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Hierarchies of Synergies in Human Movements

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Abstract

This brief review addresses the problem of motor redundancy, which exists at many levels of the neuromotor hierarchies involved in the production of voluntary movements. An approach to this problem is described based on the principle of abundance. This approach offers an operational definition for motor synergies using the framework of the uncontrolled manifold hypothesis. It is shown that hierarchical systems have inherent trade-offs between synergies at different control levels. These trade-offs have been demonstrated in experimental studies of human multi-finger pressing and prehension. They are likely to be present in other hierarchical systems, for example those involved in the control of large groups of muscles. The framework of the equilibrium-point hypothesis offers a physiologically based mechanism, which may form the basis for hierarchies of synergies.

Keywords

Synergy; motor redundancy; principle of abundance; hierarchical control; prehension

The Problem of Motor Redundancy

All the neuromotor processes within the human body associated with performing natural voluntary movements involve several few-to-many mappings that are commonly addressed as problems of redundancy. In other words, constraints defined by an input (for example by a task) do not define unambiguously patterns of an output (for example patterns of joint rotations, muscle forces, activation of motoneurons, etc.) such that many (commonly, an infinite number of) solutions exist. This problem has been appreciated by Bernstein (1935, 1967) who viewed it as the central problem of motor control: How does the central nervous system (CNS) select unique solutions from the numerous seemingly equivalent alternatives?

The problem of motor redundancy can be illustrated by examples at different levels of the neuromotor hierarchy. For example: How is a joint configuration selected for a desired endpoint limb position in the three-dimensional space given the larger than three number of individual joint rotations? How are muscle forces (or activation levels) defined for a desired joint torque given that all major joints are spanned by more than two muscles? How is a motor unit firing pattern defined for a desired muscle activation levels given the large number of motor units and a possibility to vary their frequency of firing?

A traditional method of dealing with the problems of motor redundancy has been to assume that the CNS uses a set of criteria to find unique solutions to such problems. In particular, a variety of optimization techniques have been used to address such problems including optimization of cost functions based on mechanical, psychological, and neurophysiological variables (reviewed in Prilutsky 2000; Rosenbaum et al. 1993, Latash 1993). There is an alternative view, however, on such problems. This view originated from the seminal works by Gelfand and Tsetlin (1966) and has been developed recently (Gelfand and Latash 1998, 2002; Latash et al. 2007).

The Principle of Abundance

Gelfand and Tsetlin (1966) compared the many elements involved at any step of the generation of movement to a class of lazy students who want to do minimal work compatible with the task at hand. They introduced the principle of minimal interaction to describe such behaviors of large ensembles of elements. According to this principle, each element tries to minimize its interaction with other elements, the controller, and the environment. In other words, each element tries to minimize input it receives from all the mentioned sources.

Recently, this principle has been developed into a principle of abundance (Gelfand and Latash 1998). According to the principle of abundance, the problems of motor redundancy are wrongly formulated. The few-to-many mappings typical of such problems should not be viewed as a computational problem for the controller but rather as a luxury that allows combining stable performance of a task with performing other tasks and responding to possible perturbing influences from the environment. Solving problems of motor redundancy involves not selecting a unique, optimal solution but rather facilitating families of solutions that are equally successful in solving the task. Note that this family of solutions is much smaller than the total number of possible solutions. So, a certain selection/optimization is likely to take place. For example, we do not use military parade gaits and do not walk sideway although these ambulation patterns solve the task of moving from point A to point B. The shift from searching for unique solutions to defining rules that organize families of solutions have resulted in a novel view on motor synergies, a paradigm shift that has led to an operational definition of synergies and the creation of a new computational approach to identify and quantify synergies.

Synergy – an Operational Definition

The word “synergy” has been used in studies of movements and to describe motor disorders for over 100 years. Commonly, it has not been defined beyond the direct translation from Greek meaning “work together”. Recently, however, this word has acquired a more specific meaning rooted in the principle of abundance (for a detailed review see Latash 2008). The easiest way to introduce this new meaning of the old word is with an illustration (Figure 1).

Imagine a person pressing with three fingers of a hand on three force sensors. The task is to produce a certain level of the total force, for example 20 N. This is a typical problem of motor redundancy since the equation $F_1 + F_2 + F_3 = 20$ has an infinite number of solutions. These solutions form a two-dimensional sub-space, a plane in the three-dimensional space of finger forces (Figure 1A, UCM_F , this abbreviation will become clear later). The original formulation of the problem of motor redundancy implies that a neural controller finds a unique solution, a point on that plane, that satisfies an optimality criterion (for example, point A). The principle of abundance, however, implies that a whole family of solutions are allowed by the controller; these solutions should all belong to an area within the plane shown in Figure 1 with dashed lines. Now consider that each element (each finger) has an inherent variability that cannot be reduced to zero. This means that actual observations in such a task over repetitive attempts are expected to generate a cloud of points. What could be the shape of such a cloud?

