Journal of Human Kinetics volume 12, 2004, 3-14

Motor Synergies and Their Changes with Practice

by

Mark L. Latash[1], *Slobodan Jaric*[2], *John P. Scholz*[2],
Vladimir M. Zatsiorsky[1]

We review a series of studies that used the framework of the uncontrolled manifold (UCM) hypothesis to quantify changes in motor synergies with practice. The UCM hypothesis states that control of a multi-element action, at any time, may be associated with creation of a subspace (a UCM) within the state space of the elements. This subspace corresponds to a stable value of an important performance variable or several variables. Strength of a synergy may be estimated quantitatively as proportion of the total variance of its elements, e.g. across several trials at a task, that lies within the UCM. Quantitative analysis of covariation patterns of kinematic and kinetic elemental variables with respect to stabilization of different, task-specific performance variables allowed to monitor changes in motor synergies with practice. The studies have demonstrated two stages in practice-related effects. Early in practice of novel tasks, synergies stabilizing important performance variables emerged and strengthened. Later, in some instances, variability of elemental variables which did not affect the performance variables decreased more rapidly leading to the synergies becoming seemingly weaker. Experiments with transcranial magnetic stimulation applied to the primary motor cortex have suggested that practice led to plastic changes in neural structures mediating motor response to the stimulation.
Keywords: *Synergy, practice, uncontrolled manifold, human*

---

[1] - The Pennsylvania State University, University Park, PA USA;
[2] - The University of Delaware, Newark, DE USA

Approaches to the problem of motor redundancy

There have been two major approaches to the problem of motor redundancy. One of them follows the original formulation by Bernstein (1967) that this is a problem of elimination of redundant degrees-of-freedom (DOFs). Elimination of biomechanical DOFs is commonly invoked in contemporary studies of motor behavior, while studies of motor learning commonly use notions of freezing and releasing DOFs at different stages of skill acquisition (Newell 1991; Vereijken *et al.* 1992; Piek 1995). Attempts to solve the problem of motor redundancy have involved, in particular, application of optimization methods based on certain mechanical, psychological, or complex cost functions (reviewed in Rosenbaum *et al.* 1995; Prilutsky and Zatsiorsky 2002).

The other approach follows the traditions of Gelfand and Tsetlin (1967). It views the design of the human motor system not as a source of computational problems for the central nervous system (CNS) but rather as a versatile and flexible tool. The CNS is not expected to eliminate any of the seemingly redundant DOFs but to use them to ensure stable performance with respect to particular important variables: *The motor system is viewed not as redundant but as abundant*.

We view synergies as *neural organizations of elements (or elemental variables) that stabilize important performance variables*. Synergies may be described with two major characteristics. First, elements typically share a common input or neural drive that leads to stable relationships among them over time, such as force sharing in multi-finger tasks, Li *et al.* (1998). Second, elements show “error compensation”: If the contribution of one element in a particular trial and/or at a particular time has a perturbing effect on an important performance variable, other elements are likely to modify their contributions in such a way that these modifications decrease the expected change in that performance variable or, in other words, stabilizes its desired value.

This definition makes the notion of synergy tightly linked to the phenomenon of motor variability, which is arguably the most universal characteristic of human motor actions. Apparently, humans are unable to completely eliminate variability, even for best practiced actions performed in most reproducible conditions. Arguably, one of the best known illustrations of this is a study performed by Bernstein in the nineteen-twenties (Bernstein 1927) of the kinematics of hitting movements when professional blacksmiths stroke the chisel with the hammer. These subjects were perfectly trained: They had performed the same movement hundreds of times a day for years. Bernstein noticed that the trajectory of the tip of the hammer showed visible variability across a series of strikes by a blacksmith, and that this variability was smaller than the variability of the trajectories of individual joints of the subject's arm holding the hammer. Since apparently, the brain 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 that the 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.

To put it bluntly, variability happens. A major purpose of a synergy may be viewed as minimizing effects of element variability on important performance variables.

