figure 1 presents a general scheme and a few examples of such organizations at very different scales. Just like a football coach never specifies a precise sequence of all the movements of all the players for a particular play, the CNS does not specify a precise pattern of joint rotations that

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Accepted for publication: October 10, 2001.

0091-6631/3001/26–31
Exercise and Sport Sciences Reviews

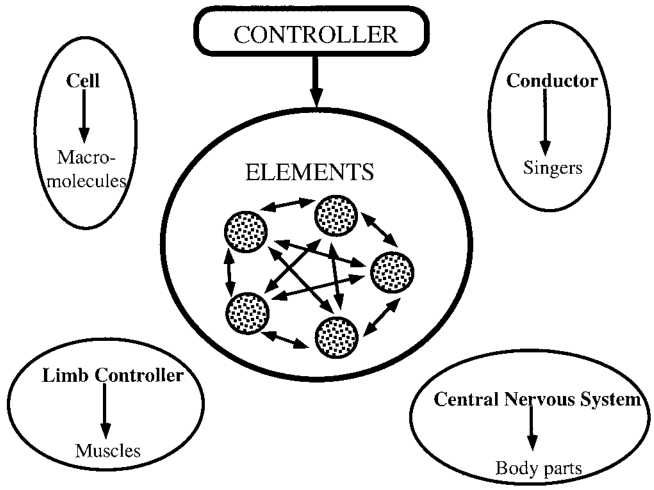

Figure 1. An illustration of an hierarchical organization of a structural unit with a few examples of structural units at different scales and levels of analysis.

would lead to a new, desired position of the endpoint of the limb. A structural unit is always organized in a task-specific way such that, if an element introduces an error into the common output, other elements change their contributions to minimize the original error, and no corrective action is required of the controller (cf. the principle of minimal interaction (4)). Only systems that function according to this principle and demonstrate error compensation among elements are going to be called synergies.

More recently, a principle of abundance (3) has been suggested; it states that all the elements (DOFs) always participate in all the tasks, assuring both stability and flexibility of the performance. As such, the principle of abundance renders the redundancy problem irrelevant: No DOFs are ever eliminated or frozen. The principle of abundance allows the introduction of elements of exactness into one of the most commonly (ab)used terms in the area of movement studies, that of a synergy. Here, we present an approach that allows one to address in a formal way the following questions: 1) how to tell a synergy from a "nonsynergy"; 2) how to measure the "strength" of a synergy; 3) how to test whether an alleged synergy contributes to a particular task; and 4) how to test whether a new synergy has been developed for a particular task (for example, as a result of practice or adaptation to an injury).

THE UNCONTROLLED MANIFOLD (UCM) HYPOTHESIS

The UCM hypothesis assumes that, when a controller of a multi-element system wants to stabilize a particular value of a performance variable, it selects a subspace within the state space of the elements such that, within the subspace, the desired value of the variable is constant. This subspace has been termed the "uncontrolled manifold" (UCM). After selecting a UCM, the controller selectively restricts the variability of elements along "essential" directions within the state space that do not belong to the UCM, but not along directions within the UCM. This means that the controller allows the elements to show high variability (have more freedom) as long as it does not affect the desired value of the variable. The term "uncontrolled manifold" refers to this basic feature of the UCM: the elements are "less controlled" as long as they remain within the UCM.

Consider the following example: A person is asked to press with two fingers to produce a total force of 10 N. Let this person perform the task 100 times and plot the values of individual finger forces on the force-force plane (state space of the system). The data points will form a cloud (Fig. 2A, the ovals indicate the data distribution shapes). Let us consider two main possibilities. First, the cloud may be circular (Fig. 2A). This means that, if one finger by chance produced a higher than usual force (introduced an error), the other finger would produce with equal probabilities higher than usual or lower than usual forces (amplify or reduce the error). By definition, this is not a synergy. In Figure 2B, the data ellipsoid is elongated along a line corresponding to the equation $F_1 + F_2 = 10$ (dashed line). Now, if by chance, one finger produced a larger force, the other finger would more likely produce a lower force to keep the sum closer to the required value. The two elements are at least partly compensating for each other's errors. This is a synergy, and the dashed line is the UCM.