If a unique solution is selected, and there is inherent variability that is approximately equal for each of the fingers, the cloud will look like a sphere centered about point A. This corresponds to a stereotypical solution that does not make use of the design of the hand and does not deserve to be called a synergy. If a whole family of solutions is selected, one may also expect some variability that goes beyond the plane shown in Figure 1, but it may be expected to be smaller than variability within the plane. In other words, different solutions may be observed across trials, but these solutions will show co-variation of finger forces such that most of the variability is confined to the plane corresponding to perfect execution of the task (illustrated with the ellipsoid in Figure 1A).

Imagine now that the force sensors are mounted on a plate that is placed on a narrow support under the middle finger (the insert in Figure 1) such that the whole system is in an unstable equilibrium. Now the subject has to balance the moments of force produced by the two lateral fingers. This task corresponds to another equation $F_1=F_3$, which also allows an infinite number of solutions corresponding to a plane in the space of finger forces (thick dashed lines in Figure 1B). Following the same logic, two strategies of dealing with this problem are possible. First, the neural controller may select a unique solution. Second, a whole family of solutions may be facilitated. In the first case, one may expect a close to spherical distribution of data points recorded in several trials centered about a point. In the second case, an ellipsoid of data points may be expected oriented parallel to the plane of perfect solutions.

Note that both tasks can be performed at the same time, that is producing a total force of 20 N and simultaneously balancing the plate. Then, both equations are satisfied, and the space of solutions becomes one-dimensional, a line formed by the intersection of the two planes shown as the thick solid line in Figure 1B.

This example allows to introduce three characteristics of synergies. First, when an apparently redundant set of elements is involved in a task, an average *sharing pattern* is selected that will characterize the average contribution of each element. Second, when several attempts at a task are analyzed, elements may show co-variation of their outputs that is beneficial for the task, i.e., that reduced variability of the important performance variable as compared to what one could expect in the absence of the co-variation. This feature is sometimes referred to as *error compensation* or *stability*. Third, the same set of elements may be used to form different synergies, i.e. different co-variation patterns that are beneficial for different performance variables produced by the whole system. This feature may be called *flexibility*. Only systems that can demonstrate all three features will be called synergies.

Synergies always do something; there are no abstract synergies. Within the current framework, we assume that they ensure low variability (high stability) of a performance variable. So, every time the word synergy is used, one has to mention what elemental variables form the synergy and what the synergy is doing. For example, an expression “a hand synergy” carries little meaning, but it is possible to say “a synergy among individual finger forces stabilizing the total force” or “a synergy among moments of force produced by individual digits stabilizing the total moment of force applied to the hand-held object.” A number of recent studies have suggested that sometimes co-variation among elemental variables contributes to a quick change in a performance variable (Olafsdottir et al. 2005; Kim et al. 2006); in such cases, one may say that a synergy acts to destabilize the performance variable.

This framework allows to offer the following definition of a synergy: *Synergy is a neural organization of a set of elemental variables with the purpose to ensure certain stability properties (stabilize or destabilize) of a performance variable produced by the whole set.*

The Uncontrolled Manifold Hypothesis

The introduced definition of synergy requires a quantitative method that would be able to distinguish a synergy from a non-synergy and to quantify synergies. Such a method has been developed within the framework of the uncontrolled manifold hypothesis (UCM hypothesis, Scholz and Schönner 1999; reviewed in Latash et al. 2002, 2007). The UCM hypothesis assumes that a neural controller acts in a space of elemental variables and selects in that space a subspace (a UCM) corresponding to a desired value of a performance variable. Further, the controller organizes interactions among the elements in such a way that the variance in the space of elemental variables is mostly confined to the UCM. There have been several attempts to offer a mechanism that could organize such type of control. In particular, feedback using peripheral sensors (Todorov and Jordan 2002), feedback using central back-coupling neural

loops (Latash et al. 2005), and a feed-forward control scheme (Goodman and Latash 2006) have all been shown to lead to data point distributions compatible with the UCM hypothesis.

