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Motor Synergies and the Equilibrium-Point Hypothesis

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Abstract

The article offers a way to unite three recent developments in the field of motor control and coordination: (1) The notion of synergies is introduced based on the principle of motor abundance; (2) The uncontrolled manifold hypothesis is described as offering a computational framework to identify and quantify synergies; and (3) The equilibrium-point hypothesis is described for a single muscle, single joint, and multi-joint systems. Merging these concepts into a single coherent scheme requires focusing on control variables rather than performance variables. The principle of minimal final action is formulated as the guiding principle within the referent configuration hypothesis. Motor actions are associated with setting two types of variables by a controller, those that ultimately define average performance patterns and those that define associated synergies. Predictions of the suggested scheme are reviewed, such as the phenomenon of anticipatory synergy adjustments, quick actions without changes in synergies, atypical synergies, and changes in synergies with practice. A few models are briefly reviewed.

Keywords

synergy; uncontrolled manifold hypothesis; equilibrium-point hypothesis; prehension; anticipatory control; hierarchical control

1. The Preamble

Some of the features of the human body, such as the sluggish muscles, relatively long time delays in neural pathways, complex mechanical interaction between moving segments, and ambiguous information from sensory receptors look like the sources of complex computational problems for the neural controller. Attempts at applying the progress in engineering and control theory to the problems of neural control of human movements have led to the recent surge in papers that view the human body as a poorly designed robot with a powerful computer on its shoulders. The brain has been assumed to contain “internal models” of the complex interactions within the body and between the body and the environment to make up for the apparent imperfection of the body’s design (as compared to the artificial moving systems with their powerful motors, no-delay electrical circuits, and other achievements of the XX-century engineering). This idea follows a seemingly natural axiom that in order to produce a movement of an effector from point A to point B, the controller has to make sure that requisite time profiles of force (and moment of force) are applied to the effector. This axiom, which is the foundation of the motor programming approach, looks so obvious that it takes an effort to realize that it may be wrong.

An alternative approach to the control of human movement starts not with the control theory and laws of classical mechanics but with the design of the human body, in particular its

central nervous system. The human system for movement production is a multi-element dynamic system, it evolves in time, and its output (including forces and moments of force) cannot be prescribed by any neural controller, no matter how smart it is (Glansdorff & Prigogine 1971). Such systems can be controlled only by setting their parameters, while their output emerges given the parameters and the interaction with the environment that proceeds according to the laws of physics. This approach to voluntary movements has been developed over the past half-a-century (reviewed in Kugler & Turvey 1987; Feldman & Levin 1995; Latash 2008) in parallel to and in competition with the motor programming approach, from the schema theory to the internal models (reviewed in Schmidt 1975; Wolpert et al. 1998; Shadmehr & Wise 2005; see also Ostry & Feldman 2003).

Movement of a human effector, from a single joint to the whole body, is a transition between its equilibrium states (equilibrium points, EPs). To perform a movement requires that the original EP disappears and a new one (or a time series of new EPs) is established. We are going to review the processes that are likely to be involved in EP shifts in the next section.

An amazing feature of motor behavior is its stability with respect to important variables (set by the goals) given the unpredictable external forces and inherently noisy elements. The notion of stability of voluntary movements has been addressed in a recent excellent review (Hasan 2005). One of the points made in that review is that stability may not be always desirable since it implies a trade-off with maneuverability. This view is very close to the recent developments of the notion of synergies as neural organizations that simultaneously ensure stability and flexibility of movements (reviewed in Latash et al. 2002b, 2007).

This paper tries to achieve two goals: (1) To merge the EP hypothesis of motor control and the mentioned notion of motor synergies; and (2) To formulate and support a hypothesis that there are two methods of ensuring stable motor behavior, non-synergic and synergic. Synergic methods of ensuring stability comply with the principle of minimal final action (a development of the famous principle of minimal interaction, described later, Gelfand & Tsetlin 1966) and are naturally compatible with the EP control of human movements. It is also suggested that stability of equilibrium states can be not only purposefully created but also purposefully destroyed.

2. The Background

This section reviews two interrelated aspects of motor control that may be referred to as “control” (the nature of neural variables that are manipulated to produce movements) and “coordination” (co-variation of the outputs of elements in a multi-element system). We are going to start with coordination and introduce the notion of motor synergies and the uncontrolled manifold (UCM) hypothesis. Further, we turn to control, review the EP-hypothesis, its recent development in the form of the referent configuration hypothesis, and relations between the latter and the notion of synergies.

2.1. Motor Synergies and the UCM Hypothesis

Assume that the neural control of movement is hierarchical and that, at each level of the hierarchy, the input is low-dimensional as compared to the output (cf. the problem of motor redundancy, Bernstein 1967; Figure 1). Hence, each hierarchical level deals with an apparent problem of redundancy: How to define the output (elemental variables) given an input that specifies what the system has to produce as a whole.

We assume that at each level, the problem is solved not by finding a unique, optimal solution but by facilitating families of solutions that are all capable of solving the task

adequately (the principle of abundance, Gelfand & Latash 1998, 2002). This is achieved by co-varying elemental variables in such a way that the overall output remains close to a required value. We will use the term “synergy” for a hypothetical neural mechanism that ensures task-specific co-variation of elemental variables providing for desired stability properties of an important output (performance) variable.

There is a natural link between the introduced notion of synergy and the uncontrolled manifold (UCM) hypothesis (Schöner 1995; Scholz & Schöner 1999; reviewed in Latash et al. 2002b, 2007). The UCM hypothesis states that the controller acts in a high-dimensional space of elemental variables and organizes in that space a subspace (the UCM) corresponding to a desired value of a particular performance variable. Further, the controller organizes co-variation among the elemental variables (across trials or across time samples) in such a way that their variance is mostly constrained to the UCM. This may be interpreted as stabilizing the performance variable. The UCM idea is close in spirit to those of the “self-motion manifold” (e.g., Demers & Kreutz-Delgado 1996), the “no-motion manifold” suggested by Laboissiere et al. (1996), and the “goal-equivalent manifold” formulated by Cusumano and Cesari (2006).

Figure 2 illustrates the main idea of the UCM hypothesis using a simple example of producing a certain level of total force with two independent effectors, for example the two index fingers. This task, obviously, has an infinite number of solutions that may be illustrated on the force-force plane by a straight line (the slanted dashed line in Figure 2; this line is the UCM for this task). The controller may prefer to share the total force between the two fingers in a certain way, for example about 40%:60%. Each finger may be expected to show some unavoidable trial-to-trial variability in its force. Three ellipses in Figure 2 illustrate three possible data point distributions. The circular distribution illustrates no co-variation between the outputs of the two fingers, that is a non-synergy according to our definition. The ellipse elongated along the dashed line corresponds to a synergy stabilizing total force because most of the finger force variance does not affect total force (we are going to call this variance component “good variance”, V_{GOOD}) and only a small fraction of variance (“bad variance”, V_{BAD}) leads to total force variations. The ellipse elongated orthogonal to the UCM corresponds to $V_{\text{BAD}} > V_{\text{GOOD}}$, which may be interpreted as a co-variation destabilizing the total force.

In the illustrated simple linear system the UCM is linear. This is not always the case. For example, commonly tasks require motion of the endpoint of a limb into a target. In such cases, individual joint rotations may be viewed as elemental variables, and the relations between small changes in these variables and endpoint coordinate shifts are nonlinear. For such tasks, analysis is typically performed within a linear approximation, using the null-space of the Jacobian matrix (\mathbf{J} , mapping small changes in the elemental variables onto changes in the global performance variable) as a local approximation of the UCM (see Scholz & Schöner 1999; Scholz et al. 2000; Latash et al. 2007). By definition, the null-space of \mathbf{J} is a set of all vector solutions \mathbf{x} of the equation $\mathbf{J}\mathbf{x} = \mathbf{0}$. Within the null-space, changes in the performance variable are nil.

Originally, the purpose of synergies was viewed as a means of organizing a system with apparently redundant degrees-of-freedom to achieve low variability (high stability) of its functionally important output (Bernstein 1967; Latash et al. 2002b). Note, however, that the definition of synergy is based on an inequality $V_{\text{GOOD}} > V_{\text{BAD}}$. The output variability is defined by V_{BAD} . Why would the controller facilitate large V_{GOOD} if it is, by definition, irrelevant to performance? Several recent studies have suggested that V_{GOOD} is truly good, not irrelevant (Gorniak et al. 2007; Shapkova et al. 2007; Zhang et al. 2008). Large V_{GOOD} does not by itself affect variance of the performance but it affords the system flexibility to

perform other tasks using the same elemental variables and, potentially, deal with unexpected perturbations applied to one (a few) of the elements. There is evidence that a purposeful increase in V_{GOOD} may be related to allowing the system to explore a variety of solutions in unusual conditions or in conditions of uncertainty (Yang et al. 2007; De Freitas et al. 2007; Freitas & Scholz 2009).