Let us introduce two measures of variance for the data clouds in Figure 2. One of them is the projection of the variance on the UCM (Var_{UCM}), whereas the other one is the projection of the variance on the orthogonal to the UCM direction (Var_{ORT}). Let us normalize both Var_{UCM} and

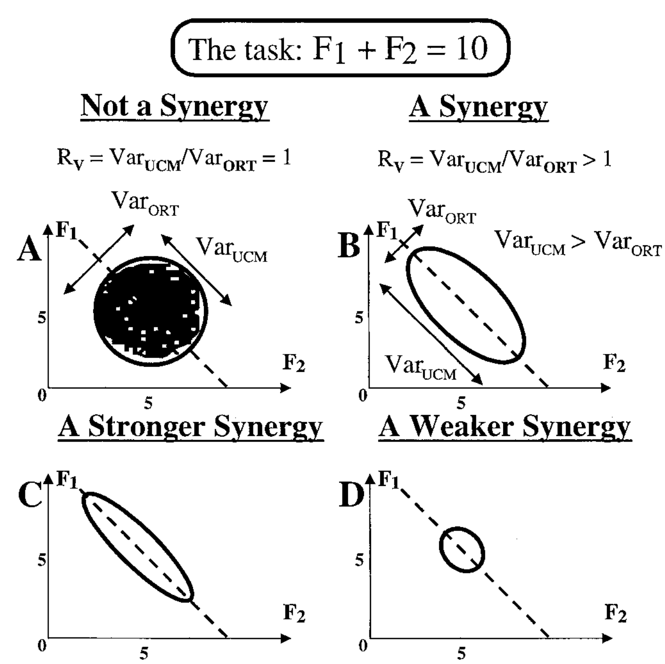

Figure 2. Examples of data clouds for the task of pressing with two effectors with a total force of 10 N. A. A spherical distribution corresponds to no error compensation between the effectors (by definition, this is not a synergy). B. An elongated distribution along a UCM line corresponds to larger variance parallel to the UCM (Var_{UCM}) than orthogonal to the UCM (Var_{ORT}). C and D. An improvement in performance can be associated with a stronger synergy (C, larger Rv) or with a weaker synergy (D, smaller Rv).

Var_{ORT} by the number of dimensions (DOFs) within the UCM and within the orthogonal subspace (in Fig. 2, no normalization is required because both dimensions are unity). If, after the normalization, Var_{UCM} is significantly higher than Var_{ORT}, as in Figure 2B, the system functions according to the UCM hypothesis. If there is no difference between Var_{UCM} and Var_{ORT}, the system controls the elements independently. This may be quantified using the ratio $R_V = Var_{UCM}/Var_{ORT}$. If $R_V > 1$, the system functions according to the UCM hypothesis with respect to the selected criterion.

Let us make a few important points with respect to the UCM hypothesis:

1) A UCM always reflects a "control hypothesis," *i.e.*, a hypothesis about a performance variable, whose value the system is assumed to stabilize. In Figure 2, the control hypothesis was that the system tried to stabilize the total force at 10 N. Other control hypotheses may assume, for example, that the total force is stabilized at a different value, or that another function of the forces is stabilized at a certain value. If $R_V > 1$ for a control hypothesis, the hypothesized performance variable is selectively stabilized. If $R_V = 1$, the organization of control is indifferent to the selected performance variable. If $R_V < 1$, the organization of control is such that the selected performance variable is destabilized, *i.e.*, an error introduced by an element is more likely to be amplified by changes in the outputs of other elements.

2) Using the UCM method of control only predicts certain relations between variance components but not their absolute magnitudes. As such, it is compatible with better, equal, or worse performance as compared with controlling each element of the system independently (as a nonsynergy).

3) An improvement in performance, for example as a result of practice, may be associated with increased or decreased R_V (see panels C and D of Fig. 2). In both cases, Var_{ORT} is decreased, implying less variable overall performance. In Figure 2C, this is associated with no changes in Var_{UCM} leading to an increase in R_V (a stronger synergy). In Figure 2D, Var_{UCM} decreased more than Var_{ORT}, leading to a drop in R_V (a weaker synergy).

4) A multi-element system may be able to selectively stabilize several performance variables at the same time. This is true as long as the number of elements is at least as high as the number of task constraints plus the number of stabilized variables.

5) The UCM method shares certain similar features with the principal component analysis. A major difference is that the principal component analysis is "objective," *i.e.*, it identifies the directions and magnitudes of the main axes of an ellipsoid describing a distribution of data points. It does not say, however, whether these directions are in any way special with respect to characteristics of the external performance of the system. The UCM always analyzes data clouds with respect to a particular control hypothesis, *i.e.*, a particular performance variable.