Consider the simplest case of a mechanically redundant system, two effectors that have to produce a certain magnitude of their summed output (Figure 2). The space of elemental variables is two-dimensional (a plane), while any magnitude of the summed output may be represented as a one-dimensional sub-space (a line). This line is the UCM corresponding to a desired value of the performance variable ($E_1 + E_2$). Now it is clear why in Figure 1, the two planes corresponding to stabilization of the total force and total moment of force are labeled as UCM_F and UCM_M , respectively. As long as the system's state belongs to that line, the task is performed perfectly, and the controller does not need to interfere. According to the UCM hypothesis, the controller is expected to organize co-variation of E_1 and E_2 over a set of trials in such a way that the cloud of points recorded in those trials is oriented parallel to the UCM. Formally, this may be expressed as an inequality $V_{UCM} > V_{ORT}$, where V_{UCM} stands for variance along the UCM and V_{ORT} stands for variance along the orthogonal sub-space (shown with the dashed slanted line in Figure 2). Another, more intuitive pair of terms have been used to describe the two variance components, "good" and "bad" variance (V_{GOOD} and V_{BAD}). V_{BAD} hurts accuracy of performance while V_{GOOD} does not while it allows the system to be flexible and deal with external perturbations and/or secondary tasks. For example, having large V_{GOOD} may help a person to open a door with the elbow while carrying a cup of hot coffee in the hand.

Analysis within the framework of the UCM hypothesis involves several important steps:

1. First, one has to select a set of elemental variables or, in other words, to commit to a certain level of analysis.
2. Then, one has to formulate a hypothesis on a possible performance variable that may or may not be stabilized by co-variation of the elemental variables. The performance variable may be complex, that is multi-dimensional. This is a very important step. It follows the basic idea that synergies always do something. We assume that they ensure certain stability properties of important features of performance.
3. One has to compute relations between small changes in the elemental variables and changes in the selected performance variable, the Jacobian of this system. This step leads to linear analysis of the system, which may not be appropriate for systems with strongly non-linear properties.
4. In general, the UCM is non-linear, for example for joint configurations corresponding to a desired endpoint position of a limb. If one accepts a linear approximation of the UCM, the null-space of the Jacobian may be computed and used instead.
5. One has to perform an experiment with repetitive measurements of the elemental variables assuming that the subject tries "to do the same thing". Then, data (values of the elemental variables) may be analyzed across trials at comparable phases of the actions or across time samples.
6. Finally, variance in the space of elemental variables has to be projected onto the null-space of the Jacobian and onto its orthogonal complement and compared per dimension in each of these sub-spaces. If $V_{GOOD} > V_{BAD}$, the hypothesis may be accepted, and one may conclude that a synergy in the space of those elemental variables stabilizes the performance variable hypothesized at step #2.

Note that the inequality $V_{GOOD} > V_{BAD}$ is not required for accurate performance. For example, the tiny circle in Figure 2 illustrates very accurate performance (small variability of the sum

E_1+E_2) without any co-variation between the two elemental variables such that $V_{\text{GOOD}}=V_{\text{BAD}}$. So, there may be very accurate non-synergies as well as very sloppy synergies.

Hierarchical Control

The idea of hierarchical control of human movements is very old. In particular, Bernstein (1947, 1967) introduced and developed a scheme involving five to six hierarchical levels. As mentioned earlier, few-to-many mappings exist at different levels of the neuromotor system. Hence, one may expect the existence of hierarchies of synergies such that outputs of a synergy serve as inputs into a hierarchically lower synergy. The input into the higher level is provided by the task, while the lowest level acts on the environment (Figure 3).

Most studies have considered at most two hierarchical levels in analysis of synergies. In particular, studies of multi-muscle postural synergies have suggested that the CNS manipulates fewer variables than the number of involved muscles; these muscle groups have been addressed as muscle synergies (d'Avella et al. 2003; Ivanenko et al. 2004; Ting and Macpherson 2005; Tresch et al. 2006) or as muscle modes (Krishnamoorthy et al. 2003a,b). In turn, muscle modes have been viewed as elemental variables that are organized into synergies with the purpose to stabilize such physical variables as coordinates of the center of pressure and shear forces acting from the supporting surface onto the body (Danna-Dos-Santos et al. 2007; Robert et al. 2008).