Many studies used the method of the UCM hypothesis to quantify synergies stabilizing a variety of performance variables by different sets of elemental variables, kinetic, kinematic, and electromyographic (reviewed in Latash 2008) in a variety of tasks. However, all those studies used peripheral performance variables produced by apparent elements (or their hypothetical direct precursors, so-called modes, Latash et al. 2001; Krishnamoorthy et al. 2003), not control variables. Partly, this problem was due to the elusive nature of the control variables, which is addressed in the next subsection.

2.2. The Equilibrium-Point Hypothesis

The EP-hypothesis (Feldman 1966, 1986) is, to our knowledge, the only theory in the field of motor control that specifies physiological variables that are used by the central nervous system as control variables. According to the EP-hypothesis, central control signals change the threshold of activation of alpha-motoneurons to afferent signals related to muscle length (threshold of the tonic stretch reflex, λ) by subthreshold depolarization of the alpha-motoneurons. Central signals are not the only ones contributing to λ , which also changes with muscle velocity (because of the velocity-sensitivity of muscle spindle endings), signals from sensory receptors in other muscles, and history of activation (Feldman & Latash 2005).

Consider control of a single muscle (Figure 3). Setting a value of λ leads to a dependence of active muscle force on muscle length (the invariant characteristic, IC). Muscle force, level of activation, and length all change along the IC. This means that setting a value of λ does not prescribe any of the mentioned peripheral variables, but they emerge depending on the external load (L in Figure 3). The point of intersection between the load characteristic (three loads, isotonic, isometric, and elastic are illustrated in Figure 3) is the equilibrium point (EP) of the system. Note that EP is not a value of muscle length but a combination of muscle length and force values. Posture-stabilizing mechanisms ensure stability of EP under transient external force perturbations. Two types of movement are possible within this scheme, passive that follow change in L without a change in λ , and active – when λ is changed by the controller. In either case, the original EP shifts to a new location that may involve a change in length, force, or both (Figure 4).

Voluntary muscle control is associated with three distinct time patterns of important variables. First, the time profile of the control variable, $\lambda(t)$ may be viewed as the **control trajectory**. Second, for each λ (given an external load), there is an instantaneous EP – a combination of muscle length and force that would have been observed if the control process stopped and the system were given time to reach an equilibrium state. Instantaneous EP is typically not directly observable, in particular because of the inertial properties of the system. A time sequence of EPs forms an **equilibrium trajectory** of the system that can be described with two variables $\{x_{\text{EP}}(t); F_{\text{EP}}(t)\}$, i.e. in units of displacement and force. And finally, there is an **actual trajectory** that can also be described in both units of displacement and force (for example, in isotonic and isometric conditions). The actual trajectory is the only reliable observable, while attempts at reconstructing the other two trajectories involved simplified models of the moving system (Latash & Gottlieb 1991; Latash 1992; Gomi & Kawato 1992) and might have led to distorted time profiles of $\lambda(t)$ and EP(t) (Gribble et al. 1998).

Control of a simple joint with one kinematic degree of freedom may be viewed as resulting from specifying the control variables for the agonist and antagonist muscles. There are at least two muscles crossing any joint. Hence, there are at least two control variables, λ_{FL} and λ_{EX} that specify the threshold of the tonic stretch reflex for each of the two opposing muscles (for example, a flexor and an extensor). Another, equivalent pair of control variables has been suggested, r and c . The r command defines the midpoint between the two λ s, and changes in r lead to reciprocal changes in muscle activation levels (reciprocal command). The c command defines a range where both muscles can be activated simultaneously, and changes in c lead to parallel changes in the muscle activation levels (coactivation command).

3. The Main Points

3.1. Referent Configuration: Linking the EP-hypothesis and the Idea of Synergies

The main idea of the EP-hypothesis – that is, neural control with shifting thresholds for muscle activation – has been generalized in the form of the referent configuration hypothesis (Feldman & Levin 1995; Feldman et al. 2007). According to this hypothesis, the neural controller sets a referent configuration of the body (or of salient points on the body), a configuration at which all the muscles are at the threshold of activation via the stretch reflex. Discrepancies between the actual and referent configurations lead to muscle activations that act to move the actual configuration towards the referent one. Commonly, actual body configuration cannot reach the referent one because of anatomical and external force constraints thus leading to non-zero muscle activation levels at equilibrium.

In other words, given a set of central variables and a set of mechanical constraints, the neuromuscular system tries to achieve a state of minimal muscle activation. This basic principle can be called **the principle of minimal final action**. It is a younger cousin of the famous principle of minimal interaction introduced by Gelfand and Tsetlin nearly half-a-century ago (1967). Gelfand and Tsetlin suggested that the interaction among elements of a multi-element system was organized so as to minimize the external input to each individual element (and, correspondingly, its output) while keeping the total output of the system compatible with the command signal from the hierarchically higher controller. Minimal final action may also be viewed as a consequence of the natural trend of physical systems to move to a state with minimal potential energy.

There are natural links between the EP-hypothesis and the introduced definition of synergies. Even at the single-muscle level, the mechanism of the tonic stretch reflex, which plays a central role in the EP-hypothesis, may be viewed as a particular feedback-based method of organizing a multi-motor-unit synergy stabilizing the level of muscle activation. Indeed, if one motor unit suddenly turns off (introduces an “error”), the muscle force will drop, the balance of forces between the muscle and the external load will be violated, the muscle will stretch, its spindle afferents will increase the frequency of firing, and this increase will lead to an increase in the overall level of activation of the motoneuronal pool, at least partly compensating for the original “error”.

Now, imagine that a person tries to perform a multi-joint reaching motion into a target. At the highest level of the hierarchy, control variables may be associated with setting two multi-dimensional variables, a referent position of the endpoint (R) and its apparent stiffness (C). R is defined as a position, at which the endpoint would be in an equilibrium, given the external force field, while C defines resistance to slow small perturbations (cf. the idea of endpoint impedance control, Hogan 1985). These variables result from $\{r,c\}_i$ pairs for each of the i kinematic degrees-of-freedom. We assume that the $\{R,C\}$ dimensionality is smaller than that of all the $\{r,c\}_i$ pairs combined. Then, the problem of defining a set of $\{r,c\}_i$ based

on $\{R,C\}$ is redundant and may involve creating a multi- $\{r,c\}$ synergy stabilizing $\{R,C\}$ (Figure 5, top).

At the next step, muscle control variables, $\{\lambda_j\}$ have to be defined for each $\{r,c\}_i$ pair. Most joints are crossed by more than two muscles; for example, the relatively simple elbow joint, which has only one kinematic degree-of-freedom, is crossed by three flexors and three extensors. Hence the problem of defining a set of $\{\lambda_j\}$ to match a pair $\{r,c\}$ is also redundant. A multi- λ synergy may be used to solve this problem based on the principle of abundance (Figure 5, bottom). Hence, the control using referent configurations may be viewed as based on a hierarchy of synergies of control variables.

Another link between the referent configuration hypothesis and the idea of synergies is that, at least some of the synergies among performance variables studied in earlier studies, might have naturally resulted from the method of control with referent configurations. Consider grasping an object with two opposing digits (Figure 6). According to the referent configuration hypothesis, this action is associated with setting a referent aperture (AP_{REF}) between the digits (Pilon et al. 2007). The object does not allow the digits to move to AP_{REF} . As a result, the difference between the actual aperture (AP_{ACT}) and AP_{REF} leads to active grip force production.

Consider now the task of preventing the object in Figure 6 from moving along the X-axis. To achieve this result, the forces produced by the opposing effectors have to be equal in magnitude: $F_1 + F_2 = 0$. This is one equation with two unknowns – a problem of redundancy – and it may be expected to involve a two-digit synergy stabilizing the resultant force at a close to zero level (confirmed experimentally, Zhang et al. 2009; Gorniak et al. 2009a,b). Note, however, that setting AP_{REF} by itself leads naturally to such a synergy. Setting a smaller or larger AP_{REF} (certainly, within reasonable limits), centered closer to one digit or closer to the other digit, is always expected to result in $F_1 + F_2 = 0$, while the forces produced by each of the digits and the spatial location of the handle where the forces are balanced may differ across trials. Note that if the two opposing effectors belong to two persons, this method of control becomes unavailable, and the two participants have to set referent coordinates for each of the effectors, rather than a referent aperture value. This leads to significantly lower indices of synergies stabilizing the resultant force in the X-direction (Gorniak et al. 2009b).

This simple example illustrates how the principle of control involving setting referent values for important points on the body, $\{R,C\}$ in combination with the principle of minimal final action may lead to synergic relations among elemental variables without any additional smart controlling action. To realize this principle, sensory feedback on the salient variable (AP_{ACT}) has to be used as an input into a neuron whose threshold is set at AP_{REF} by the controller. If $AP_{ACT} > AP_{REF}$, the neuron generates action potentials leading to shifts of λ for muscles producing closure of the opposing digits (possibly using a hierarchical scheme illustrated in Figure 5). The digits move towards each other until $AP_{ACT} = AP_{REF}$ or, if the digits are prevented from moving, active grip force production occurs.

