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Intentional and Unintentional Multi-Joint Movements: Their Nature and Structure of Variance

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Abstract

We tested predictions of a hierarchical scheme on the control of natural movements with referent body configurations. Subjects occupied an initial hand position against a bias force generated by a HapticMaster robot. A smooth force perturbation was applied to the hand consisting of an increase in the bias force, keeping it at a new level for 5 s, and decreasing it back to the bias value. When the force returned to the bias value, the arm stopped at a position different from the initial one interpreted as an involuntary movement. We then asked subjects to make voluntary movements to targets corresponding to the measured end-position of the unintentional movements. No target for hand orientation was used. The joint configuration variance was compared between intentional and unintentional movements within the framework of the uncontrolled manifold hypothesis. Our central hypothesis was that both unintentional and intentional movements would be characterized by structure of joint configuration variance reflecting task-specific stability of salient performance variables, such as hand position and orientation. The analysis confirmed that most variance at the final steady states was compatible with unchanged values of both hand position and orientation following both intentional and unintentional movements. We interpret unintentional movements as consequences of back-coupling between the actual and referent configurations at the task level. The results suggested that both intentional and unintentional movements resulted from shifts of the body referent configuration produced intentionally or as a result of the hypothesized back-coupling. Inter-trial variance signature reflects similar task-specific stability properties of the system following both types of movements, intentional and unintentional.

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Author contributions

Tao Zhou: developed apparatus and methods; performed the experiment; designed, performed, and reviewed statistical analysis; wrote the first draft and reviewed the manuscript.

Lee Zhang: performed the experiment; reviewed statistical analysis; and reviewed the manuscript.

Mark L. Latash: conceived the experiment; developed apparatus and methods; designed and reviewed statistical analysis; and reviewed the manuscript.

Keywords

redundancy; synergy; referent configuration; uncontrolled manifold hypothesis; back-coupling

1. Introduction

Redundancy is a central feature of the human system for the production of voluntary movements (Bernstein 1967): At any level of analysis, typically there are more elements and variables that they produce (elemental variables) than task-defined constraints. Recently, the problem of motor redundancy has been reformulated based on the principle of abundance (Gelfand and Latash 1998; Latash 2012), which suggests that the central nervous system (CNS) is not trying to find unique (optimal) solutions for this apparent problem but facilitates families of solutions that ensure stability of important performance variables. A unique action from a family of solutions emerges as a result of unpredictable interactions between the body and the environment. Analysis of multi-element, abundant systems has been developed within the framework of the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999) based on quantifying inter-trial variance in two sub-spaces. One of the sub-spaces (UCM) corresponds to no changes in a selected performance variable (e.g., coordinate of the end-effector), to which all elemental variables (e.g., joint rotations) contribute. The other sub-space is orthogonal to the UCM; variance in that sub-space leads to variance in the selected performance variable. If the former variance component (V_{UCM}) is larger than the latter one (V_{ORT}), both quantified per degree-of-freedom in the corresponding sub-spaces, a conclusion is drawn that a synergy in the space of elemental variables stabilizes the performance variable (reviewed in Latash et al. 2007).

In this study we use variance across repetitive trials as proxy for stability. Assuming that each trial starts from slightly different initial conditions, variance is expected to be larger in directions of relatively low stability and smaller in directions of high stability (Schöner 1995; Martin et al. 2009). So, while analysis of variance is essentially a snapshot analysis at a particular movement phase (e.g., in a steady state), it reflects the time evolution of the action.

Several recent studies (Martin et al. 2009; Latash 2010) have attempted to combine the principle of abundance with the idea of control with referent body configurations (RCs; Feldman 2009). Within the RC hypothesis, the neural control of a voluntary movement is described as defining a time course of neural variables associated with subthreshold depolarization of neuronal pools leading to time changes in spatial referent coordinates related to salient task-specific variables (RC at the task level). Actual body coordinates are attracted towards the RC and either achieve the RC or produce non-zero forces on the environment if external forces oppose the movement.

Within the RC hypothesis, a transient change in the external force is not expected to lead to changes in the final steady state of the moving system assuming that the subject does not react to the perturbation (cf. equifinality, Bizzi et al. 1976; Kelso and Holt 1980; Schmidt and McGown 1980; Latash and Gottlieb 1990). Several recent studies explored the effects of smooth transient changes in the external forces (perturbations) on redundant systems under

such conditions (Wilhelm et al. 2013; Zhou et al. 2014). In these studies, elemental variables showed large deviations from their initial values and large inter-trial variance of these deviations following the perturbations (non-equifinality), while the task-specific performance variables showed small deviations from the initial values and low variance (equifinality). These results have been viewed as reflections of task-specific differences in stability in different directions within the abundant space of elemental variables.

The cited studies also mention a relatively slow drift of the task-specific performance variables following the perturbations. Further studies have confirmed that a longer-lasting transient perturbation leads to a substantial, consistent change of the task-specific performance variable, i.e., violations of equifinality at the task level (Ambike et al. 2014; Zhou et al. in press). In the study of a multi-joint positional task (Zhou et al. in press), the amount of such unintentional movement was about 50% of the maximal distance of the hand deviation produced by the perturbation. Similar effects have been observed in the absence of perturbations, for example when a person is asked to maintain a constant force against a stop for several tens of seconds (Slifkin et al. 2000; Vaillancourt and Russell 2002). A hypothesis has been offered that the unintentional RC drift can be caused by the difference between the actual and referent body configurations moving the RC towards the actual configuration; this mechanism has been referred to as RC-back-coupling (cf. back-coupling in Latash et al. 2005; Martin et al. 2009). This term implies a drift in RC, which may or may not be accompanied by a change in the co-activation command (c-command, Feldman 1980, 1986; see Discussion for more detail).

Obviously, unintentional movements can be produced by a change in the external force field assuming unchanged RC. We imply here, however, unintentional shifts in an effector's position observed when the external forces are the same. Such movements are presumably produced by unintentional RC shifts.

This interpretation suggests that intentional and unintentional movements share a common feature: They both result from shifts of the body RC produced intentionally or as a result of the hypothesized RC-back-coupling. This hypothesis leads to a prediction that the structure of inter-trial joint configuration variance would lead to an inequality $V_{UCM} > V_{ORT}$ with respect to task-specific variables such as hand position and orientation (cf. Scholz et al. 2000; Zhou et al. 2014). The main purpose of this study was to test this prediction by comparing the structure of inter-trial joint configuration variance during intentional and unintentional movements: A comparison that has never been done before. While the inequality $V_{UCM} > V_{ORT}$ has been demonstrated in many studies (reviewed in Latash 2008), it should not be taken for granted. In the early study of sit-to-stand, this inequality was confirmed for the horizontal position of the center of mass, but not for its vertical coordinate (Scholz and Schöner 1999). Moreover, in a later study (Latash et al. 2001), the variable specified for the subjects as the task variable (total force produced by a set of fingers) failed to show consistent $V_{UCM} > V_{ORT}$, while this inequality was observed for another mechanical variable (total moment of force), which was not an explicit part of the task. Those and other studies have shown that the ratio of V_{UCM} to V_{ORT} can be modulated within a broad range depending on the task and the performance variable with respect to which analysis is performed.

