

Chapter 7

Use of the Uncontrolled Manifold (UCM) Approach to Understand Motor Variability, Motor Equivalence, and Self-motion

John P. Scholz and Gregor Schöner

7.1 Characterizing Variability in Motor Performance

Variability of motor output often has been considered a form of noise that interferes with reliable performance. This assumption, however, depends on the level of the motor system under consideration. For targeting tasks, variability of the end-effector position will affect the consistency of targeting, depending on the task requirements and the size of the target. Variability of coordination patterns used in artistic performance may impact the aesthetics of performance. However, variability at the level of the motor elements, including small variations in coordination patterns, often reflect task flexibility that is only possible when the motor system exhibits sufficient motor abundance (Latash 2012). Consider, for example, performing cardiopulmonary resuscitation (CPR) on an infant, with the index and middle fingers exerting the necessary force to produce adequate chest compression. If fluctuation in the compression force of one finger leads to a tendency for higher total force output, then reduction in the forces exerted by the other fingers is necessary to compensate and maintain a consistent total compression force. This is only possible because there are two fingers contributing to a single total force output. Note that an alternative approach would be to attempt to control precisely, to the extent possible, the variability of individual finger forces such that each finger generates approximately the same force on each repetition. The presence of compensatory finger forces, however, has been well documented (Latash et al. 2001, 2002a, 2002b), and is consistent with the notion of a functional synergy among the motor elements (Latash et al. 2007).

Determining whether variability of motor output reflects motor noise or flexible motor patterns is not trivial, however. Bernstein observed that when blacksmiths hit

G. Schöner (✉)

Institut für Neuroinformatik, Ruhr-Universität Bochum, Bochum 44780, Germany
e-mail: gregor.schoener@ini.ruhr-uni-bochum.de

J. P. Scholz

Department of Physical Therapy and Biomechanics and Movement Sciences Program,
University of Delaware, Newark, DE 19716, USA

© Springer Science+Business Media New York 2014

M. Levin (ed.), *Progress in Motor Control*, Advances in Experimental Medicine and Biology 826, DOI 10.1007/978-1-4939-1338-1_7

1

24 the chisel with the hammer there appeared to be more variability of the trajectories
25 of individual joints than there was for the trajectory of the hammer (Bernstein 1967).
26 This led him to conclude that a movement is never repeated in exactly the same
27 manner. Although his intuition was correct, there was no way to clearly establish
28 this fact. For one thing, the trajectory of the joints and the end effector (hammer) are
29 measured in different units and the number of degrees of freedom of each is quite
30 different. How does one compare variability of up to 10 joint motions (including
31 scapular motion) measured in radians to the variability of three dimensions of end-
32 effector motion measured in meters? Schöner and Scholz (Schöner 1995; Scholz and
33 Schöner 1999) developed the uncontrolled manifold (UCM) approach to overcome
34 this problem and to quantify statistically the extent to which variability of motor
35 elements tends to lead to noise or error in performance versus reflecting the use of
36 flexible patterns of coordination. In this approach, all analysis to answer this question
37 is performed at the level of the motor components, e.g., joint motions, finger forces,
38 and muscle modes.

39 To accomplish this, the UCM approach requires a model that relates how changes
40 in elemental variables affect the task level (e.g., hand position in space, total force
41 output). This model can be obtained formally, as when relating joint motions to
42 movement of the hand in space (e.g., $\Delta x = l_1 \cos \theta_1 + \cos(\theta_1 + \theta_2) + \dots$) or via
43 regression analysis when a formal model is not readily available or excessively com-
44 plicated (Freitas and Scholz 2010). The null space of the equation relating the task
45 space to the space of motor elements provides a linear estimate of all combinations
46 of the motor elements that do not affect the value of the task variable at that point
47 in a movement trajectory or in time (e.g., $J(\theta_{\text{mean}}) \Delta \theta_i = 0$ where J is the Jaco-
48 bian matrix of partial derivatives relating small changes in the elemental variables
49 to changes in the task variable). The null space is computed around the mean value
50 of the motor elements (θ_{mean}) at each point in the movement trajectory. Experimen-
51 tally measured mean-free values of the motor elements ($\Delta \theta_i = \theta_i - \theta_{\text{mean}}$) for each
52 movement repetition at a given point in the normalized movement are projected into
53 the null space and its complement, or range space (the subspace of motor elements
54 in which different combinations of the motor elements lead to different values of
55 the task variable of interest). This is done for each repetition and the variance of
56 the projection lengths is then computed and normalized to the dimensions of the
57 subspace to make the analysis more conservative. Greater variance in the null space
58 or UCM subspace than in the range space suggests a control strategy in which the
59 central nervous system provides stabilizing control signals that restrict variations of
60 the motor elements when they affect the desired value of the task variable but allows
61 for some degree of variability in combinations of those variables if they have no
62 effect on the task variable (i.e., variations within the UCM).