3.2. Two Methods of Ensuring Motor Stability

Given a centrally specified referent configuration, the neuromotor system moves to a state with minimal weighted muscle activations (minimal final action) compatible with the external forces and anatomy. However, we know that positioning the endpoint of a limb into a target does not limit what humans can do; they can also co-contract limb muscles without moving from the target but “stiffening” the limb. Hence, we assume that the minimal final action may be scaled by a second component of control related to desired stability of the endpoint at the target and, possibly, with a trade-off between stability and muscle activation.

Many studies invoked and explored this method of achieving stability, via muscle co-contraction (Woollacott et al. 1988; Bouisset & Zattara 1990; McIntyre et al. 1996; Zatsiorsky 2002). In particular, direct links between postural instability and modulation of an index of muscle co-contraction (associated with the c-command within the EP-hypothesis) have been demonstrated in experiments on subjects who stood with and without additional destabilizing factors (Slijper & Latash 2000).

The idea of synergies suggests that stability may also be achieved by another method, not directly associated with increased muscle activations (and higher apparent joint stiffness). Stability of a performance variable (for example, the endpoint coordinate) may be increased by organizing proper co-variation among elemental variables that make sure that any deviations of elemental variables are mostly channeled into “good variability” (see V_{GOOD} in Figure 2).

So, there are two methods of increasing stability of performance: (1) increasing muscle co-contraction by changing the outputs of the muscles in a properly scaled manner; and (2) organizing a multi-muscle synergy that arranges appropriate co-variation of muscle activation levels that, on average, may remain unchanged. The first method is more typical of poorly practiced tasks, tasks performed in novel and/or unpredictable conditions, and tasks performed by an impaired neuromuscular system. This view is supported by a number of studies documenting increased indices of muscle co-contraction during early stages of motor learning and in persons with motor impairments (Woollacott et al. 1998; Darainy et al. 2004; Latash & Anson 2006; Darainy & Ostry 2008). The second method reflects an important feature of motor synergies, that is their ability to ensure two features, stability and flexibility (the last word means an ability to achieve the same value of an important performance variable with variable combinations of elemental variables, cf. “repetition without repetition”, Bernstein 1935, 1967).

Figure 7 illustrates a hypothetical control scheme with two types of control variables, CV1 related to a desired value of a performance variable, and CV2 related to synergies that do or do not stabilize that variable. The EP-hypothesis suggests the nature of CV1 – referent configuration translated into thresholds for muscle activation. There is no equivalent hypothesis for CV2 at this time. There are, however, several models that will be reviewed in a future section.

The hypothesis on the existence of two groups of control variables entails a few consequences (predictions):

Prediction-1: There is a possibility to change one of these variables without changing the other. This means, in particular, that synergies may be changed without changing the overall output of a multi-element system and, vice versa, an action (a purposeful change in a performance variable) may start without a change in pre-existent synergies stabilizing that variable.

Prediction-2: Practice may lead to changes in patterns of both CV1 and CV2. A change in CV1 is expected to lead to an improvement of an average across trials performance. A change in CV2 is expected to lead to higher or lower proportion of V_{GOOD} in the total variance and, correspondingly, to less or more stereotypical performance.

Prediction-3: Impaired (atypical) motor performance may be associated with impaired (atypical) patterns of CV1 and/or CV2. If the former variables are affected, changes in average movement patterns may be expected. Impaired CV2 patterns may lead to problems with stability of motor patterns without necessarily affecting their overall time profiles.

Certainly, in cases of long-standing disorders, adaptive changes in both CV1 and CV2 may be expected (Latash & Anson 1996, 2006).

4. Experimental Support

4.1. Are There Multi- $\{r,c\}$ and Multi- λ Synergies?

Most evidence supporting existence of multi- $\{r,c\}$ and multi- λ synergies is indirect. It comes partly from studies of multi-joint actions at a kinematic level and partly from (very few) studies of control variables during two- and multi-joint actions in the presence of motor redundancy.

Several studies have shown that natural kinematic variability at a joint level is partly compensated such that important kinematic variables show relatively little variance across trials. These involve the classical study of blacksmiths by Bernstein (1930), as well as more recent studies of reaching (Domkin et al. 2002, 2005), pointing (Jaric & Latash 1999), swaying (Freitas et al. 2006), and taking a sip from the glass (Latash & Jaric 2002). Some of these studies used the framework of the UCM hypothesis and analyzed variance in the joint configuration space with respect to several performance variables that the controller might care about (Scholz & Schöner 1999; Scholz et al. 2000; Reisman et al. 2002; Freitas et al. 2006). In particular, across trials variance of the joint configurations during quick-draw pistol shooting (Scholz et al. 2000) was associated with a strong synergy (in a sense that $V_{\text{GOOD}} > V_{\text{BAD}}$, see Figure 2) stabilizing the orientation of the barrel with respect to the target, stronger than a synergy stabilizing the pistol trajectory in space. This is a non-trivial result, given that the barrel orientation was stabilized even at earlier phases of the action when the pistol was pointing at a large angle away from the target.

These observations, however, cannot be easily interpreted at the level of control variables, that is $\{r,c\}$ pairs for each joint or λ s for individual muscles. To remind, elemental performance variables, such as joint rotations, reflect both control variables and external forces, including interaction forces that depend on movement of other joints. Hence, specific patterns of co-variation at the level of joint rotations do not automatically imply co-variation of control variables such as $\{r,c\}$ pairs. Even when movements are performed very slowly, joint coupling is still present due, in particular, to the action of bi- and multi-articular muscles and inter-joint reflexes (Nichols 1989 1994).

There have been only a handful of studies that tried to reconstruct control variables during a multi-joint action within the framework of the EP-hypothesis (Latash et al. 1998; Domen et al. 1999). The first of those studies explored quick flexion and extension movements of one of the two joints in the wrist-elbow system, when the subject sat, placed his/her right upper arm on the table and oriented the forearm and the hand vertically (Figure 8, top). Moving one of the joints quickly is associated with moments of force acting on the other joint. As a result, preventing flapping of the apparently “static” joint requires accurate control of the muscles acting at that joint (Koshland et al. 1991; Latash et al. 1995). Reconstruction of the equilibrium trajectories of the two joints (under an assumed simplified model!) has shown similarly timed profiles of the EP(t) at the two joints, which were spatially different: For the instructed joint, the equilibrium trajectory led to a new joint position, while for the other joint, it ended up at the same joint position representing a control pattern with the purpose to avoid joint motion (Figure 8, bottom). The similar time patterns and scaling of the peak-to-peak equilibrium trajectories at the two joints are signatures of a two-joint synergy at a control level, a synergy between $\{r,c\}_{\text{ELBOW}}$ and $\{r,c\}_{\text{WRIST}}$ that stabilized $\{R,C\}$ for the arm endpoint (cf. Figure 5).

4.2. Lessons from Studies of Prehension Synergies

The method of control with referent configurations can be applied simultaneously to several variables salient for the task of holding an object. These components may be viewed as involving changes in the referent vertical position of the hand (to counterbalance the weight of the object at a certain vertical location), in the referent aperture (to ensure a certain object location in the horizontal direction and to provide sufficient grip force given the friction), and in the referent pronation-supination angle of the hand (to counterbalance the external torque). They all project onto the same group of elemental variables, forces and moments of force produced by individual digits.

Consider, for simplicity, a planar case when the external torque acts in the plane of the grasp (the plane that passes through all the points of digit contact with the object). The equations of statics require that:

$$-F_{th}^n = F_i^n + F_m^n + F_r^n + F_l^n \quad (1)$$

$$-W = F_{th}^t + F_i^t + F_m^t + F_r^t + F_l^t \quad (2)$$

$$-T = \underbrace{F_{th}^n d_{th} + F_i^n d_i + F_m^n d_m + F_r^n d_r + F_l^n d_l}_{\text{Moment of the normal forces} \equiv M^n} + \underbrace{F_{th}^t r_{th} + F_i^t r_i + F_m^t r_m + F_r^t r_r + F_l^t r_l}_{\text{Moment of the tangential forces} \equiv M^t} \quad (3)$$

where the subscripts *th*, *i*, *m*, *r*, and *l* refer to the thumb, index, middle, ring, and little finger, respectively; the superscripts *n* and *t* stand for the normal and tangential force components, respectively; *W* is weight of the object, *T* is external torque, and coefficients *d* and *r* stand for the moment arms of the normal and tangential force with respect to a pre-selected center, respectively. The number of equations is smaller than the number of the variables, that is the system is redundant; this is true even for only two digits opposing each other.

As described in an earlier section, setting referent aperture satisfies Eq. (1) and allows to generate grip force. Similarly, setting a referent vertical position of the hand and a referent pronation/supination position allow to satisfy Eqs. (2) and (3). Several consequences may be expected from such control.

First, if we assume that the three mentioned referent values may be changed by the controller independently of each other, there should be no interactions of the effects of external load (*W*) and torque (*T*) on all the elemental mechanical variables produced by individual digits. This prediction has been confirmed experimentally (Shim et al. 2003; Zatsiorsky et al. 2003, 2004). Hence, this type of control entails the principle of superposition in prehension (see Arimoto et al. 2001; Zatsiorsky et al. 2004) as a direct consequence.

