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RESEARCH ARTICLE

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Structure of joint variability in bimanual pointing tasks

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Abstract Changes in the structure of motor variability during practicing a bimanual pointing task were investigated using the framework of the uncontrolled manifold (UCM) hypothesis. The subjects performed fast and accurate planar movements with both arms, one moving the pointer and the other moving the target. The UCM hypothesis predicts that joint kinematic variability will be structured to selectively stabilize important task variables. This prediction was tested with respect to selective stabilization of the trajectory of the endpoint of each arm (unimanual control hypotheses) and with respect to selective stabilization of the timecourse of the vectorial distance between the target and the pointer tip (bimanual control hypothesis). Components of joint position variance not affecting and affecting a mean value of a selected variable were computed at each 10% of normalized movement time. The ratio of these two components (R_V) served as a quantitative index of selective stabilization. Both unimanual control hypotheses and the bimanual control hypothesis were supported both prior to and after practice. However, the R_V values for the bimanual control hypothesis were significantly higher than for either of the unimanual control hypothesis, suggesting that the bimanual synergy was not simply a simultaneous execution of two unimanual synergies. After practice, an improvement in both movement speed and accuracy was accompanied by counterintuitive changes in the structure of kinematic variability. Components of joint position variance affecting and not affecting a mean value of a selected variable decreased, but there was a significantly larger drop in the latter when applied on each of the three selected task variables corresponding to the three control hypotheses. We conclude that the UCM hypothesis allows quantitative assessment of the degree of stabilization of selected performance variables and provides information on changes in the structure of a multijoint synergy that may not be reflected in its overall performance.

Keywords Coordination · Variability · Voluntary movement · Bimanual · Human

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Introduction

Human voluntary movements are characterized by the production of functionally appropriate motor outputs by apparently redundant systems. There have been two major approaches to the problem of motor redundancy. The first approach originated from the original formulation by Bernstein that the main issue of motor control was the elimination of the redundant degrees of freedom (Bernstein 1967). A number of researchers have been trying to discover rules used by the central nervous system (CNS) when it generates a unique solution for an apparently ill-posed problem (for reviews, see Seif-Naraghi and Winters 1990; Latash 1996; Prilutsky 1999).

An alternative approach follows the traditions of Gelfand and Tsetlin (1962, 1966), who have gone beyond the original Bernstein's formulation and suggest that all elements within a redundant motor system are always involved in solving all motor tasks so that no degrees of freedom are eliminated (later reformulated as the principle of abundance; Gelfand and Latash 1998). The concept of motor equivalence (Hughes and Abbs 1976; Cole and Abbs 1986) suggests a low variability in task variable while variability of individual elements (such as joint angles) remain high. A recent development of this line of thinking has led to the formulation of an uncontrolled manifold hypothesis (UCM hypothesis; Schoner 1995; Scholz and Schoner 1999; Scholz et al. 2000). This hypothesis suggests that the CNS generates families of solutions such that functionally important, task-related variables are selectively stabilized. According to the UCM hypothesis, each motor task is associated with stabilizing a time series of a particular variable(s). For each moment of time, the CNS selects, within the state space of elements participating in the task, a manifold (uncontrolled manifold, UCM) corresponding to a fixed instantaneous value of the selected variable. Links are established among individual elements such that they can show relatively large variability within the UCM as compared to variability outside the UCM.

Earlier studies of the sit-to-stand action (Scholz and Schoner 1999), quick-draw shooting (Scholz et al. 2000), and multifinger force production (Latash et al. 2000) have tested the UCM hypothesis by performing kinematic analyses of individual joint rotations and individual finger forces. Further, the structure of motor variability was tested by quantifying components of joint variance (or finger force variance) within and orthogonal to particular UCMs. The data provided support for the UCM hypothesis and also allowed to compare different "control hypotheses", i.e., hypotheses related to different performance variables that the CNS may be stabilizing selectively in such tasks. The latter possibility allows testing of some of the earlier formulated hypotheses related to the coordination of multielement motor systems.

Until now, all studies of motor coordination within the UCM hypothesis framework have been performed using, as objects, tasks that were well practiced by the subjects. Within this study, we decided to look at changes in the structure of motor variability within a redundant multijoint system in the process of practicing a motor task.