To summarize, the UCM method combines a hypothesis on a particular type of control and a toolbox that allows one to analyze the output of a multi-element system to discover which variables the system stabilizes preferentially.

To use the UCM approach to analyze a multi-element system, one needs to have a Jacobian (**J**) of the system, *i.e.*, a set of coefficients that describe how small changes in the outputs of individual elements are reflected in the magnitude of a selected performance variable. This is formalized as a matrix of partial derivatives of the selected variable with respect to outputs of the elements. In some cases, the **J** matrix can be computed based on the geometrical properties of the system, for example, when one is interested in how individual joint rotations are organized to produce a particular motion of the endpoint of the multi-joint limb. In other situations, however, getting an estimate of the **J** matrix itself becomes a major problem, in particular when one deals with a system whose apparent output elements may not be independently controlled. For example, when a person tries to produce force with a finger of a hand, other fingers of the hand also show involuntary force production. This phenomenon is called "enslaving" (15). It is a result of both peripheral connections among the fingers, such as shared muscles and inter-digit tendinous connections, and neural factors such as overlapping cortical representations for individual fingers. Such "built-in" dependences among the finger forces require one to look for another set of variables that the CNS manipulates independently. Let us term these hypothetical variables "modes." Figure 3 illustrates the notion of modes. Each mode induces force production by all the fingers, whereas separate modes can be independently involved to different degrees by the CNS. In the case of multi-finger force production, modes can be assessed by asking a subject to press with only one finger at a time and observing force changes in all four fingers.

In other cases, the situation may be even more complicated. For example, most contemporary scientists would probably agree that muscles are not controlled independently by the CNS. Imagine that you want to analyze multi-muscle synergies. You cannot simply tell your subject "and now activate only your left soleus." So, multi-muscle modes need to be discovered with other, more subtle means. Such means do not exist yet.

KINEMATIC STUDIES WITHIN THE UCM HYPOTHESIS FRAMEWORK

Until now, there have been a few studies that used the UCM hypothesis to analyze motor systems and tasks of different complexity. The tasks included whole-body motion, joint coordination during a bimanual task, joint coordination during a single-limb task, and finger coordination in a multi-

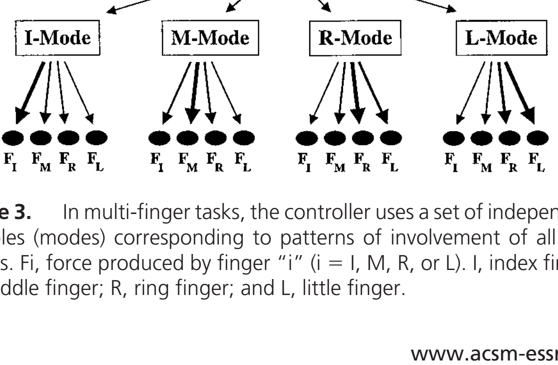

Figure 3. In multi-finger tasks, the controller uses a set of independent variables (modes) corresponding to patterns of involvement of all four fingers. Fi, force produced by finger "i" (i = I, M, R, or L). I, index finger; M, middle finger; R, ring finger; and L, little finger.

TABLE 1
A summary of studies within the UCM approach

Study	Task	Analysis	Hypotheses	Results
Scholz and Schoner (12)	Sit-to-stand	Planar, kinematic	H1StS - center of mass (CM) path H2StS - head position	$R_V > 1$ for H1StS, horizontal and vertical CM path; for H2StS, horizontal path only
Scholz *et al.*, Reisman *et al.* (9,11)	Sit-to-stand	Planar, kinematic, kinetic	H1StS - CM path H2StS - head path H3StS - linear momentum of CM	$R_V > 1$ for H1StS, H2StS, and H3StS for horizontal but not vertical path; $R_V \gg 1$ for H1StS, when task is more challenging
Domkin *et al.* (2)	Bimanual pointing	Planar, kinematic	H1P - target trajectory H2P - pointer trajectory H3P - vectorial distance between pointer and target	All hypotheses confirmed; H3P showed higher R_V; practice led to better performance and smaller R_V
Scholz *et al.* (13)	Quick-draw shooting	3D, kinematic	H1Sh - pistol orientation H2Sh - pistol position H3Sh - center of mass position	H1Sh - confirmed over the whole movement; H2Sh and H3Sh - confirmed only during early phase
Scholz *et al.* (10)	Four-finger cyclic force production	Kinetic	H1F - total force H2F - total moment	H1F confirmed only at high forces; H2F confirmed over the whole cycle
Latash *et al.* (7)	Marginally redundant; two- and three-finger cyclic force production	Kinetic; stable and unstable conditions	H1F - total force H2F - total moment	H1F confirmed only at high forces; H2F confirmed over much of the cycle; moment was stabilized while force was destabilized