Second, if the load and/or torque are removed unexpectedly and the person does not try to correct the action, motion of the hand is expected towards the three referent values. This prediction has been confirmed in a recent experiment (Latash, Friedman, Kim, Feldman, Zatsiorsky, unpublished). In this experiment, the subjects were required to lift very quickly a handle instrumented with six-component force/torque sensors from a resting position on the table to a target. The handle had a certain weight and a certain torque with respect to its geometrical center. In catch trials, the handle happened to be fixed to the table, the subject's

fingers slipped off the sensors, and the hand was lifted without the handle. In the catch trials, the hand stopped at a new, higher vertical location, its digits moved towards each other, and it showed rotation in pronation/supination, as expected from setting the three referent values. Figure 9 illustrates the changes in the horizontal coordinates of the thumb and index finger tips (A) and in the hand aperture (B) in the perturbed (thick traces) and unperturbed trials.

4.3. Changes in Synergies prior to Action: Anticipatory Synergy Adjustments

Several recent studies have provided experimental support for the prediction that the controller can adjust synergies (using CV2 in Figure 7) without a change in the overall output of the system (defined by CV1 in Figure 7). Figure 10 illustrates one of these studies (Olafsdottir et al. 2005). The subjects were instructed to keep a constant level of total force by pressing naturally with the four fingers of the right (dominant) hand on individual force sensors. Then, at a self-selected time, the subjects produced a very quick force pulse to a target. An index of synergy was computed across trials after the trials were aligned by the force pulse initiation. This index (ΔV) reflected the normalized difference between the good and bad components of variance (V_{GOOD} and V_{BAD} in Figure 2). The index showed highly positive values during the steady-state corresponding to a very strong multi-finger synergy stabilizing the total force. The ΔV index showed a drop starting 100–150 ms prior to the first detectable changes in the total force but only when the subjects performed the task in a self-paced manner (Figure 10).

This phenomenon has been termed anticipatory co-variation or anticipatory synergy adjustment (ASA). It was later documented in a variety of tasks (Shim et al. 2005, 2006; Kim et al. 2006). Its purpose has been viewed as turning off synergies stabilizing a performance variable in preparation to its quick change. Indeed, trying to change quickly a variable that is stabilized at a certain value by a strong synergy is obviously suboptimal because the controller has to fight its own synergy.

Several features make ASAs similar to a well-known phenomenon in movement studies, that is anticipatory postural adjustments (APAs). APAs represent changes in the activation of apparently postural muscles when a person performs a quick action leading to a postural perturbation (Belenkiy et al. 1967; reviewed in Massion 1992). They are typically seen about 100 ms prior to the initiation of the instructed action. Both ASAs and APAs show a delayed start (about the time of action initiation) when a person is instructed to perform a similar action not in a self-paced manner but under a typical simple reaction time instruction: as quickly as possible following an imperative signal (Lee et al. 1987; De Wolf et al. 1998; Olafsdottir et al. 2005, see Figure 10). Both ASAs and APAs are delayed and reduced in magnitude in elderly persons (Woollacott et al. 1988; Olafsdottir et al. 2007). These coincidences are too many to be ignored. They suggest that ASAs and APAs share the same central mechanism, at least partly.

The traditional view on APAs is that they produce forces and moments of force acting against those expected from the action and associated postural perturbation (Bouisset & Zattara 1987; Massion 1992). Indeed, most published results are compatible with this view, although changes in salient mechanical variables during APAs are commonly very small and not very reproducible as compared to more substantial changes in the muscle activation levels (e.g., Aruin & Latash 1995). There have, however, been several reports documenting reversals of APAs such that their mechanical effects could act in the direction of the expected perturbation, not against it (Hirschfeld & Forssberg 1991; Krishnamoorthy & Latash 2005).

The APA reversals and the presented data on similarities between APAs and ASAs suggest a hypothesis that APAs reflect at least two processes. One of them is associated with the

generation of forces and moments of force that the controller views as adequate for the expected perturbation and the current state of the postural system. The other reflects turning down (or even off) pre-existent synergies stabilizing performance variables that the controller plans to change quickly after the perturbation takes place.

Recently, the method of synergy studies within the framework of the UCM hypothesis has been developed to studies of multi-muscle synergies stabilizing potentially important variables such as coordinate of the center of pressure (COP) during postural tasks (Krishnamoorthy et al. 2003; Danna-Dos-Santos et al. 2007). These experiments have shown, in particular, early changes in indices of corresponding synergies stabilizing COP coordinates at the initiation of a quick voluntary COP shift (Wang et al. 2006). These results corroborate the idea that, at least partly, APAs are actually ASAs.

4.4. Actions without Changes in Synergies

Several studies have shown that quick changes in performance variables may happen without a change in the index of synergies stabilizing those variables. These studies confirm that CV1 in Figure 6 can be changed without a change in CV2, which, by definition, is expected to change the relative amounts of V_{GOOD} and V_{BAD} resulting in a changed synergy index.

In particular, in the mentioned study of quick-draw pistol shooting (Scholz et al. 2000), the action was very quick, it took about 250–300 ms from the movement initiation to pressing the trigger. During that time, the pistol barrel rotated over more than 90°. Nevertheless, there were no changes in the relative amount of V_{GOOD} in the total joint configuration variance; V_{GOOD} was consistently larger than V_{BAD} .

A study of multi-muscle synergies stabilizing the coordinate of the center of pressure in the anterior-posterior direction (COP_{AP}) during voluntary whole-body sway explored a broad range of sway frequencies, from 0.25 to 1.5 Hz (Danna-Dos-Santos et al. 2007). During the sway, both the direction and rate of COP_{AP} shift varied within a cycle. Nevertheless, there were no major changes in the relative amount of V_{GOOD} in the total variance computed in the space of muscle modes (hypothetical variables manipulated by the controller, Krishnamoorthy et al. 2003), corresponding to COP_{AP} stabilizing synergies both across the frequencies and across the cycle within each frequency.

4.5. Lessons from Studies of Motor Learning

Motor learning has been traditionally viewed as a process involving a few stages such as freezing and freeing degrees-of-freedom (Bernstein 1967; Newell 1991; Vereijken et al. 1992). In contrast, the scheme in Figure 6 suggests that motor learning can bring about changes in CV1 and/or CV2 leading, respectively, to improved average performance and/or to changes in the relative amounts of good and bad components of variability. This scheme contrasts two possible effects of practice, learning how to produce desired time profiles of performance variables and learning relevant synergies.

If one practices to become more accurate at a certain motor task, an expected drop in variability of a performance variable with practice means that V_{BAD} drops. What can be expected from V_{GOOD} , which, by definition, does not affect performance? Does the central nervous system care about this seemingly irrelevant component of variability? Several recent studies suggest that it does.

Figure 11 illustrates three possible scenarios of synergy changes using the earlier example of accurate force production with two index fingers. It assumes that before practice a synergy existed stabilizing the total force across repetitive trials ($V_{\text{GOOD}} > V_{\text{BAD}}$ in panel A). With

practice, V_{BAD} drops as expected. If V_{GOOD} stays unchanged, decreases less than V_{BAD} , or increases, this may be interpreted as the synergy becoming stronger (panel B). If V_{GOOD} decreases in proportion to V_{BAD} , more accurate performance is accompanied by an unchanged synergy (panel C). V_{GOOD} can also drop more than V_{BAD} leading to a more spherical data distribution (panel D), a weaker synergy. Data compatible with all three scenarios have been reported suggesting that improved performance may indeed be accompanied by stronger, weaker, or unchanged synergies.

It is natural to expect synergies to strengthen with practice and indeed several studies reported results compatible with Figure 11B. Two of these studies investigated typical subjects who practiced Frisbee throwing (Yang & Scholz 2006) and the production of an accurate force pattern with unusual finger combinations (Kang et al. 2004). One more study studied the ability of persons with Down syndrome to produce accurate profiles of the total force while pressing with the four fingers of the dominant hand (Latash et al. 2002). In that study, prior to practice, the participants showed an atypical inequality $V_{\text{BAD}} > V_{\text{GOOD}}$ that apparently destabilized the total force. After three days of practice, the inequality reversed, $V_{\text{BAD}} < V_{\text{GOOD}}$, at least within a certain force range, corresponding to a force-stabilizing synergy (Scholz et al. 2003).

One of the early studies of changes in kinematic synergies with practice led to the most unusual outcome corresponding to a decrease in the synergy strength with practice (Figure 11D; Domkin et al. 2002). In that study, the subjects practiced a rather simple task of bi-manual pointing when one hand moved the target and the other hand moved the pointer. In a follow-up (Domkin et al. 2005) that involved a more complex task, the second scenario (Figure 11C) was observed with proportional changes in both components of variance, V_{BAD} and V_{GOOD} .

Finally, one more study observed a sequence of opposite effects starting with an increase in the synergy index early in practice followed by its decrease (Latash et al. 2003). In that study, the subjects reached very high accuracy (very low V_{BAD}) in the performance of the task (accurate multi-finger force production with constraints on the moment of force) about the mid-point over the practice time. With further practice, they apparently adjusted their control strategies to handle other components of the task without changing V_{BAD} . This led to shrinking V_{GOOD} and to an apparent drop in the synergy index. This study suggests the existence of stages in the process of motor learning, but the stages are not associated with changes in the number of degrees of freedom (cf. Vereijken et al. 1992) but with emergence of and changes in appropriate synergies.