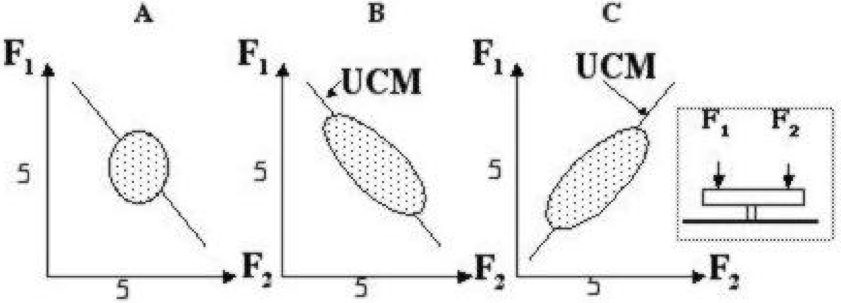

Fig. 1

Panel A demonstrates a distribution of data points for a “non-synergy” in the task of force production with two fingers. Panel B corresponds to a force-stabilizing synergy (more variance lies within the UCM$_F$). Panel C illustrates a moment-stabilizing synergy with respect to UCM$_M$.

Figure 1 illustrates the notion of synergy with a two-finger task to produce the total force of 10 N. Individual points on the graphs correspond to force combinations produced by the fingers in different trials, while the ellipses outline the point distributions. All three panels show a certain average sharing pattern between the two fingers, close to 50%:50%. In panel A, if one finger produces too much force, the other finger with equal probabilities produces more than average or less than average force, i.e. the fingers do not show error compensation with respect to the total force. In panel B, if one finger produces more force than average, the other finger will more likely produce less force than average, i.e. the fingers show error compensation. Panel A illustrates a “non-synergy”, while panel B illustrates a force-stabilizing synergy. We will get to panel C in the next subsection.

The Uncontrolled Manifold (UCM-) hypothesis and analysis of variance

The UCM hypothesis (Scholz and Schöner 1999; reviewed in Latash *et al.* 2002b) assumes that the controller acts in the space of independent elemental variables and selects in that space a subspace (a manifold, UCM) corresponding to a stable value of an important performance variable (or several important variables). Further, the controller organizes covariation of elemental variables to limit their variability in directions that are orthogonal to the UCM (“bad variability”) while allowing relatively more variability within the UCM (“good variability”). In Fig. 1A,B, the UCM corresponding to the total force of 10 N is shown by the lines with a negative slope. *The UCM-hypothesis allows to introduce a quantitative measure for a synergy by comparing the amounts of the total variance per DOF within the UCM (V_{UCM}) and orthogonal to the UCM (V_{ORT})*, termed in some studies compensated and uncompensated variance. If $V_{UCM} = V_{ORT}$ (panel A), this is a non-synergy with respect to the analyzed performance variable; if $V_{UCM} > V_{ORT}$ (panel B), this is a synergy. If $V_{UCM} < V_{ORT}$ (panel C), this is a non-synergy with respect to the analyzed variable but may be a synergy with respect to another variable. In Fig. 1C, the presented distribution may be interpreted as a synergy stabilizing the total moment produced by the finger forces with respect to a midpoint (insert). In other words, *the total motor variance of a multi-element system consists of “bad variance” (which affects important performance variables) and “good variance” (which does not) – just like cholesterol (sorry!). A synergy turns most variance good.*

The UCM hypothesis allows asking an apparently redundant neuromotor system a question: *Are you organized into a synergy with respect to a particular performance variable?* This question can be answered by analysis of variance of data distributions across repetitions of a task. Comparisons of the two variance components (V_{UCM} and V_{ORT}) allows to introduce an index of strength of a synergy, for example, $?V = (V_{UCM}-V_{ORT})/V_{TOT}$ where V_{TOT} stands for the total amount of variance per DOF (Scholz *et al.* 2003). Larger positive values of $?V$ correspond to stronger synergies. Such analysis has been applied to studies of multi-finger interactions in the process of motor learning (Kang *et al.* 2004) and in comparisons between different subject subpopulations (Scholz *et al.* 2003; Shinohara *et al.* 2004). An alternative computational approach has recently been suggested, based on a similar logic, that uses a randomization method when surrogate data sets assuming no task-specific covariation among elemental variables are compared to actual data sets (Kudo *et al.* 2000; Martin *et al.* 2002; Muller and Sternad 2004; Latash *et al.* 2004b).