We selected, as an object of study, a pointing task performed "as fast and accurately as possible," when one hand moved the target and the other hand moved the pointer (cf. Mottet et al., in press). Such a task may be considered as requiring coordination at two levels. First, joints within each arm need to be coordinated to produce a certain trajectory of the endpoint (the target or the pointer tip). Second, the trajectories of the endpoints need to be coordinated to result in a fast and accurate pointing movement. We hypothesize that the UCM analysis will show higher stability of the time series of the vectorial difference between the pointer tip and the target as compared to the trajectories of the pointer tip and of the target analyzed separately. This hypothesis is in line with a number of recent publications (Turvey 1990; Scholz and Latash 1998; Mottet et al., in press).

The UCM hypothesis makes predictions with respect to relative magnitudes-of-variance components computed within a UCM and orthogonal to it. We are going to address these two components as compensated variance (V_{COMP}) and uncompensated variance (V_{UN}), respectively. These terms reflect the fact that, by definition, errors in the outputs of individual elements that lie within a UCM do not affect a selected variable, with respect to which the UCM was computed, i.e., they compensate for each other. The other component of variance contains combinations of errors of elements that affect the selected variable, i.e., their effects are uncompensated. We used the ratio of these two variance components ($R_V=V_{COMP}/V_{UN}$) as an index of selective stabilization of a variable.

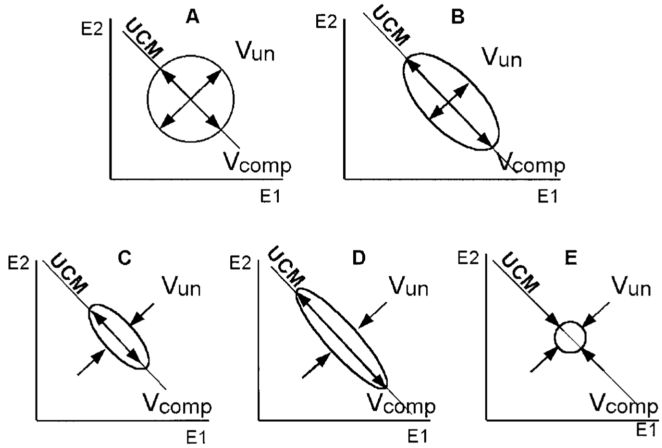

Fig. 1A–E Possible changes in the components of variance (V_{COMP} and V_{UN}) between the pre-test (**A, B**) and post-test (**C–E**). Notice that V_{COMP} is oriented along the line E1+E2=constant that reflects the motor task. The pre-test panels demonstrate equal sums of V_{COMP} and V_{UN}, while all the post-test panels depict the same value of V_{UN}. (*UCM* Uncontrolled manifold)

Let us explain the main predictions of the study with an illustration of a very simple task when two elements, E1 and E2, are acting together to produce a required output equal to the sum of their individual outputs (Fig. 1; for example, when a person pushes with two hands to produce a constant total force). Let us also imagine that a subject performed this task many times and the values of the outputs of the two elements measured in individual trials were plotted as clouds of data points on a two-dimensional state space. For simplicity, we are going to illustrate these hypothetical data point distributions with ellipses whose axes correspond to components of variance. If both elements are controlled independently with a certain variability, one may expect a circular cloud of data points, since errors in the output of one element are not expected to correlate with possible errors in the output of the other element (Fig. 1A). However, the UCM hypothesis predicts the cloud of points to be ellipsoidal, elongated along the UCM line, providing that $R_V=V_{COMP}/V_{UN}$ is significantly more than unity (Fig. 1B). Note that, from this prospective, R_V depicted in Fig. 1A is expected to be unity. Therefore, although the total variance ($V_{COMP}+V_{UN}$) is the same in Fig. 1A and B, the V_{UN} component of the total variance is less in Fig. 1B, corresponding to a lower variance in the production of the task variable. The "concealed" variance component V_{COMP} is significantly higher in Fig. 1B, but it does not affect the task variable.