In the language of the EP-hypothesis, stages in motor learning may be associated with a shift in the variables that are manipulated at the highest level of the hierarchy. Imagine practicing a very unusual multi-joint task associated with a time function of a performance variable, PV. The neural controller might have never faced such tasks before, and it has to control each joint action individually. This may be associated with specifying and refining a set of $\{r,c\}_i$ functions to match the task at hand (cf. Figure 5). Weak or no synergies stabilizing PV may be expected at this stage. Further, a set of variables related to equilibrium states of PV (for example, the endpoint trajectory) may be elaborated, $\{R,C\}$. The projection of $\{R,C\}$ onto $\{r,c\}_i$ may be expected to lead to synergies stabilizing that PV that will become stronger with practice. If the person continues to practice the task, further improvement in performance may be associated with optimization of aspects of the task that are not directly related to PV time profile such as, for example, esthetics, energy expenditure, fatigue, etc. Such additional constraints are expected to limit the space of acceptable solutions that lead to the same PV values, i.e. limit the amount of good variance. This is expected to be associated with a drop in the synergy index. Since the number of levels in a hypothetical

control hierarchy may be more than two, the number of stages in the process of motor learning may also be higher than two.

4.6. Lessons from Studies of Impaired and Atypical Populations

Only a handful of studies quantified synergies within the suggested framework during movements performed by atypical persons or persons with motor impairments. More typically, clinical studies use the word “synergy” to describe atypical *average* patterns of motor variables, not patterns of their co-variation (Bobath 1978; Dewald et al. 1995).

A study of the kinematics of reaching movements after stroke has resulted in unexpected findings (Reisman and Scholz 2003). Although there was a significant deterioration of the movement characteristics such as longer movement time, poorly reproducible shape of the endpoint trajectory, and poor accuracy (cf. Levin 1996), the index of multi-joint synergy was similar for movements performed by the more impaired limb and by the less impaired limb. Hence, in our language, stroke led to major problems with time profiles of CV1 variables, but no comparable problems were seen in the CV2 variables (Figure 7).

The mentioned study of multi-finger accurate force production tasks by persons with Down syndrome (Latash et al. 2003) documented atypical patterns of finger force co-variation: The persons with Down syndrome showed strong positive co-variation of finger forces across trials. In a sense, they used the hand as a fork turned upside down such that the forces produced by the “prongs” always scaled together. That study also showed that three days of practice were sufficient to turn the atypical patterns into more typical ones that involved flexible finger involvement and higher proportion of good variability.

Finally, a series of studies explored changes in multi-finger synergies that happen with healthy aging. Those studies documented significantly reduced indices of multi-digit synergies, particularly those related to stabilization of the rotational hand action (Olafsdottir et al. 2007a). Elderly persons also showed reduced anticipatory synergy adjustments (ASAs, see earlier) in preparation to a quick action and to a self-triggered mechanical perturbation (Olafsdottir et al. 2007b). A recent study of the effects of hand strength training in elderly persons showed a significant correlation between changes in the accuracy of performance of a multi-finger force production task and changes in the indices of multi-finger force stabilizing synergies (Olafsdottir et al. 2008).

Taken together, these few studies suggest the following conclusions. First, motor synergies are not obligatory, they may disappear, emerge, and change. Second, the method of quantifying synergies is sensitive to such factors as atypical development, healthy aging, and neurological injury, as well as to specific and less-specific (strength training) practice. Third, the area of studying synergies in patients with motor disorders is inherently rich and largely unexplored. It is California waiting for the Gold Rush.

4.7. Links to Models

Most existing models of motor synergies have a common drawback, they use a language of performance variables instead of trying to link performance to changes in control variables. As mentioned in the earlier sections, such variables as muscle forces, joint torques, joint angles, and their derivatives are all performance variables. Any analysis of synergies that tries to link co-variation of elemental performance variables to a global performance variable (for example, trying to link co-variation of digit forces to the resultant force acting on a hand-held object; see Zatsiorsky & Latash 2004) suffers from the same basic flaw: It assumes implicitly that this language is adequate to represent control strategies of the central nervous system. As illustrated earlier (for example, see Figure 6), such apparent synergies

may emerge not because the controller organizes covariation among a set of elemental variables but due to the basic mechanism of control with referent configurations of the body.

There seem to be two types of co-variation patterns among elemental variables, those induced by the control with referent configurations and those that are not dictated by this control mechanism. For example, imagine holding an object with a prismatic grasp (the four fingers opposing the thumb). Setting a referent aperture (Pilon et al. 2007; Figure 6) leads to co-variation between the normal force of the thumb and the resultant normal force produced by the four fingers. So, this pattern of co-variation belongs to the first type. The next question is: How will referent positions of the individual fingers covary given a fixed referent aperture? This question has no simple answer. The four fingers may be characterized by four referent positions, $X_{R,i}$ (i = index, middle, ring, and little fingers). There is an infinite number of $X_{R,i}$ combinations that satisfy a given referent aperture. Even if an additional constraint is introduced (for example, related to a required total rotational hand action), this still results in only two equations with four unknowns. Setting values of the referent aperture (and referent hand orientation) imposes constraints on the “bad variability” in the space of finger referent positions, but the person is free to combine this V_{BAD} with any amount of V_{GOOD} , leading or not leading to multi-finger synergies stabilizing the overall hand action. These are synergies of the second type. Their existence is exemplified, in particular, by their presence or absence in different subpopulations and after different amounts of practice (Latash et al. 2002a; Kang et al. 2004; Olafsdottir et al. 2007).

Current models of motor synergies typically operate with performance variables at two levels, elemental and global. Some of these models use a feedback mechanism that adjust individual elemental variables based on the combined output of all the elemental variables. An optimal feedback control model by Todorov and Jordan (2002) implies using feedback loops from peripheral receptors or within the central nervous system to structure variance in the space of elemental variables. Another model of this kind (Latash et al. 2005) assumes that stabilization of particular performance variables is realized with central back-coupling loops (similar to the feedback effects on alpha-motoneurons from Renshaw cells, Katz et al. 1993; Hultborn et al. 2004). Both models have been able to account for certain features of motor synergies such as the structure of variance. The latter model has also accounted for the mechanism of anticipatory synergy adjustments (ASAs, see earlier) and the very short time delays from the initiation of an action to the first signs of an appropriate synergy (cf. Shim et al. 2003b).

A recent model (Goodman & Latash 2006) has been based on an assumption that a hypothetical controller has information on the mapping between small changes in elemental variables and changes in an important global performance variable (the Jacobian of the system). Sensory feedback within this model is used only to update this knowledge, not to correct the ongoing control signals. This model is similar in spirit to an approach advocated by Bullock et al. (1993), who proposed a neuronal network that learns coordinate transformations from end-effector to joint coordinates resulting in a structure that selects one solution out of a set of motor-equivalent solutions.

As of now, the most comprehensive model has been developed by Martin, Scholz and Schöner (Martin et al., 2004; Martin et al., 2009) for a particular case of multi-joint reaching movement. This is also the only model that links explicitly the ideas of the UCM hypothesis and the EP-hypothesis. The model views each joint as being driven by a time profile of its equilibrium point (which is assumed to be noisy) produced by an artificial neural network. The network receives an input timing signal from a set of oscillators that define the progression of the end-effector along its trajectory.

5. Concluding Comments and Future Directions

Let me summarize the main points made in this paper. The recent developments of the notion of synergies, the uncontrolled manifold hypothesis, and the equilibrium-point hypothesis suggest that these, previously separate, issues can be merged in a natural and productive way. This is achieved based on two principles, the principle of abundance and the principle of minimal final action. A number of distinct experimental findings, such as the structure of variance in multi-effector tasks, anticipatory changes in motor synergies, prehension synergies, changes in synergy indices in certain special populations and with practice can all fit a physiologically based theory of motor control, namely the referent configuration (equilibrium-point) hypothesis supplemented with the idea of synergic control of multi-element systems.

Synergic control is not obligatory for natural human movements, in some tasks it may be absent, it can be learned and modified. Its main advantage is in allowing the central nervous system to use a set of elemental variables to perform several tasks simultaneously without sacrificing accuracy (stability) of performing either of them. The handful of studies performed on special populations so far have demonstrated that this is a potentially powerful framework to address applied issues of motor control such as effects of specialized practice (athletics), disordered movements, and effects of rehabilitation.

One of the current main challenges is the lack of tools to study patterns of control variables (such as time patterns of λ for muscles and related control variables at the joint and whole-body levels) with sufficient accuracy. This seems to be a major obstacle on the way to studying motor synergies using the language of control variables rather than elemental performance variables.