The idea of a two-level hierarchical control has been developed for prehensile tasks such as holding an object with the digits of a hand. Within this scheme, at the higher level, the task is assumed to be shared between the thumb and the virtual finger (VF, an imagined finger with the action equivalent to the summed action of the four actual fingers, Arbib et al. 1985). At the lower level, the action of the VF is shared among the actual fingers. Patterns of co-variation of elemental variables stabilizing aspects of the combined action have been demonstrated at each of the two levels (reviewed in Zatsiorsky and Latash 2004). In particular, the combined action of the thumb and VF has been shown to stabilize the grasping action and the rotational action of the hand in accordance with the principle of superposition introduced in robotics (Arimoto et al. 2001). The combined action of the fingers has been reported to stabilize the grasping force applied to the hand-held object (Shim et al. 2004).

Trade-offs Inherent to Hierarchical Control Schemes

Consider a very simple task: To press with two hands, two fingers per hand, such that the total force is constant (Gorniak et al. 2007a). Panel A of Figure 4 illustrates a distribution of data points across a number of trials with an ellipse elongated along the line $F_{\text{LEFT}}+F_{\text{RIGHT}}=\text{const}$. This line represents the UCM in the space of two elemental variables (F_{LEFT} and F_{RIGHT}) corresponding to the required constant value of the total force. The illustrated data show a much larger variance along the UCM (V_{GOOD}) than orthogonal to the UCM (V_{BAD}). So, we may conclude that a two-hand synergy stabilizes the magnitude of the total force. Note that the variance of each of the hands (for example V_{RIGHT}) may be rather large because it reflects both V_{GOOD} and V_{BAD} . Hence, a strong synergy with a large V_{GOOD} is expected to show large variance of each of the two forces.

Consider now the lower level of the hierarchy where each hand's force is shared between the two fingers (Figure 4B). By definition, at this level, variance of that hand's force is V_{BAD} . It is large due to the large V_{GOOD} at the upper level of the hierarchy (panel A). So, to show a synergy at the lower level, V_{GOOD} at the lower level should be very large to satisfy the inequality $V_{\text{GOOD}}>V_{\text{BAD}}$ (the large, dashed ellipse). It is more likely, therefore, that V_{GOOD} will not be large enough such that there will be no synergy (the smaller ellipse). So, there seems to be an inherent trade-off between synergies at two hierarchical levels: V_{GOOD} at the higher

level contributes to a synergy at that level but potentially hurts chances of the lower level to show a synergy stabilizing its output. Two studies (Gorniak et al. 2007a,b) provided experimental support for this conclusion by showing that during one-hand tasks, there are strong synergies among the fingers stabilizing the total force, while during two-hand tasks there are such synergies between the two hands but not between the fingers within each of the hands. Moreover, when a one-hand task turned into a two-hand tasks (by instruction), within-a-hand force stabilizing synergies disappeared; when a two-hand task turned into a one-hand task, such synergies emerged.

Does the mentioned trade-off present an insurmountable obstacle for the central nervous system? In general, it is possible to have synergies at both hierarchical levels if the inequality $V_{GOOD} > V_{BAD}$ is satisfied at both levels, as illustrated with the very large ellipse in panel B of Figure 4. However, is this feasible during natural behaviors?

A recent study (Gorniak, Zatsiorsky, Latash, unpublished) explored multi-digit synergies stabilizing components of the hand action during a variety of tasks that involved holding an object steadily. As mentioned earlier, the hand has commonly been viewed as being controlled by a two-level hierarchy in prehensile tasks (Arbib et al 1985; MacKenzie and Iberall 1994). The total force and moment of force produced on an object are distributed at the higher level of the hierarchy between the thumb and the virtual finger (VF). At the lower level of the hierarchy, the VF action is distributed among the fingers that form the VF. Let us assume for simplicity that all the points of digit contacts belong to one plane (the grasp plane), and the external moment of force acts in the same plane. Then, the problem becomes two-dimensional. Holding an object steadily is associated with equilibrium constraints at the upper hierarchical level:

1. The sum of normal (superscript N) forces of the individual fingers on the object should be equal and opposite to the normal force of the thumb.

$$0 = F_{VF}^N + F_{TH}^N$$

$$F_{VF}^N = F_i^N + F_m^N + F_r^N + F_l^N$$

2. The sum of tangential (load resisting, superscript L) forces of the individual fingers and of the thumb (along the Y-axis) should be equal to the weight of the object (W).