A hypothesis has recently been advanced by Todorov and Jordan (2002) suggesting an optimal feedback control structure can replicate UCM-like effects. However, recent simulations of their linear model in a pointing task revealed that it cannot account for the experimentally observed time course of variance in the UCM or for components of the motion that do not affect performance variables; these are commonly addressed in robotics as “self-motion” (a component of joint velocities with no effect on endpoint motion). Instead, the observed time course of variance changes throughout the movement and the structure of self-motion in the joint space were better accounted for by a mathematical model of the UCM in which nonlinear muscle models for each joint drive the nonlinear biomechanical dynamics of the arm (Martin *et al.* 2004). In this model, muscle activation is governed by neural signals that generate a stable equilibrium trajectory (cf. Feldman 1986; Latash 1993) in the joint space using an approach similar to that of Gribble and his colleagues (1998). Such an equilibrium trajectory is specific to a particular performance variable that needs to be stabilized. The process involves noise sources at all levels, including "neuronal" noise affecting the equilibrium trajectory. There are back-coupling effects from actual joint trajectories onto the neuronal structures generating the equilibrium trajectory. The strength of these feedback effects can be modified by the controller in a task-specific way. This model has been able to account for experimental observations including the patterns of joint variability within the UCM and orthogonal to the UCM.

Effects of practice on multi-finger synergies

The observations of better moment stabilization in earlier studies (Latash *et al.* 2001; Scholz *et al.* 2002) have led to a hypothesis that patterns of covariation of force modes are conditioned by the everyday experience over the lifetime, which commonly places more strict requirements on moment variations during prehension tasks. We performed three experiments to study changes of finger interaction with practice.

In one study (Latash *et al.* 2003), subjects practiced a ramp force production task for about 1.5 hours (200 trials) while pressing with three fingers on three force sensors. The frame with the sensors rested on a very narrow support placed under the middle finger. In each trial, at some time during the ramp, unexpectedly, a transcranial magnetic stimulus (TMS) was applied over the contralateral M1 cortical area. The stimulus induced a quick jerk of the fingers and perturbed both the total force and the total moment. Effects of practice were assessed using brief series of unperturbed ramp trials. Over the first 100 trials, subjects showed a decrease in the finger force variance related to the total force, but there was little additional improvement after the second 100 trials (Fig. 2A). Similar changes were observed in the variance related to the total moment with respect to the pivot. In contrast, finger force variance that did not affect either total force or total moment showed little change after the first 100 trials and a decline over the next 100 trials (Fig. 2B). These results suggest the existence of two stages of practice: Over the first stage, performance was optimized with respect to the explicit task requirements, i.e. “bad variability” dropped. Over the second stage, however, “good variability” of elements decreased, possibly related to optimizing other task components such as preparation and reaction to the TMS stimuli.