Another obstacle is the necessity to perform analysis of the structure of variance across many repetitive trials. In clinical studies, this may present a major obstacle, for example because of quick fatigue. It is, in principle, possible to extend the computational approach within the UCM framework to analysis of single trials. This has been done in a study of multi-finger isometric accurate force production (Scholz et al. 2003). However, the method has not yet been developed to tasks that involve major changes in the Jacobian matrix in the course of the movement, for example to multi-joint pointing.

However, even the available tools, with their obvious limitations, offer a productive approach to analysis of unimpaired and disordered motor synergies. Issues of changes in synergies with practice, fatigue, disorder, and rehabilitation remain largely unexplored despite the availability of the well developed computational approach based on the UCM hypothesis. I hope that the readers of this paper will become interested in exploring and developing this framework and addressing zillions of exciting and practically highly relevant problems related to the control of natural human movement.

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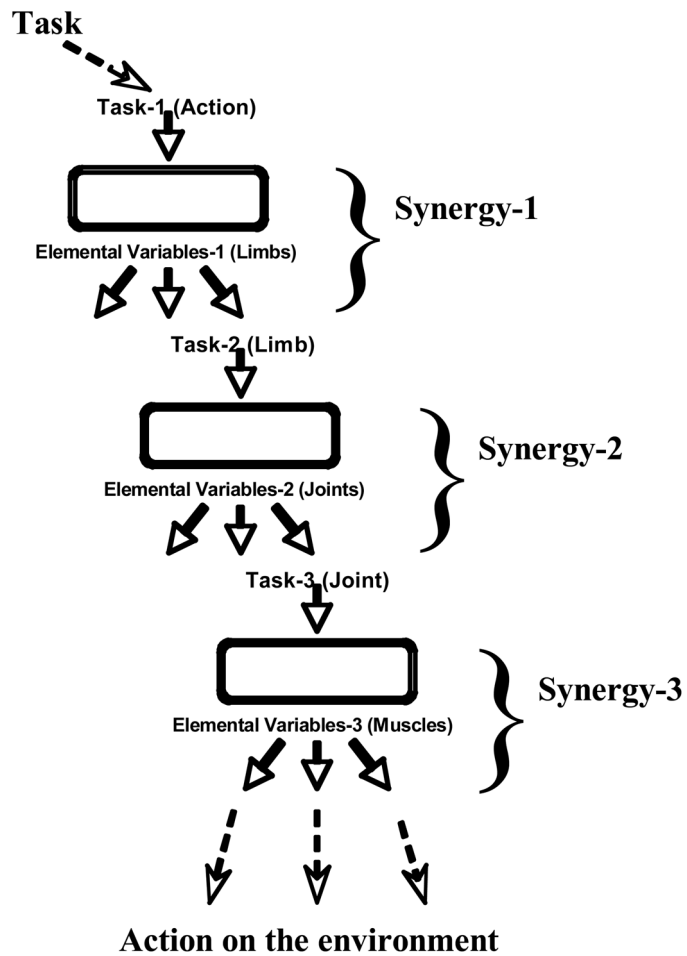


Figure 1. A scheme of a control hierarchy. At each level, a few-to-many mapping takes place (the input is low-dimensional as compared to the output). Output signals serve as the inputs into a hierarchically lower level. Feedback loops are not shown not to overload the scheme but they are assumed both within each level and across levels.

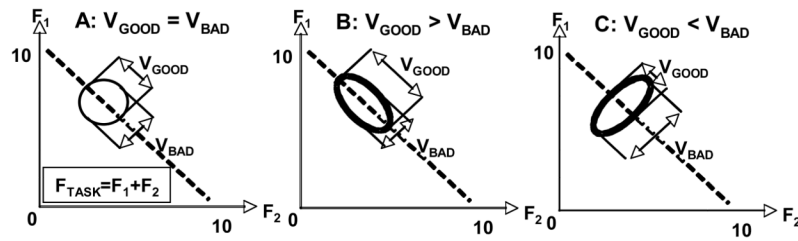


Figure 2.

An illustration of the idea of “good” and “bad” components of variance (V_{GOOD} and V_{BAD}). The task is to produce a constant force level (F_{TASK}) using two effectors that generate forces F_1 and F_2 . The dashed line corresponding to the equation $F_{TASK} = F_1 + F_2$ defines the uncontrolled manifold (UCM) for this performance variable. Three ellipses illustrate possible data point distributions. The circular distribution (A) implies no co-variation between F_1 and F_2 , a non-synergy. The ellipse elongated along the dashed line (B) corresponds to $V_{GOOD} > V_{BAD}$ - a synergy stabilizing F_{TASK} . The ellipse elongated orthogonal to the UCM corresponds to $V_{BAD} > V_{GOOD}$, which may be interpreted as a co-variation destabilizing F_{TASK} .

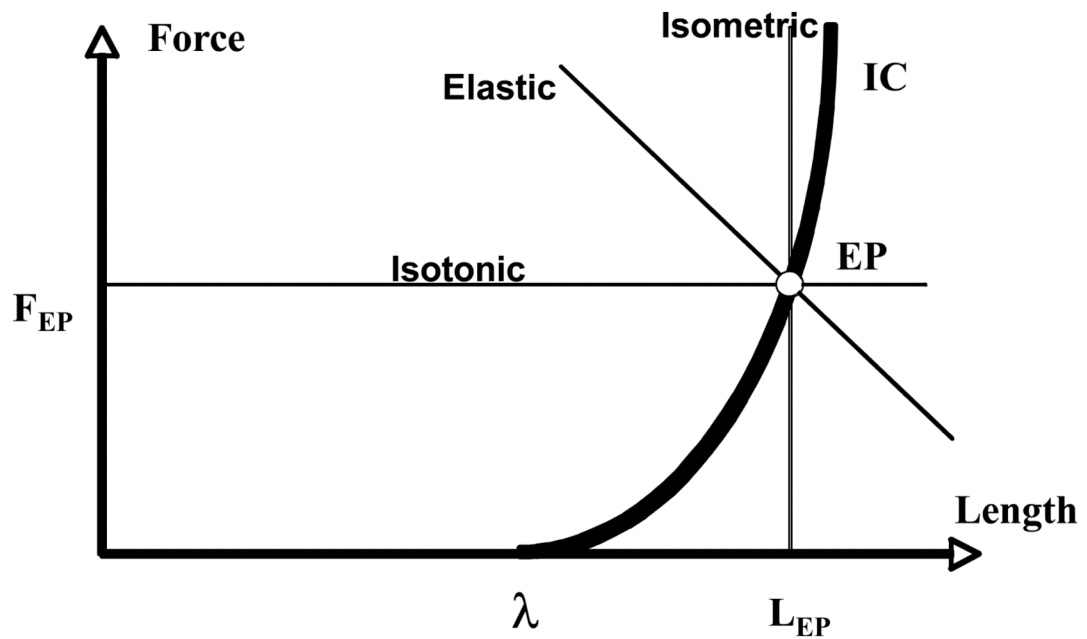


Figure 3.

An illustration of the EP-hypothesis for a single muscle. Setting a value of λ defines a dependence of active muscle force on muscle length (IC). Muscle force, level of activation, and length all change along IC. The point of intersection between the load characteristic (L, isotonic load, isometric load, and elastic load are illustrated with the solid, dashed, and dotted lines respectively) is the equilibrium point (EP) of the system corresponding to a combination of muscle length (L_{EP}) and muscle force (F_{EP}).

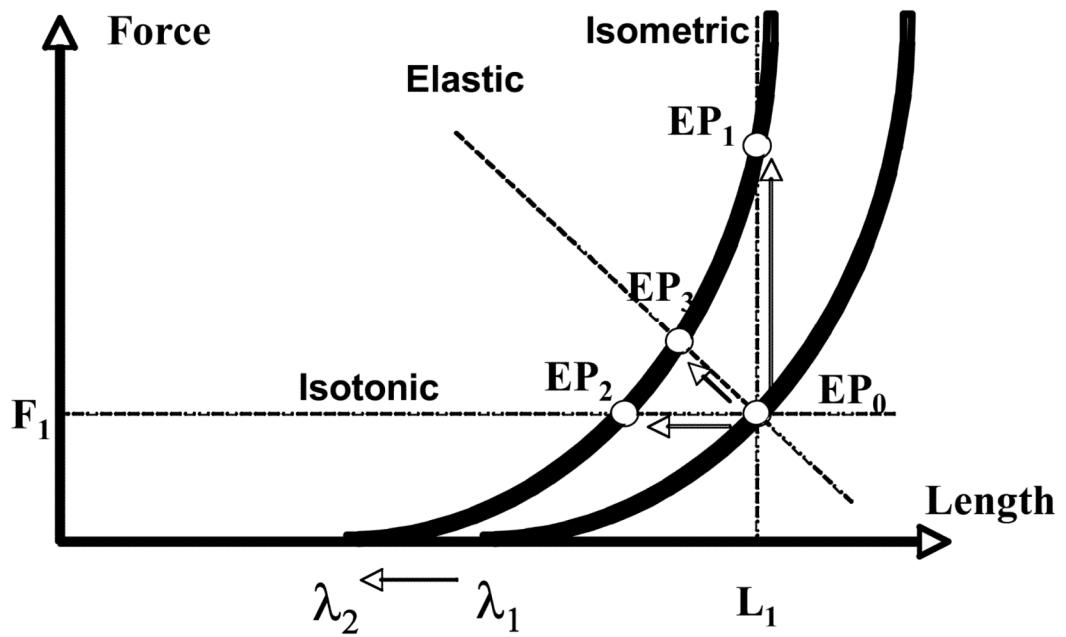


Figure 4. Within the EP-hypothesis, movement can emerge following a change in the external load (L) or a shift in the central control variable λ . A shift from λ_1 to λ_2 may lead to a change in muscle force (isometric conditions, $EP_0 - EP_1$), muscle length (isotonic conditions, $EP_0 - EP_2$), or both ($EP_0 - EP_3$).