$$W = F_{TH}^L + F_{VF}^L$$

$$F_{VF}^L = F_i^L + F_m^L + F_r^L + F_l^L$$

3. The total moment in the grasp plane (M^{TOT}) should be equal to the external moment of force (M^{EXT}).

$$M^{TOT} = M^N + M^L = M^{EXT}, \text{ where } M^N = M_{VF}^N + M_{TH}^N \text{ and } M^L = M_{VF}^L + M_{TH}^L$$

$$M_{VF}^N = F_{VF}^N d_{VF} = F_i^N d_i + F_m^N d_m + F_r^N d_r + F_l^N d_l$$

$$M_{VF}^L = F_{VF}^L r_{VF} = F_i^L r_i + F_m^L r_m + F_r^L r_r + F_l^L r_l$$

In these equations, superscripts relate to forces that produce mechanical effects (N – normal and L – load resisting), subscripts refer to digits (TH – thumb, i – index, m – middle, r – ring, and l – little fingers), d and r stand for lever arms for the normal and load forces respectively.

Note that the same elemental variables enter different equilibrium constraints. This fact, in combination with the mentioned inherent trade-off between synergies at different hierarchical

levels. leads to rather complex interactions between V_{GOOD} and V_{BAD} for different variables and different levels of analysis. Note that these interactions are not dictated by the task mechanics but rather constrained by them. To make the long story short, experiments have shown that some of the variables (for example, the load force) can show synergies stabilizing their values at both levels of the hierarchy. Some variables (for example, the grip force) show synergies only at the upper level (similar to the mentioned study of pressing tasks), while other variables (for example, the total moment of force) show synergies only at the lower level. These interactions can be analyzed similarly to the chain effects described in earlier studies of relations among the magnitudes of elemental variables (reviewed in Zatsiorsky and Latash 2004), while here we are interested in relations among their variance components.

Ideas of multi-level hierarchical control have also been applied to analysis of multi-muscle synergies. Most experimental studies have addressed multi-muscle synergies at only one level. In particular, some studies applied matrix factorization techniques to muscle activation indices to discover muscle groups that may be viewed as controlled with only one central variable (Ting and Macpherson 2005; Tresch et al. 2006). Such groups have been addressed as multi-muscle synergies. Other studies viewed those groups not as synergies but as elemental variables and explored co-variations among the magnitudes of those variables that could be related to stabilization of such mechanical variables relevant to postural control during standing as coordinate of the center of pressure, horizontal force, and moment of force about the longitudinal axis of the body (Danna-Dos-Santos et al. 2007; Robert et al. 2008). A few recent studies have shown, however, that the composition of muscle modes can change under challenging conditions (Krishnamoorthy et al. 2004) and as a result of practice (Asaka et al. 2008) supporting the view that the modes are flexible muscle groupings that may be viewed as synergies in the space of muscle activations.

Synergies and the Equilibrium-Point Hypothesis

The equilibrium-point hypothesis of single-muscle control (reviewed in Feldman 1986; Feldman and Levin 1995) may be viewed as an example of how a large set of elements (motor units) can be united by a physiological mechanism (the tonic stretch reflex) to stabilize an important feature of performance – the equilibrium point characterized by values of muscle force and length. According to this hypothesis, the central nervous system specifies a value of the threshold of the tonic stretch reflex, while muscle activation level as well as its mechanical output are defined by both the central command and the reflex feedback from peripheral receptors.

The main idea of threshold control has been generalized to the control of multi-effector systems using the notion of *reference configuration* as a control variable at a higher level of a control hierarchy involved in the production of natural multi-muscle movements (Feldman et al. 2007; Pilon et al. 2007). Reference configuration defines, in the external space, a configuration, at which all the muscles would attain a minimal level of activity – a set of threshold values for muscle activation. If external conditions and/or anatomical constraints prevent a system from reaching its current reference configuration (as it commonly happens), muscles generate non-zero forces. In particular, fingertip forces on an external object emerge when a reference hand configuration corresponds to shorter flexor muscles as compared to the actual configuration. The general idea of control using reference configurations may be described as following a *principle of minimal end-state action*: The body tries to achieve an end-state, compatible with the external force field, where its muscles show minimal activation levels. This principle is a natural extension of the principle of minimal interaction (Gelfand and Tsetlin 1966).

The notion of *reference configuration* offers an attractive framework to analyze motor synergies. This framework assumes a hierarchical control system where, at each level of the

hierarchy, the system is redundant, that is, it produces more output variables than the number of constraints specified by input variables (as in Figure 3). Other characteristics of action may be allowed to vary based on secondary considerations, possibly reflecting optimization of certain features of performance. Because the system is redundant, a reference configuration at a higher hierarchical level does not specify unambiguously all the reference configurations at a lower level. Emergence of particular lower-level reference trajectories may be based on a feedback mechanism or on a feed-forward mechanism. Hence, a hierarchy of control levels, where each level functions based on the equilibrium-point control principle, seems like a plausible control structure leading to motor synergies.