63 Studies of many different motor tasks have shown that variability at the level of
64 motor elements is more consistent with the use of flexible combinations of those
65 elements that preserve a stable state (e.g., posture) or produce a consistent trajectory
66 (e.g., reaching) of a task-level variable (e.g., center of mass position, trajectory of
67 the hand). In contrast, range space variability typically is shown to be significantly
68 smaller (Scholz and Schöner 1999; Scholz et al. 2000; Latash et al. 2001; Scholz

69 et al. 2001, 2002; Krishnamoorthy et al. 2003, 2007; Latash et al. 2002a). UCM
70 analysis also has been able to differentiate between movement synergies in persons
71 with neurological dysfunction and healthy control subjects (Reisman and Scholz
72 2006; Park et al. 2012, 2013). In addition, different hypothesized task variables
73 can be evaluated with this approach to help determine what variables are of greatest
74 importance to task performance (Scholz et al. 2000). The results are in agreement
75 with the minimum intervention principle, which suggests that allowing variability
76 in redundant (abundant) dimensions is the optimal control strategy in the face of
77 uncertainty (Todorov and Jordan 2003), although a control structure more in line
78 with the UCM hypothesis than optimal control has been shown to better account for
79 detailed characteristics of movement trajectories (Martin et al. 2009).

80 The dependence of the outcome of a UCM analysis of motor variability on the
81 variables used to describe the effector system has recently been criticized (Sternad
82 et al. 2010). For example, the authors suggest that movements may equally well be
83 planned in joint or segment angle coordinates. They provide an example of a mini-
84 mally redundant effector system in which the UCM method leads to quite different
85 results when either of these sets of variables is used. This criticism is relevant and
86 emphasizes that researchers must make considered choices of the variables used for
87 analysis. Three clarifications are in order, however:

- 88 1. A choice of variables fixes the space in which configurations of the effector are
89 described. If we choose joint angles as variables, then we describe the effector
90 in joint space. A point in that space represents one particular configuration of
91 the effector. A metric must be fixed as well, which assesses the distance between
92 any two points in that space, that is, between two configurations of the effector.
93 Typically, the Euclidian metric is used, in which the squared distances along each
94 of a set of orthogonal coordinate axes are summed and the square root is taken.
95 The UCM approach is then actually invariant under any change of coordinate
96 frame that leaves the metric invariant (Schöner and Scholz 2007). This includes,
97 in particular, rotations of the coordinate frame. This invariance reflects the fact that
98 the UCM analysis is based on a geometrical view of variance, in which the shape
99 of the cloud of points in joint space is observed across trials at a particular point
100 during a movement. If that shape is elongated along the direction of the null space,
101 then the UCM hypothesis is confirmed. The shape of the cloud of points is invariant
102 under any coordinate transform that preserves the metric of the space spanned
103 by the chosen variables. This is useful in some cases, such as for the shoulder
104 joint, for which there is no principled way to select a particular coordinate frame
105 to represent the three degrees of freedom that reside in that joint. Any orthogonal
106 set of coordinate axis is equally meaningful, so that invariance under rotation of
107 a coordinate frame is desirable. The randomization method (Müller and Sternad
108 2004), in contrast, is essentially a form of nonlinear, multivariate correlation. In
109 that approach, the coordinate frames matter as they do for correlation. If the cloud
110 of points is elongated along a coordinate axis, for instance, then that shape is not
111 picked up as correlation but as inherent variability of that particular degree of
112 freedom.

