

Toward a New Theory of Motor Synergies

Mark L. Latash, John P. Scholz, and Gregor Schöner

Driven by recent empirical studies, we offer a new understanding of the degrees of freedom problem, and propose a refined concept of synergy as a neural organization that ensures a one-to-many mapping of variables providing for both stability of important performance variables and flexibility of motor patterns to deal with possible perturbations and/or secondary tasks. Empirical evidence is reviewed, including a discussion of the operationalization of stability/flexibility through the method of the uncontrolled manifold. We show how this concept establishes links between the various accounts for how movement is organized in redundant effector systems.

Key Words: force production, motor learning, movement, posture, redundancy, synergy

The central nervous system knows nothing about muscles, it only knows movements.

J. Hughlings Jackson (1889, p. 358)

The Degrees-of-Freedom (DOFs) Problem

Voluntary actions consist of movements directed at motor tasks. Humans reach for objects, and then grasp and handle them. Humans locomote, transporting their body through space to desired locations while remaining upright. At every level of analysis of the system for the production of voluntary movements, there are more elements contributing to performance than are absolutely necessary to solve these motor tasks. For instance, the body has more joints than needed to position the center of mass in space, the human arm has more joints than needed to configure the spatial position and orientation of the hand on an object. Similarly, the hand has more fingers than needed to generate a grasp.

This problem of redundancy has been recognized as a central one from the earliest days of the scientific study of motor control. N.A. Bernstein developed

Latash is with the Dept of Kinesiology, Pennsylvania State University, University Park, PA 16802. Scholz is with the Dept of Physical Therapy and Biomechanics and Movement Science Program, University of Delaware, Newark, DE 19716. Schöner is with the Lehrstuhl Theoretische Biologie, Institut für Neuroinformatik, Ruhr-Universität Bochum, 44780 Bochum, Germany.

his theory of multi-level hierarchical control of voluntary movement (1947, 1967) around the degrees of freedom (DOF) problem. He had performed, for instance, a study of the kinematics of hitting movements when professional blacksmiths stroke the chisel with the hammer. His subjects were perfectly trained: They had performed the same movement hundreds of times a day for years. Bernstein noticed that variability of the trajectory of the tip of the hammer across a series of strikes was smaller than variability of the individual joint trajectories of the subject's arm holding the hammer. Since the brain obviously could not send signals directly to the hammer, Bernstein concluded that the joints were not acting independently but correcting each other's errors. This observation suggested to him that the central nervous system (CNS) did not try to find a unique solution for the problem of kinematic redundancy by eliminating redundant DOFs but rather used the apparently redundant set of joints to ensure more accurate (less variable) performance of the task. Of course, his observations were suggestive rather than conclusive. For instance, variability in the spatial position of the hammer cannot be compared to the degree to which joint angles are reproducible, as these variables are in incommensurate units. Moreover, the initial joint configuration was not controlled, so Bernstein's finding likely reflected, more generally, the nervous system's ability to generate flexible solutions to the motor task, allowing the hammer to reach the same terminal point from slightly different initial conditions and to compensate for disturbances in the course of the movement.

Analogous problems arise at other levels of analysis. Typically, more than one muscle contributes to the torque generated at any individual joint. Which combination of muscle forces does the CNS select to achieve a particular amount of torque? Muscles consist of a large number of motor units, which together are capable of generating a particular amount of muscle activation (or force) in many different ways. How and in what sense the CNS solves the DOF problem (the "Bernstein problem," Turvey, 1990; Latash, 1996) is one of the fundamental problems of motor control. A number of different approaches to this problem exist in the literature.

Elimination

A first position is that the CNS solves the problem by reducing the number of DOFs to the ones necessary to perform the task. Such "freezing" of DOFs had been postulated by Bernstein, and is commonly invoked in contemporary studies of human motor behavior (e.g., Newell, 1991; Vereijken et al., 1992).

A related position comes from the observation that in some circumstances, movement takes place within a sub-space of the full space of mechanically possible movements. Evidence for such constraints comes from Donders's law which, when applied to eye movements, states that the angular gaze positions do not routinely make use of all three DOFs but are constrained to a two-dimensional surface when the head is stationary (Donders, 1847). Donders's law has been shown to be valid for some four-DOF arm movements, but to break down for arm movements with more DOFs (Gielen et al., 1997). When valid, the phenomenon captured by this law would reflect a more abstract form of "freezing" in which combinations of DOFs are constrained to change along a particular direction in the space of movement elements.

The notion of elimination of DOFs has been invoked primarily at the kinematic level, not to our knowledge to account for redundancy at the levels of forces, muscles, motor units, or during multi-limb tasks.

Optimization

These approaches to the problem of motor redundancy involve application of optimization principles based on certain mechanical, engineering, psychological, or complex cost functions (reviewed in Seif-Naraghi and Winters, 1990; Rosenbaum et al., 1995). Most straightforward optimization approaches essentially select a cost function and find a unique solution that ensures its maximal or minimal value. More sophisticated optimization methods are compatible with the ideas advocated in this paper (e.g., Mussa-Ivaldi & Hogan, 1991; Todorov, 2004) and may be viewed as complementary to the analysis described later.

Synergy

The third class of solutions can be traced back to classical works by Hughlings Jackson (1889; see the epigraph), Babinski (1899), and Sherrington (1910). However, in contemporary motor control literature, this notion is most commonly associated with the name of N.A. Bernstein. The idea is clearest in the context of muscle synergies: Multiple muscles are bound together such that a central control signal jointly and proportionally activates all muscles in the synergy. When task demands vary, the control signal to the synergy changes, leading to parallel changes in all muscles bound together in the synergy. By extending the notion of muscle synergies to groups of muscles that span multiple joints, the coordination of multiple DOF may be understood in a similar way. To avoid misunderstanding, we would like to state upfront that this understanding of synergies differs qualitatively from what we propose further in this article.

There is a common feature across the three mentioned approaches. They all view the existence of numerous DOFs as the source of computational problems for the CNS (even if it is ultimately useful for adaptive, flexible behaviors). For example, the idea of eliminating (“freezing”) redundant DOFs assumes that it is easier for the central nervous system to control movements if it has to manipulate fewer variables. This is questionable. For example, not moving a joint of a limb does not relieve that joint of being controlled. To the contrary, the interaction forces and moments of force that arise as the other joints along the kinematic chain are moved require active control to stabilize the joint at its frozen value. Latash, Aruin, and Zatsiorky (1999), for instance, showed complex control signals to a “frozen” wrist joint when a pure elbow movement was generated.

Our view on the apparently redundant design of the system for movement production is quite different. We do not consider the numerous DOFs as a source of problems for the CNS but rather as a luxury that allows the controller to ensure both stability of important performance variables and flexibility of patterns to deal with other task components and possible perturbations. As follows from a few models, discussed later in this article, this luxury does not necessarily mean an increased cost (for example, computational). To us, the main question with respect

to the problem of motor redundancy is: How does the solution to the DOFs problem leave the motor control system more powerful than a system that would start with fewer DOFs from the outset?

In this article, we will argue that current approaches to the DOFs problem deal predominantly with how combinations of DOFs are selected by freezing, by optimization, or by binding into groups with proportional scaling of the DOFs within a group. We will identify the concept of “sharing” as the thread common to these approaches (see the section headed “Quantitative Approaches to Studying Synergies: Sharing Patterns”). We will then argue that these approaches to the DOF problem fail to address another important feature of behavior of multi-element systems, namely how performance is allowed to show both stability against perturbations and flexibility to solve concurrent tasks. In the section “Quantitative Approaches to Studying Synergies: Flexibility and Stability,” we will show how analyzing the structure of motor variability enables the quantification of this second feature.

We start with an explicit definition of synergy that is going to be analyzed and explored in further sections: Synergy is a neural organization of a multi-element system that (1) organizes sharing of a task among a set of elemental variables; and (2) ensures co-variation among elemental variables with the purpose to stabilize performance variables. Further, we will use several examples of systems and tasks with different sets of elemental variables and different performance variables. For brevity, we will use “synergy” in reference to patterns of co-variation of elemental variables, rather than to the underlying neural circuitry.

Two Components of Synergies: Sharing and Flexibility/Stability

Individual finger forces are expected to vary from trial to trial. These variations may be independent leading to circular distributions of data points or they may co-vary. For example, if finger forces always satisfy the equation $F_1 + F_2 = 20$ (the slanted thin line in Figure 1), the task is performed perfectly despite possible variations in finger forces. Generally, if smaller than expected forces produced by one finger are accompanied by larger than expected forces produced by the other finger (negative co-variation, ellipses in Figure 1), the total force may be expected to vary less as compared to the circular force distributions. We will refer to such a synergy as stabilizing the total force and view co-variation patterns among finger forces as reflecting how well the synergy stabilizes the performance variable and how much flexibility it allows in the space of finger forces. Note that the average location of the data distributions (sharing) and the shape of the distributions (stability/flexibility) are generally independent and hence may be viewed as two basic characteristics of a synergy. We conclude from this example that synergies must be characterized not only by sharing patterns but also by patterns of co-variation reflecting the feature of stability/flexibility.

Consider an example from a different level of analysis. The equilibrium-point (EP) hypothesis of motor control (Feldman, 1966) states that the CNS uses time functions of variables that parameterize the neuromotor system in a task-specific way and define sequences of equilibrium states of this system. These variables

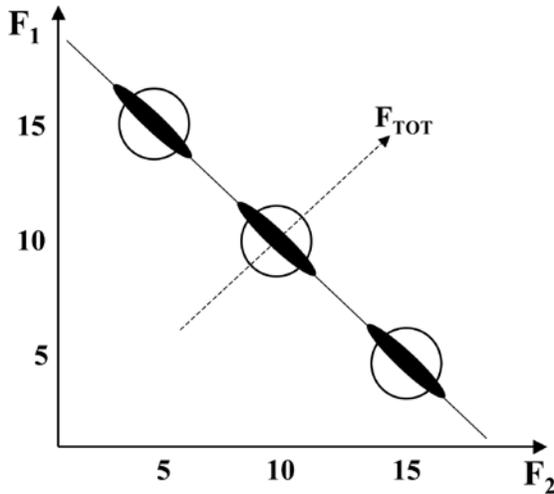


Figure 1—An illustration of the two basic features of synergies. A person tried to produce the same total force of 20 N with two fingers. Three sharing patterns are illustrated: 5:15 N, 10:10 N, and 15:5 N. This means that with changes of total force (F_{TOT}) both finger forces change in the same direction (i.e., positive co-variation along the dashed lines). Data distributions over repetitive trials may form circles (not a synergy) or ellipses (force stabilizing synergies, or negative force co-variation). Individual finger force variations are similar for the circles and ellipses while the total force (F_{TOT}) shows smaller variations for the ellipses.

have been associated with thresholds (λ) of the tonic stretch reflex of participating muscles. In the simplest case, single muscles composed of multiple motor units may be viewed as a multi-element system. When the CNS defines a time shift of λ , this results in a certain pattern of motor unit recruitment.

A set of involved motor units may show both preference for particular sharing patterns (for example, based on the well-established size principle, Henneman et al., 1965) and the stability/flexibility feature. Imagine, for instance, that for some reason, in one of the trials, one motor unit stops firing. The muscle force will drop, and given unchanged external load, the muscle fibers will stretch. This will lead to an increase in the spindle activity and an increase in the excitatory input into the alpha-motoneuron pool via the tonic stretch reflex loop. Other motor units will increase their firing rate and/or new motor units will be recruited such that the muscle will reach the same equilibrium state defined by λ and the external load. In this example, a particular neurophysiological mechanism, the tonic stretch reflex, unites motor units within a muscle into a synergy. Such co-varied changes in the contributions of alpha-motoneurons to muscle activation may be analyzed both in time (as above) and across repetitive attempts to oppose the same external force at the same muscle length.

Quantitative Approaches to Studying Synergies: Sharing Patterns

Discovering Sharing Patterns Through Pair-Wise Correlation and Matrix Factorization

As a movement unfolds, such as the hand pointing towards a target, the different DOFs typically change their values simultaneously and systematically to effect the change in hand position. The fact that there is a well-defined trajectory at all implies that changes in the values of individual motor elements, e.g., changes in joint angles, are coupled along time. It has been assumed that such regularities of motor output are accomplished not by the control of the individual motor elements, but by uniting the elements into groups (e.g., structural units in Gelfand and Tsetlin, 1966; Turvey, 1990).