Concluding Comments

This review offers a new look at the century-old concept of synergy. It suggests an operational definition that makes synergies quantifiable using the framework of the UCM hypothesis. It shows how synergies may compete or co-exist at different levels of the neuromotor hierarchy involved in the production of any voluntary action. It also links the idea of an hierarchy of synergies to a physiologically-based hypothesis of motor control, namely the equilibrium-point hypothesis. This approach seems to be applicable to apparently suboptimal movements performed by persons with movement disorders (Reisman et al. 2006), following atypical development (e.g., Latash et al. 2002a), and resulting from healthy aging (Shim et al. 2004; Olafsdottir et al. 2007).

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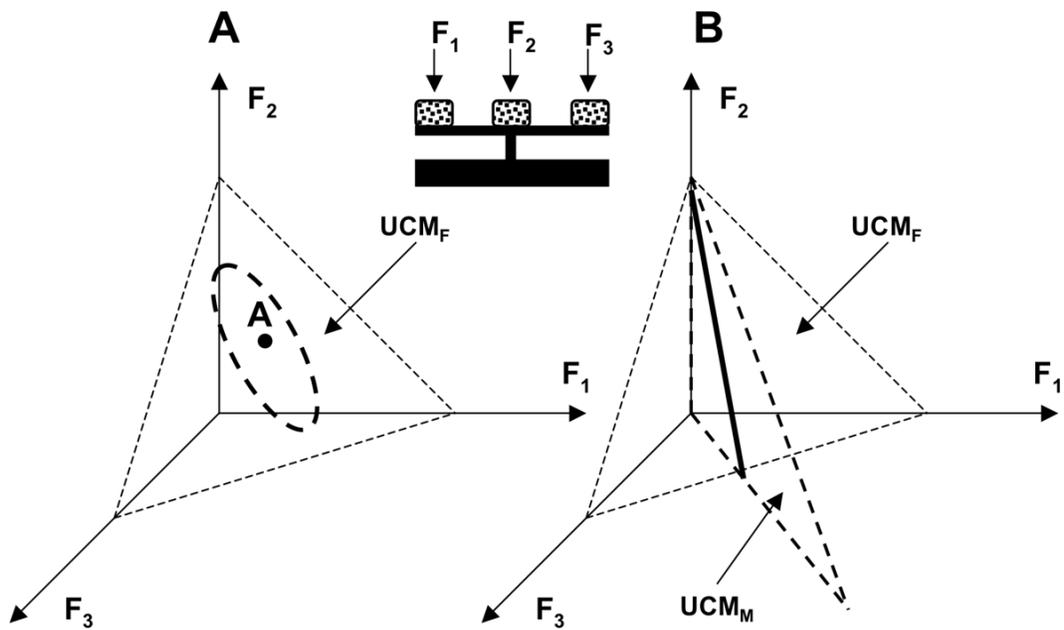


Figure 1. The task of constant total force production with three fingers acting in parallel. A: The sub-space corresponding to constant total force (UCM_F), an average sharing of force among the fingers (point A), and a possible data distribution across a series of trials (the ellipsoid); B: The sub-space corresponding to constant total moment of force, UCM_M (with respect to a pivot shown in the insert). The thick solid lines belongs to both sub-spaces shown by dashed lines.