Let us consider possible scenarios of changes in components of variance with practice, naturally assuming that the variability in the production of the task variable (E1+E2) will drop. A drop in the overall variability may be associated with different changes in the structure of variance in the element state space. The original ellipse illustrated in Fig. 1B may simply scale down without a change in its shape, i.e., preserving the ratio R_V (Fig. 1C). Alternatively, only one component of variance may scale down, namely V_{UN}, since V_{COMP} is irrelevant to task success (Fig. 1D), leading to an increase in R_V. It is also possible that the "irrelevant" V_{COMP} will decrease more than V_{UN}, leading to a more circular distribution of data points (Fig. 1E), corresponding to a drop in R_V. Figure 1C–E shows that accuracy of performance of a task variable and R_V may be independent of each other. Accuracy of performance depends on only one component used in calculating R_V, namely V_{UN}. Changes in V_{COMP} do not affect the variability of reproducing the task variable but are reflected in R_V.

We expect that the ratio R_V, computed prior to practice for variables related to success at the practiced task (such as endpoint trajectories or changes in the distance between the pointer tip and the target), will be significantly more than unity, supporting the UCM-type of control.

We expect the performance of the pointing task to improve with practice (Jaric and Latash 1998, 1999).We also expect that the CNS will improve the overall degree of error compensation among individual joint rotations such that the V_{UN} component of variance will drop more than the V_{COMP} component for hypotheses related to selective stabilization of endpoint trajectories and of the distance between the endpoints. This is expected to lead to an increase in the R_V ratios as illustrated in Fig. 1D.

Methods

Subjects

Subjects were nine neurologically healthy, right-handed men, aged between 26 and 43 years (mean 32 years), recruited among the personnel of the Centre for Musculo-Skeletal Research. Their height and body mass were 181±5 cm (mean ± SD) and 74±13 kg, respectively. All subjects signed the informed consent form in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki approved by the Ethical Committee of the Umea University.

Apparatus and task

The subject was seated in a rigid chair with the shoulders tightly strapped to the chair back with wide belts. A horizontal table was positioned in front of the subject's chest about 15 cm below the shoulders level. The subject grasped a pointer with the right hand. The pointer was a light-weight (mass 0.1 kg) plastic, "gun-like" object 23 cm long from the center of the handle to the pointer tip (see Fig. 2A). The subject's right index finger was tightly strapped to the pointer, preventing sliding of the pointer's handle within the hand grasp. The subject also grasped a semicircular target (diameter 11 cm, mass 0.04 kg) with the left hand, having his thumb and index finger extended along the semicircle and strapped to it. In order to stress the difference between the mechanical object and its center, in further text we will refer either to the "target-object" (i.e., the mechanical object held in the left hand) or to the "target" (the center of the semicircular part of the object).

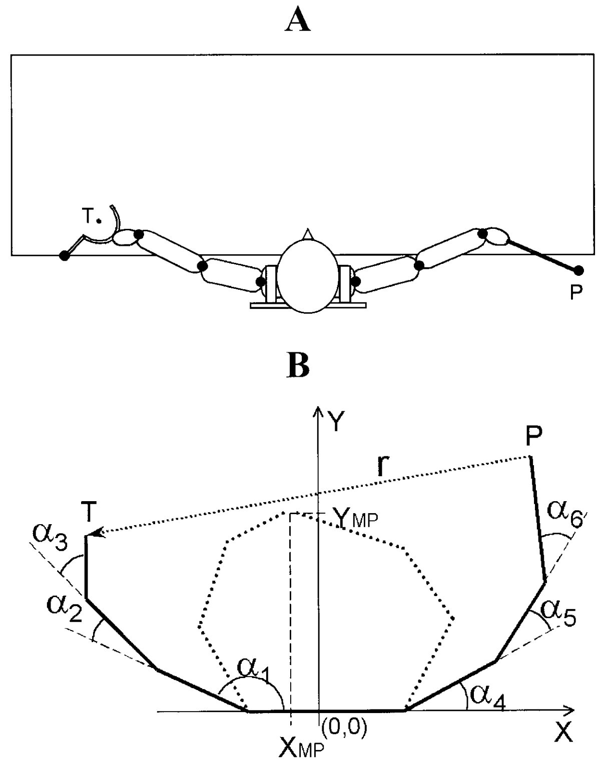

Fig. 2A, B Experimental conditions and measured kinematic variables. **A** Starting position depicted in the horizontal plane. *Filled circles* illustrate positions of the reflexive markers. **B** An intermediate position of body segments (*thick full line*) during the movement represents the recorded joint angles (from α_1 to α_6), while *r* represents the vectorial distance from the pointer tip (*P*) to the target (*T*). The final position of body segments (*dotted line*) depicts the meeting point position (coordinates x_{MP} and y_{MP}) of the pointer tip and target with respect to the coordinate system of the movement plane anchored between the shoulders