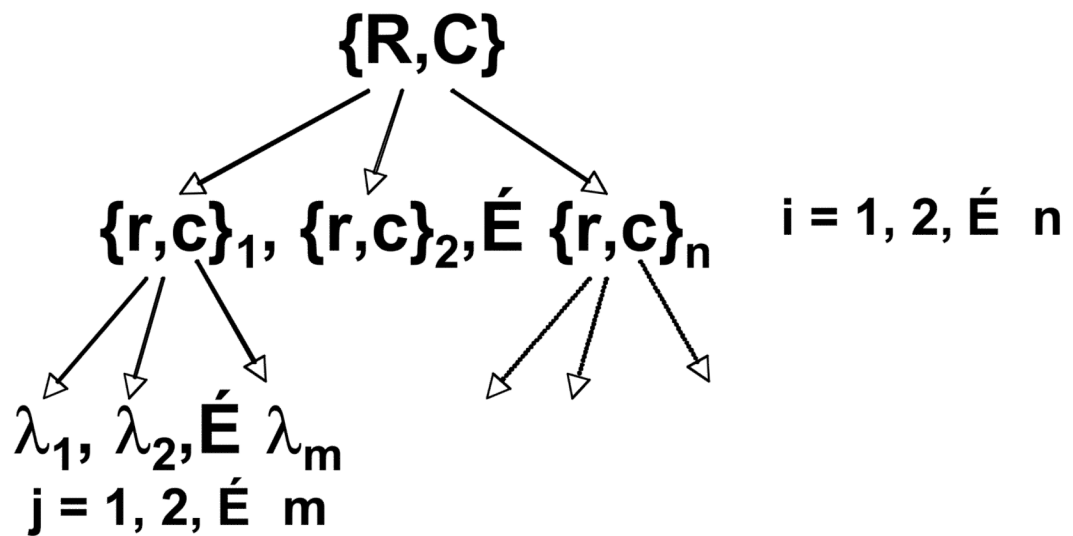


Figure 5.

A hypothetical hierarchy of control variables within the referent configuration hypothesis illustrated with the task of placing the endpoint of a redundant kinematic chain into a target. At the higher level, based on the task, a referent configuration $\{R,C\}$ is selected. At the next level, these signals project on n $\{r,c\}$ pairs for individual joints. At the next level, each $\{r,c\}$ pair serves as the input into a synergy that defines m λ values for the participating muscles.

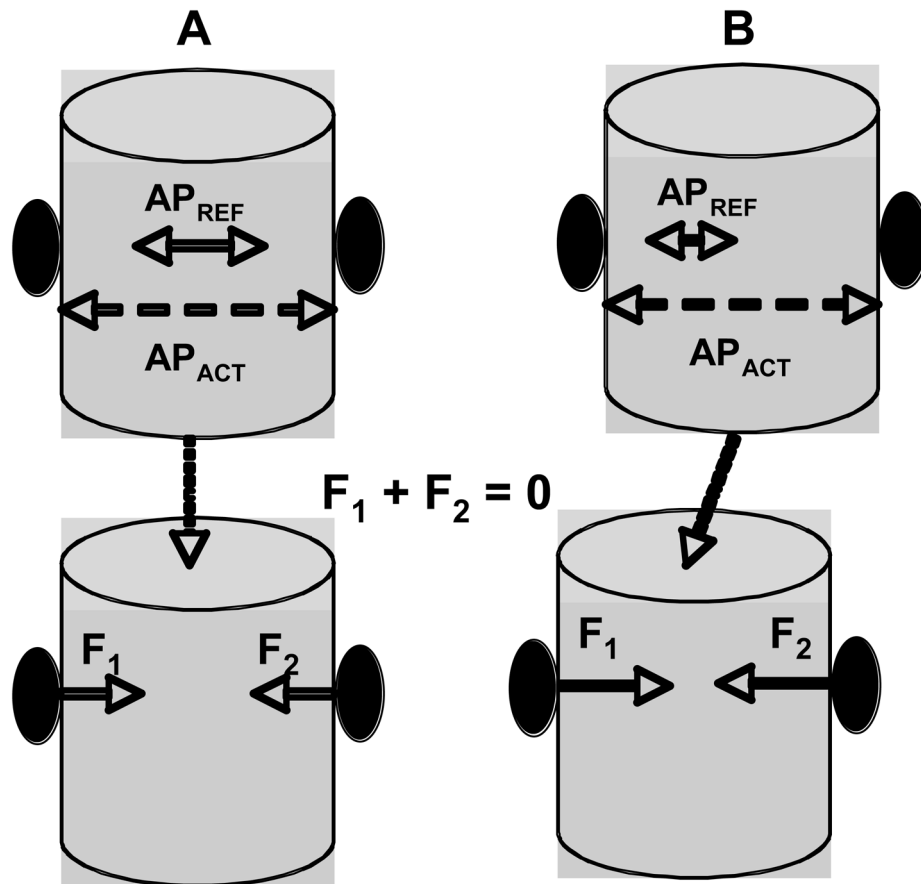


Figure 6.

Setting a value of referent aperture (AP_{REF}) leads to active force production against the walls of the hand-held object because of the difference between the actual aperture (AP_{ACT}) and AP_{REF} (upper panels). This mode of control would always lead to equality of the two opposing forces ($F_1 + F_2 = 0$; lower panels) that may be achieved at different spatial locations if AP_{REF} is located off-center (as in panel B).

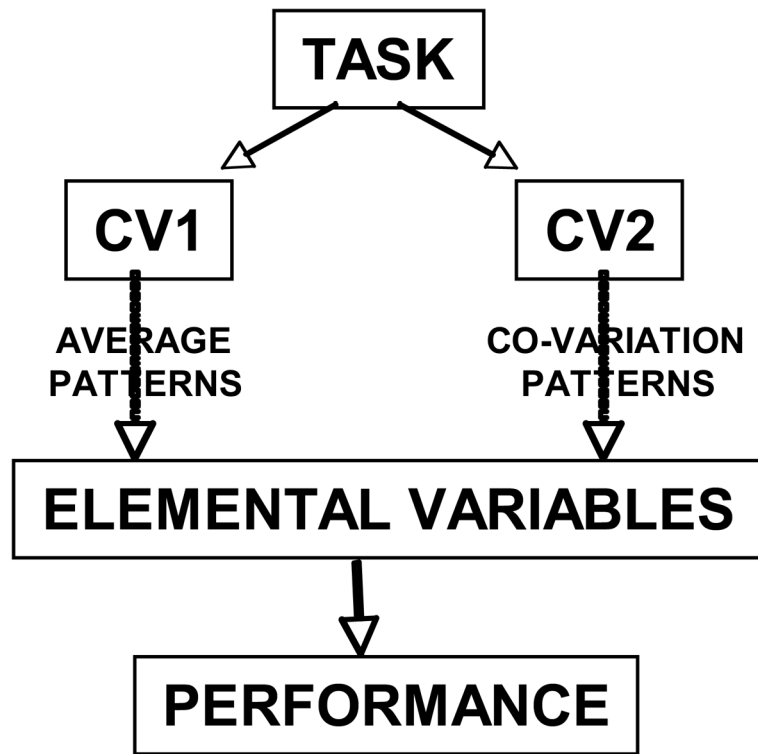


Figure 7.

A hypothetical control scheme with two types of control variables, CV1 related to a desired value of a performance variable, and CV2 related to synergies that do or do not stabilize that variable.