A HapticMaster robot was used to introduce smooth, transient changes in the external force applied to the handle held by the subjects who were instructed not to interfere voluntarily (“allow the robot to move your arm”). The quick and smooth force change was followed by a dwell time, after which the force returned to the bias level. At the new steady state, the subject’s hand undershot its initial position, i.e., showed an unintentional movement. Further, subjects were instructed to make series of intentional movements to the same final position without a change in the robot force. Joint configuration variance was analyzed across trials for intentional and unintentional movement separately to test the main hypothesis ($V_{UCM} > V_{ORT}$).

2. Methods

2.1. Participants

Eight self-reported right-handed male subjects took part in this study (age: 29.6 ± 0.7 years, height: 1.75 ± 0.04 m, and mass: 68.5 ± 4.7 kg; mean $\pm$ SE). All subjects were healthy and had no history of hand injury. All subjects provided informed consent in accordance with the procedures approved by the Office for Research Protection of the Pennsylvania State University.

2.2. Apparatus and Procedure

2.2.1. Experimental setup—The HapticMaster (Moog, The Netherlands) is an admittance-controlled robot with an arm that possesses three degrees of freedom (DOFs). A handle with three kinematic DOFs -pitch, roll and yaw - was attached to the end of the robot arm. The HapticMaster integrates the force sensor into the control loop to get high-quality haptic rendering. The advantage of this method is that the actual mass and friction of the device can be eliminated. A virtual mass is always needed though, in order to avoid commanding infinite accelerations. The default value of the virtual mass was 3 kg; for smaller values, the robot started to oscillate. Thus, when the subject was holding the handle steadily, he could not sense the weight of the handle; however, during movement, the subject could feel the virtual mass of the robot. The robot arm was used to generate both baseline force (F_{BASE}) and perturbation force (F_{PERT}) (details in Procedures). Visual feedback was presented with a 20-inch monitor placed 0.8 m from the subject.

Each subject sat upright in the chair and held the handle attached to the robot arm with the right hand; gravity forces acting on the hand/arm were not compensated. One reflective marker was placed on the suprasternal notch (SN) and another marker was placed 2 cm below the acromion process (AP). Three-dimensional coordinates of the SN marker were used as the origin of the XYZ global coordinate system $\{G\}$. The X-axis was a horizontal axis in a sagittal plane pointing forward, the Y-axis was a horizontal axis in a frontal plane pointing to left side of the subject, and the Z-axis pointed upward. The axes of the robot coordinate system $\{r\}$ (x^r y^r z^r) were parallel to the axes of $\{G\}$ (XYZ). The directions of x^r and y^r were opposite to the directions of X and Y, while the direction of z^r coincided with that of Z. The global and robot coordinate systems, as well as the initial joint configuration of the subject, are illustrated in Figure 1.

The height of the robot arm and the position of the chair were adjusted in such a way that the subject's hand moved primarily in a parasagittal plane. Note that we performed analysis of joint configuration variance in 3D (see later). So, keeping the movement within a plane was not crucial. The subject selected a comfortable hand position, from which the hand could move 25 cm freely along Y positive ($Y+$), Y negative ($Y-$), and X positive ($X+$) directions in $\{G\}$. The 3D position of the handle of the robot arm was set as the initial position by the robot control program. The initial position was also set as the origin of the robot coordinate system.

2.2.2. Kinematic data collection—A Qualisys Motion Capture System (Qualisys AB, Sweden), consisting of five ProReflex MCU240 infrared light-emitting cameras, was used to record three-dimensional (3D) kinematic data at 120 Hz. The cameras were mounted on tripods positioned around the experimental space. Calibration was considered to be successful if the standard deviation of the wand length (30 cm) was less than 1 mm. The 3D tracking maximum residual of the camera system was set as 5 mm.

Marker clusters, molded to fit body segments, (four markers per cluster, see Mattos et al. 2011) were used to track positions and orientations of right arm segments. These clusters were placed at: (1) the upper torso, at two-thirds of the distance between the neck and the acromion process; (2) the upper arm, at the half-distance of the lateral midline; (3) the dorsal surface of the forearm, at two-thirds of the length; and (4) the dorsal surface of the hand. Self-adherent wrap (Coban™ LF, 3M) and surgical tape (Transpore™, 3M) was used to fasten the clusters.

Four more markers were used to calibrate the kinematical model of the subject's right arm and removed before the main experiment procedure. These markers were attached at: 1) medial and 2) lateral epicondyles of humerus; 3) ulnar and 4) radial styloid processes. These markers were used to calculate limb segment lengths and joint rotation centers. For this procedure, subjects maintained a steady calibration posture with the right arm parallel to the floor in a parasagittal plane, elbow joint fully extended, and wrist in a neutral position. The zero angle of each joint was defined using this posture. Each limb segment had its own local xyz coordinate system whose origin was at the proximal joint center and the axes were aligned with XYZ . Euler angles were calculated based on the rotation of these local coordinate axes. Before experiment, local coordinate axes were defined using posture calibration.

2.2.3. Experimental procedure—The experiment involved two movement types: unintentional and intentional. For both movement types, the subject sat in the chair holding the handle with the right arm before each trial started. The robot generated a constant baseline force ($F_{BASE} = 10$ N) along the $X+$ axis to obtain a certain reproducible combination of force and position vectors in the initial state. The magnitude of the bias force was selected based on an earlier study (Zhou et al. 2014). The subject was instructed to resist F_{BASE} and maintain the initial posture (Figure 1). At any time, the hand was free to move in any direction, including vertical direction (along Z axis).

During unintentional movements, each trial consisted of three parts. The first part, *Preparation*, was a steady state lasting 2–4 s until a change in F_{BASE} was initiated (perturbation force, F_{PERT} starting at T_0 , Figure 2A, B). During the second part, *Perturbation*, F_{PERT} increased in magnitude over 0.5 s, reached a peak value, was kept at that value for 5 s, and then removed. During the final part, *Recovery*, the robot force was back to F_{BASE} . Note that F_{PERT} increased smoothly over 0.5 s to avoid inducing so-called triggered responses (Hammond 1954; Tatton et al. 1978; reviewed in Shemmell et al. 2010). A recent study of the electromyographic patterns in arm muscles using similar perturbations (Falaki et al. 2014) has shown no visible phasic muscle reactions that would resemble triggered responses.

Before the experiment, the subject performed a few practice trials. During these trials, a magnitude of F_{PERT} was selected, such that the handle moved over about 20–25 cm away from its initial position. Across subjects, F_{PERT} along X-axis ranged between 20 and 30 N. As a result, the handle excursion was approximately matched across subjects (see Results) while F_{PERT} magnitude varied from subject to subject.

During the Perturbation and Recovery parts, the subject was instructed not to interfere voluntarily (“allow the robot to move your arm, do not relax and do not resist”) (Feldman 1966; Latash 1994). After T_0 , F_{PERT} increased in $Y+$, $Y-$ or $X+$ direction and, as a result, the subject’s hand was pulled away from its initial position. During this phase, peak velocity (V_{PEAK}) of the handle was computed on-line. F_{PERT} increased to a new level over 500 ms and was kept at that level. Movement time was defined as the time interval between T_0 and the time when the handle velocity dropped under 10% V_{PEAK} .

After movement time, the robot kept its force unchanged for 5 s (dwell time, T_{DWELL}). Perturbation time was defined as the sum of movement time and dwell time. Then, the robot force returned to F_{BASE} and, as a result, the subject’s hand moved towards the initial position, typically with an undershoot (see Results). The subject kept the final posture for 2–3 s and then released the handle. After the handle returned to the initial position, the system was ready for the next trial. Besides, blocks of five trials with $T_{\text{DWELL}} = 0$ for each perturbation direction were performed (see Figure 2A).