The identification of sharing patterns is often based on pair-wise correlations between elemental DOFs that result from their simultaneous change as a task evolves in time or in conjunction with global changes in movement parameters, for example, velocity. For example, Jensen et al., (1994) correlated rotations in the proximal and distal joints of the leg to determine changes in their coupling during the development of kicking. Similar descriptions of what we call sharing patterns were provided for a variety of tasks including vertical posture, locomotion, reaching, finger force production, etc. (Smith et al., 1985; Macpherson et al., 1986; Desmurget et al., 1995; Li et al., 1998; Santello & Soechting, 2000; Pelz et al., 2001). Correspondingly, synergies have been associated with correlated outputs of muscles/joints/effectors in voluntary multi-joint limb movements, force production tasks, quiet standing, locomotion, anticipatory postural adjustments, quick corrective reactions to perturbations, and other motor actions and reactions (Nashner & Cordo, 1981; Alexandrov et al., 1998; Li et al., 1998; Gottlieb et al., 1996; Vernazza-Martin et al., 1999; Saltiel et al., 2001; Ivanenko et al., 2004). Clinical studies reported atypical sharing patterns among elemental variables in different patient groups and interpreted them as atypical synergies (Levin et al., 2002; Cirstea et al., 2003; Beer et al., 2004).

Pair-wise correlation techniques may be useful in addressing questions of coordination involving a limited set of effectors but are, of course, inadequate when studying more common functional tasks that involve large redundant sets of effectors. A more comprehensive approach to identifying correlated changes in the values of motor elements requires the use of more robust matrix factorization techniques such as principal component analysis or PCA (Mah et al., 1994). PCA results in the identification of a smaller set of linear combinations of the original variables, which some authors refer to as synergies. For example, Mah et al. (1994) used PCA to identify normal and atypical linear combinations of joint and segmental angles for human locomotion. Combinations of original variables identified with PCA and similar procedures are sometimes considered basic synergies that can be combined to form functional synergies for particular behaviors (e.g., Tresch et al., 2006). PCA has provided a powerful tool for identifying stable groupings of elemental variables (modes) for a variety of motor behaviors (Alexandrov et al., 1998; Ivanenko et al., 2004; Sanger, 2000; Santello et al., 1998; Shim et al., 2005).

Alternative multivariate approaches to the use of PCA have been introduced recently (Tresch et al., 2006; Hart & Giszter, 2004). For example, Saltiel et al (2001) applied non-negative matrix factorization procedures, involving gradient descent, to identify modes of muscle action underlying the frog withdrawal reflex. Tresch et al. (2006) recently evaluated the ability of a number of these approaches, including PCA, to identify the appropriate mode combinations in simulated data sets for which the muscle modes were known.

What Are the Elemental Variables That Form the Basis for Synergies?

When performing infant cardiopulmonary resuscitation, the rescuer's index, middle, and ring fingers apply force to the infant's chest to facilitate circulation but not so forceful as to injure the infant (American Heart Association, 2005). Control of the total force applied can be considered to result from a synergy that includes the individual finger forces as elements. But should individual fingers be considered the elemental variables of the synergy? In our approach to synergies, elemental variables are defined as those DOFs whose values can be changed, in principle, by the controller while keeping the values of other DOFs unchanged. When a person tries to produce force with an individual finger, other fingers of the hand also show force production, a phenomenon called "enslaving" (Ohtsuki, 1981; Li et al., 1998). Enslaving is due to both peripheral connections among the fingers such as shared muscles, inter-digit tendon connections, and to neural factors such as overlapping cortical representations for individual fingers (Leijnse et al., 1993; Kilbreath & Gandevia, 1994; Schieber, 2001). Enslaving is not task specific but may induce co-variations of finger forces that may be confused with task-specific sharing patterns (Latash et al., 2001).

To disambiguate these two sources of co-variation, the notion of modes as elemental variables has been introduced (Latash et al., 2001; Scholz et al., 2002; Danion et al., 2003). As illustrated in Figure 2, there is one mode corresponding to desired involvement of each specific finger, but each mode leads to force production by all fingers.

Formally, a finger force vector F may be represented as a linear transformation of a mode vector M (both M and F have the dimension n equal to the number of fingers) as:

$$F = [E]*M, \quad (1)$$

where E is a $n \times n$ transformation matrix. Hence, the E matrix can be computed for a subject based on data from trials when the subject tries to produce total force ramp profiles by pressing with one finger at a time. For example, if only index (I) and middle (M) fingers of a hand are involved in a task:

$$E = \begin{bmatrix} \Delta f_{i,I}/\Delta F_I & \Delta f_{i,M}/\Delta F_M \\ \Delta f_{m,I}/\Delta F_I & \Delta f_{m,M}/\Delta F_M \end{bmatrix} \quad (2)$$

where $\Delta f_{j,k}$ and ΔF_k are the changes of individual finger force j ($j = I, M$) and the change of total force produced during the ramp when subjects were instructed to press only with finger k ($k = I, M$). This experimentally reconstructed matrix can

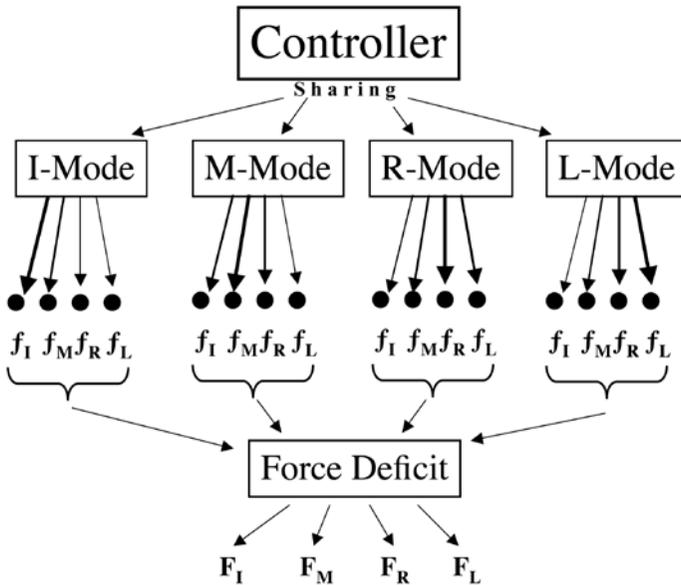


Figure 2—An illustration of the mode hypothesis. The controller defines a pattern of sharing among elemental variables (modes) corresponding to desired involvement of individual fingers. Each variable leads to force production by all fingers because of enslaving. The effects of elemental variables are summed up and attenuated (reflecting the force deficit phenomenon, Li et al. 1998) to produce finger forces.

now be used to compute changes in force modes based on experimentally recorded changes in finger forces:

$$dM = E^{-1} \begin{bmatrix} df_I \\ df_M \end{bmatrix} \tag{3}$$

The mode concept is not always needed. For example, at the kinematic level, joints are considered to be elemental variables because voluntary motion of a joint while keeping the other joint angles constant seems to be possible. Activation of an individual muscle, by contrast, does not seem to be generally possible without specific feedback, and the mode concept is needed in that domain to arrive at candidate elemental variables (Krishnamoorthy et al., 2003b; 2004).

Quantitative Approaches to Studying Synergies: Flexibility and Stability

Concept of the Uncontrolled Manifold (UCM)

While most research in motor control has focused primarily on the average performance over trials, investigators of rhythmic movement coordination have found that the variance of performance is an equally fundamental measure. This was based

on the notion that movement patterns emerge as stable states from the coupling of DOFs. This approach, invoking terms like “coordinative structures” (Easton, 1978; Turvey, 1990) or “dynamical patterns” (Schöner & Kelso, 1988), builds on the language of dynamical systems theory, in which “stability” is the capacity of a pattern to resist internal or external perturbations (sometimes addressed as “noise”). The variability from trial to trial or, in rhythmic movement, from cycle to cycle, is therefore one of several possible measures of stability.

Most work based on a dynamical systems perspective has been concerned with the relative timing among limbs, among effectors, or between effectors and perceived external rhythms (reviewed in Schöner, 2002). Transferring these ideas from relative timing to posture and trajectory formation, Schöner (1994; 1995) postulated that the patterns of elemental variables could be interpreted in terms of stability of relevant performance variables. Later, Scholz and Schöner (1999) developed a technical procedure, the method of the “uncontrolled manifold” (UCM), for testing whether trial-to-trial variability of elemental variables shows a structure interpretable as stabilizing particular performance variables. The method and approach have been refined and elaborated over the past several years as a result of experimental studies of a number of functional tasks (Scholz & Schöner, 1999; Scholz et al., 2000, 2001, 2002, 2003; Latash et al., 2001, 2002b; Tseng et al., 2002, 2003; Krishnamoorthy et al., 2003b, 2004; Domkin et al., 2002; Yang & Scholz, 2005; Kang et al., 2004). Here we propose that the structure discovered in the variance of multi-DOF systems using the UCM approach reflects the stability/flexibility feature of synergies. The UCM method may therefore be used to characterize that feature quantitatively.

Consider a planar three-joint arm, which controls the tip of a pointer in two dimensions (Figure 3A). This arm is redundant, in that multiple combinations of the three joint angles may achieve the same two-dimensional pointer-tip position along its path from a starting position (S) to a target (T). Two such configurations are shown in Figure 3A at three different time points along the pointer’s path. The path of the pointer in end-effector space illustrated in Figure 3A can be represented as well in the space of the three joints (Figure 3B, block dots correspond to the illustrated joint configurations), where the dashed line represents the average joint trajectory across a series of reaches. The black lines orthogonal to this path represent ensembles of joint configurations compatible with the same end-effector position at that point in time, or a manifold of joint angles (the UCM). These are illustrated for the three different end-effector positions in Figure 3B.

The idea is to use the UCM concept to partition the variance of the elemental variables into two components, one that affects and one that does not affect the value of a particular performance variable. Note that the variance analyzed here is across repetitions of the task at a particular movement phase.

In the example of Figure 3, the joint configuration realized at a particular movement phase (e.g., at t_1) can be represented as a point in the three-dimensional joint space. Plotting the joint angles across all such trials for the same phase results in a cloud of data points in joint space. The shape of this cloud in relation to a particular UCM reveals the extent to which coordination of the joints acts to stabilize the performance variable (pointer-tip coordinate) at its average value and, related, provides an indication of how flexible is the coordination (Figure 4). If the cloud of data points is elongated along the UCM, then most variability of

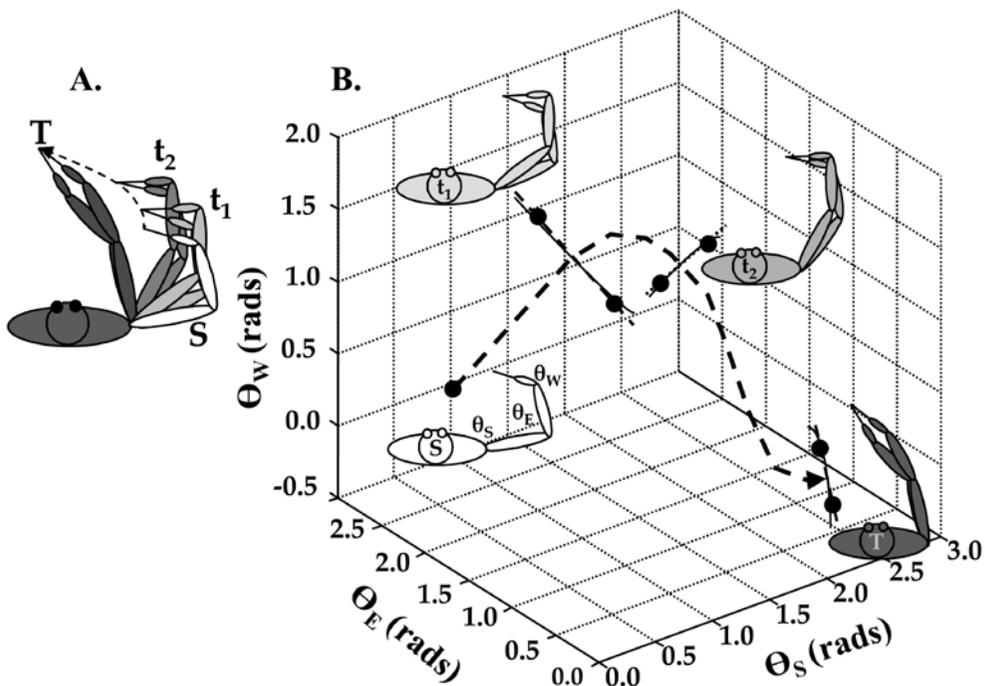


Figure 3—An illustration of a planar three-joint arm, which controls the tip of a pointer in two dimensions (A). The pointer moves from a starting position (S) to a target (T). Two such configurations are shown at three different time points along the pointer’s path. The path of the pointer in the space of the three joints is shown in panel B. The black dots correspond to the illustrated joint configurations. The dashed line represents the average joint trajectory across a series of reaches. The black lines orthogonal to this path represent ensembles of joint configurations compatible with the same end-effector position at that point in time, or a manifold of joint angles (the UCM).

the joint configuration lies in directions in joint space that do not affect the value of the relevant performance variable represented by the UCM (here, the Cartesian coordinates of the pointer-tip; Figure 4A or particularly C). If the cloud of data points is spherical (Figure 4D), then there is no synergy among the joints acting to stabilize the endpoint coordinate, although the joints may be united in a synergy that stabilizes a different performance variable. Please keep in mind that here we consider a very simple example with a uni-dimensional UCM sub-space in a two-dimensional space of elemental variables. In general (see later), indices of variance have to be normalized by the number of dimensions (DOFs) within corresponding sub-spaces. Note also that this example assumes that “all DOFs are created equal,” i.e., the effects of their deviations from an average value on a selected performance variable are adequately reflected in the formal relation between small changes in the DOFs and changes in the performance variable (the Jacobian).