The subjects were instructed to keep the centers of their wrists at proper initial positions that required full arm extension, and to keep the wrists fully extended. Thereafter, on a verbal command, the subjects performed a fast and accurate movement with both arms in order to accurately place the pointer tip into the center of the target object. The subjects were instructed to execute the movement just above the table surface without touching it. Hence, the orientation of all the upper limb segments as well as of the pointer and the target object remained approximately horizontal during the movement execution. The subjects were also instructed not to correct the final position. There were no instructions regarding the point in space where the pointer tip and the target should meet.

Experimental design

The subjects practiced the pointing task over four sessions, performed within a week. The first three sessions consisted of 100 trials each, while only the first 15 movements of the first session were recorded (i.e., movements 1–15; the pre-test). The fourth session consisted of one recorded movement block of 15 trials (i.e., movements 301–315; the post-test). No additional practice trials were allowed prior to the pre- and post-test.

Data collection

Passive spherical markers of an optoelectronic system, APAS (Ariel Performance Analysis System; Ariel Dynamics), were applied to the standard surface bony landmarks that corresponded to the vertical projections of the shoulders, elbows, and wrists. In particular, those were acromion processes, the lateral epicondyle of elbows, and wrist folds on the lateral surface of hands (Zhang and Chaffin 2000). Additional markers were placed on the pointer tip, as well as on the lateral tip of the target object (see Fig. 2A). The latter marker position was chosen in order to avoid the interference with the pointer tip marker at the end of the movement.

Calibration of the two-camera system and calculation of the coordinates was performed in such a way that the origin of the coordinate system was positioned between the subject's shoulders. *x*- and *y*-axes were oriented horizontally along the subject's frontal and sagittal plane, respectively, while the *z*-axis was oriented vertically (see Fig. 2B). Since the tested movement was predominantly performed within the *x*-*y* plane, in the further text we refer to the horizontal plane at the level of shoulders as "movement plane."

The data were recorded at the rate of 60 frames/s. The standard APAS software was used to calculate the positions and velocities of the markers, as well as the intersegmental joint angles in the movement plane (see Fig. 2B).

Kinematic variables

Movement planarity was tested by comparing motion intervals of the markers in the orthogonal direction as a percentage of their motion intervals in the movement plane. Movement initiation and movement termination were assessed for each arm separately from the velocity profiles of the markers placed on the tip of the pointer and on the target object (for right and left arm, respectively). This initiation and termination corresponded to the instant of time when the velocity of the respecive marker exceeded 10% of its maximal value and the instant when the velocity of the marker dropped below the same value, respectively. Since the differences in either the initiation or termination time between two arms proved to be insignificant (see Results), movement time of each particular trial was calculated from the earlier initiation time to the later termination time.

A pilot analysis of the obtained data revealed that the first zero of both the target and the pointer tip velocity in either *x*- or *y*-axis direction appeared approximately 100 ms after the end of movement time (averaged across the subjects and trials). Hence, it was assumed that the final movement position was attained at that instant of time in all trials. Constant and variable errors were calculated from the relative positions of the pointer tip and target in the final movement position in the movement plane. Constant errors were separately measured along the *x*- and *y*-axis directions as mean distances between the target and the pointer tip in the final position. Variable error was calculated as the standard deviation of the distance between the final positions in individual trials and mean position of the pointer tip.

The position where the pointer tip and target met in the final movement position (i.e., the meeting point position) was measured within the movement plane. Thereafter, the variability of the meeting point position was calculated in the movement plane as standard deviation of the planar distance of the individual meeting point position from the averaged one (see Fig. 2B for illustration of a meeting point position).