During intentional movements, a target marker was placed on a tripod at the averaged across trials final position of the hand calculated from all the unintentional movement trials with F_{PERT} along one of the three directions ($Y+$, $Y-$ and $X+$). The subject was instructed to hold the handle in the initial position (same as during the unintentional movements) against F_{BASE} . After the verbal command “Go!”, the subject moved the handle to the target marker with natural speed in one motion (movement time was about 1 s). After the handle reached the target, the subject held the handle for 2–3 s and then released the handle. The handle returned to the initial position, and the system was ready for the next trial. This procedure was repeated for the averaged final positions calculated from the unintentional movements along all three directions of F_{PERT} .

Given different combinations of F_{PERT} direction (factor *Direction*, three levels, $Y+$, $Y-$ and $X+$) and movement type (factor *Movement*, two levels, intentional and unintentional), there

were six conditions. Subjects performed each condition 22 times (132 trials in total). Trials within each condition were blocked, while conditions were randomized with respect to the *Direction* factor. Intentional movements were always performed after unintentional movements because setting targets for intentional movement series required knowing the final steady-state hand coordinate during unintentional movements. Short rest intervals were offered between trials within a condition (about 5 s), while 1-min rest was given between conditions.

2.3. Data Processing

The data were analyzed with a customized Matlab program (Mathworks Inc, MA, USA). Marker coordinates were low-pass filtered at 5 Hz with a zero-phase 4th-order Butterworth filter. Joint angles between two adjacent segments were calculated in the following steps; first, the relationship between the orientation of each segment and its orientation in the anatomical calibration posture was derived from marker coordinates to compute the rotation matrices. Next, rotation matrices were obtained for the relative orientation of distal segments with respect to proximate segments. Next, matrices of relative orientation were parsed into angles between adjacent segments using Euler's *Zx'y'* sequence. The second rotation was performed around the local *x*-axis, which was rotated previously around the global *Z*-axis. The third rotation was around the local *y*-axis, which was rotated previously around the global *Z*-axis and then around the *x*-axis. Finally, ten angles were computed for further analyses (Figure 1): three angles for the clavicular rotation relative to the trunk (θ_1 —about *z*-axis, θ_2 —about *x*-axis, and θ_3 —about *y*-axis), three angles for the relative rotation of the upper arm (θ_4 —about *z*-axis, θ_5 —about *x*-axis, and θ_6 —about *y*-axis), two angles for the relative rotation of the forearm (θ_7 —about estimated *x*-axis oblique to the local coordinate system and θ_8 —about *y*-axis), and two angles for the relative rotation of the hand (θ_9 —about *z*-axis, θ_{10} —about *x*-axis). The ten angles formed the joint configuration vector, θ .

The trials were aligned in time according to perturbation onset (T_0). At each frame, joint angles were averaged across trials for each condition separately to obtain the average joint configuration vector (θ_{AV}). Elemental variables (θ) and two performance variables, hand position (*X*-, *Y*- and *Z*- coordinates) and hand orientation (α , β and γ —orientation angles of the hand, the first rotation about *Z*-axis by α , the second rotation about *x'* by β , the third rotation about *y* “ by γ), were linked by a forward kinematic model (Scholz et al. 2000). A Jacobian matrix, $J(\theta_{AV})$, was computed from the forward kinematic model for each time step to determine the relationship between infinitesimal deviations of joint angles from the average configuration vector and the change of selected performance variables. Subsequently, singular value decomposition (SVD) was used to compute the null-space of $J(\theta_{AV})$. This null-space was taken as a linear approximation of the uncontrolled manifold (UCM).

Variance per DOF within the UCM and orthogonal sub-space was computed as:

$$V_{UCM} = (\sum |\theta_{UCM} - \theta_{AV,UCM}|^2) / N_{trial} \cdot (n - d) \quad (1)$$

$$V_{ORT} = (\sum |\theta_{ORT} - \theta_{AV,ORT}|^2) / N_{trial} \cdot (d) \quad (2)$$

Where θ_{UCM} and θ_{ORT} are projections of joint configuration onto the UCM and its orthogonal complement; $\theta_{AV,UCM}$ and $\theta_{AV,ORT}$ are the corresponding averaged joint configuration projections across trials, $n = 10$ is the dimensionality of joint angles, θ , and N_{trial} is the number of trials used in the analysis. The dimensionality of each performance variable, position and orientation, was $d = 3$.

The total variance V_{TOT} was computed as:

$$V_{TOT} = (\sum |\theta - \theta_{AV}|^2) / N_{trial} \cdot (n) \quad (3)$$

All variance indices in (1) – (3) were computed per DOF in the corresponding spaces. Further, an index of synergy (V) was computed:

$$\Delta V = (V_{UCM} - V_{ORT}) / V_{TOT} \quad (4)$$

For parametric statistical analysis V was log-transformed using modified Fisher's z - transform (Solnik et al. 2013):

$$\Delta V_z = 0.5 \cdot \log [(|\Delta V_{low}| + \Delta V) / (\Delta V_{up} - \Delta V)] - 0.5 \cdot \log [|\Delta V_{low}| / \Delta V_{up}] \quad (5)$$

Here V_{upper} and V_{lower} are the upper limit and the lower limit of V , respectively. $V_{UCM} > V_{ORT}$ ($V > 0$) was interpreted as a synergy in the joint configuration space stabilizing the performance variable (cf. Latash et al. 2007).

Overall, six dependent variables were calculated: V_{UCM-P} , V_{ORT-P} , and V_{Z-P} with respect to hand position and V_{UCM-O} , V_{ORT-O} , and V_{Z-O} with respect to hand orientation. We did not perform analysis with respect to the combined variable (position and orientation) but separated the two analyses to contrast results for the variable that was defined as an explicit target for unintentional movements (position) and for the variable that was not (orientation).

For unintentional movement, three time intervals (phases) were extracted from the three phases of each trial. During *Preparation*, the 0.5 s time interval prior to T_0 was defined as Phase-1. During *Perturbation*, Phase-2 was defined as the final 0.5 s time interval of the perturbation time for trials with $T_{DWELL} = 5$ s, while the final 0.1 s time interval of the perturbation time for trials with $T_{DWELL} = 0$ (Fig. 2A, B). During *Recovery*, Phase-3 was defined as the 0.5 s time interval that ended 0.5 s before the end of the trial. For intentional movement, only the data at the end of the movement (corresponding to Phase-3) were analyzed. These data were taken over the 0.5 s time interval that ended 0.5 s before the end of the trial (Fig. 2C).

The coordinates of the suprasternal notch (SN) marker were subtracted from the coordinates of all markers. To obtain the hand coordinates, one marker within the hand marker cluster was selected to represent the hand. The hand coordinates were averaged over each of the three phases in each trial and the Euclidean distance of the hand was calculated between 1)

Phase-1 and Phase-2 (D12), and 2) Phase-2 and Phase-3 (D23). Return ratio (R-ratio) was defined as the absolute value of D23/D12. Note that R-ratio = 1 means that the hand moved to the initial position after F_{PERT} had been removed, while R-ratio = 0 means that no return movement happened after F_{PERT} had been removed. In Phase-3, the hand position variance was quantified along different axes (X, Y and Z) separately. For each subject, hand position variance was calculated across trials for each time sample. The variance was then averaged across time samples.