Note that a spherical cloud of data points may be large (sloppy control of each elemental variable) or small (very precise control of each elemental variable, Figure 4D). In the latter case, an acceptable level of performance is achieved using a

different control strategy, that of producing a stereotypical time profile of all elemental variables and not making use of the flexibility afforded by the redundancy of the motor system. Such a control strategy might be acceptable in reaching the goal, but it may make it more difficult to respond to unexpected external perturbations and to perform secondary tasks simultaneously with a primary task (e.g., flipping a light switch with the elbow while transporting a full glass of wine in the hand).

The UCM itself may be non-linear (solid, slightly curved lines in Figure 3B). Because analysis of variance is a linear formalism, the UCM must be approximated linearly to make this idea quantitatively operational (dashed lines in Figure 3B). This linearization is obtained by computing the null space of the Jacobian, a matrix of partial derivatives representing the effect of small changes in each elemental variable (joint motions in our example) on the value of the task-relevant performance variable (endpoint position). The null space is tangential to the UCM

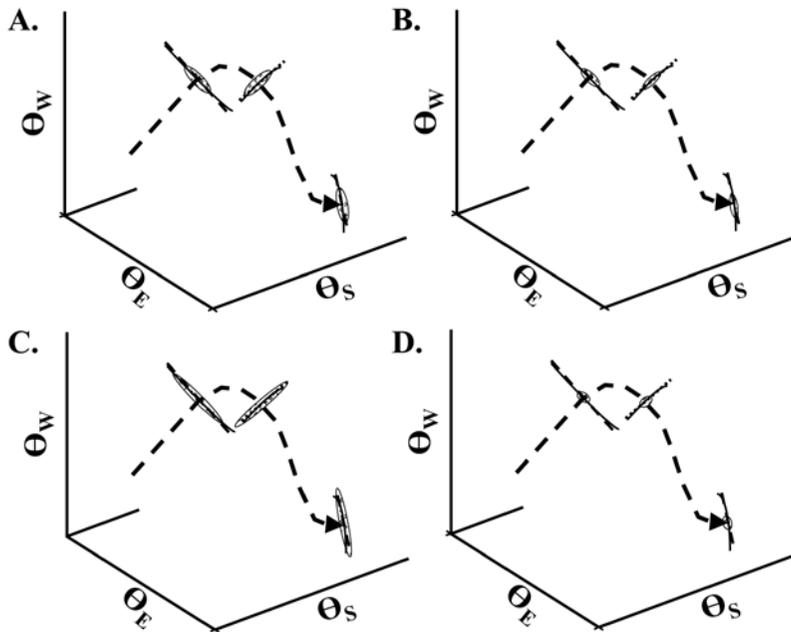


Figure 4—Schematics of clouds of data points from different trials (ellipses) and their relationship to the UCMs (dashed, short lines approximated by the straight solid lines are shown for three endpoint locations) at three phases along the joint space trajectories (dashed, thick lines) of Figure 3. (A) Structure of the data is such that the major axes of the ellipses are oriented parallel to the UCMs, indicating that variability is compressed in the orthogonal direction, stabilizing the pointer position. As a result of learning, both axes of the data ellipses may be compressed (B), there may be variance compression orthogonal to the UCMs and an increase along the UCMs (C), or greater variance compression along the UCMs than orthogonal to the UCMs (D). See text for details.

at a particular configuration of elemental variables. Typically, the mean configuration across trials is chosen as an approximation of the desired configuration. The subspace in joint space orthogonal to the null space is termed the range space of the Jacobian. In robotics, null space and range space are used to partition effector velocities. Here, by contrast, these subspaces are used to partition variance of effector configurations.

Each point in the cloud of data points is then projected into the null and into the range space of the Jacobian. The variance of the projections within each subspace is then obtained. The variance of the null space projections (V_{UCM}) provides an indication of the extent to which flexible combinations of elemental variables across repetitions lead to the same value of the performance variable under consideration. The variance of the range space projections (V_{ORT}) reflects combinations of the elemental variables that lead to changes in that performance variable across repetitions.* Thus, $V_{UCM} \gg V_{ORT}$ indicates that flexible combinations of elemental variables produce a relatively invariant, stable value of the performance variable. For a more formal description of how the UCM method can be applied to analysis of particular tasks, we refer the reader to our earlier publications (Scholz & Schöner, 1999; Scholz et al., 2000; Latash et al., 2001; Krishnamoorthy et al., 2003b).

A General Scheme of Analysis Within the UCM Approach

Practical application of the UCM method for quantitative analysis of synergies involves a number of steps that may be non-trivial. These involve:

Step 1: Selection of Elemental Variables. We have partly addressed this step in the earlier section “What are the elemental variables that form the basis for synergies?” Selection of elemental variables is intimately related to selection of an appropriate level of analysis. Depending on the particular research questions, the variables can be mechanical (such as forces, moments of forces, angular and linear displacements, etc.) or electrophysiological (for example, levels of muscle activation). Since the ultimate goal of analysis is to discover patterns of task-specific co-variation among elemental variables that may or may not stabilize a particular feature of performance, one would like a set of elemental variables to be free of task-independent co-variations. Examples of such co-variations are effects of enslaving among finger forces (Zatsiorsky et al., 2000) and muscle groups with parallel scaling of the muscle activity within a group (Merkle et al., 1998; Ivanenko et al., 2004, 2005; Ting & Macpherson, 2005). To deal with this problem, an idea of modes has been introduced (see the earlier section “What are the elemental variables that form the basis for synergies?”; Danion et al., 2003; Krishnamoorthy et al., 2003a). The idea of modes is similar to the concept of functional DOFs (reviewed in Li, 2006).

Another important issue is not to include into analysis elemental variables that are irrelevant to the task. If changes in an elemental variable have no effect

*In earlier papers, different (confusing) terms have been used for V_{UCM} and V_{ORT} such as V_{COMP} (compensated variance) and V_{UN} (uncompensated variance), and GEV (goal-equivalent variance) and NGEV (non-goal-equivalent variance) (Latash et al., 2001; Tseng et al., 2003). We apologize for the messy terminology and in this article will stick to the V_{UCM} and V_{ORT} nomenclature.

on performance, obviously all its variance will be within the UCM (V_{UCM}) thus artificially inflating that index.

Step 2: Selection of a Performance Variable. One of the most exciting opportunities afforded by the UCM method is to analyze the same data set with respect to different performance variables, as if asking the system: “Are you a synergy stabilizing such-and-such performance variable?” This question has been referred to as a “control hypothesis” (Scholz & Schöner, 1999; Scholz et al., 2000). In general, any performance variable that is affected by changes of a set of elemental variables can be selected.

Step 3: Creating a Linear Model of the System. At this step, relations between small changes in elemental variables and the selected performance variable are computed and united into the Jacobian matrix, J . In some cases, J may be computed based on the geometrical properties of the system, for example, in analysis of multi-joint kinematic synergies (e.g., Scholz et al., 2000). In other cases, J has to be discovered experimentally, for example, using methods of linear regression (e.g., Krishnamoorthy et al., 2003b). After a J matrix is computed, its null-space can be used as a linear approximation of the UCM. The null-space is computed for given values of J . These values will be different for each point in the movement, consistent with the changing geometry of the system. Typically, we use the average value of the joint configuration and assume this to be a reasonable approximation to the desired value of the control system.

Step 4: Partitioning Variance into V_{UCM} and V_{ORT} . Finally, a set of data can be used to compute projections of variance in the space of elemental variables onto the UCM and onto its orthogonal complement (V_{UCM} and V_{ORT} respectively). Such analyses were typically run across data measured in a number of trials at comparable phases. However, in certain special cases, the analysis has also been applied to analysis of data points collected within a single trial (Scholz et al., 2003). The magnitudes of V_{UCM} and V_{ORT} are further normalized by the number of DOFs in the corresponding sub-spaces and compared quantitatively. If V_{UCM} is statistically higher than V_{ORT} , the control hypothesis may be considered supported, and an index of a synergy may be computed, for example, the ratio of the two variance components or their normalized difference.

Example Application of UCM Analysis: Sit-to-Stand Action

As an example, we review how the UCM approach has been used to determine the flexible patterns of joint coordination that stabilize the path of the center of mass of the body or of the head position during a sit-to-stand task (Reisman et al., 2002a; Scholz et al., 2001). In all such studies, individual axes of joint rotation were assumed to be independent elemental variables. The Jacobian was computed based on the geometry of the effectors.

In these studies, subjects performed the sit-to-stand task under different constraints, in each case controlling for subjects' starting position. Performances were studied on normal and narrow bases of support with the eyes open or closed (Scholz & Schöner, 1999; Scholz et al., 2001). Several performance variables were evaluated, for example, the horizontal and vertical position of the center of mass (CM), head position and orientation, and momentum of the CM (Reisman

et al., 2002a). In each case, a different geometric model was developed relating each performance variable to the space of joint motions. Thus, the variance in joint space was partitioned with respect to the appropriate Jacobian matrix, depending on the performance variable being tested. Regardless of the task constraints, the instantaneous horizontal CM position led to $V_{UCM} > V_{ORT}$ while this was not true for the vertical CM position ($V_{UCM} \approx V_{ORT}$). This effect was strongest in the middle of the sit-to-stand movement and when standing up under challenging task constraints such as on a narrow support surface, compared to a normal support surface (Figure 5) (Reisman et al., 2002a; Scholz et al., 2001). When the sitting down portion of the task was examined, where subjects could not directly see the seat behind them, stabilization of the vertical position of the CM was also observed by the use of flexible patterns of joint combinations (i.e., $V_{UCM} > V_{ORT}$; Reisman et al., 2002b). Thus, the use of flexible patterns of joint coordination to stabilize different task-related variables depended on the phase and context of the task's performance.

Example Application of UCM Analysis: Multi-Finger Force Production

The non-independence of the individual fingers during force-production tasks, mentioned earlier, must be taken into account in analysis of multi-finger synergies. This was done in a series of studies by using the force mode approach described in the earlier section “What are the elemental variables that form the basis for

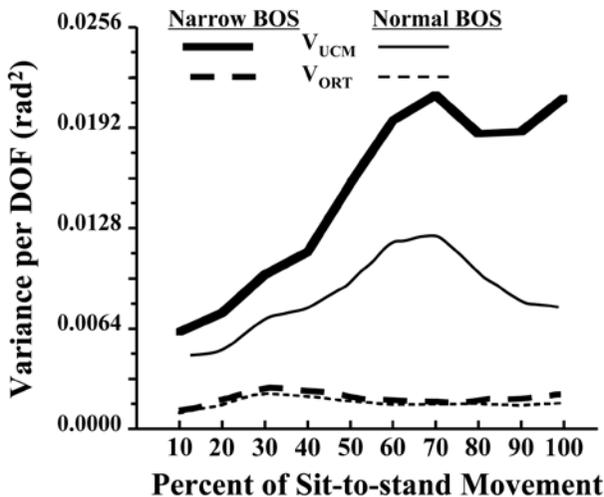


Figure 5—Variance of joint angles reflecting flexible patterns of joint coordination (V_{UCM}), consistent with a stable value of the horizontal path of the body's center of mass, and variance leading to fluctuations in the horizontal CM path (V_{ORT}) when standing up from either a narrow (thick solid line) or normal (thin solid line) base of support, computed at each percentage of normalized movement time. V_{ORT} for narrow base is represented by a thick dashed line, while that for the normal base is represented by a thin dashed line. Reproduced with permission from Scholz et al., 2001.

synergies?” The experiments studied whether flexible patterns of force modes during multi-finger pressing tasks could be related to stabilization of such performance variables as total force and total moment produced by finger forces with respect to the mid-point between the two most lateral fingers involved in the task. In most experiments, the subjects were required to produce certain time profiles of the total force (Latash et al., 2001, 2002b; Scholz et al., 2002). It was expected, therefore, that the analysis would reveal structure of the mode variance compatible with total force stabilization. However, the results were rather unexpected. During fast cyclic force production with two, three, or four fingers, the modes co-varied across cycles to stabilize total force only within a narrow range of the force cycle around the peak total force (Figure 6, left panel), while they stabilized the moment of force over most of the cycle (Figure 6, right panel). This occurred despite the fact that the subjects received instruction and visual feedback on the total force but not on the total moment. Note that in three- and four-finger tasks, the motor abundance of the system allows the stabilization of both force and moment at the same time.