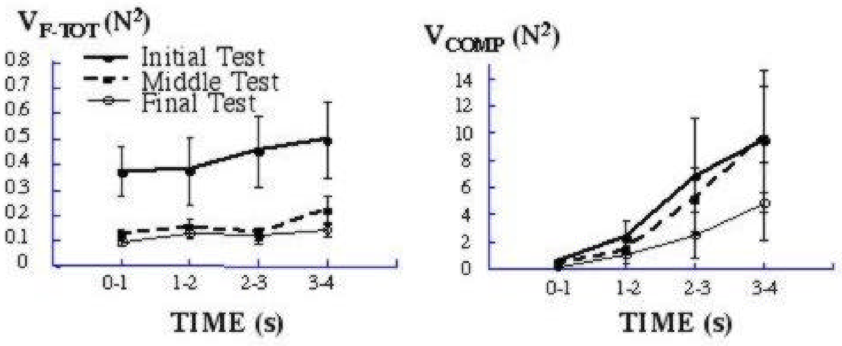

Fig. 2

Finger force variance related to the total force (left) and compensated variance that did not affect force or moment (right) at the three tests. Note the different scales of the Y-axes. Averaged across subjects data are shown with standard error bars.

TMS-induced changes in the finger forces showed a gradual decline in the overall force response. The differences in the responses of the index and ring fingers, which perturbed the total moment with respect to the pivot, declined as well. This study has shown that a *brief practice can induce plastic changes in neural structures involved in the TMS-induced responses and these changes are specific to the practiced task.*

In another study (Latash *et al.* 2002a; Scholz *et al.* 2003), effects of practice on finger interaction in persons with Down syndrome (DS) were studied. In that study, the 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 covariation among individual finger forces that destabilized the total force, while the pronation/supination moment was stabilized. After two days of practice, these persons improved their performance and showed a multi-finger synergy that stabilized the total force profile without deterioration of the moment-stabilizing synergy.

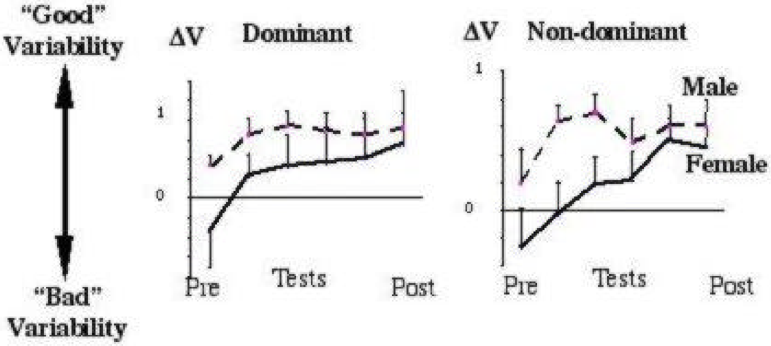

Fig. 3

Practice-related changes in an index (?V) reflecting the relation between variance within the UCM and orthogonal to the UCM during practice of an unusual mult-finger force production task (Kang et al. 2004). Positive values of ?V correspond to a synergy stabilizing the contribution of a hand to the task force. Note the emergence of force-stabilizing synergies with practice, in particular in female subjects in both dominant and non-dominant hands.

In a third study (Kang *et al.* 2004), young, healthy subjects practiced a multi-finger slow ramp force production task. The task was purposefully made very unusual to make room for improvement. The subjects were required to produce a ramp profile with a signal (FTASK) representing the sum of the forces produced by asymmetrical finger pairs in the two hands (e.g., the I and R fingers of the right hand plus the M and L fingers of the left hand), from which the forces produced by the other four fingers were subtracted. Prior to practice, subjects showed high error indices and failed to show stabilization of each hand's contribution to FTASK. However, the pronation-supination moment was stabilized by the fingers of each hand despite the lack of instruction on this moment. Over two days of practice, the performance of the subjects improved considerably. This was accompanied by the emergence of within-a-hand force stabilization in both hands without deterioration of moment stabilization.

Taken together, *these three studies show that finger synergies during multi-finger force production tasks can change under practice*. There are computational methods that can be used to quantify the processes of emergence and modification of synergies. As the first study suggests, major changes in the finger coordination may happen after only 100 trials (under one hour). Even very unusual patterns of finger interaction (as in the third study) or patterns of finger interaction in atypical persons (as in the second study) can be learned over the course of a couple of days.