- 113 2. Transformations that do not leave the metric invariant matter in the analysis of
114 variance and this is how the choices of variables that set up the configuration
115 space come into play. For instance, representing joint configurations through
116 segment angles or through joint angles does not lead to the same shape of the
117 cloud of points. Mathematically, going from segment angles to joint angles is a
118 transformation that does not leave distances invariant: It is not a metric preserv-
119 ing transformation, unlike the rigid rotations that may be used to link different
120 orthogonal axes for joint angles anchored in the shoulder. This dependence on
121 the embedding space is shared, of course, by all approaches to the analysis of
122 multidimensional variance (e.g., Müller and Sternad 2004; Cusumano and Cesari
123 2006).
- 124 3. Fortunately, the choice of embedding space can be guided by what we know
125 about physiology. Specifically, the choice of joint over segment angles is not
126 arbitrary. Known sensory receptors provide information to the nervous system
127 about changes in joint angles (Grigg 1994). There are no known sensory receptors
128 signaling orientation of a limb segment in external space, although transformation
129 of sensory receptor information can be used to estimate limb orientation (Popele
130 et al. 2001). Segment angles are inherently dependent on each other. For example,
131 a flexion of the ankle brought about by a signal sent to muscles that act on the
132 ankle joint leads to changes of all segment angles along the kinematic chain of the
133 upright body, including joints not linked to the ankle by any muscle. Similarly,
134 changing the segment angle that the humerus forms with an external reference
135 frame also changes the segment angles of the forearm and hand, without any
136 activity by muscles acting on these more distal joints. Thus, distal segment motion
137 in an open kinematic chain is not independent of proximal segment motion. This
138 is not the case with joint angles. Changing one joint angle does not necessarily
139 affect another joint angle, unless there are particular mechanisms that bring about
140 such dependence like multi-articular muscles or coordinated neural signals.

141 Thus, it seems to us that the best of two worlds is achieved by combining the ge-
142 ometrical view of the UCM approach, which is conceptually attractive, with the
143 analytical power of the correlational approach. This is now routinely done by re-
144 searchers who select a set of variables and a particular coordinate frame based on
145 substantive hypotheses. They can then use the surrogate data procedure of the cor-
146 relational approach to verify if the shape of the variance in the UCM analysis truly
147 comes from covariation among the variables identified as meaningful rather than
148 from inherent differences in variance among the different degrees of freedom (see,
149 for example, Yen and Chang 2009; Verrel et al. 2010).

150 7.2 Quantifying Motor Equivalence

151 More recently, the geometrical perspective of the UCM approach has been used
152 to address additional issues in motor control, namely, motor equivalence and self-
153 motion. The term motor equivalence has been used in a variety of ways, but is defined

154 here as a change in the configuration of motor elements after a perturbation that tends
155 to preserve the outcome of a task or the stability of a task-relevant variable. Kelso
156 and colleagues (Kelso et al. 1984) performed a seminal study of motor equivalence
157 in the context of the control of speech utterances. They found that adjustments in
158 the articulators were task-specific, dependent on the nonsense syllable that subjects
159 spoke when a perturbation was delivered to depress the jaw. Further evidence was
160 provided when naïve subjects were unable to distinguish utterances performed during
161 perturbed and nonperturbed trials. However, in many cases, distinguishing between
162 adjustments of motor coordination that lead to disturbance of the task versus being
163 a reflection of motor equivalent adjustments to preserve the task is not trivial. For
164 example, when reaching to a target, a transient perturbation of a joint will lead to at
165 least some effect on the motion of the end effector. If the end effector still reaches
166 the target, this suggests that motor equivalence must be present. What if the hand,
167 however, hits the target but deviates from its position on nonperturbed trials or what
168 effect does the perturbation have on the path of the hand itself? Presuming that
169 there are readjustments in the joint configuration or muscle firing patterns due to the
170 perturbation, how can one determine the extent to which the adjustments account for
171 observed deviations in the hand path or whether more of the adjustments tend to act
172 to preserve the hand path? A modification of the UCM approach allows this question
173 to be addressed quantitatively. If one takes a set of nonperturbed trials, the null space
174 of the Jacobian matrix relating small changes in the motor elements to changes in a
175 hypothesized task variable (e.g., the hand position) can be computed using the mean
176 value of the motor elements across trials. This null space corresponds, as in UCM
177 variance analysis, to a linear estimation of all combinations of joint configurations
178 that lead to the same value of the task variable. Again, this analysis is performed at
179 each point in the normalized (to 100 %) movement.