These seemingly unexpected findings were interpreted as reflecting patterns of multi-finger interaction elaborated by the CNS during the lifetime based on everyday tasks, such as eating with a spoon, drinking from a glass, writing with a pen, etc. which impose stronger constraints on permissible errors in total moment than in total force. For example, when taking a sip from a glass, grip force should only be above the slipping threshold and below the crushing threshold. These are relatively weak constraints. The moment of force, however, needs to be controlled much more precisely if one wants to avoid spilling the contents of the glass.

The Task Dependency of the Uncontrolled Manifold (UCM)

The structure of variance observed through the UCM approach is task dependent. For instance, when the arm is used to point at targets in three dimensions, the Cartesian position of the pointer tip is stabilized by structured variance in joint space (Tseng et

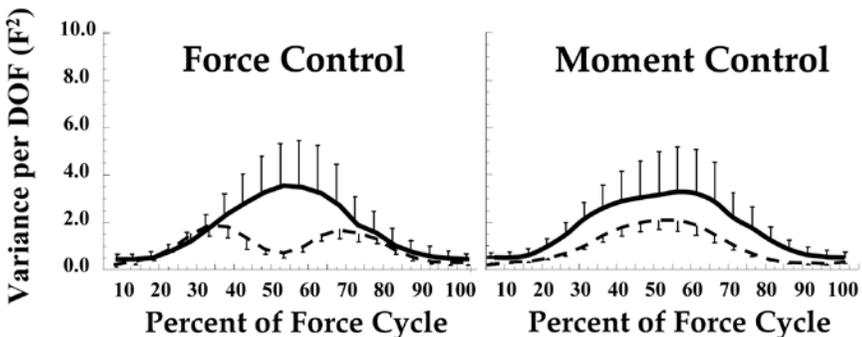


Figure 6—Left panel: Variance of finger force modes at every 10% of the force oscillation that is consistent with a stable value of the performance variable total force (V_{UCM} , solid line) and variance of finger force modes that leads to variability of total force (V_{ORF} ; dashed line); Right panel: Same components of finger force variance evaluated with respect to the performance variable force moment. Error bars are standard errors of the means.

al., 2002, 2003). By contrast, when that same effector is used to shoot at a target with a hand-held laser gun, then the spatial position of the gun is no longer stabilized by co-varied changes in joint angles, particularly during the second half of the movement, crucial for shooting accuracy (Scholz et al., 2000). Instead, a different two-dimensional constraint that determines if the target will be hit by the gunshot generates a UCM that captures most of the joint angle variance during that stage of the movement.

Multiple performance variables should therefore be tested to explore the task-dependent structure of variance in the space of elemental variables. The method provides a means to quantify the levels of stabilization of different variables. Quantitative measures of synergies, such as the normalized difference $[V_{UCM} - V_{ORT}]/V_{TOTAL}$ or the ratio V_{UCM}/V_{ORT} can be used to help separate synergies ($V_{UCM} > V_{ORT}$) from “non-synergies” ($V_{UCM} \leq V_{ORT}$).

Such information, in conjunction with analyses that address changes in the sharing pattern across time or changes in other task parameters can provide useful insights about a variety of motor phenomena, including motor learning (Domkin et al., 2002, 2005; Kang et al., 2004; Yang & Scholz, 2005) and deficits in coordination in patients and atypically developing persons (Reisman & Scholz, 2003; Scholz et al., 2003) as well as among elderly subjects (Shinohara et al., 2004).

Note that matrix factorization procedures such as PCA applied to the movement data across time may serve as an important first step to the UCM method by helping to identify the elemental variables (modes). These modes can then be used to experimentally estimate the Jacobian, relating small changes in modes to changes in specific performance variables, when an analytical model is not available, as a precursor to UCM analysis. This approach has recently been used by Krishnamoorthy et al. (2003a, 2003b) and extended by Danna-Dos-Santos et al., (2007) to study how flexible patterns of muscle activation relate to changes in the center of pressure during the performance of postural tasks.

One limitation of the UCM method as formalized here is that it is based on decomposing variance into linear subspaces even though the UCM itself may be curved and thus highly nonlinear. An alternative to the UCM method is an approach based on the creation of uncorrelated, surrogate data sets from the original data (Kudo et al., 2000; Martin et al., 2002; Müller & Sternad, 2003, 2004; Latash et al., 2004) that can deal with non-linear forms of correlation. Unlike the UCM approach, this method does not perform the variance analysis in the space of elemental variables but in the space of task-relevant performance variables, in which the variances in the original and in a surrogate data set are compared. Recently, a related approach has been developed by Cusumano and Cesari (2006) that tries to link manifold geometry analysis and analysis of variance by introducing a notion of goal-equivalent manifold (GEM). This approach considers, in particular, such factors as sensitivity of solutions within the UCM (different sharing patterns) to deviations of elemental variables.

General Discussion

Theoretical Approaches to Synergy

Theoretical work on the DOFs problem has focused largely on the problem of selecting a solution from the range of possible solutions, in particular, through

optimization principles (e.g., Uno et al., 1989; Hasan, 1986; Rosenbaum et al., 1995; Lan, 1997). The stability and flexibility aspect of the DOFs problem, and the associated variance analysis, have not been central to most theoretical accounts.

Harris and Wolpert (1998) address variance by hypothesizing that an optimal trajectory is selected by minimizing signal-dependent terminal variance at the target of reaching and of saccadic eye movements. Their account has not been extended to redundant effector systems. Todorov and Jordan (2002; Todorov, 2004), by contrast, deal with redundant systems by postulating a “minimal intervention” principle within the framework of optimal feedback control. The model minimizes the weighted sum where the first summand is the squared difference between a function of effectors signals and its preset value, and the second summand is the effort defined as the variance of the control signals. However, as the authors of this approach admit, the computational part of the model introduces substantial complications. There are other disadvantages of systems with feedback loops such as time delays and a chance of self-excitation for some values of system parameters. Nevertheless, this principle is conceptually consistent with the UCM approach. The probability distributions of observed states of elemental variables generated by the stochastic optimal control model are elongated in directions compatible with the UCM hypothesis (i.e., $V_{\text{UCM}} > V_{\text{ORT}}$). One limitation of the model is that it does not clearly address how the CNS re-computes a new optimal trajectory plan at any moment in time based on the (sensed?) current state of the effector. Such optimization involves knowing the control effort associated with different possible trajectories, which includes a complete model of the effector. It may also be expected to involve substantial time delays in the sensory feedback signals, which is not compatible with recent studies (see the section “Issues of Timing in Synergy Formation,” below).

A less formal, more physiologically based approach has been pursued by Bullock et al. (1993), who proposed a neuronal network that learns coordinate transformations from end-effector to joint coordinates, in effect developing a structure that selects one solution out of a set of “motor-equivalent” solutions. An analysis of variance and of underlying noise sources was not a topic in that work, although extending the model to address the structure of variance seems feasible.

Another physiologically based model has recently been proposed by Latash et al. (2005) using, as an example, multi-finger force production tasks. Within the model, outputs of individual neurons are mapped onto each elemental variable. This “central back-coupling model” is based on a plausible neural mechanism of self- and lateral inhibition (e.g., similar to the system of Renshaw cells) among the elements (output neurons). As illustrated in Figure 7, a command signal (level A) is being distributed over a set of elements producing a particular sharing pattern. This signal is assumed to be noisy (Gaussian noise with zero average magnitude is added) leading to inputs to individual neurons (level B). The output of the level B neurons m is transformed by an enslaving matrix resulting in finger forces: $f = [E]m$. The output of each of the level B elements also serves as input into an interneuron (IN in Figure 7, level C), which projects back to all the level B neurons. These back-coupling loops are characterized by gains (g_{ji} comprising a matrix G), time delays, and thresholds. The model generates similar variance structure as predicted by the UCM hypothesis. Moreover, the model has been able to replicate the finding of a time delay of the order of 100–300 ms between the initiation of a

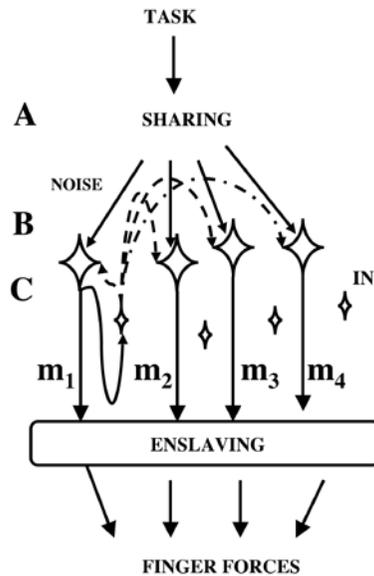


Figure 7—A scheme illustrating the back-coupling (CBC) hypothesis. Control signal (A) is shared among four “neurons” (B) with added noise. The outputs of the “neurons” excite inhibitory “interneurons” (C) that project back to all four “neurons” at the B level. Further, the outputs of the B “neurons” are modified with a finger interconnection matrix (enslaving matrix) producing finger forces. Modified with permission from Latash et al., 2005.

slow ramp force production and the emergence of a force-stabilizing synergy (see the right panel of Figure 7; cf. Shim et al., 2003; Latash et al., 2004).

A comprehensive model of both features of synergies in redundant effector systems has been developed by Martin and colleagues (Martin, 2005; Martin et al., 2004). A biomechanical model of the effector system is augmented by physiologically based muscle models. At each joint, the group of agonist and antagonist muscles is described by a simplified version of the nonlinear equilibrium-point model of Gribble et al. (1998). The equilibrium points of these muscle-joint systems are considered dynamical variables, whose temporal evolution is described by a dynamical neural network. The network receives input from a set of neural oscillators that generate a timing signal defining the progression of the end-effector along its trajectory. The model has been validated in experiments involving planar movement of a four-DOF system to various targets. In particular, the model has been able to account for the structure of variance observed in the experiment, including the amount and temporal evolution of self-motion (joint motion that does not move the end-effector) and of the variance within the UCM during the movement. In the model, three factors contribute to the observed structure of variance: First, the neuronal computations of equilibrium-point trajectories are assumed to be noisy. Second, the dynamics of the equilibrium points within the two subspaces (UCM and orthogonal to the UCM) of joint space are assumed to be decoupled.

Third, the realized joint configuration is fed back into the neural computation of the equilibrium trajectory, keeping the performance variable unchanged. This back-coupling could be viewed as a neural mechanism that performs something akin to Todorov and Jordan's (2002) "minimum intervention" principle. From the perspective of Martin et al.'s theoretical account, the structure of variance reveals control priorities, which enhance the flexibility of the system to satisfy multiple task constraints and enable the system to satisfy these constraints in varying contexts and for varying initial configurations.

A feed-forward control model has recently been suggested by Goodman and Latash (2006). The model assumes the existence of two input signals at an upper level of the control hierarchy, related and unrelated to a task variable. Knowledge of the Jacobian of the system is assumed at the level of generation of elemental variables. Several phenomena have been simulated including data point distributions corresponding to presence and absence of force-stabilizing synergies in two-finger tasks, changes in synergies with practice, and changes in synergy indices in preparation to a fast action (cf. Shim et al., 2005; Olafsdottir et al., 2005).

The basic notions underlying the UCM approach and reflected in the mentioned models can be traced back to ideas of Gelfand and Tsetlin (1966) who assumed that movements were controlled in a hierarchical but not prescriptive manner, so that relations among variables at a hierarchically lower level ensured stable motor performance with respect to a performance variable produced by a hierarchically higher level. More recently, Gelfand and Latash (1998, 2002) suggested that all the DOFs at all levels always participate in all the tasks ensuring both stability and flexibility of the performance, a hypothesis they call the "principle of abundance."