Effects of practice on multi-joint pointing tasks

Two studies were performed within the framework of the UCM-hypothesis on the effects of practice on multi-joint coordination during two-arm pointing tasks. In both studies, the subjects were required to perform “fast and accurate” movements of the pointer and the target, each held by different hands and moving towards each other, and stop the pointer in the center of the target. In the first study (Domkin *et al.* 2002), the planar analysis has shown that joint trajectories within each arm co-varied across trials to stabilize the trajectory of the endpoint, while all the joints acted as a two-arm synergy. An improvement in the performance with practice was associated with an unexpected drop in the ratio between the two variance components $R_V=V_{UCM}/V_{ORT}$ i.e. in a weaker synergy. We interpreted this finding as resulting from over-practicing the relatively easy task. Hence, in the next study (Domkin *et al.* in press), a more complex task was designed using three targets and three-dimensional movements. A similar amount of practice (3 days) resulted in the lack of changes in R_V, which was short of the expectated increase in this index. Apparently, the task was still too simple, and the subjects mastered it too quickly to show an increase in the synergy index. It remains a challenge to devise a multi-joint task that would have enough room for practice-related improvement to demonstrate that practice does indeed involve two stages of synergy formation/changes for such tasks as well.

Effects of practice on a multi-joint throwing task

A recent study of learning a Frisbee throwing task evaluated changes in the amounts of “good” and “bad” variance with practice using the UCM approach

(Yang and Scholz 2005). Following a pre-test, the main experiment consisted of subjects practicing a Frisbee throw to a laterally-placed target for 5-days, making 150 throws per day, followed by a post-test. There was also a subgroup of three subjects who continued to practice for an extended period amounting to 1800-2700 additional throws each. Analysis of kinematic variability in the joint space (ten major arm joints, including scapular motion) was performed with respect to several selected performance variables including movement extent, movement direction, hand path velocity, and the hand's orientation with respect to the target. Changes in the relative amounts of V_{UCM} and V_{ORT} across practice with respect to each of the hypothesized performance variables were evaluated using the method of the UCM hypothesis. In addition, changes in the amount of joint motion that did not affect performance variables (self-motion) with practice, in particular apparently extraneous joint velocities that have no effect on the hand's motion, was determined.

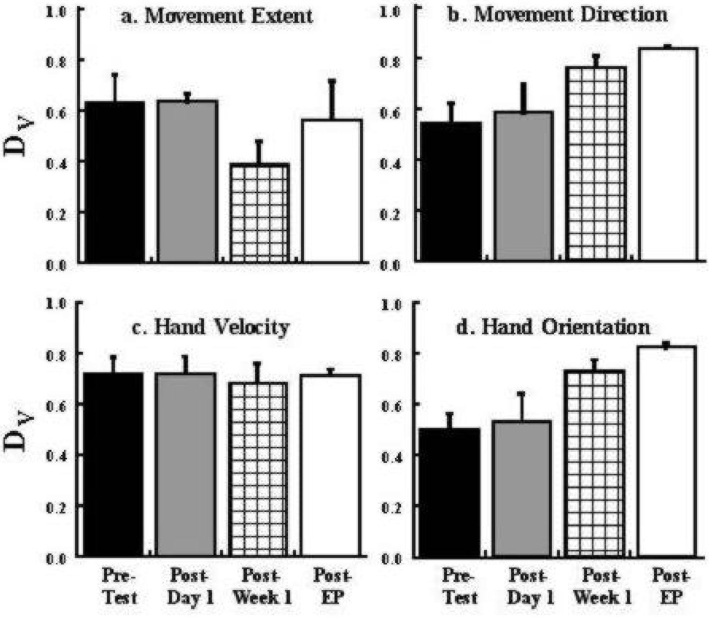

Fig. 4

An index of the structure of joint variance, D_V [$D_V = (V_{UCM}-V_{ORT})$/total variance per DOF] evaluated with respect to control of (a) movement extent, (b) movement direction, (c) hand path velocity, and (d) hand orientation with the target for each phase of practice (EP = extended practice). Higher positive values of D_V correspond to better stabilization of particular performance variables.