180 One can then obtain the vector of the configuration of motor elements from a
181 perturbed (pert) trial, subtract it from the mean of the nonperturbed (nonpert) trials
182 ($\theta_{\text{pert}} - \theta_{\text{non-pert}}$), and project this difference vector into the null space (UCM) and
183 range space of the nonperturbed trials. If the null space projection is significantly
184 larger than the range space projection, then this suggests that more of the adjustment
185 in the joint configuration due to the perturbation is motor equivalent, tending to pre-
186 serve the nonperturbed value of the relevant task variable. This approach, therefore,
187 provides a statistical method for determining the extent to which motor equivalence
188 is present.

189 In a collaborative study with Fay Horak and John Jeka, motor equivalence relative
190 to the position of the center of mass of the body was measured in persons standing
191 on a moveable force platform that was perturbed by different amplitudes, keeping
192 the velocity of perturbation constant (Scholz et al. 2007). An example of the results
193 obtained immediately after the transient perturbation are presented in Fig. 7.1. Note
194 that the projection into the UCM subspace or null space was larger, and significantly
195 so, than the projection into the range space, both computed based on the nonperturbed
196 trials. This difference increased with greater amplitudes of perturbation. Thus, most
197 of the change in the joint configuration as a result of the perturbation was motor
198 equivalent, tending to preserve the pre-perturbation position of the center of mass of
199 the body.

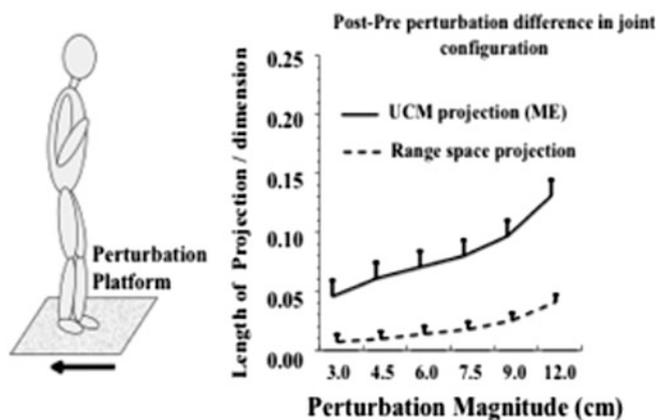


Fig. 7.1 *Left:* Participants stood upright when the support platform was abruptly moved by a varied amount (perturbation amplitude). *Right:* Six degrees of freedom were included in a motor equivalence analysis. The difference vector between joint configurations in perturbed trials from the mean configuration in unperturbed trials was projected into the UCM subspace (*solid line*) and the range spaced (*dashed line*). The plot shows the average length of these differences vectors across perturbation trials per degree of freedom together with the SME (*error bars*) as functions of the perturbation amplitude. The data are from Scholz et al. 2007 (Fig. 4 there)

200 7.2.1 Quantifying Self-Motion

201 UCM variance analysis indicates how fluctuations of the motor elements across
 202 repetitions or, in the case of relatively steady state behavior, across time are structured.
 203 For example, in upright posture, to what extent do joint fluctuations over time lead to
 204 postural sway of the center of mass versus being coordinated to flexibly stabilize the
 205 center of mass location? Nonetheless, fluctuations of the motor elements could be
 206 relatively small or large, depending on the task. The amount of self-motion provides
 207 an estimate of the magnitude of changes in the motor elements that lie in the UCM
 208 subspace and, therefore, do not affect the value of a task variable and those that
 209 change the value of the task variable. The concept of self-motion comes from the
 210 robotics of redundant effectors and, in that context, refers to the magnitude of the
 211 vector of time-dependent changes (e.g., velocity) in the motor elements that lies
 212 in the null space or UCM subspace. In contrast, range space motion refers to that
 213 component of this vector that lies in the range space, or actually moves the task
 214 variable with reference to which the analysis is applied.