2.4. Statistics

All descriptive statistics are reported in the text and figures as means and standard errors unless stated otherwise. Two-way repeated-measures ANOVAs were used to test effect of *Direction* (Y+, Y- and X+) and *Movement* (unintentional and intentional) on the variance indices computed within the UCM-based analysis in Phase-3, V_{UCM-P} , V_{ORT-P} , V_{UCM-O} , V_{ORT-O} . A three-way repeated-measure ANOVA was used to test effect of *Direction*, *Movement* and *Variable* (two levels: position and orientation) on V_Z in Phase-3. A two-way repeated-measure ANOVA was used to test effect of *Direction* and T_{DWELL} (two levels, 5 s and 0 s) on the Return ratio. A three-way repeated-measure ANOVA was used to test effect of *Direction*, *Movement* and *Axis* (X, Y and Z) on the hand positional variance. To fulfill the assumption of normality, dependent variables were log-transformed when needed. Pairwise comparisons with Bonferroni corrections were used to explore significant effects, while post-hoc ANOVAs were performed to explore interaction effects in the three-way analysis. The statistical tests were performed with SPSS 20.0 (IBM Corporation, USA) and Matlab (Mathworks Inc, MA, USA).

3. Results

3.1. Kinematic characteristics of movements

During trials with transient force perturbations applied to the hand, changes in the baseline force (F_{BASE}) produced by the perturbation force (F_{PERT}) resulted in hand motion to a new position. The hand moved back towards the initial position after F_{PERT} was removed. The amount by which subjects undershot the initial position changed consistently with both perturbation direction and dwell time. When $T_{DWELL} = 0$ s, little difference was observed between the hand positions in Phase-1 and Phase-3, especially when the perturbation was exerted along the Y direction. However, when $T_{DWELL} = 5$ s, the subject's final hand position undershot the initial position consistently. The Return ratio (R-ratio, see Methods) is illustrated in Figure 3A. This index shows to what extent the hand moved back to its initial position. It is clear from the figure that movements with no dwell time (open bars) showed high R-ratio values (return closer to the initial position) as compared to movements with the dwell time of 5 s (black columns).

Two-way, repeated-measures ANOVA confirmed that R-ratio depended on *Direction* and T_{DWELL} . In particular, R-ratio for X+ (0.66 ± 0.03) was significantly smaller than for Y+ (0.85 ± 0.03) and Y- (0.87 ± 0.04) [$F_{(2, 14)} = 7.09$, $p < 0.01$]. Besides, R-ratio value for $T_{DWELL} = 5$ s (0.7 ± 0.06) was significantly smaller than for $T_{DWELL} = 0$ s (0.89 ± 0.02) [$F_{(1, 14)} = 13.75$, $p < 0.01$]. There was also a *Direction* $\times$ T_{DWELL} interaction [$F_{(2, 14)} = 4.48$,

$p < 0.05$] reflecting the larger difference between the $X+$ and $Y\pm$ directions of F_{PERT} for the trials with $T_{DWELL} = 5$ s.

After the transient perturbation was over (Phase-3), the hand coordinate variance along each of the global coordinate axes depended on *Direction* of F_{PERT} , *Movement* and *Axis* (Figure 3B–D). In this comparison, the factor *Movement* had two levels, intentional and unintentional. We viewed changes in the hand position produced by the transient force change as unintentional movements (to remind, the subjects were instructed not to interfere voluntarily with hand movements induced by changes in the robot force). Intentional movements were performed by the subjects without any change in F_{BIAS} to targets placed at the same location as those observed, on average, during unintentional movements (see Methods for more detail). As a result, on average, the initial and final hand positions did not differ significantly between the two classes of movements, and the external force was also the same (F_{BIAS}). The biggest variance was seen along the perturbation direction, i.e., variance along X when F_{PERT} was along $X+$ and variance along Y when F_{PERT} was along $Y\pm$. Variance along the vertical handle coordinate axis (Z , Figure 3D) did not show significant effects of F_{PERT} direction. Overall, variance indices for unintentional movements (open bars; 159 ± 36 mm²) were much larger than those for intentional movements (26 ± 5 mm²; black bars) [$F_{(1, 7)} = 155.88$, $p < 0.01$]. Besides, variance along Y axis (104 ± 38 mm²) was significantly larger than along Z axis (83 ± 13 mm²) [$F_{(2, 14)} = 7.09$, $p < 0.01$].

There were also two-way interactions *Axis* $\times$ *Movement* [$F_{(2, 14)} = 9.68$, $p < 0.01$] and *Axis* $\times$ *Direction* [$F_{(4, 28)} = 8.0$, $p < 0.01$] and the three-way interaction [$F_{(4, 28)} = 6.31$, $p < 0.01$]. The interactions reflected the facts that: 1) For intentional movements, variance along Y axis was smaller than along the other two axes (the open bars in Figure 3C are smaller than in Figure 3B and 3D); besides, variance along Y axis was also smaller for F_{PERT} along $X+$ during unintentional movements (the black bar for $X+$ in Figure 3C is smaller than in Figures 3B and 3D); and 2) For unintentional movements, variance along X axis for F_{PERT} along $X+$ was larger as compared to F_{PERT} along $Y\pm$ (the black bar for $X+$ in Figure 3B is larger than for $Y\pm$) while variance along Y showed an opposite pattern (the black bar for $X+$ in Figure 3C is smaller than for $Y\pm$).

3.2. Joint configuration variance

Two components of the inter-trial variance in the joint configuration space were calculated: V_{UCM} compatible with no changes in a selected performance variable (hand position or orientation, both three-dimensional) and V_{ORT} leading to changes in that variable (for details see Methods). This analysis was run for hand position and orientation separately based on the data in Phase-3 when both unintentional and intentional movements stopped about a new steady state. The two analyses were run to compare the structures of joint configuration variance for a variable specified by the target (position) and for a variable that had no target (orientation).

Figure 4 illustrates the indices of joint configuration variance for Phase-3 quantified per degree-of-freedom in the corresponding spaces. For both position-related and orientation-related analyses, typically both variance components were larger for unintentional movements than for intentional movements. This was confirmed by the main effect of

Movement ($F_{(1,7)} = 6.55, p < 0.05$). Across all six combinations of different directions of F_{PERT} and *Movement*, most joint configuration variance was consistently within the UCM ($V_{UCM} > V_{ORT}$). This was true for both the position-related ($1.76 \times 10^{-3} \pm 0.64 \times 10^{-3}$ vs. $0.62 \times 10^{-3} \pm 0.2 \times 10^{-3} \text{ rad}^2$) and the orientation-related ($1.73 \times 10^{-3} \pm 0.6 \times 10^{-3}$ vs. $0.69 \times 10^{-3} \pm 0.3 \times 10^{-3} \text{ rad}^2$) analyses as illustrated in the top two panels on Figure 4 (black columns are consistently larger than white columns).