The column "Hypotheses" identifies variables that were tested for selective stabilization during the studied tasks. H stands for "hypothesis," whereas the letters following the number stand for the study: StS, sit-to-stand; P, pointing; Sh, shooting; and F, force production.

finger force production task. Table 1 summarizes methods of analysis, control hypotheses, and main results obtained in these studies.

Two-dimensional kinematic studies of a sit-to-stand action (9,11,12) and two-arm pointing (2) have shown that the UCM apparatus is capable of distinguishing among different control hypotheses related to selective stabilization of time patterns of particular performance characteristics of these actions. In particular, the studies of the sit-to-stand action showed differences in the stabilization of the horizontal and vertical displacements of the center of mass. The pointing study has provided quantitative support for the hypothesis that joints of the two arms were indeed united into a bimanual synergy rather than being a simple superposition of two unimanual synergies. The latter study also looked at the effects of practice on the structure of joint variability. The UCM analysis showed that both Var_{UCM} and Var_{ORT} decreased with practice. However, Var_{UCM} decreased more, leading to smaller R_V values (see Fig. 2D). This is an unexpected finding. It may be a result of the task being very simple, such that there was not much room for decreasing Var_{ORT}. Other factors, outside the explicit task, could play a role in making the movements more stereotypical, *e.g.*, postural stability. Finally, the path of end-effector positions requires a sequence of different UCMs. The subjects may have learned to limit the range of joint combinations used for a given UCM to improve efficiency of transitions between UCMs.

A three-dimensional study of quick-draw pistol shooting (13) was performed based on an intuitive consideration that accurate shooting depends on two angles (pitch and yaw) describing the orientation of the pistol at the time the trigger is pressed, but not on the third angle (roll) and not on the position of the pistol along the line of shooting (Fig. 4). The results have shown that instantaneous orientation of the pistol barrel with respect to the direction from the backsight to the target was selectively stabilized by the coordinated rotation at the seven major joint axes. Other control hypotheses were tested; they, however, were supported only during the initial phase of the movement. Supporting several hypotheses during the movement initiation was possible because of the relatively large redundancy of the system.

ANALYSIS OF MULTI-FINGER FORCE PRODUCTION

Studies of multi-finger cyclic force production (7,10) used the mode approach as described earlier (Fig. 3). Patterns of finger forces were recomputed into force-mode patterns; then, force-mode patterns were analyzed with respect to two

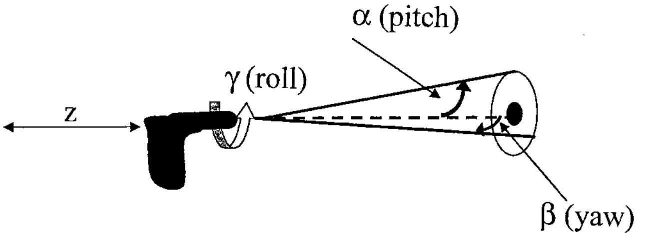

Figure 4. An illustration of important and unimportant errors in pistol's position during shooting. Errors in pitch (α) and yaw (β) lead to inaccurate shooting, whereas errors in roll (γ) and coordinate of the pistol along the shooting line (z) do not.

control hypotheses: (H1) individual finger forces were coordinated to stabilize the average total force profile; and (H2) individual finger forces were coordinated to stabilize the average profile of total moment generated by all involved fingers with respect to the midpoint between the two "lateral" fingers. When only two fingers participated in the task, the requirements of force and moment stabilization were incompatible, such that the subjects were forced to choose which of the two variables to stabilize at the expense of the other variable being destabilized. In two-finger tasks, the subjects stabilized total force only within a narrow phase range of the force cycle, close to the peak total force, while the moment-control hypothesis (H2F) was confirmed over most of the cycle (Fig. 5B). Note that the subjects were explicitly asked to reproduce a pattern of total force with no explicit feedback on total moment.