Possible Neurophysiological Foundations of Synergies

There is ample evidence that task-specific and relatively high-level features of motor tasks are represented in the brain. Studies of cortical neuronal populations have revealed patterns of activity related to performance variables such as the spatial trajectory of the effector's endpoint or the force vector applied by an end-effector (Georgopoulos et al., 1982; Schwartz, 1993; Coltz et al., 1999; Cisek & Kalaska, 2005).

Studies with spinal cord electrical stimulation have been interpreted as pointing at the existence of motor "primitives" in the spinal cord that produce certain force fields at the endpoint of a hindlimb (Hart & Giszter, 2004; Giszter et al., 1993; Giszter & Kargo, 2000; Kargo & Giszter, 2000; Mussa-Ivaldi et al., 1994). Recently, similar effects of micro-stimulation of the spinal cord in cats have been reported (Lemay & Grill, 2004). Most studies of motor primitives measured forces produced by the endpoint of a limb in isometric conditions; making these findings unlikely to generalize for non-isometric conditions. Note also that by limiting analysis to end-effector force fields these studies did not address how redundant effectors generate these forces (although such analysis is possible; see Gandolfo & Mussa-Ivaldi, 1993). Another series of studies have shown that spinal frogs can produce a successful wiping response on the first trial after a joint has been constrained (Berkinblit et al., 1986). These observations provide evidence that flexible patterns of joint and muscle coordination are used to stabilize task-relevant performance even at this low level of control.

A number of supraspinal structures, such as the cerebellum and the motor cortex, have been viewed as potential contributors to motor synergies (Houk & Gibson, 1987; Bloedel, 1992; Lemon et al., 1998; Schieber, 2001; Holdefer & Miller, 2002; Kargo & Nitz, 2003; Thach & Bastian, 2003). In particular, phenomena of divergence and convergence in cortical representations of individual digits of the human hand have been discussed as providing the neural basis for multi-finger synergies (Lemon et al., 1998; Schieber, 2001; Schieber & Santello, 2004), always in the sense of the sharing aspect of synergies. Single neurons in the medial vestibulospinal tract have been shown to innervate functional sets of neck muscles possibly contributing to the head movement synergy (Sugiuchi et al., 2003).

The basis of flexibility is also very broad. Studies in which individual motor elements were perturbed within a variety of complex actions have revealed fast, online correction mechanisms (Abbs & Gracco, 1984; Kelso et al., 1984; Latash, 2000). There is the potential for flexibility and stability to arise based on neurophysiological principles. Indeed, dynamic stability is a fundamental feature of the biophysics of neuronal nets, which restores the state of the network after an external or internal perturbation (e.g., Wilson, 1999). This fact is exploited in recurrent neuronal networks that afford continuous linkage to sensory inputs. The basis of dynamic stability is thus entirely generic in the CNS. However, as of now stability is the aspect of synergies which has the least specific grounding in neurophysiology.

An exception to the last statement is the central back-coupling model of synergies described earlier (see the section “Theoretical Approaches to Synergy”; Latash et al., 2005). It uses short-latency back-coupling as a particular mechanism to ensure error compensation among elemental variables, one of the signatures of flexibility. Short-latency negative feedback loops, also addressed as lateral inhibition and surround suppression, are rather common in the CNS. They have been described and/or postulated for sensory systems of different modalities (Lund et al., 2003; Schoppa & Urban, 2003; Wehr & Zador, 2003; Ozeki et al., 2004) as well as for brain circuits traditionally associated with the production of movement (Fukai, 1999). The well-known system of Renshaw cells (recurrent inhibition) may be viewed as a particular instantiation of this scheme. Renshaw cells have recently become incorporated into several hypotheses on the control of movement (van Heijst et al. 1998; Uchiyama et al., 2003). There is substantial variability in the organization and the strength of inhibitory projections mediated by Renshaw cells in different muscles (Katz et al., 1993). These projections can be modulated pharmacologically and by descending projections (Mattei et al., 2003; Hultborn et al., 2004), which may be the basis for how Renshaw cells stabilize the output of a motoneuronal pool in a way that could be muscle and task specific (cf. Hultborn et al., 2004).

Issues of Timing in Synergy Formation

The two aspects of synergies, sharing and flexibility/stability, can be related to the generation of a time course of a performance variable (sharing it among the elemental variables) and stabilization of the combined output of the elemental variables to actually achieve the sequence of states (stability/flexibility). We will address these two components as “timing” and “control.” The theory of optimal

control is really about the former, while the theory of feedback control systems is about the latter (Sontag, 1990).

The concept of the equilibrium trajectory (Feldman, 1986; Feldman & Levin, 1995; Feldman & Latash, 2005) postulates a separation between the two components, specification of the time course of the equilibrium trajectory and stabilization of a movement modeled through more or less sophisticated variants of the equilibrium-point hypothesis (Feldman et al., 1998; Latash & Gottlieb, 1991; Gribble et al., 1998). Other motor control models have also frequently invoked the concept of a desired trajectory, often assumed to arise from an optimization principle (Miyamoto et al., 1988; Kawato, 1990, 1999), which feeds into the more complex control system that may include forward and/or inverse modeling.

During slow movements, the equilibrium or desired trajectory can be seen as a series of postural states, to which the control system steers the effector system independently of its previous motor state. For fast movements, however, variance at a given phase may be affected by earlier states.

One of the studies of multi-finger force production showed that the temporal evolution of variance within the UCM, V_{UCM} followed closely the evolution of variability of the total force, while the temporal evolution of V_{ORT} was correlated with the first force derivative (Latash et al., 2002c). These observations suggest that variation of a timing parameter across trials may be mostly reflected in V_{ORT} while errors in the magnitude of finger forces were mostly reflected in V_{UCM} .

Recently, Goodman and colleagues (Goodman et al., 2005) have developed for multi-element actions an earlier suggested model of motor variability based on assumed errors in the timing and amplitude parameters (Gutman & Gottlieb, 1992; Gutman et al., 1993). They have demonstrated, in particular, that variance in the space of elemental variables (force modes for the task of fast multi-finger force production) can show non-spherical distributions elongated along the direction of the first derivative of force in the absence of any specific control strategy. These results suggest that patterns of co-variation among elemental variables during fast actions should be interpreted with caution since they may conceal a synergy stabilizing a performance variable among elemental variables because of the effects of timing errors.

Learning Motor Synergies

Where do synergies come from, and how do they arise? Many of the synergies that have been experimentally identified are probably deeply ingrained as they are the basis for the most common motor activities such as upright balance or reaching for objects. Others are more likely derived from more specific and learned skills such as shooting or throwing a Frisbee. Those of us who have tried to influence synergies by shaping environments know that it is not trivial to do so. Just because a movement environment affords, for instance, to relax the control of particular DOFs, this does not mean that the CNS will actually release the associated DOFs from control. In the experiment of Scholz and Schöner (1999), for example, we explored a condition in which participants made the sit-to-stand transition with their feet in tightly fitting ski boots that were fit into ski bindings and attached to the floor. This released participants, in principle, from control of the horizontal position of their center of mass in the anterior-posterior direction as they could transmit angular momentum

in this direction without risk of falling over. Just providing this constraint did not lead to a restructuring of motor variance, however. Only skilled skiers were able to adapt to this condition and to alter their patterns (unpublished).

Acquiring motor skills has, of course, been a central topic of research in motor control for a long time (Schmidt, 2004). Different conceptions of learning have been considered. The earliest relevant approach might be Bernstein's theory of staged skill acquisition (Bernstein, 1996), which stated that practicing a movement leads to a sequence of changes in the number of DOFs. Early stages of skill acquisition were assumed to be associated with a reduction in the number of DOFs, which was assumed to make it easier for the controller to deal with the task. Additional DOFs were to be released or recruited over the course of learning. This view has not been challenged, to our knowledge, and many studies describe changes in the number of DOFs with practice. Both reducing the amount of motion in a particular DOF ("freezing") and increasing the amount of motion (DOF "freed" or "released") with practice have been reported (Newell et al., 2003). Note, however, that keeping one joint of a multi-joint effector motionless during a fast movement requires precise modification of the control signals to muscles crossing the joint (Koshland et al., 1991; Latash et al., 1995). Moreover, the number of DOFs does not change when some of them have smaller amounts of movement within a motor task.

Much recent work on motor learning has been based on the paradigm of exposing people to unknown force fields or sensory distortions and analyzing adaptation to such conditions (Shadmehr & Mussa-Ivaldi, 1994). The theoretical setting for such work has been that of learning as the elaboration of new or the refinement of existing internal models (Wolpert et al., 2001; Shadmehr, 2004).

A recent study used the adaptation paradigm to look at changes in patterns of joint variance to a velocity-dependent force field when a multi-joint reaching task was performed by a kinematically redundant limb (Yang et al., 2007). The study showed, in particular, an increase in the variability within the UCM (V_{UCM}) after the adaptation. Since this variability, by definition, has no effect on the endpoint trajectory, its increase seems to pose major problems for any idea of a refined internal model designed to optimize task performance in the new conditions.

An approach to motor learning closer in spirit to the problem of learning synergies has been developed in the domain of relative timing. When a new pattern of relative timing of bimanual movements is learned, for instance, the stability of the pattern increases in time, with an associated reduction in variability (Schöner et al., 1992; Zanone & Kelso, 1997). Moreover, after learning the new pattern, other patterns of relative timing are systematically biased toward the learned patterns and are more stable the closer they are to the learned pattern. Similarly, practice has been shown to lead to changes in the correlation among motions of body segments occurring in time (Vereijken et al., 1992). Unfortunately, these studies have generally examined changes in the coordination of non-redundant sets of joints and, therefore, do not address how flexibility in redundant motor patterns emerges during learning.

Within our current framework, we conceive of learning as potentially leading to changes in either component of synergies, sharing pattern and/or flexibility/stability reflected in patterns of co-variation of elemental variables. Thus, an important area of investigation is to determine whether, how, and in what sequence the two features of synergies are learned. Can practice lead to better or worse stabilization of an

important performance variable by changing the relations among the elemental variables?

Assuming that learning ultimately leads to stabilization of task-relevant performance variables, there are three possible scenarios for how the structure of variance in the space of elemental variables may evolve during learning: (a) V_{ORT} (task-relevant variance) is reduced more strongly than V_{UCM} , leading to a strengthening or even the first emergence of a synergy stabilizing the performance variable. V_{UCM} may be reduced less, remain constant or even increase in this scenario; (b) V_{UCM} is reduced along with V_{ORT} , keeping the strength of the synergy (for example, the ratio $V_{\text{UCM}}/V_{\text{ORT}}$) relatively invariant; and (c) V_{UCM} is reduced more strongly than V_{ORT} , leading to a reduction of indices of synergy.

A number of recent studies of learning have begun to shed light on these issues. In particular, experiments have shown that all three scenarios are possible at different stages of motor learning.

Scenario (a) amounts to creating or learning the synergy. This may involve learning anew or refining a Jacobian to be able to form an appropriate structure that stabilizes salient performance variables, i.e., forming a UCM (e.g., producing a function of finger forces that is not their sum, Kang et al., 2004). This may also involve elaborating an optimal sharing pattern of elemental variables given a set of constraints (e.g., prehension tasks constrained by requirements to keep the total force and the total moment of forces within a particular range; Zatsiorsky and Latash, 2004) and maybe other goals such as comfort, smoothness of trajectory, etc. (e.g., as in pointing and multi-finger force production tasks; Domkin et al., 2002, 2005; Latash et al., 2003).

Results consistent with scenario (a) were observed in a study of the effects of practice of an accurate multi-finger force production task in persons with Down syndrome (DS; Latash et al., 2002a; Scholz et al., 2003). Participants produced ramp profiles of the total force while pressing on force sensors with all four fingers of the dominant hand. Prior to practice, persons with DS showed predominantly positive co-variation among individual finger modes that destabilized the total force, while the pronation/supination moment of force was stabilized. After 2 days of practice, these persons learned to use their fingers more flexibly and showed improved co-variation of force modes, which stabilized the total force profile without a concomitant deterioration in the moment stabilization. These patterns of co-variation of force modes were similar to those observed in persons without DS.

In the study of Frisbee throwing (Yang & Scholz, 2005), both V_{UCM} and V_{ORT} decreased over practice. However, the decrease in V_{UCM} was significantly smaller than that in V_{ORT} consistent with scenario (a). This change was limited to synergies that stabilized movement direction (deviations from a straight line path to the target) and the hand's orientation to the target. The relation $V_{\text{UCM}} > V_{\text{ORT}}$ with respect to stabilization of movement extent or hand path velocity persisted from the outset and did not change with practice, more consistent with scenario (b). In both experiments, the structure $V_{\text{UCM}} > V_{\text{ORT}}$ was present from the onset of practicing the task.