After a week of practice, all subjects showed improvement in terms of accuracy of their throws. Hand path variability also decreased with practice, and this was associated with a decrease in the overall variance in the joint space, although there was no evidence that one joint showed a greater decrease in variability than another. Although both "good" and "bad" variance (V_{UCM} and V_{ORT}) decreased significantly with practice, V_{UCM} was always significantly larger than V_{ORT} with respect to all four performance variables. Moreover, the decrease in V_{UCM} with practice was significantly smaller than the decrease in V_{ORT} in relation to two performance variables, movement direction and the hand's orientation with the target, while both components decreased equally with respect to the other two performance variables (Figure 4). Thus, improvement of throwing performance in this experiment was mostly related to improved stabilization of movement direction and of the hand's orientation with respect to the target. In addition, the amount of self-motion related to control of the hand's path showed a significant increase with practice, possibly reflecting better compensation for perturbations due to the limb's dynamics. In this study there was no evidence for a greater decrease in V_{UCM} than V_{ORT} with practice.

Concluding comments

Recent developments of quantitative methods to analyze motor synergies have allowed application of these methods to study effects of practice. The reviewed studies have challenged the predominant view on stages of practice involving "freezing" and "releasing" degrees-of-freedom. In contrast, practice has typically led to changes in patterns of covariation of elemental variables (DOFs) related to stabilization of certain performance variables. These changes have not been unambiguous and monotonic. Early in practice of challenging tasks, we observed an increase in the introduced quantitative indices of synergies. However, further practice of challenging tasks or pactice of relatively easy tasks was associated with the emergence of relatively stereotypical motor patterns associated with a drop in such quantitative indices. We believe that the computational apparatus associated with the UCM hypothesis offers new potentially powerful methods to study changes in motor synergies with practice. Analysis of the structure of motor variability goes far beyond the more traditionalapproaches to effects of practice such as those that are based on quantifying changes in performance variables and in the number of "frozen" or "released" DOFs.

Acknowledgments:

We are grateful to Mats Djupsobacka, Dmitry Domkin, Ning Kang, John Rothwell, Jozsef Laczko, Minoru Shinohara, and Kielan Yarrow for their participation in the reviewed studies. Preparation of the manuscript has been supported by grants from the National Institutes of Health NS-035032, AG-018751, and AR-048563, and from the National Science Foundation IBN-0078127.

References

Bernstein NA (1927). Kymozyclographion, ein neuer Apparat fur Bewegungsstudium. *Pflugers Arch. ges. Physiol. Menschen und Tiere*, 217: 783-793.

Bernstein NA (1967). The Co-ordination and Regulation of Movement. Pergamon Press, Oxford.

Domkin D, Laczko J, Jaric S, Johansson H, Latash ML (2002). Structure of joint variability in bimanual pointing tasks. *Exp Brain Res*, 143: 11-23.

Domkin D, Jozsef J, Djupsjöbacka M, Jaric S, Latash ML (in press).Joint angle variability in 3D bimanual pointing: uncontrolled manifold analysis. *Exp Brain Res.*

Feldman AG (1986). Once more on the equilibrium-point hypothesis (lambda model) for motor control. *J Mot Behav*, 18: 17-54

Gelfand IM, Tsetlin ML (1966). On mathematical modeling of the mechanisms of the central nervous system. In: IM Gelfand, VS Gurfinkel, SV Fomin, ML Tsetlin (Eds.) Models of the structural-functional organization of certain biological systems, pp. 9-26, Nauka: Moscow

Gribble PL, Ostry DJ, Sanguineti V, Laboissiere R (1998). Are complex control signals required for human arm movement? *J Neurophysiol*, 79: 1409-1424.