The synergy index (ΔV) reflecting the difference between V_{UCM} and V_{ORT} was consistently positive for both the position-related and orientation-related analyses (the bottom panels in Figure 4). A significant difference between z-transformed synergy indices (ΔV_Z) during intentional (0.60 ± 0.04) and unintentional movements (0.48 ± 0.03) was found [$F_{(1,7)} = 7.37, p < 0.05$]. Along all F_{PERT} directions, position-related analysis showed higher ΔV_Z for intentional movements than for unintentional movements (the lower left panel in Fig. 4). Orientation-related analysis produced similar ΔV_Z values along Y direction for the two movement types and was higher along $X+$ during unintentional movements. This was reflected in two-way interactions: *Variable* $\times$ *Direction* [$F_{(2,14)} = 15.85, p < 0.01$] and *Variable* $\times$ *Movement* [$F_{(1,7)} = 12.53, p < 0.01$]. The interactions reflected the facts that ΔV_{Z-P} for $Y+$ was larger than for $X+$ while ΔV_{Z-O} for $Y+$ was smaller than for $X+$, and ΔV_{Z-P} for unintentional movements was smaller than for intentional movements.

Figure 5 illustrates the time profiles of the z-transformed synergy index ΔV for both position-related (thin dashed lines, ΔV_{Z-P}) and orientation-related (thin solid lines, ΔV_{Z-O}) analyses for a representative subject for both unintentional (top panel) and intentional (bottom panel) movements. The corresponding average kinematic profiles are shown with thick lines with standard error shades. Note that the synergy index was consistently positive at all steady-state phases of the movements. This was true for all the subjects. There were no visible consistent changes in the synergy index at the final steady state that would suggest intentional movement corrections in any of the subjects.

To explore whether the results of the position-related and orientation-related analyses could reflect correlated changes in the handle position and orientation we ran an additional correlation analysis between hand position and orientation across trials in each subject separately. Since both variables are three-dimensional, we ran all possible pair-wise correlations between the position and orientation components. No significant correlations were found in any of those. The range of R^2 values was from 0 to 0.04 with the median value of 0.02.

4. Discussion

The main hypothesis formulated in the Introduction has been supported by the results. Longer-lasting ($T_{DWELL} = 5 \text{ s}$) transient perturbations led to consistent undershoots of the initial hand position when the external force returned to its baseline value (similar to results of Zhou et al. in press). When these unintentional movements were compared to intentional movements to about the same locations performed within about the same movement time, the structure of the joint configuration variance confirmed the $V_{UCM} > V_{ORT}$ inequality both classes of movements. In both cases, variance that did not affect handle position (V_{UCM-P})

was larger than variance affecting the handle position (V_{ORT-P}). The inequality $V_{UCM} > V_{ORT}$ was also confirmed for another performance variable that was not emphasized in the task, namely hand orientation. There were, however, quantitative differences in indices of joint configuration variance between the intentional and unintentional movements. In the following sections we offer an interpretation for these findings based on a general scheme for the control of natural, multi-joint movements.

4.1. Origins of task-specific stability in abundant systems

Stability of motor actions in the unpredictable environment is paramount for successful biological movement. The notion of task-specific stability (Schöner 1995) suggests that, within a redundant system, the central nervous system has the ability to ensure high stability in directions corresponding to changes in a salient variable while allowing relatively low stability in directions that keep this variable unchanged. During analysis of inter-trial variance, directions of low stability are expected to show disproportionately more variance reflecting the time evolution of the movements.

Task-specific stability is a natural consequence of a recently developed scheme (reviewed in Latash 2010) combining several earlier ideas: Hierarchical control of multi-element natural actions (Arbib et al. 1985; Martin et al. 2009), synergy organization based on back-coupling loops within the CNS (Latash et al. 2005), and control with subthreshold depolarization of neuronal pools (Feldman 2009). According to this scheme, referent spatial coordinates for body parts related to salient performance variables (we will address those as *referent configuration*, RC) are specified at the highest level of the hierarchy, while RCs at lower levels emerge as results of a cascade of few-to-many mappings, all the way down to the individual muscle level, where RC is equivalent to the threshold of the tonic stretch reflex as in the classical equilibrium-point hypothesis (Feldman 1966, 1986).

Within this scheme, synergies at each of the few-to-many transformations are organized with the help of back-coupling loops (Latash et al. 2005; Martin et al. 2009) that channel variance at the higher-dimensional lower level primarily into the uncontrolled manifold (UCM) for RC at the lower-dimensional higher level (Scholz and Schöner 1999; reviewed in Latash et al. 2007). There is also a back-coupling loop from the discrepancy between the referent and actual values of task-specific variables to the hierarchically highest level that drives the system to the desired values for the task-related performance variables.

Our experiments suggest that this scheme may be incomplete. They show that, even when the subject tries his or her best not to react to changes in the external forces, a drift in the referent values for task-specific variables (RC_{TASK}) takes place if the hand position is moved away from its initial position and then kept there for a few seconds. These observations suggest that a drift in RC_{TASK} may be caused by a discrepancy between RC_{TASK} and actual body configuration (Wilhelm et al. 2013; Ambike et al. 2014; Zhou et al. in press). This process has been addressed as RC-back-coupling to distinguish it from the back-coupling schemes suggested earlier to account for the observed structure of inter-trial variance (Latash et al. 2005; Martin et al. 2009).

During natural voluntary movements, a person shifts RC_{TASK} and it plays the role of an attractor for the actual body configuration. This process of direct coupling leads to a movement assuming that no external force prevents the movement. Our results show that, if movement is prevented by an external force, RC_{TASK} starts to shift towards the actual body configuration. This assumption offers an interpretation for a variety of observations such as a slow force drift in isometric tasks when visual feedback is turned off (Slifkin et al. 2000; Vaillancourt and Russell 2002; Shapkova et al. 2008) and phenomena of *slacking* reflecting reduction in the subject's motor output when the kinematic error is small (Reinkensmeyer et al. 2009; Seol et al. 2011). It also suggests that violation of movement equifinality may be common in conditions when transient perturbations have a dwell time of a few seconds.

We would like to emphasize that, while perturbations were used in our current experiments, they are not crucial to observe a drift in performance variables suggesting a drift in the corresponding RC. This is exemplified by the aforementioned studies of the force drift in the absence of visual feedback. A recent study (unpublished) quantified the force drift under such conditions and reported a much slower process with the characteristic time of about 15 s (using exponential fitting). This time is much longer than the one reported in experiments with perturbations (about 1 s, Zhou et al. in press). It is possible that, while perturbations are not needed to observe the RC drift, they accelerate the process by mechanisms that are currently unknown.

Note that the hand did not show visible motion during the dwell time in our experiment. This is not a trivial observation. It suggests that the drift of RC_{TASK} was accompanied by an increase of the hand apparent stiffness (Latash and Zatsiorsky 1993). Figure 5 illustrates this with a force-coordinate plot assuming that the force and displacement are limited to a single dimension. In the initial condition, a certain combination of hand force and coordinate corresponds to point A. F_{PERT} moves the hand to a new combination of force and coordinate (point B). After a dwell time, removal of F_{PERT} results to the system moving to a point C where the force equals F_{BIAS} but the coordinate is different from the initial state. Assuming, for simplicity, that the hand behavior can be represented as that of a linear spring, it is obvious from Fig. 5 that the slope of the line connecting points B and C is higher than that of the line connecting points A and B. This analysis requires further experimental exploration.