Results consistent with scenarios (b) and (c) were observed in studies of the effects of practice on multi-joint, bi-manual pointing (Domkin et al., 2002, 2005). During a rather simple planar task of placing the tip of the pointer held by one hand into the center of a target held by the other hand (Domkin et al., 2002) an improvement in overall accuracy was reflected in a decrease in V_{ORT} that was accompanied

by an even larger decline in V_{UCM} [consistent with scenario (c)]. When a similar task was made more complex by using three-dimensional movements and three possible targets, the relative declines in V_{ORT} and V_{UCM} became similar [consistent with scenario (b)].

Experiments with accurate multi-finger force production have suggested the existence of two stages in the effects of practice, not in terms of freezing or releasing of DOFs, but in terms of changes in the structure of variance (Latash et al., 2003; Kang et al., 2004). The first stage is associated with a greater drop in V_{ORT} than in V_{UCM} computed for the stabilization of the important performance variable leading to an increase in the index of a corresponding synergy, consistent with scenario (a). Further practice led to a larger drop in V_{UCM} than in V_{ORT} consistent with scenario (c).

A drop in an index of a synergy could be a bottom effect if the stability of the task-relevant performance variable has reached its maximum leading to minimal V_{ORT} . On the other hand, a decrease in an index of stability of a performance variable may indeed be a purposeful outcome of learning. Stability of performance comes at a price of decreased flexibility and adaptability (see Hasan, 2005). In particular, if a task requires changing a performance variable quickly when required by external conditions, increasing its stability may be counter-productive and learning may indeed lead to a drop in indices of synergies stabilizing that variable.

Conclusions

What is the contribution of the refined concept of synergy to our understanding of the control of redundant systems? We think it offers a broader approach to the DOF problem. Binding DOFs into sharing patterns reduces the need to generate detailed time courses for all elemental variables in a given task. This has been widely recognized by previous researchers. However, the task-specific structure of variability observed in multi-DOF systems forces us to also account for how synergies provide for stabilization against perturbations while at the same time allowing for the amazing adaptability and flexibility of voluntary movement. We propose that this is achieved in two ways. First, the synergies are task-dependent. Through learning processes, the DOFs are bound not into universal “motor primitives” (that seem more similar to the concept of “modes”), but into task-specific synergies, whose activation by a single, potentially simple timing signal leads to competent performance. Second, the binding is flexible itself, stably linking combinations of DOFs that are essential to achieve the task, but releasing from tight control combinations of DOFs that lead to the same task performance. This makes it possible to achieve motor goals under varied environmental circumstances, coming from different initial postures, or even simultaneously achieving multiple tasks.

Although our knowledge to date is still limited, it is plausible that the extent to which flexibility is challenged during practice plays a major role in the learning process. What is being learned, in other words, is not only a particular movement in joint space, but rather how to achieve a motor goal from varied initial conditions and in the face of varied environmental constraints [very close to the concept of dexterity in Bernstein (1996)].

Such insights into learning might become important with respect to pathologies and strategies of their treatment. For instance, helping a stroke patient to actively

explore flexibility rather than merely learning a rigid substitute solution to a motor problem could shift emphasis in movement therapy. At a more basic level, however, the first step may be to recognize that the characterization of movement patterns and their pathologies needs to look at two aspects, sharing and stability/flexibility, or, simply put, the mean but also the variance (cf. Reisman & Scholz, 2003)!

Despite the many challenges still ahead of us, we feel that the refined concept of synergy may be an element of a language for motor control, the inadequacy of which has been considered a chief problem for the discipline (Gelfand, 1991). Combining methods that establish sharing patterns (e.g., matrix factorization methods such as PCA) with methods that establish patterns of stability and flexibility (e.g., the UCM method) makes it possible to characterize synergies, track their evolution during learning, and diagnose their pathological failure.

Acknowledgments

We are grateful to our colleagues and former students Frederic Danion, Simon Goodman, Valere Martin, Vijaya Krishnamoorthy, Darcy Reisman, Ya-weng Tseng, Jeng-Feng Yang, Jae Kun Shim, Sheng Li, Ning Kang, Minoru Shinohara, and Vladimir Zatsiorsky. We are also very grateful to Sandro Mussa-Ivaldi for his productive comments on earlier versions of the manuscript. This work was supported in part by NIH grants AG-018751, NS-35032, NS-044907, NS-050880, and M01 RR-10732, and NSF grant IBN-0078127.

References

- Abbs, J.H., & Gracco, V.L. (1984). Control of complex motor gestures: Orofacial muscle responses to load perturbations of the lip during speech. *Journal of Neurophysiology*, **51**, 705-723.
- Alexandrov, A., Frolov, A., & Massion, J. (1998). Axial synergies during human upper trunk bending. *Experimental Brain Research*, **118**, 210-220.
- American Heart Association. (2005). Overview of CPR. *Circulation*, **112**, 12-15.
- Babinski, F. (1899). De l'asynergie cerebelleuse. *Revue Neurologique*, **7**, 806-816.
- Beer, R.F., Dewald, J.P., Dawson, M.L., & Rymer, W.Z. (2004). Target-dependent differences between free and constrained arm movements in chronic hemiparesis. *Experimental Brain Research*, **156**, 458-470.
- Berkinblit, M.B., Feldman, A.G., Fukson, O.I. (1986). Adaptability of innate motor patterns and motor control mechanisms. *Behavioral and Brain Sciences*, **9**, 585-638.
- Bernstein, N.A. (1947). *On the construction of movements*. Moscow: Medgiz (in Russian).
- Bernstein, N.A. (1967). *The co-ordination and regulation of movements*. Oxford: Pergamon Press.
- Bernstein, N.A. (1996). On dexterity and its development. In: Latash ML, Turvey MT (Eds.) *Dexterity and Its Development* (pp. 3-246). Mahwah, NJ: Lawrence Erlbaum Associates.
- Bloedel, J.R. (1992). Functional heterogeneity with structural homogeneity: How does the cerebellum operate? *Behavioral and Brain Sciences*, **15**, 666-678.
- Bullock, D., Grossberg, S., Guenther, F. (1993). A self-organizing neural model of motor equivalence reaching and tool use by a multijoint arm. *Journal of Cognitive Neuroscience*, **5**, 408-435.
- Cirstea, M.C., Mitnitski, A.B., Feldman, A.G., & Levin, M.F. (2003). Interjoint coordination dynamics during reaching in stroke. *Experimental Brain Research*, **151**, 289-300.
- Cisek, P., & Kalaska, J.F. (2005). Neural correlates of reaching decisions in dorsal premotor cortex: specification of multiple direction choices and final selection of action. *Neuron*, **45**, 801-814.

- Coltz, J.D., Johnson, M.T.V., & Ebner, T.J. (1999). Cerebellar Purkinje cell simple spike discharge encodes movement velocity in primates during visuomotor arm tracking. *Journal of Neuroscience*, **19**, 1782-1803.
- Cusumano, J.P., & Cesari, P. (2006). Body goal variability mapping in an aiming task. *Biological Cybernetics*, **94**, 367-379.
- Danion, F., Schöner, G., Latash, M.L., Li, S., Scholz, J.P., & Zatsiorsky, V.M. (2003). A force mode hypothesis for finger interaction during multi-finger force production tasks. *Biological Cybernetics*, **88**, 91-98.
- Danna-Dos-Santos, A., Slomka, K., Zatsiorsky, V.M., & Latash, M.L. (2007). Muscle modes and synergies during voluntary body sway. *Experimental Brain Research* (in press).
- Desmurget, M., Prablanc, C., Rossetti, Y., Arzi, M., Paulignan, Y., Urquizar, C., & Mignot, J.C. (1995). Postural and synergic control for three-dimensional movements of reaching and grasping. *Journal of Neurophysiology*, **74**, 905-910.
- Domkin, D., Laczko, J., Jaric, S., Johansson, H., & Latash, M.L. (2002). Structure of joint variability in bimanual pointing tasks. *Experimental Brain Research*, **143**, 11-23.
- Domkin, D., Laczko, J., Djupsjöbacka, M., Jaric, S., & Latash, M.L. (2005). Joint angle variability in 3D bimanual pointing: uncontrolled manifold analysis. *Experimental Brain Research*, **163**, 44-57.
- Donders, F.C. (1847). Beitrag zur Lehre von den Bewegungen von den menschlichen Augen. *Hollandischen Beiträgen zu den Anatomischen und Physiologischen Wissenschaften*, **1**, 104-145.
- Easton, T.A. (1978). Coordinative structures—the basis for a motor program. In Landers, D. & Christina, R. (Eds.). *Psychology of motor behavior and sport*. Champaign, IL: Human Kinetics.
- Feldman, A.G. (1966). Functional tuning of the nervous system with control of movement or maintenance of a steady posture. II. Controllable parameters of the muscle. *Biophysics*, **11**, 565-578.
- Feldman, A.G. (1986). Once more on the equilibrium-point hypothesis (λ model) for motor control. *Journal of Motor Behavior*, **18**, 17-54.
- Feldman, A.G., & Latash, M.L. (2005). Testing hypotheses and the advancement of science: Recent attempts to falsify the equilibrium-point hypothesis. *Experimental Brain Research*, **161**, 91-103.
- Feldman, A.G., & Levin, M.F. (1995). Positional frames of reference in motor control: their origin and use. *Behavioral and Brain Sciences*, **18**, 723-806.
- Feldman, A.G., Ostry, D.J., Levin, M.F., Gribble, P.L., & Mitnitski, A.B. (1998). Recent tests of the equilibrium-point hypothesis (λ model). *Motor Control*, **2**, 189-205.
- Fukui, T. (1999). Sequence generation in arbitrary temporal patterns from theta-nested gamma oscillations: a model of the basal ganglia-thalamo-cortical loops. *Neural Networks*, **12**, 975-987.
- Gandolfo, F., & Mussa-Ivaldi, F.A. (1993). Vector summation of end-point impedance in kinematically redundant manipulators. In: Proceedings of the 1993 IEEE/RSJ International Conference on Intelligent Robots and Systems (IROS93), pp.1627-1634.
- Gelfand, I.M. (1991). Two archetypes in the psychology of man. *Nonlinear Science Today*, **1**, 11-16.
- Gelfand, I.M., & Latash, M.L. (1998). On the problem of adequate language in movement science. *Motor Control*, **2**, 306-313.
- Gelfand, I.M., Latash, M.L. (2002). On the problem of adequate language in biology. In: Latash, M.L. (Ed.) *Progress in motor control. vol. 2: structure-function relations in voluntary movement* (pp. 209-228). Champaign, IL: Human Kinetics.
- Gelfand, I.M., & Tsetlin, M.L. (1966). On mathematical modeling of the mechanisms of the central nervous system. In: Gelfand, I.M., Gurfinkel, V.S., Fomin, S.V., & Tsetlin, M.L. (Eds.) *Models of the structural-functional organization of certain biological systems* (pp. 9-26). Moscow: Nauka (in Russian; a translation is available in 1971 edition by MIT Press, Cambridge, MA).