In three- and four-finger tasks, the redundancy of the system allows the stabilization of both force and moment at the same time. However, in three-finger tasks, the results were similar to those in two-finger tasks. Actually, the third finger was used to stabilize moment over the whole cycle, not to stabilize force better! Only when all four fingers were used, were the subjects able to avoid force destabilization. However, they still stabilized force only within a relatively narrow phase range, while moment was stabilized over the whole cycle.

These seemingly unexpected findings are likely to reflect the multi-finger synergies elaborated by the CNS during a lifetime based on everyday tasks. Most everyday tasks such as eating with a spoon, drinking from a glass, and writing with a pen impose stronger constraints on permissible errors in moment than in force. In tasks illustrated in Figure 6, grip force should only be sufficiently large to prevent the glass or the pen from slipping out of the hand. It should also be under a magnitude that could potentially crush the glass or the pen.

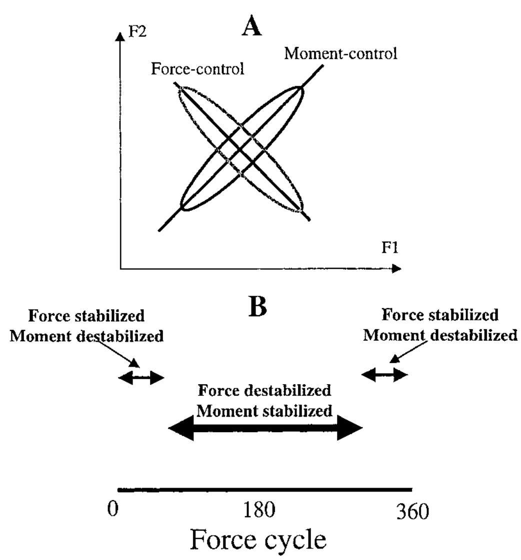

Figure 5. A. When two fingers produce total force oscillating at a comfortable frequency, force control and moment control are incompatible because they require data distributions (ellipsoids) elongated along orthogonal lines. B. In experiments, moment was stabilized and force destabilized over most of the force cycle; force was stabilized and moment was destabilized close to peak force values only.

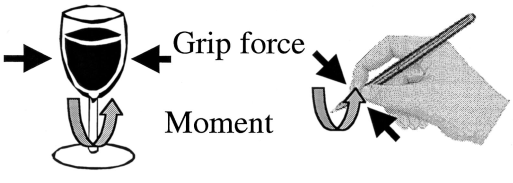

Figure 6. In many everyday tasks, accurate stabilization of moment is very important, while grip force may show relatively large errors.

These are relatively weak constraints. The moment, however, needs to be controlled much more precisely if one wants to write legibly and to avoid spilling the contents of the glass.

POTENTIAL APPLICATIONS OF THE UCM APPROACH

The UCM hypothesis and toolbox allow the following issues to be addressed that are central to aspects of motor rehabilitation and motor skill acquisition:

One can test whether an alleged element of a multi-element synergy actually contributes to stabilization of a particular performance variable: if considering the contribution of this element leads to better error compensation (higher R_V values) with respect to the selected variable, the element indeed takes part in the synergy.

If a new technique of performing a motor task has emerged, it is possible to test whether the new coordination actually stabilizes performance variables that are essential for the task.

One can test hypotheses about different performance variables being stabilized by apparently atypical coordination patterns. Patients with motor disorders commonly show atypical motor patterns that may result from their pathology or may be consequences of an adaptation within the CNS (6). In the latter case, atypical coordination patterns may be directed not at an apparent motor task but at less obvious performance characteristics related to postural stabilization, avoiding uncomfortable or painful body postures, preserving larger safety margins, etc.

Until now, applications of the UCM approach have been limited to analysis of kinematic and kinetic variables. It is theoretically possible to apply this general theoretical framework and the associated computational approaches to more physiological variables such as muscle activation patterns and patterns of neural signals associated with motor tasks. There are methodological challenges to be met. However, at the present time, we do not see alternatives to studies of the central organization of motor synergies.

Acknowledgments

This study was supported in part by National Institutes of Health grants HD-35857, AG-018751, and NS-35032, and by NSF grant IBN-0078127.

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