The drawing in Figure 6 suggests that the RC drift involved a change in the coactivation command (c-command, Feldman 1980; Feldman and Latash 1982). While the notions of reciprocal command (r-command) and c-command were introduced originally for single-joint control, they have been generalized for whole-body motion (Feldman and Levin 1995; Latash 1998; Feldman 2011). The c-command defines a spatial range of joint motion where the two opposing muscle groups, agonist and antagonist, are activated. As a result, even when the external load is zero, the agonist-antagonist muscles show non-zero activation levels at steady state. Changing the c-command is an effective method to change the apparent stiffness of the corresponding joint or of the endpoint of a multi-joint effector (see Flash 1987). We view the c-command as a component of RC at a multi-muscle level, and the drawing in Figure 6 suggests that the unintentional RC drift may have, as its component, a drift of the corresponding c-command. Other contributors to the change in the apparent

stiffness may include the non-linearity of the force-length relationships for the involved muscles and tendons.

4.2. Voluntary neural command as a perturbation

The UCM hypothesis is based on the assumption that the central nervous system has an ability to modify selectively, in a task-specific way, stability of a redundant system in different directions within the high-dimensional space of elemental variables (Scholz and Schoner 1999; reviewed in Latash et al. 2007). Within this hypothesis, analysis of variance across repetitive trials has been developed (reviewed in Latash et al. 2002) to probe stability of the system in different directions. Another, complementary, method of analysis of stability used unexpected perturbations of multi-joint movements to a target (Scholz et al. 2000; Mattos et al. 2011). If a system is less stable in certain directions, perturbations are expected to lead to larger deviations along those directions – a prediction confirmed in the cited studies.

Recently, analysis of equifinality (cf. Bizzi et al. 1976; Kelso and Holt 1980; Schmidt and McGown 1980; Latash and Gottlieb 1990) at the level of task-related variables and at the level of elemental variables has shown that smooth and quick transient perturbations lead to close to equifinal behavior at the level of task variables but not at the level of elemental variables (Wilhelm et al. 2013; Zhou et al. 2014). These results are naturally expected within the aforementioned hierarchical control scheme with RCs assuming high stability in directions leading to changes in task-related variables and low stability in directions that keep those variables unchanged (within the corresponding UCM). Our observations of the inequality $V_{UCM} > V_{ORT}$ with respect to task-specific variables (hand position and orientation) in trials without dwell time confirm the mentioned findings.

We have assumed that the subjects in our experiments did not change task RC_{TASK} intentionally, as required by the instruction (this assumption remains a weakness, see the next section). Under this assumption, unintentional RC_{TASK} shifts in the trials with dwell time were expected to result in the inequality $V_{UCM} > V_{ORT}$ with respect to hand position and orientation. This signature is a natural consequence of the task-specific stability inherent to the described control scheme. We would like to emphasize that, in those trials, the subjects had no explicit spatial target, and their behavior (including the $V_{UCM} > V_{ORT}$ signature) was a natural consequence of the physics/physiology of the system. The fact that the $V_{UCM} > V_{ORT}$ signature was seen across conditions with very different muscle and joint involvement (in trials with perturbations in different directions) is an additional argument in favor of the advocated general scheme for the movement production, which is not muscle or joint specific. We would like to remind that the relations between V_{UCM} and V_{ORT} potentially can vary within a broad range as mentioned in the Introduction and supported by many earlier studies.

A simple scheme in Figure 7 illustrates how similar structure of variance could emerge within the suggested theoretical framework in response to three inputs: An external perturbation, an unintentional RC_{TASK} drift, and an intentional RC_{TASK} shift. Indeed, in all three cases, the task-specific stability ensured by the neural structures in the middle “box” is expected to reveal itself in such phenomena as motor equivalent motion (Mattos et al. 2011,

2013), lack of equifinality at the level of elements (Wilhelm et al. 2013; Zhou et al. 2014), and $V_{UCM} > V_{ORT}$. Note that similar structure of variance in the joint configuration space was observed in earlier studies of multi-joint intentional movements (Domkin et al. 2002, 2005; Gera et al. 2010).

During intentional movements, our subjects were instructed to move to a visual target. Thus, it was not much of a surprise that those movements were characterized by lower V_{ort} as compared to unintentional movements to about the same point in space, which happened without any target. This resulted in significantly larger V indices computed for the hand position. Note that hand orientation was not constrained by the task and, as a result, the V indices for hand orientation were not significantly different between the intentional and unintentional movements providing further support for our central hypothesis that both types of movements shared the same task-specific stability properties.

4.3. Shortcomings and future plans

We acknowledge a few shortcomings of the present study. In our analyses of joint configuration variance, we have assumed that individual joint rotations form a set of elemental variables, that is, that they could be modified by the central nervous system one at a time. In other words, we have assumed that there is no task-independent co-variation of joint rotations. This assumption is far from being obvious, particularly given the presence of bi-articular muscles and inter-joint reflexes (e.g., Nichols 1989). While many earlier studies performed analysis of inter-trial variance in joint configuration space under the same assumption (e.g., Scholz and Schöner 1999; Scholz et al. 2000; Domkin et al. 2002, 2005; reviewed in Latash et al. 2007), the assumption may happen to be wrong. Unfortunately, we are unaware of experimental studies addressing this issue, for example asking a person to move one joint at a time and quantifying motion of the other joints as this is done, for example, in studies of multi-finger action (Latash et al. 2001; Danion et al. 2003). Until such a study is performed, assuming potential independence of joint rotations remains a drawback of the analysis.

Although we trained the subjects to ignore the arm motion induced by F_{PERT} , this point remains a weakness. There is no objective method to judge whether the subjects follow the instruction “do not intervene voluntarily” since reflex pathways are expected to lead to changes in electromyographic signals even if the subject follows the instruction perfectly. This instruction has been used in many earlier studies (e.g., Feldman 1966; Latash 1992; Zhou et al. 2014) and led to consistent findings both within and across subjects. It was also shown to lead to more consistent behavior as compared to an instruction requiring the subjects to react to external force changes (Latash 1994). Earlier studies have suggested that humans can relatively consistently keep RC unchanged during perturbations leading to unloading of active muscles (Archambault et al. 2005) while loading (stretching) active muscles could lead to an inability to keep the RC (Feldman and Levin 1995).

We have not studied perturbations in the unloading direction, which is a limitation of the study. However, our prediction would be compatible with the aforementioned suggestions: Indeed, an unloading would lead to movement of the actual body configuration towards the RC and, hence, no unintentional RC drift is expected – a prediction to be tested in future.

Another shortcoming is the lack of further exploration of possible changes in the hand apparent stiffness (as illustrated in Fig. 5). We plan experiments with double perturbations designed to explore this unusual phenomenon.

5. Conclusions

To summarize, our experiments show that intentional and unintentional shifts of the hand position in space share an important feature, namely the structure of inter-trial variance in the joint configuration space. These findings fit the general scheme for the production of movements by a redundant system and may be viewed as reflections of task-specific stability properties of the system probed with two different means – external perturbations and changes in descending neural command.

Consider the following example (cf. Valero-Cuevas et al. 2003). Imagine that you are holding between the index finger and the thumb a small metal spring from a typical pen (actually, the reader can take a spring and run this experiment). If an external force is suddenly applied to one of the digits, the spring will likely deform orthogonally to its main axis and may jump out of the hand. This is likely to happen even if the force is applied along the main spring axis. If you try to squeeze the spring quickly, it will again likely jump out of the hand. So, both external perturbations and voluntary actions result in behaviors defined primarily by the stability properties of the object. The idea of task-specific stability, which is in the heart of this line of research, suggests that the brain can modify the “main spring axis” depending on the task and intention.