215 Consider reaching to a target with the hand. One might suspect that the most
 216 efficient movement of the hand would occur if the joints were coordinated such that
 217 their velocities were directed primarily toward that goal. If so, then the range space
 218 velocity component of the joints, which actually moves the hand in space, would be
 219 expected to be substantially larger than the self-motion or UCM component. Self-
 220 motion might be advantageous in some circumstances, however. For example, when
 221 carrying a relatively full glass of Guinness stout, if a fly lands on your elbow, you

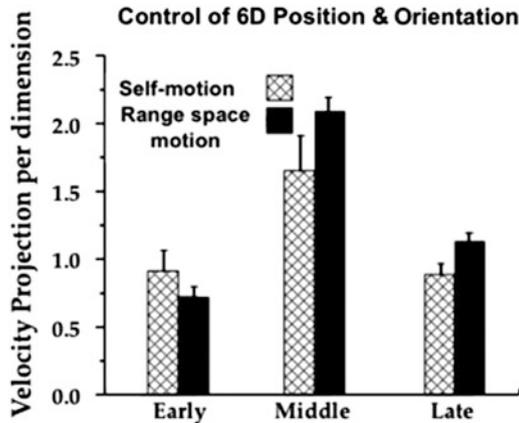


Fig. 7.2 Reaching with ten degrees of freedom to a target was analyzed with respect to self-motion, using a Jacobian that took into account both the 3D end-effector position and the 3D orientation of the hand for a total of six degrees of freedom in task space. Mean self-motion and range space motion per degree of freedom averaged across participants is shown for the early, middle, and late phase of reaching when reaching at a fast speed to a target. Data are from Scholz et al. (2011; compare to Fig. 3 there, which includes other conditions as well)

222 might want to flick the elbow to get it to go away without spilling the precious
 223 stout! Internal motion of the arm joints that does not affect the hand position is, by
 224 definition, self-motion. But how much self-motion is present for a given task when
 225 motion to achieve a secondary task is not required?

226 To answer this question, we developed a method of analysis that can be carried out
 227 on individual trials or on means across trials. The method was adapted from the UCM
 228 approach to the analysis of variance. The Jacobian, J , that relates the joint velocity
 229 vector, $\dot{\theta}$, to the velocity of the hand, $\dot{x} = J(\theta)\dot{\theta}$, is computed from a geometrical
 230 model of the effector. It is evaluated at the instantaneous joint configuration, θ , at
 231 each point in time. Based on this Jacobian, the null (UCM) and range spaces can
 232 be determined. The joint velocity vector, $\dot{\theta}$, is computed from the time series by
 233 numerical differentiation and is projected into either subspace. Finally, the length
 234 of these projections is computed and divided by the number of dimensions of each
 235 subspace.

236 Figure 7.2 presents an example of this analysis from a recent article investigat-
 237 ing self-motion at different speeds of reaching (Scholz et al. 2011). The results for
 238 reaching at a self-selected fast speed are depicted. Note that although range space
 239 motion (component of the joint velocity vector projection that moves the hand in
 240 space) generally was larger than self-motion, self-motion was nonetheless quite sub-
 241 stantial. The results were similar at slow and moderate speeds of reaching, although
 242 self-motion was not quite as large as compared to range space motion. Of interest
 243 was that at all speeds of reaching, self-motion actually was larger than range space
 244 motion at the early stage of reaching, probably because the arm had to be adjusted
 245 to exit the trough in which it rested as the reach was initiated.