- Georgopoulos, A.P., Kalaska, J.F., Caminiti, R., & Massey, J.T. (1982). On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *Journal of Neuroscience*, **2**, 1527-1537.
- Gielen, C.C.A.M., Vrijenhoek, E.J., Flash, T., & Neggers, S.F.W. (1997). Arm position constraints during pointing and reaching in 3-D space. *Journal of Neurophysiology*, **78**, 660-673.
- Giszter, S.F., & Kargo, W.J. (2000). Conserved temporal dynamics and vector superposition of primitives in frog wiping reflexes during spontaneous extensor deletions. *Neurocomputing*, **32-33**, 775-783.
- Giszter, S.F., Mussa-Ivaldi, F.A., & Bizzi, E. (1993). Convergent force fields organized in the frog's spinal cord. *Journal of Neuroscience*, **13**, 467-491.
- Goodman, S.R., & Latash, M.L. (2006). Feedforward control of a redundant motor system. *Biological Cybernetics*, **95**, 271-280.
- Goodman, S.R., Shim, J.K., Zatsiorsky, V.M., & Latash, M.L. (2005). Motor variability within a multi-effector system: Experimental and analytical studies of multi-finger production of quick force pulses. *Experimental Brain Research*, **163**, 75-85.
- Gottlieb, G.L., Song, Q., Hong, D.A., Almeida, G.L., & Corcos, D. (1996). Coordinating movement at two joints: a principle of linear covariance. *Journal of Neurophysiology*, **75**, 1760-1764.
- Gribble, P.L., Ostry, D.J., Sanguineti, V., & Laboisiere, R. (1998). Are complex control signals required for human arm movements? *Journal of Neurophysiology*, **79**, 1409-1424.
- Gutman, S.R., & Gottlieb, G.L. (1992). Basic functions of variability of simple pre-planned movements. *Biological Cybernetics*, **68**, 63-73.
- Gutman, S.R., Latash, M.L., Gottlieb, G.L., & Almeida, G.L. (1993). Kinematic description of variability of fast movements: Analytical and experimental approaches. *Biological Cybernetics*, **69**, 485-492.
- Hasan, Z. (1986). Optimized movement trajectories and joint stiffness in unperturbed, inertially loaded movements. *Biological Cybernetics*, **53**, 373-382.
- Hasan, Z. (2005). The human motor control system's response to mechanical perturbation: should it, can it, and does it ensure stability? *Journal of Motor Behavior*, **37**, 484-493.
- Harris, C.M., & Wolpert, D.M. (1998). Signal-dependent noise determines motor planning. *Nature*, **394**, 780-784.
- Hart, C.B., & Giszter, S.F. (2004). Modular premotor drives and unit bursts as primitives for frog motor behaviors. *Journal of Neuroscience*, **24**, 5269-5282.
- Henneman, E., Somjen, G., & Carpenter, D.O. (1965). Excitability and inhibibility of motoneurons of different sizes. *Journal of Neurophysiology*, **28**, 599-620.
- Holdefer, R.N., & Miller, L.E. (2002). Primary motor cortical neurons encode functional muscle synergies. *Experimental Brain Research*, **146**, 233-243.
- Houk, J.C., & Gibson, A.R. (1987). Sensorimotor processing through the cerebellum. In: King J.S. (Ed.) *New concepts in cerebellar neurobiology* (pp. 387-416). Liss: New York.
- Hughlings Jackson, J. (1889). On the comparative study of disease of the nervous system. *British Medical Journal*, **355-362**, Aug. 17, 1889.
- Hultborn, H., Brownstone, R.B., Toth, T.I., & Gossard, J.P. (2004). Key mechanisms for setting the input-output gain across the motoneuron pool. *Progress in Brain Research*, **143**, 77-95.
- Ivanenko, Y.P., Poppele, R.E., & Lacquaniti, F. (2004). Five basic muscle activation patterns account for muscle activity during human locomotion. *Journal of Physiology*, **556**, 267-282.
- Ivanenko, Y.P., Cappellini, G., Dominici, N., Poppele, R.E., & Lacquaniti, F. (2005). Coordination of locomotion with voluntary movements in humans. *Journal of Neuroscience*, **25**, 7238-7253.

- Jensen, J.L., Schneider, K., Ulrich, B.D., Zernicke, R.F., & Thelen, E. (1994). Adaptive dynamics of the leg movement patterns of human infants: I. The effects of posture on spontaneous kicking. *Journal of Motor Behavior*, **26**, 303-312.
- Kang, N., Shinohara, M., Zatsiorsky, V.M., & Latash, M.L. (2004). Learning multi-finger synergies: An uncontrolled manifold analysis. *Experimental Brain Research*, **157**, 336-350.
- Kargo, W.J., & Giszter, S.F. (2000). Rapid correction of aimed movements by summation of force-field primitives. *Journal of Neuroscience*, **20**, 409-426.
- Kargo, W.J., & Nitz, D.A. (2003). Early skill learning is expressed through selection and tuning of cortically represented muscle synergies. *Journal of Neuroscience*, **23**, 11255-11269.
- Katz, R., Mazzocchio, R., Penicaud, A., & Rossi, A. (1993). Distribution of recurrent inhibition in the human upper limb. *Acta Physiologica Scandinavica*, **149**, 183-198.
- Kawato, M. (1990). Computational schemas and neural network models of multijoint arm trajectory. In Miller, W.T. III, Sutton, R.S., & Werbos, P.J. (Eds). *Neural networks for control* (pp. 197-228). Cambridge, MA: The MIT Press.
- Kawato, M. (1999). Internal models for motor control and trajectory planning. *Current Opinions in Neurobiology*, **9**, 718-727.
- Kelso, J.A.S., Tuller, B., Vatikiotis-Bateson, E., & Fowler, C.A. (1984). Functionally specific articulatory cooperation following jaw perturbations during speech: evidence for coordinative structures. *Journal of Experimental Psychology: Human Perception and Performance*, **10**, 812-832.
- Kilbreath, S.L., & Gandevia, S.C. (1994). Limited independent flexion of the thumb and fingers in human subjects. *Journal of Physiology*, **479**, 487-497.
- Koshland, G.F., Gerilovsky, L., & Hasan, Z. (1991). Activity of wrist muscles elicited during imposed or voluntary movements about the elbow joint. *Journal of Motor Behavior*, **23**, 91-100.
- Krishnamoorthy, V., Goodman, S.R., Latash, M.L., & Zatsiorsky, V.M. (2003a). Muscle synergies during shifts of the center of pressure by standing persons: Identification of muscle modes. *Biological Cybernetics*, **89**, 152-161.
- Krishnamoorthy, V., Latash, M.L., Scholz, J.P., & Zatsiorsky, V.M. (2003b). Muscle synergies during shifts of the center of pressure by standing persons. *Experimental Brain Research*, **152**, 281-292.
- Krishnamoorthy, V., Latash, M.L., Scholz, J.P., & Zatsiorsky, V.M. (2004). Muscle modes during shifts of the center of pressure by standing persons: Effects of instability and additional support. *Experimental Brain Research*, **157**, 18-31.
- Kudo, K., Ito, T., & Tsutsui, S. (2000). Compensatory coordination of release parameters in a throwing task. *Journal of Motor Behavior*, **32**, 337-345.
- Lan, N. (1997). Analysis of an optimal control model of multi-joint arm movements. *Biological Cybernetics*, **76**, 107-117.
- Latash, M.L. (1996). How does our brain make its choices? In: Latash, M.L., & Turvey, M.T. (Eds.) *Dexterity and its development* (pp. 277-304). Mahwah, NJ: Lawrence Erlbaum Associates.
- Latash, M.L. (2000). The organization of quick corrections within a two-joint synergy in conditions of unexpected blocking and release of a fast movement. *Clinical Neurophysiology*, **111**, 975-987.
- Latash, M.L., Aruin, A.S., & Shapiro, M.B. (1995). The relation between posture and movement: A study of a simple synergy in a two-joint task. *Human Movement Science*, **14**, 79-107.
- Latash, M.L., Aruin, A.S., & Zatsiorsky, V.M. (1999). The basis of a simple synergy: Reconstruction of joint equilibrium trajectories during unrestrained arm movements. *Human Movement Science*, **18**, 3-30.
- Latash, M.L., & Gottlieb, G.L. (1991). Reconstruction of elbow joint compliant characteristics during fast and slow voluntary movements. *Neuroscience*, **43**, 697-712.

- Latash, M.L., Kang, N., & Patterson, D. (2002a). Finger coordination in persons with Down syndrome: Atypical patterns of coordination and the effects of practice. *Experimental Brain Research*, **146**, 345-355.
- Latash, M.L., Scholz, J.F., Danion, F., & Schöner, G. (2001). Structure of motor variability in marginally redundant multi-finger force production tasks. *Experimental Brain Research*, **141**, 153-165.
- Latash, M.L., Scholz, J.F., Danion, F., & Schöner, G. (2002b). Finger coordination during discrete and oscillatory force production tasks. *Experimental Brain Research*, **146**, 412-432.
- Latash, M.L., Scholz, J.F., Danion, F., & Schöner, G. (2002c). Finger coordination during discrete and oscillatory force production tasks. *Experimental Brain Research*, **146**, 419-432.
- Latash, M.L., Shim, J.K., & Zatsiorsky, V.M. (2004). Is there a timing synergy during multi-finger production of quick force pulses? *Experimental Brain Research*, **159**, 65-71.
- Latash, M.L., Shim, J.K., Smilga, A.V., & Zatsiorsky, V. (2005). A central back-coupling hypothesis on the organization of motor synergies: a physical metaphor and a neural model. *Biological Cybernetics*, **92**, 186-191.
- Latash, M.L., Yarrow, K., & Rothwell, J.C. (2003). Changes in finger coordination and responses to single pulse TMS of motor cortex during practice of a multi-finger force production task. *Experimental Brain Research*, **151**, 60-71.
- Leijnse, J.N., Snijders, C.C.J., Bonte, J.E., Landsmeer, J.M., Kalker, J.J., Van Der Meulen, J.C., Sonneveld, G.J., & Hovius, S.E. (1993). The hand of the musician: the kinematics of the bidigital finger system with anatomical restrictions. *Journal of Biomechanics*, **26**, 1169-1179.
- Lemay, M.A., & Grill, W.M. (2004). Modularity of motor output evoked by intraspinal microstimulation in cats. *Journal of Neurophysiology*, **91**, 502-514.
- Lemon, R.N., Baker, S.N., Davis, J.A., Kirkwood, P.A., Maier, M.A., & Yang, H.S. (1998). The importance of the cortico-motoneuronal system for control of grasp. *Novartis Foundation Symposium*, **218**, 202-215.
- Levin, M.F., Michaelsen, S.M., Cirstea, C.M., & Roby-Brami, A. (2002). Use of the trunk for reaching targets placed within and beyond the reach in adult hemiparesis. *Experimental Brain Research*, **143**, 171-180.
- Li, Z.M. (2006). Functional degrees of freedom. *Motor Control*, **10**, 301-310.
- Li, Z.M., Latash, M.L., & Zatsiorsky, V.M. (1998). Force sharing among fingers as a model of the redundancy problem. *Experimental Brain Research*, **119**, 276-286.
- Lund, J.S., Angelucci, A., & Bressloff, P.C. (2003). Anatomical substrates for functional columns in macaque monkey primary visual cortex. *Cerebral Cortex*, **13**, 15-24.
- McDonald, P.V., van Emmerik, R.E.A., & Newell, K.M. (1989). The effects of practice on limb kinematics in a throwing task. *Journal of Motor Behavior*, **21**, 245-264.
- Macpherson, J.M., Rushmer, D.S., & Dunbar, D.C. (1986). Postural responses in the cat to unexpected rotations of the supporting surface: evidence for a centrally generated synergic organization. *Experimental Brain Research*, **62**, 152-160.
- Mah, C.D., Hulliger, M., Lee, R.G., & O'Callaghan, I. (1994). Quantitative analysis of human movement synergies: constructive pattern analysis for gait. *Journal of Motor Behavior*, **26**, 83-102.
- Martin, T.A., Norris, S.A., Greger, B.E., & Thach, W.T. (2002). Dynamic coordination of body parts during prism adaptation. *Journal of Neurophysiology*, **88**, 1685-1694.
- Martin, V. (2005). A dynamical systems account of the uncontrolled manifold and motor equivalence in human pointing movements. PhD thesis, Ruhr-Universität, Bochum, Germany.
- Martin, V., Scholz, J.P., Schöner, G. (2004). Theory of the uncontrolled manifold: variance, self-motion, and neuronal noise. Program No. 871.17. *Abstract Viewer and Itinerary Planner*. Washington: Society for Neuroscience, 2004. Online.