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References

- Ambike S, Paclet F, Zatsiorsky VM, Latash ML. Factors affecting grip force: anatomy, mechanics, and referent configurations. *Exp Brain Res.* 2014; 232:1219–1231. [PubMed: 24477762]
- Arbib, MA.; Iberall, T.; Lyons, D. Coordinated control programs for movements of the hand. In: Goodwin, AW.; Darian-Smith, I., editors. *Hand Function and the Neocortex*. Berlin: Springer Verlag; 1985. p. 111-129.
- Archambault PS, Mihaltchev P, Levin MF, Feldman AG. Basic elements of arm postural control analyzed by unloading. *Exp Brain Res.* 2005; 164:225–241. [PubMed: 15856209]
- Bernstein, NA. *The Co-ordination and Regulation of Movements*. Oxford: Pergamon Press; 1967.
- Bizzi E, Polit A, Morasso P. Mechanisms underlying achievement of final head position. *J Neurophysiol.* 1976; 39:435–444. [PubMed: 815518]
- Danion F, Schöner G, Latash ML, Li S, Scholz JP, Zatsiorsky VM. A force mode hypothesis for finger interaction during multi-finger force production tasks. *Biol Cybern.* 2003; 88:91–98. [PubMed: 12567224]
- Diedrichsen J, Shadmehr R, Ivry RB. The coordination of movement: optimal feedback control and beyond. *Trends Cogn Sci.* 2010; 14:31–39. [PubMed: 20005767]
- Domkin D, Laczko J, Jaric S, Johansson H, Latash ML. Structure of joint variability in bimanual pointing tasks. *Exp Brain Res.* 2002; 143:11–23. [PubMed: 11907686]
- Domkin D, Laczko J, Djupsjöbacka M, Jaric S, Latash ML. Joint angle variability in 3D bimanual pointing: uncontrolled manifold analysis. *Exp Brain Res.* 2005; 163:44–57. [PubMed: 15668794]

- Falaki A, Towhidkhah F, Zhou T, Latash ML. Task-specific stability in muscle activation space during unintentional movements. *Exp Brain Res*. 2014; 232:3645–3658. [PubMed: 25092272]
- Feldman AG. Functional tuning of the nervous system with control of movement or maintenance of a steady posture. II. Controllable parameters of the muscle. *Biophysics*. 1966; 11:565–578.
- Feldman AG. Superposition of motor programs. I. Rhythmic forearm movements in man. *Neurosci*. 1980; 5:81–90.
- Feldman AG. Once more on the equilibrium-point hypothesis (λ -model) for motor control. *J Mot Behav*. 1986; 18:17–54. [PubMed: 15136283]
- Feldman AG. Origin and advances of the equilibrium-point hypothesis. *Adv Exp Med Biol*. 2009; 629:637–643. [PubMed: 19227525]
- Feldman AG. Space and time in the context of equilibrium-point theory. *Wiley Interdisc Rev: Cogn Sci*. 2011; 2:287–304.
- Feldman AG, Latash ML. Interaction of afferent and efferent signals underlying joint position sense: Empirical and theoretical approaches. *J Mot Behav*. 1982; 14:174–193. [PubMed: 15153409]
- Feldman AG, Levin MF. Positional frames of reference in motor control: their origin and use. *Behav Brain Sci*. 1995; 18:723–806.
- Flash T. The control of hand equilibrium trajectories in multi-joint arm movements. *Biol Cybern*. 1987; 57:257–274. [PubMed: 3689835]
- Gelfand IM, Latash ML. On the problem of adequate language in movement science. *Motor Control*. 1998; 2:306–313. [PubMed: 9758883]
- Gera G, Freitas SMSF, Latash ML, Monahan K, Schöner G, Scholz JP. Motor abundance contributes to resolving multiple kinematic task constraints. *Motor Control*. 2010; 14:83–115. [PubMed: 20237405]
- Hammond PH. Involuntary activity in biceps following the sudden application of velocity to the abducted forearm. *J Physiol*. 1954; 127:23P–25P. [PubMed: 14354685]
- Kelso JA, Holt KG. Exploring a vibratory systems analysis of human movement production. *J Neurophysiol*. 1980; 43:1183–1196. [PubMed: 7373360]
- Latash ML. Virtual trajectories, joint stiffness, and changes in natural frequency during single-joint oscillatory movements. *Neurosci*. 1992; 49:209–220.
- Latash ML. Reconstruction of equilibrium trajectories and joint stiffness patterns during single-joint voluntary movements under different instructions. *Biol Cybern*. 1994; 71:441–450. [PubMed: 7993931]
- Latash, ML. Control of multi-joint reaching movement: The elastic membrane metaphor. In: Latash, ML., editor. *Progress in Motor Control: vol. 1: Bernstein's Traditions in Movement Studies*. Urbana, IL: Human Kinetics; 1998. p. 315-328.
- Latash, ML. *Synergy*. New York, NY: Oxford University Press; 2008.
- Latash ML. Motor synergies and the equilibrium-point hypothesis. *Motor Control*. 2010; 14:294–322. [PubMed: 20702893]
- Latash ML. The bliss (not the problem) of motor abundance (not redundancy). *Exp Brain Res*. 2012; 217:1–5. [PubMed: 22246105]
- Latash ML, Gottlieb GL. Compliant characteristics of single joints: Preservation of equifinality with phasic reactions. *Biol Cybern*. 1990; 62:331–336. [PubMed: 2310787]
- Latash ML, Shim JK, Smilga AV, Zatsiorsky VM. A central back-coupling hypothesis on the organization of motor synergies: A physical metaphor and a neural model. *Biol Cybern*. 2005; 92:186–191. [PubMed: 15739110]
- Latash ML, Scholz JF, Danion F, Schöner G. Structure of motor variability in marginally redundant multi-finger force production tasks. *Exp Brain Res*. 2001; 141:153–165. [PubMed: 11713627]
- Latash ML, Scholz JP, Schöner G. Motor control strategies revealed in the structure of motor variability. *Exer Sport Sci Rev*. 2002; 30:26–31.
- Latash ML, Scholz JP, Schöner G. Toward a new theory of motor synergies. *Motor Control*. 2007; 11:276–308. [PubMed: 17715460]
- Latash ML, Zatsiorsky VM. Joint stiffness: Myth or reality? *Hum Move Sci*. 1993; 12:653–692.