246 The results suggest that even during the performance of goal-oriented targeting
247 tasks there is a substantial amount of self-motion, i.e., joint configuration motion
248 within the UCM subspace of joint space, even when an obvious secondary task is not
249 involved. It is hypothesized that this amount of self-motion is a reflection of the nature
250 of the control system that minimally restricts combinations of motor elements for a
251 task that do not interfere with successful performance even when the configurations
252 deviate from the initially planned configuration.

253 7.3 Conclusion

254 The UCM approach was developed originally to investigate the role of motor vari-
255 ance and has been successfully applied to a variety of motor tasks from finger force
256 production to reaching to postural control. In most cases, variance consistent with
257 flexible combinations of the motor elements that maintain a consistent value of an
258 important task variable has been shown to be significantly greater than variance
259 leading to variability of the task variable. The approach allows one to test hypothe-
260 ses about the importance of different task-relevant variables based on the structure
261 of variance of the underlying motor elements and to evaluate how different motor
262 elements contribute to that structure.

263 Recently, the approach has been extended to address additional important issues
264 in motor control such as motor equivalence in the presence of a perturbation and
265 the extent to which motor abundance is used in the control of motor tasks through
266 self-motion analysis. A model of a control strategy based on the UCM hypothesis
267 and consistent with the recent results was developed by Martin, Scholz, and Schöner
268 (Martin et al. 2009) and applied to postural control by Reimann et al. (2011). We
269 believe that the geometrical perspective offered by UCM thinking will be useful both
270 to interpret experimental signatures of control hypotheses and to investigate possible
271 neural processes that bring about the coordination of the many degrees of freedom
272 of the motor system. Ultimately, we will need to understand how spatial information and
273 timing constraints for the motion of effectors in space can be translated to control
274 signals at the level of each muscle (Bullock et al. 1993; Butz et al. 2007). That
275 transformation sets up the geometry uncovered by the UCM method.

276 **Acknowledgments** Work reviewed here was supported by NINDS Grant R01-NS050880 to John
277 Scholz and DFG (Germany) Grant SCHO 336/7-1 to Gregor Schöner. Thanks to Dr. Hendrik
278 Reimann for a critical reading. A draft of this paper was completed by John Scholz shortly before
279 he passed away.