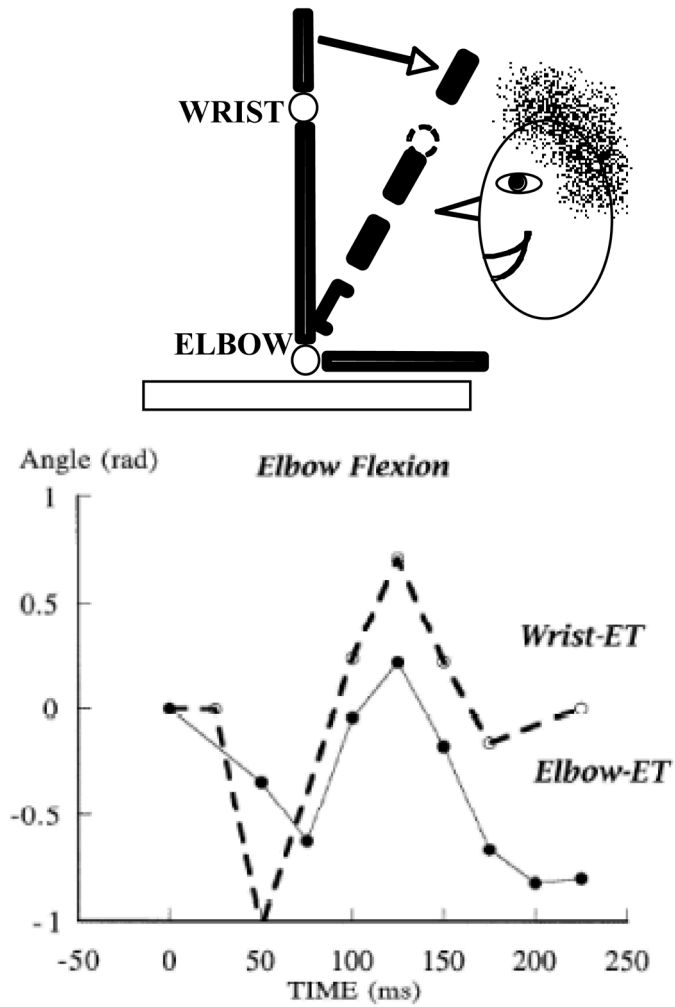


Figure 8.

Top: The subject placed the upper arm on the table and performed quick elbow flexion movements. Bottom: Equilibrium trajectories reconstructed for the wrist and elbow joints when only the elbow joint was instructed to perform a fast movement. Note the large peak-to-peak amplitude of the wrist equilibrium trajectory and the similar timing of the trajectory peaks. The purpose of the control of the wrist is to prevent its motion under the action of interaction torques. ET – equilibrium trajectory. Modified by permission from Latash ML, Aruin AS, Zatsiorsky VM (1999) The basis of a simple synergy: Reconstruction of joint equilibrium trajectories during unrestrained arm movements. *Human Movement Science* 18: 3–30.

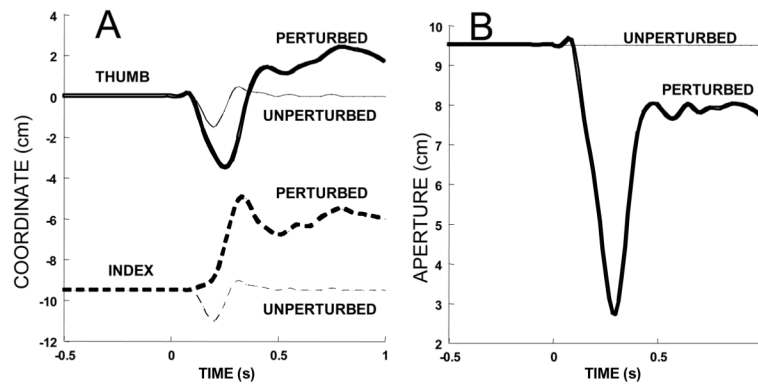


Figure 9.

The subject lifted an instrumented handle quickly in the vertical direction towards a target. The handle could be pre-loaded to introduce a non-zero moment of force in a static condition. Two typical trials are illustrated. In one trial (perturbed trial), the handle was fixed to the table, the digits slipped off the sensors, and the hand moved without the handle. Panel A shows the time profiles of the thumb and index finger coordinates under the two conditions. Panel B shows the time changes in the hand aperture in the two trials. Note the transient closure of the index finger and the thumb and the smaller aperture in the final state.

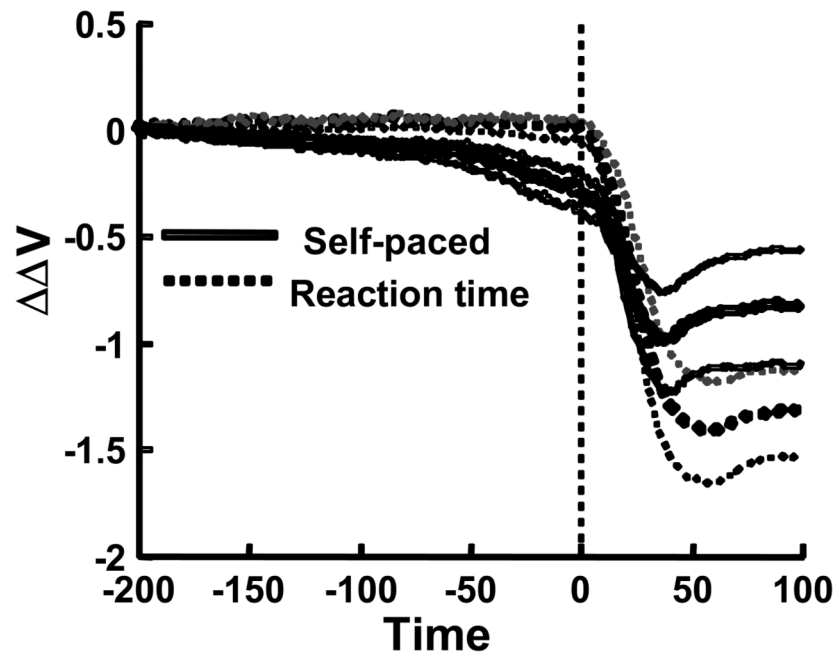


Figure 10.

Changes in the index of multi-finger synergy stabilizing total force ($\Delta\Delta V$) prior to a quick force pulse production at a self-selected time and “as quickly as possible” following an auditory signal. Note the early drop in ΔV in the self-paced trials (solid lines), but not in the reaction-time trials (dashed lines). Average time profiles are shown with standard deviation (thin lines). Reproduced by permission from Olafsdottir H, Yoshida N, Zatsiorsky VM, Latash ML (2005) Anticipatory covariation of finger forces during self-paced and reaction time force production. *Neuroscience Letters* 381: 92–96.

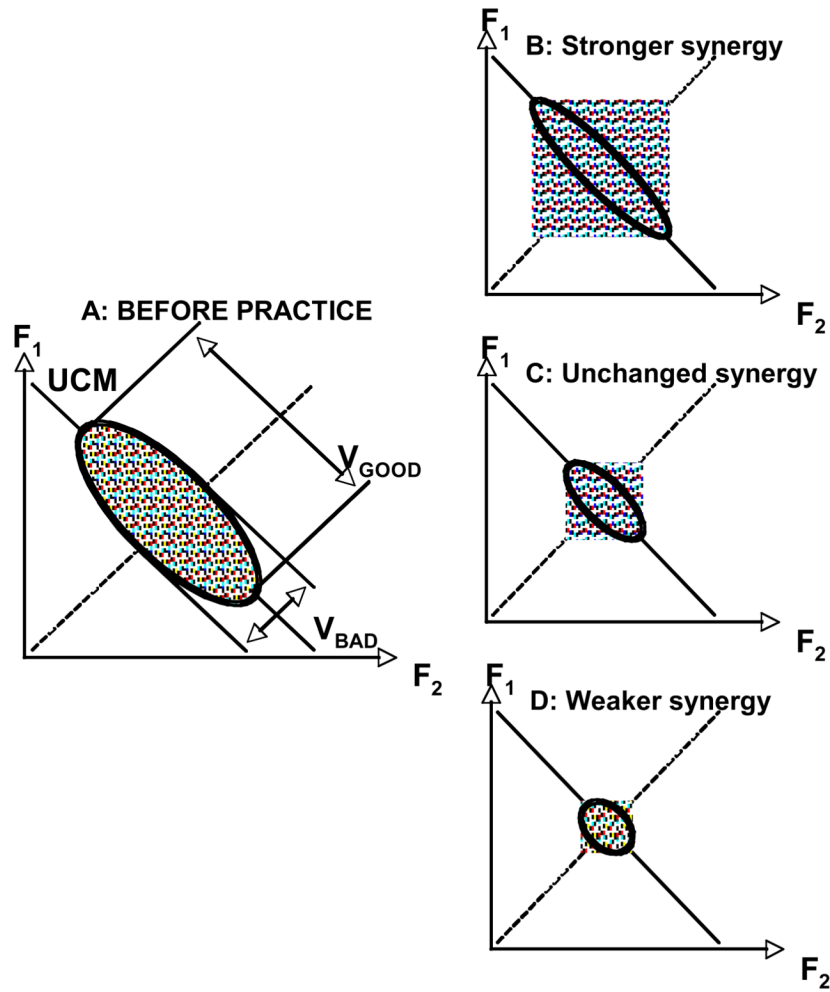


Figure 11. Three possible scenarios of synergy changes during force production with two index fingers. Before practice a synergy existed stabilizing the total force across repetitive trials ($V_{GOOD} > V_{BAD}$ in panel A). With practice, V_{BAD} drops. If V_{GOOD} stays unchanged, decreases less than V_{BAD} , or increases, this may be interpreted as the synergy becoming stronger (panel B). If V_{GOOD} decreases in proportion to V_{BAD} , more accurate performance is accompanied by the unchanged synergy (panel C). V_{GOOD} can also drop more than V_{BAD} leading to a more spherical data distribution (panel D), a weaker synergy.