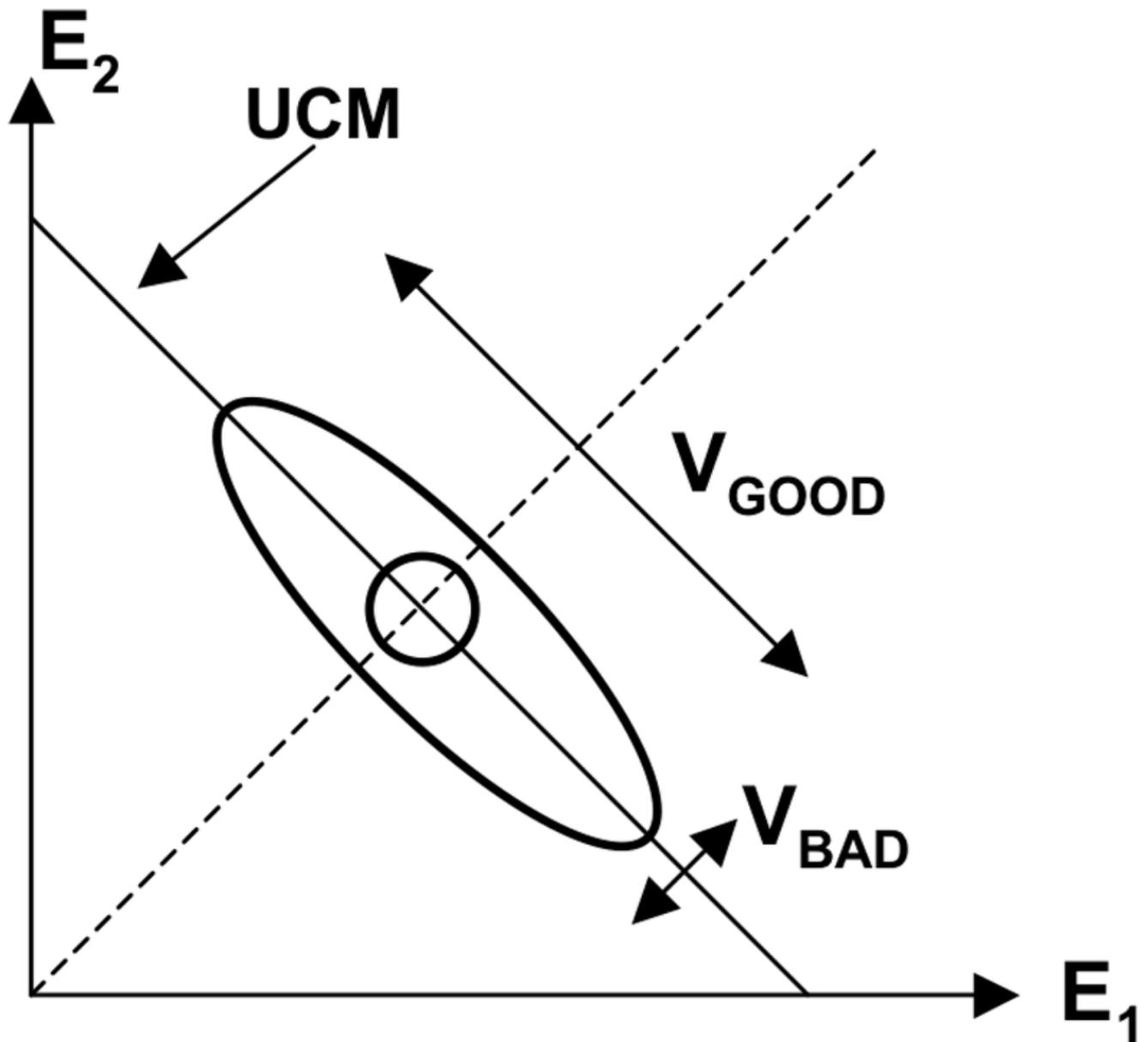


Figure 2. The task of constant output production by two effectors, E_1 and E_2 . The circle and the ellipse show data distribution across repetitive trials. The slanted solid line is the UCM for the task. The ellipse shows more variance parallel to the UCM (V_{GOOD}) as compared to variance orthogonal to it (V_{BAD}), while the circle has equal amount of variance in the two directions. The ellipse illustrates a not very accurate synergy, while the circle illustrates a very accurate non-synergy.