References

- Bernstein N. 1967. *The co-ordination and regulation of movements*. Oxford: Pergamon Press.
- Bullock D, Grossberg S, Guenther F. 1993. A self-organizing neural model of motor equivalence reaching and tool use by a multijoint arm. *J Cogn Neurosci* 5:408–435.
- Butz MV, Herbert O, Hoffmann J. 2007. Exploiting redundancy for flexible behavior: unsupervised learning in a modular sensorimotor control architecture. *Psychol Rev* 114(4):1015–1046.
- Cusumano JP, Cesari P. 2006. Body-goal variability mapping in an aiming task. *Biol Cybern* 94:367–379.
- Freitas SMSF, Scholz JP. 2010. A comparison of methods for identifying the Jacobian for uncontrolled manifold analysis. *J Biomech* 43:775–777.
- Grigg P. 1994. Peripheral neural mechanisms in proprioception. *J Sport Rehabil* 3:2–17.
- Kelso JA, Tuller B, Vatikiotis-Bateson E, Fowler CA. 1984. Functionally specific articulatory cooperation following jaw perturbations during speech: evidence for coordinative structures. *J Exp Psychol Hum Percept Perform* 10(6):812–832.
- Krishnamoorthy V, Latash ML, Scholz JP, Zatsiorsky VM. 2003. Muscle synergies during shifts of the center of pressure by standing persons. *Exp Brain Res* 152(3):281.
- Krishnamoorthy V, Scholz JP, Latash ML. 2007. The use of flexible arm muscle synergies to perform an isometric stabilization task. *Clin Neurophysiol* 118(3):525–537.
- Latash ML. 2012. The bliss of motor abundance. *Exp Brain Res* 217(1):1–5.
- Latash ML, Scholz JF, Danion F, Schoner G. (2001). Structure of motor variability in marginally redundant multifinger force production tasks. *Exp Brain Res* 141:153–165.
- Latash ML, Scholz JF, Danion F, Schoner G. (2002a). Finger coordination during discrete and oscillatory force production tasks. *Exp Brain Res* 146(4):419–432.
- Latash ML, Scholz JF, Schoner G. (2002b). Motor control strategies revealed in the structure of motor variability. *Exerc Sport Sci Rev* 30(1):26–31.
- Latash ML, Scholz JF, Schoner G. 2007. Toward a new theory of motor synergies. *Motor Control* 11(3):276–308.
- Martin V, Scholz JP, Schöner G. 2009. Redundancy, self-motion, and motor control. *Neural Comp* 21(5):1371–1414.
- Müller 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.
- Park J, Wu Y-H, Lewis MM, Huang X, Latash ML. 2012. Changes in multi-finger interaction and coordination in Parkinson's disease. *J Neurophysiol* 108:915–924.
- Park J, Lewis MM, Huang X, Latash ML. 2013. Effects of olivo-ponto-cerebellar atrophy (OPCA) on finger interaction and coordination. *Clin Neurophysiol* 124:991–998.
- Poppele RE, Bosco G, Rankin AM. 2001. Independent representations of limb axis length and orientation in spinocerebellar response components. *J Neurophysiol* 87:409–422.
- Reimann H, Schöner G, Scholz JP. (2011). Visual information is sufficient for maintaining upright stance – a multi-joint model of human posture. Program No. 184.05 2011 Neuroscience Meeting Planner. Washington: Society for Neuroscience. Online
- Reisman D, Scholz JP. 2006. Workspace location influences joint coordination during reaching in post-stroke hemiparesis. *Exp Brain Res* 170:265–276.
- Scholz JP, Schoner G. 1999. The uncontrolled manifold concept: identifying control variables for a functional task. *Exp Brain Res* 126(3):289–306.
- Scholz JP, Schöner G, Latash ML. 2000. Identifying the control structure of multijoint coordination during pistol shooting. *Exp Brain Res* 135:382–404.
- Scholz JP, Reisman D, Schöner G. 2001. Effects of varying task constraints on solutions to joint coordination in a sit-to-stand task. *Exp Brain Res* 141(4):485.
- Scholz JP, Danion F, Latash ML, Schoner G. 2002. Understanding finger coordination through analysis of the structure of force variability. *Biol Cybern*, 86(1):29–39.
- Scholz JP, Schöner G, Hsu WL, Jeka JJ, Horak FB, Martin V. 2007. Motor equivalent control of the center of mass in response to support surface perturbations. *Exp Brain Res* 180:163–179.

- 332 Scholz JP, Dwight-Higgin T, Lynch JE, Tseng Y, Martin V, Schöner G. 2011. Motor equivalence
333 and self-motion induced by different movement speeds. *Exp Brain Res* 209:319–332.
- 334 Schöner G. 1995. Recent developments and problems in human movement science and their
335 conceptual implications. *Ecol Psych* 7(4):291–314.
- 336 Schöner G, Scholz JP. 2007. Analyzing variance in multi-degree-of-freedom movements: uncover-
337 ing structure versus extracting correlations. *Motor Control* 11:259–275.
- 338 Sternad D, Park S-W, Müller H, Hogan N. 2010. Coordinate dependence of variability analysis.
339 *PLoS Comp Biol* 6(4 (e1000751)), 1–16.
- 340 Todorov E, Jordan MI. 2003. A minimal intervention principle for coordinated movement. In T.
341 Becker, Obermayer (Ed.), *Advances in Neural Information Processing* (Vol. 15, pp. 27–34).
342 Boston: MIT Press.
- 343 Verrel J, Lövdén M, Lindenberger U. 2010. Motor-equivalent covariation stabilizes step parameters
344 and center of mass position during treadmill walking. *Exp Brain Res* 207(1–2):13–26.
- 345 Yen JT, Chang Y-H. 2009. Rate-dependent control strategies stabilize limb forces during human
346 locomotion. *J R Soc Interface* 7(46):801–810.