- Loeb GE. What might the brain know about muscles, limbs and spinal circuits? *Prog Brain Res.* 1999; 123:405–409. [PubMed: 10635735]
- Martin V, Scholz JP, Schoner G. Redundancy, self-motion, and motor control. *Neural Comput.* 2009; 21:1371–1414. [PubMed: 19718817]
- Mattos D, Latash ML, Park E, Kuhl J, Scholz JP. Unpredictable elbow joint perturbation during reaching results in multijoint motor equivalence. *J Neurophysiol.* 2011; 106:1424–1436. [PubMed: 21676927]
- Mattos D, Kuhl J, Scholz JP, Latash ML. Motor equivalence (ME) during reaching: Is ME observable at the muscle level? *Motor Control.* 2013; 17:145–175. [PubMed: 23370796]
- Nichols TR. The organization of heterogenic reflexes among muscles crossing the ankle joint in the decerebrate cat. *J Physiol.* 1989; 410:463–477. [PubMed: 2795487]
- Reinkensmeyer DJ, Akoner O, Ferris DP, Gordon KE. Slaking by the human motor system: computational models and implications for robotic orthosis. *IEEE Eng Med Biol Soc.* 2009; 2009:2129–2132.
- Schmidt RA, McGown C. Terminal accuracy of unexpected loaded rapid movements: Evidence for a mass-spring mechanism in programming. *J Mot Behav.* 1980; 12:149–161. [PubMed: 15215060]
- Scholz JP, Schöner G. The uncontrolled manifold concept: Identifying control variables for a functional task. *Exp Brain Res.* 1999; 126:289–306. [PubMed: 10382616]
- Scholz JP, Schöner G, Latash ML. Identifying the control structure of multijoint coordination during pistol shooting. *Exp Brain Res.* 2000; 135:382–404. [PubMed: 11146817]
- Schöner G. Recent developments and problems in human movement science and their conceptual implications. *Ecol Psychol.* 1995; 8:291–314.
- Secoli R, Milot MH, Rosati G, Reinkensmeyer DJ. Effect of visual distraction and auditory feedback on patient effort during robot-assisted movement training after stroke. *J Neuroeng Rehabil.* 2011; 8:21. [PubMed: 21513561]
- Shapkova EY, Shapkova AL, Goodman SR, Zatsiorsky VM, Latash ML. Do synergies decrease force variability? A study of single-finger and multi-finger force production. *Exp Brain Res.* 2008; 188:411–425. [PubMed: 18425506]
- Shemmel J, Krutky MA, Perreault EJ. Stretch sensitive reflexes as an adaptive mechanism for maintaining limb stability. *Clin Neurophysiol.* 2010; 121:1680–1689. [PubMed: 20434396]
- Slifkin AB, Vaillancourt DE, Newell KM. Intermittency in the control of continuous force production. *J Neurophysiol.* 2000; 84:1708–1718. [PubMed: 11024063]
- Solnik S, Pazin N, Coelho C, Rosenbaum DA, Scholz JP, Zatsiorsky VM, Latash ML. End-state comfort and joint configuration variance during reaching. *Exp Brain Res.* 2013; 225:431–442. [PubMed: 23288326]
- Tatton WG, Bawa P, Bruce IC, Lee RG. Long loop reflexes in monkeys: an interpretive base for human reflexes. *Prog Clin Neurophysiol.* 1978; 4:229–245.
- Vaillancourt DE, Russell DM. Temporal capacity of short-term visuomotor memory in continuous force production. *Exp Brain Res.* 2002; 145:275–285. [PubMed: 12136377]
- Valero-Cuevas FJ, Smaby N, Venkadesan M, Peterson M, Wright T. The strength-dexterity test as a measure of dynamic pinch performance. *J Biomech.* 2003; 36:265–270. [PubMed: 12547365]
- Wilhelm L, Zatsiorsky VM, Latash ML. Equifinality and its violations in a redundant system: Multi-finger accurate force production. *J Neurophysiol.* 2013; 110:1965–1973. [PubMed: 23904497]
- Zhou T, Solnik S, Wu YH, Latash ML. Equifinality and its violations in a redundant system: Control with referent configurations in a multi-joint positional task. *Motor Control.* 2014; 18:405–424. [PubMed: 24717213]
- Zhou T, Solnik S, Wu YH, Latash ML. Unintentional movements produced by back-coupling between the actual and referent body configurations. *Exp Brain Res.* in press (in press); e-pub: PMID: 25150552.

Highlights

- Transient force perturbations can produce unintentional changes in the hand position
- Both intentional and unintentional movements show stability of salient variables
- Structure of joint angle variance shows stability of hand position and orientation
- The results fit a scheme of hierarchical control with referent body configurations

Figure 1.

An illustration of the initial posture. The subject sits in a chair, using the right arm to hold the handle in an initial position. The robot arm is aligned such that the subject's hand moves primarily in a parasagittal plane. The marker clusters and additional markers that are used to determine the joint locations and segment lengths are shown. $\{G\}$ designates the Global Coordinate System and $\{r\}$ the robot coordinate system. Joint angles are shown.

Figure 2.

A: A typical hand trajectory along X-axis in the global coordinate system with zero dwell time during the unintentional movement trials. The time before T_0 is *Preparation* (shown by the left arrow). The time between T_0 and the time when the force returns to its baseline value is *Perturbation* (shown by the double arrow). The two dashed lines show the start and the end of the perturbation force (F_{PERT}). The *Recovery* phase is shown with the right arrow to the right of the second dashed line. Three phases selected for analysis are shown. B: A typical hand trajectory along X-axis with dwell time of 5 s during the unintentional movement trials. C: A typical hand trajectory along X-axis for an intentional movement.

Figure 3.

The top left panel (A) shows R-ratio defined as the absolute ratio of D23 to D12; D23 is the difference between Phase-2 and Phase-3; D12 is the difference between Phase-1 and Phase-2. Y+, Y- and X+ indicate three different perturbation directions. Black bars show the data for $T_{DWELL} = 5$ s while white columns show the data for $T_{DWELL} = 0$ s. The panels (B) – (D) show the handle position variance along each of the axes (X, Y and Z) for unintentional (UNI) and intentional (INT) movements. Note that all variance indices for UNI are greater than for INT.

Figure 4.

A: Indices of joint configuration variance computed over the final steady state (Phase-3). Top panels: Variance within the UCM for position- and orientation-related analyses (V_{UCM-P} and V_{UCM-O}) and variance orthogonal to the UCM for position- and orientation-related analyses (V_{ORT-P} and V_{ORT-O}). Bottom panels: z-transformed synergy indices for position- and orientation-related analyses (ΔV_{Z-P} and ΔV_{Z-O}). Averages across subjects with standard error bars are presented. Note that $V_{UCM} > V_{ORT}$ ($\Delta V > 0$) across all conditions and variables.

Figure 5.

The time profiles of the z-transformed synergy index for the position-related (thin dashed lines, ΔV_{Z-P}) and orientation-related (thin solid lines, ΔV_{Z-O}) analyses for a representative subject for both unintentional (top panel) and intentional (bottom panel) movements. The corresponding average kinematic profiles are shown with thick lines with standard error shades. Note that the synergy index was consistently positive at all steady-state phases of the movements. Note the different time scales adjusted to the typical kinematic profiles of the two types of movement.

Figure 6.

A plot of the drift of the hand equilibrium position (EP) shown on a force-coordinate (F_X vs. X) plane. The initial EP of the hand is shown as point A (F_{BIAS} , X_{INIT}). A perturbation force F_{PERT} leads to the hand motion to a new coordinate, point B. After a dwell time, the robot force returns back to F_{BIAS} , and the hand moves to a new position, point C (F_{BIAS} , X_{FIN}).

Figure 7.

Within the suggested scheme, the task results in the creation of a referent configuration (RC_{TASK}) reflecting referent values for salient task-specific variables. The task-specific stability is ensured by the neural structures in the middle “box”. Similar structure of variance emerges in response to three inputs: an external force perturbation, an unintentional RC_{TASK} drift, and an intentional RC_{TASK} shift. The force field can be introduced to perturb elemental variables and task-specific performance variables (AC); the RC_{TASK} drifts towards AC unintentionally if AC is kept at a certain position where differs from RC. RC_{TASK} can also be changed intentionally and AC follows.