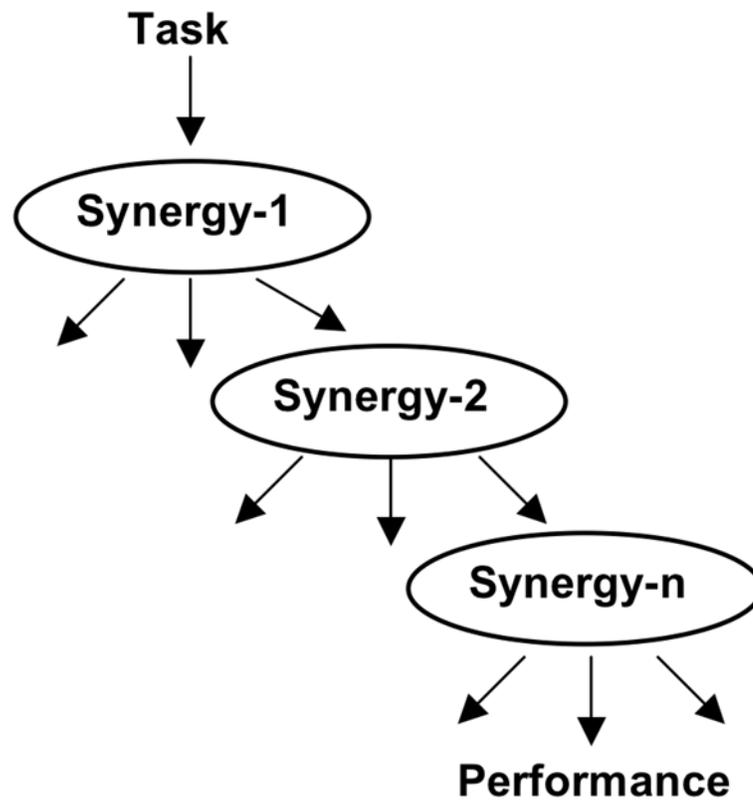


Figure 3.

An illustration of a hierarchy of synergies. At each level, the number of output variables is larger than the number of input variables. The output of each synergy serves as an input into a hierarchically lower synergy. Task serves as an input into the hierarchically highest synergy, while the hierarchically lowest one acts on the environment.

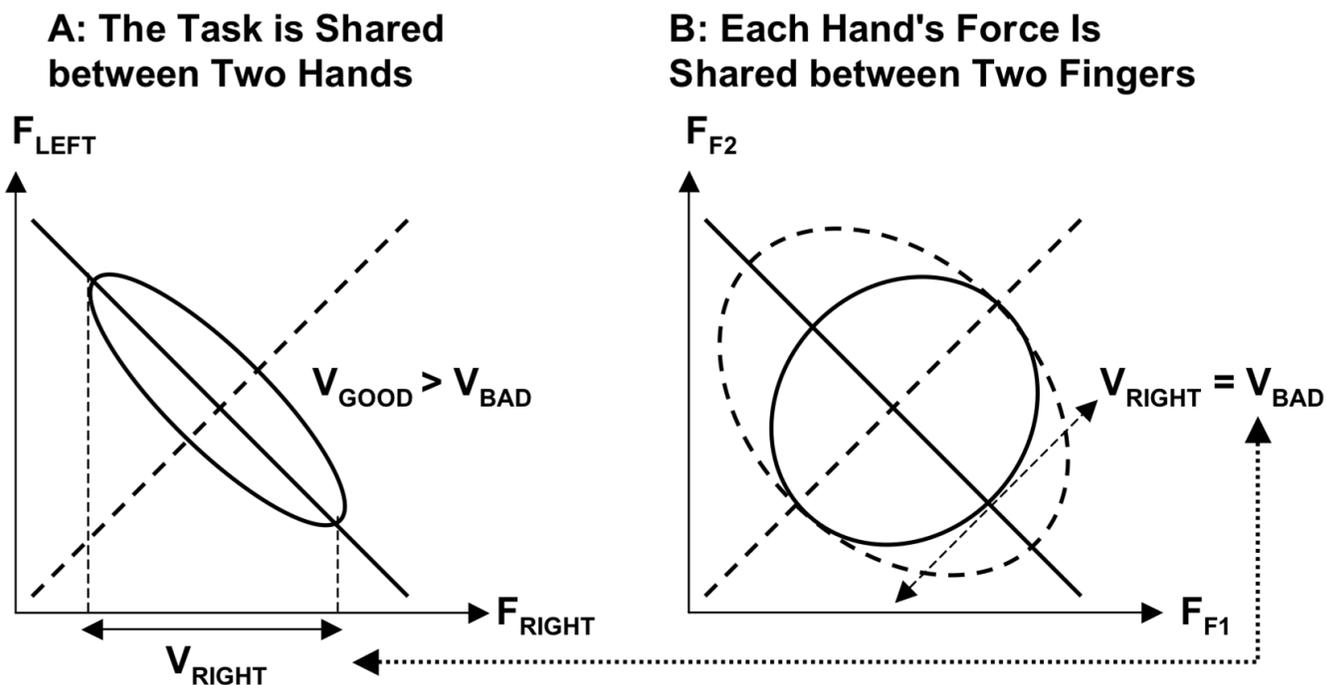


Figure 4. An illustration of data distributions for a task of producing a constant force level by four fingers, two per each hand. A force stabilizing synergy at the two-hand level (panel A) implies an inequality $V_{GOOD} > V_{BAD}$, which may result in large variance of each hand's output (e.g., V_{RIGHT}). This results in large V_{BAD} at the two-finger within-a-hand level, which may prevent a force stabilizing synergy at that level.