- Mattei, B., Schmied, A., Mazzocchio, R., Decchi, B., Rossi, A., & Vedel, J.P. (2003). Pharmacologically induced enhancement of recurrent inhibition in humans: effects on motoneurone discharge patterns. *Journal of Physiology*, **548**, 615-629.
- Merkle, L.A., Layne, C.S., Bloomberg, J.J., & Zhang, J. (1998). Using factor analysis to identify neuromuscular synergies during treadmill walking. *Journal of Neuroscience Methods*, **82**, 207-214.
- Miyamoto, H., Kawato, M., Setoyama, T., & Suzuki, R. (1988). Feedback-error-learning neural network for trajectory control of a robotic manipulator. *Neural Networks*, **1**, 251-265.
- Müller, H., & Sternad, D. (2003). A randomization method for the calculation of covariation in multiple nonlinear relations: illustrated with the example of goal-directed movements. *Biological Cybernetics*, **89**, 22-33.
- Müller, H., & Sternad, D. (2004). Decomposition of variability in the execution of goal-oriented tasks: Three components of skill improvement. *Journal of Experimental Psychology: Human Perception and Performance*, **30**, 212-233.
- Mussa-Ivaldi, F.A., Giszter, S.F., & Bizzi, E. (1994). Linear combinations of primitives in vertebrate motor control. *Proceedings of the National Academy of Sciences USA*, **91**, 7534-7538.
- Mussa-Ivaldi, F.A., & Hogan, N. (1991). Integrable solutions of kinematic redundancy via impedance control. *The International Journal of Robotics Research*, **10**, 481-491.
- Nashner, L.M., & Cordo, P.J. (1981). Relation of automatic postural responses and reaction-time voluntary movements of human leg muscles. *Experimental Brain Research*, **43**, 395-405.
- Newell, K.M. (1991). Motor skill acquisition. *Annual Reviews in Psychology*, **42**, 213-237.
- Newell, K.M., Broderick, M.P., Deutsch, K.M., & Slifkin, A.B. (2003). Task goals and change in dynamical degrees of freedom with motor learning. *Journal of Experimental Psychology: Human Perception and Performance*, **29**, 379-387.
- Ohtsuki, T. (1981). Inhibition of individual fingers during grip strength exertion. *Ergonomics*, **24**, 21-36.
- Olafsdottir, H., Yoshida, N., Zatsiorsky, V.M., & Latash, M.L. (2005). Anticipatory covariation of finger forces during self-paced and reaction time force production. *Neuroscience Letters*, **381**, 92-96.
- Ozeki, H., Sadakane, O., Akasaki, T., Naito, T., Shimegi, S., & Sato, H. (2004). Relationship between excitation and inhibition underlying size tuning and contextual response modulation in the cat primary visual cortex. *Journal of Neuroscience*, **24**, 1428-1438.
- Pelz, J., Hayhoe, M., & Loeber, R. (2001). The coordination of eye, head, and hand movements in a natural task. *Experimental Brain Research*, **139**, 266-277.
- Reisman, D., Scholz, J.P., & Schöner, G. (2002a). Coordination underlying the control of whole body momentum during sit-to-stand. *Gait and Posture*, **15**, 45-55.
- Reisman, D., Scholz, J.P., & Schöner, G. (2002b). Differential joint coordination in the tasks of standing up and sitting down. *Journal of Electromyography and Kinesiology*, **12**, 493-505.
- Reisman, D., & Scholz, J.P. (2003). Aspects of joint coordination are preserved during pointing in persons with post-stroke hemiparesis. *Brain*, **126**, 2510-2527.
- Rosenbaum, D.A., Loukopoulos, L.D., Meulenbroek, R.G.M., Vaughan, J., & Engelbrecht, S.E. (1995). Planning reaches by evaluating stored postures. *Psychological Reviews*, **102**, 28-67.
- Saltiel, P., Wyler-Duda, K., D'Avella, A., Tresch, M.C., & Bizzi, E. (2001). Muscle synergies encoded within the spinal cord: evidence from focal intraspinal NMDA iontophoresis in the frog. *Journal of Neurophysiology*, **85**, 605-619.
- Sanger, T.D. (2000). Human arm movements described by a low-dimensional superposition of principal components. *Journal of Neuroscience*, **20**, 1066-1072.
- Santello, M., Flanders, M., & Soechting, J.F. (1998). Postural hand synergies for tool use. *Journal of Neuroscience*, **18**, 10105-10115.

- Santello, M., & Soechting, J.F. (2000). Force synergies for multifingered grasping. *Experimental Brain Research*, **133**, 457-467.
- Schieber, M.H. (2001). Constraints on somatotopic organization in the primary motor cortex. *Journal of Neurophysiology*, **86**, 2125-2143.
- Schieber, M.H., & Santello, M. (2004). Hand function: peripheral and central constraints on performance. *Journal of Applied Physiology*, **96**, 2293-2300.
- Schmidt, R.A. (2004). *Motor learning and performance*. Champaign, IL: Human Kinetics.
- Scholz, J.P., & Schöner, G. (1999). The uncontrolled manifold concept: Identifying control variables for a functional task. *Experimental Brain Research*, **126**, 289-306.
- Scholz, J.P., Schöner, G., & Latash, M.L. (2000). Identifying the control structure of multijoint coordination during pistol shooting. *Experimental Brain Research*, **135**, 382-404.
- Scholz, J.P., Reisman, D., & Schöner, G. (2001). Effects of varying task constraints on solutions to joint coordination in a sit-to-stand task. *Experimental Brain Research*, **141**, 485-500.
- Scholz, J.P., Danion, F., Latash, M.L., & Schöner, G. (2002). Understanding finger coordination through analysis of the structure of force variability. *Biological Cybernetics*, **86**, 29-39.
- Scholz, J.P., Kang, N., Patterson, D., & Latash, M.L. (2003). Uncontrolled manifold analysis of single trials during multi-finger force production by persons with and without Down syndrome. *Experimental Brain Research*, **153**, 45-58.
- Schöner, G. (1994). From interlimb coordination to trajectory formation: common dynamical principles. In: Swinnen, S., Heuer, H., Massion, J., & Casaer, P. (Eds.). *Interlimb coordination: neural, dynamical, and cognitive constraints* (pp. 339-368). San Diego: Academic Press.
- Schöner, G. (1995). Recent developments and problems in human movement science and their conceptual implications. *Ecological Psychology*, **8**, 291-314.
- Schöner, G. (2002). Timing, clocks, and dynamical systems. *Brain and Cognition*, **48**, 31-51.
- Schöner, G., & Kelso, J.A.S. (1988). Dynamic pattern generation in behavioral and neural systems. *Science*, **239**, 1513-1520.
- Schöner, G., Zanone, P., & Kelso, J.A.S. (1992). Learning as change of coordination dynamics: theory and experiment. *Journal of Motor Behavior*, **24**, 29-48.
- Schoppa, N.E., & Urban, N.N. (2003). Dendritic processing within olfactory bulb circuits. *Trends in Neuroscience*, **26**, 501-506.
- Schwartz, A.B. (1993). Motor cortical activity during drawing movements: population representation during sinusoid tracing. *Journal of Neurophysiology*, **70**, 28-36.
- Seif-Naraghi, A.H., & Winters, J.M. (1990). Optimized strategies for scaling goal-directed dynamic limb movements. In: Winters, J.M., & Woo, S.L.-Y. (Eds.) *Multiple muscle systems. Biomechanics and movement organization* (pp. 312-334). New York: Springer-Verlag.
- Shadmehr, R. (2004). Generalization as a behavioral window to the neural mechanisms of learning internal models. *Human Movement Science*, **23**, 543-568.
- Shadmehr, R., & Mussa-Ivaldi, F.A. (1994). Adaptive representation of dynamics during learning of a motor task. *Journal of Neuroscience*, **14**, 3208-3224.
- Sherrington, C.S. (1910). Flexion reflex of the limb, crossed extension reflex, and reflex stepping and standing. *Journal of Physiology*, **40**, 28-121.
- Shim, J.K., Latash, M.L., & Zatsiorsky, V.M. (2003). The central nervous system needs time to organize task-specific covariation of finger forces. *Neuroscience Letters*, **353**, 72-74.
- Shim, J.K., Olafsdottir, H., Zatsiorsky, V.M., & Latash, M.L. (2005). The emergence and disappearance of multi-digit synergies during force production tasks. *Experimental Brain Research*, **164**, 260-270.

- Shinohara, M., Scholz, J.P., Zatsiorsky, V.M., & Latash, M.L. (2004). Finger interaction during accurate multi-finger force production tasks in young and elderly persons. *Experimental Brain Research*, **156**, 282-292.
- Smith, J.L., Hoy, M.G., Koshland, G.F., Phillips, D.M., & Zernicke, R.F. (1985). Intralimb coordination of the paw-shake response: a novel mixed synergy. *Journal of Neurophysiology*, **54**, 1271-1281.
- Sontag, E.D. (1990). Further facts about input to state stabilization. *IEEE Transactions on Automatic Control*, **35**, 473-477.
- Sugiuchi, Y., Kakei, S., Izawa, Y., Shinoda, Y. (2003). Functional synergies among neck muscles revealed by branching patterns of single long descending motor-tract axons. In: Mori, S., Stuart, D.G., & Wisendanger, M. (Eds.) *Brain mechanisms for the integration of posture and movement* (pp. 353-368). Amsterdam: Elsevier.
- Thach, W.T., & Bastian, A.J. (2003). Role of the cerebellum in the control and adaptation of gait in health and disease. In: Mori, S., Stuart, D.G., & Wisendanger, M. (Eds.) *Brain mechanisms for the integration of posture and movement* (pp. 411-422). Amsterdam: Elsevier.
- Ting, L.H., & Macpherson, J.M. (2005). A limited set of muscle synergies for force control during a postural task. *Journal of Neurophysiology*, **93**, 609-613.
- Todorov, E. (2004). Optimality principles in sensorimotor control. *Nature Neuroscience*, **7**, 907-915.
- Todorov, E., & Jordan, M.I. (2002). Optimal feedback control as a theory of motor coordination. *Nature Neuroscience*, **5**, 1226-1235.
- Tresch, M.C., Cheung, V.C.K., & d'Avilla, A. (2006). Matrix factorization algorithms for the identification of muscle synergies: evaluation on simulated and experimental data sets. *Journal of Neurophysiology*, **95**, 2199-2212.
- Tseng, Y., Scholz, J.P., & Schoner, G. (2002). Goal-equivalent joint coordination in pointing: affect of vision and arm dominance. *Motor Control*, **6**, 183-207.
- Tseng, Y., Scholz, J.P., Schöner, G., Hotchkiss, L. (2003). Effect of accuracy constraint on the underlying joint coordination of pointing movements. *Experimental Brain Research*, **149**, 276-288.
- Turvey, M.T. (1990). Coordination. *American Psychologist*, **45**, 938-953.
- Uno, Y., Kawato, M., & Suzuki, R. (1989). Formation and control of optimal trajectory in human multijoint arm movement. Minimum torque-change model. *Biological Cybernetics*, **61**, 89-101.
- Uchiyama, T., Johansson, H., & Windhorst, U. (2003). Static and dynamic input-output relations of the feline medial gastrocnemius motoneuron-muscle system subjected to recurrent inhibition: a model study. *Biological Cybernetics*, **89**, 264-273.
- van Heijst, J.J., Vos, J.E., & Bullock, D. (1998). Development in a biologically inspired spinal neural network for movement control. *Neural Networks*, **11**, 1305-1316.
- Vereijken, B., van Emmerick, R.E.A., Whiting, H.T.A., & Newell, K.M. (1992). Free(z)ing degrees of freedom in skill acquisition. *Journal of Motor Behavior*, **24**, 133-142.
- Vernazza-Martin, S., Martin, N., & Massion, J. (1999). Kinematic synergies and equilibrium control during trunk movement under loaded and unloaded conditions. *Experimental Brain Research*, **128**, 517-526.
- Wehr, M., & Zador, A.M. (2003). Balanced inhibition underlies tuning and sharpens spike timing in auditory cortex. *Nature*, **426**, 442-446.
- Wilson, H.R. (1999). Simplified dynamics of human and mammalian neocortical neurons. *Journal of Theoretical Biology*, **200**, 375-388.
- Wolpert, D.M., Ghahramani, Z., & Flanagan, J.R. (2001). Perspectives and problems in motor learning. *Trends in Cognitive Science*, **5**, 487-494.
- Yang, J.-F., & Scholz, J.P. (2005). Learning a throwing task is associated with differential changes in the use of motor abundance. *Experimental Brain Research*, **164**, 1-17.

- Yang, J.-F., Scholz, J.P., & Latash, M.L. (2007). The role of kinematic redundancy in adaptation of reaching. *Experimental Brain Research*, **176**, 54-69.
- Zanone, P.G., & Kelso, J.A. (1997). Coordination dynamics of learning and transfer: collective and component levels. *Journal of Experimental Psychology: Human Perception and Performance*, **23**, 1454-1480.
- Zatsiorsky, V.M., Li, Z.-M., & Latash, M.L. (2000). Enslaving effects in multi-finger force production. *Experimental Brain Research*, **131**, 187-195.
- Zatsiorsky, V.M., & Latash, M.L. (2004). Prehension synergies. *Exercise and Sport Science Reviews*, **32**, 75-80.

***Motor Control* Mission Statement**

Motor Control, the official journal of the International Society of Motor Control, is designed to provide a multidisciplinary forum for the exchange of scientific information on the control of human movement across the lifespan, including issues related to motor disorders.

Motor Control encourages submission of papers from a variety of disciplines including, but not limited to, biomechanics, kinesiology, neurophysiology, neuroscience, psychology, physical medicine, and rehabilitation. The journal will publish a wide variety of types of research papers including clinical experimental, modeling, and theoretical studies. To be considered for publication, papers should clearly demonstrate a contribution to the understanding of control of movement.

In addition to publishing research papers, *Motor Control* will publish review articles, quick communications, commentaries, target articles, and book reviews. When warranted, an entire issue may be devoted to a specific topic within the area of motor control.