Kang N, Shinohara M, Zatsiorsky VM, Latash ML (2004). Learning multi-finger synergies: An uncontrolled manifold analysis. *Exp Brain Res*, 157: 336-350.

Kudo K, Tsutsui S, Ishikura T, Tomoki I, Yamamoto Y (2000). Compensatory coordination of release parameters in a throwing task. *J Mot Behav*, 32: 337-345

Latash ML (1993) Control of Human Movement. Human Kinetics: Urbana, IL.

Latash ML, Scholz JF, Danion F, Schöner G (2001). Structure of motor variability in marginally redundant multi-finger force production tasks. *Exp Brain Res*, 141: 153-165.

Latash ML, Kang N, Patterson D (2002a) Finger coordination in persons with Down syndrome: Atypical patterns of coordination and the effects of practice. *Exp Brain Res*, 146: 345-355.

Latash ML, Scholz JP, Schöner G (2002b). Motor control strategies revealed in the structure of motor variability. *Exer Sport Sci Rev*, 30: 26-31.

Latash ML, Yarrow K, Rothwell JC (2003). Changes in finger coordination and responses to single pulse TMS of motor cortex during practice of a multi-finger force production task. *Exp Brain Res*, 151: 60-71.

Li Z-M, Latash ML, Zatsiorsky VM (1998) Force sharing among fingers as a model of the redundancy problem. Exp Brain Res 119: 276-286

Martin TA, Norris SA, Greger BE, Thach WT (2002) Dynamic coordination of body parts during prism adaptation. J Neurophysiol 88: 1685-1694

Martin V, Scholz JP, Schöner G. (2004) Theory of the uncontrolled manifold: variance, self-motion, and neuronal noise. Program No. 871.17. *Abstract Viewer and Itinerary Planner.* Washington, DC: Society for Neuroscience, 2004. Online.

Muller H, Sternad D (2004). Decomposition of variability in the execution of goal-oriented tasks: three components of skill improvement. *J Exp Psychol: Hum Percept Perform*, 30: 212-233

Newell KM (1991). Motor skill acquisition. *Ann Rev Psychol*, 42: 213-237

Piek JP (1995). The contribution of spontaneous movements in the acquisition of motor coordination in infants. In: Glencross DJ, Piek JP (Eds.) Motor Control and Sensory Motor Integration: Issues and Directions, pp. 199-230, Elsevier: Amsterdam.

Prilutsky BI, Zatsiorsky VM (2002). Optimization-based models of muscle coordination. *Exerc Sport Sci Rev*, 30: 32-38.

Rosenbaum DA, Loukopoulos LD, Meulenbroek RGM, Vaughan J, Engelbrecht SE (1995). Planning reaches by evaluating stored postures. *Psychol Rev*, 102: 28-67.

Scholz JP, Schöner G (1999). The uncontrolled manifold concept: Identifying control variables for a functional task. *Exp Brain Res*, 126, 289-306

Scholz JP, Danion F, Latash ML, Schöner G (2002). Understanding finger coordination through analysis of the structure of force variability. *Biol Cybern*, 86: 29-39.

Scholz JP, Kang N, Patterson D, Latash ML (2003). Uncontrolled manifold analysis of single trials during multi-finger force production by persons with and without Down syndrome. *Exp Brain Res*, 153: 45-58.

Shinohara M, Scholz JP, Zatsiorsky VM, Latash ML (2004). Finger interaction during accurate multi-finger force production tasks in young and elderly persons. *Exp Brain Res*, 156: 282-292.

Todorov E, Jordan MI (2002). Optimal feedback control as a theory of motor coordination. *Nature Neurosci*, 5: 1226-1235

Vereijken B, van Emmerick REA, Whiting HTA, Newell KM (1992). Free(z)ing degrees of freedom in skill acquisition. *J Mot Behav*, 24: 133-142.

Yang JF, Scholz JP (2005). Learning a throwing task is associated with differential changes in the use of motor abundance. *Exp Brain Res*, in press.