The length of the trajectories of the shoulder markers was on average about 1 cm. This finding suggests that strapping the shoulders to the back of the chair successfully reduced possible contributions of the trunk and sternoclavicular joint motion to pointer tip and target displacements. Therefore, only the three major joints of each arm were considered involved in the movements. Their angles were calculated using approximations of segment longitudinal axes as straight lines connecting pairs of markers (see Fig. 2B):

1. α_1: Horizontal abduction-adduction in the left shoulder (the angle between the left upper arm longitudinal axis and the right-directed line connecting the two shoulder markers)
2. α_2: Flexion-extension in the left elbow (the angle between the left lower arm and the upper arm longitudinal axes)
3. α_3: Flexion-extension in the left wrist (the angle between the line connecting the marker placed on the left wrist with the target and the left lower arm longitudinal axis)
4. α_4: Horizontal abduction-adduction in the right shoulder (the angle between the right upper arm longitudinal axis and the line connecting the two shoulder markers)
5. α_5: Flexion-extension in the right elbow (the angle between the right lower arm and the upper arm longitudinal axes)
6. α_6: Flexion-extension in the right wrist (the angle between the line connecting the marker placed on the right wrist with the pointer tip and the right lower arm longitudinal axis)

The contribution of these joints to the movements was assessed using their ranges of motion (i.e., the difference between the maximal and the minimal joint angle during the movement time).

Calculation of total joint variance of joint configuration

Variance was calculated from blocks of 15 consecutive trials. Angular trajectories were time-normalized to allow trial alignment within a block. A cubic spline interpolation was applied while normalizing angular trajectories in order to allow trial alignment within a block. Movement time (MT) was divided into ten evenly spread time bins. The mean joint configuration across trials [$M(t)$] was computed for each of the studied 10% bins of MT. Thereafter, the joint configuration in each particular trial [$\mathbf{A}_k(t)$] was compared with $\mathbf{M}(t)$ for each time bin:

$$\Delta\mathbf{k}(t) = \mathbf{M}(t) - \mathbf{A}_k(t) \tag{1}$$

where $\Delta\mathbf{k}$ represents the deviation of the joint configuration of the *k*th trial from the mean joint configuration at the end of a time bin (t).

Total variance of joint configuration per degree of freedom [$V_{TOT}(t)$] of the joint configuration vectors for a particular time bin was calculated using the following equation:

$$V_{TOT}(t) = \sum_{k=1}^{N} |\Delta\mathbf{k}(t)|^2 / (N * DF) \tag{2}$$

where *N* is the number of trials, while DF is the number of degrees of freedom (i.e., the number of available joint rotations), being 6 for both arms analyzed together, and 3 for the analysis of each arm separately.

Control hypotheses and task variables

The goal of our variance analysis was to partition the total joint variance observed across the blocks of movements into components that affect and do not affect a value of a task variable. Hence, the first step was formulating a control hypothesis, i.e., selecting a task variable, that was assumed to be selectively stabilized. Three control hypotheses were compared: H1, the vectorial distance between the target and the pointer tip is selectively stabilized by joint interaction of both arms; H2, the trajectory of the target is selectively stabilized by joint interaction within the left arm; and H3, the trajectory of the tip of the pointer is selectively stabilized by joint interaction within the right arm. We will refer to H1 as "bimanual control hypothesis", and to H2 and H3 as "unimanual control hypotheses."

Partitioning of joint variance

The next step of the analysis was partitioning the total joint variance of joint configuration per degree of freedom (V_{TOT}) into two components that do and do not affect a hypothesized task variable. The first component is compensated variance (V_{COMP}) and it corresponds to the variance observed within the UCM subspace. The second one is uncompensated variance (V_{UN}) and it corresponds to the variance observed within a subspace orthogonal to the UCM. This decomposition was linearly approximated for each bin of MT and for each control hypothesis separately. Then, the ratio of the two components of variance was computed: $R_V=V_{COMP}/V_{UN}$. The computational methods are described in detail in the Appendix.

Statistics

In addition to descriptive statistics, we used two-way ANOVAs. In particular, we tested the range of motion of each joint separately (“test” and “side” being the main factors), as well as movement planarity (“test” and “marker position”), V_{TOT} (“test” and “side”), and R_V (“test” and “control hypothesis”). Paired *t*-tests were applied in order to examine differences in constant errors, variable errors, variability of the meeting point position and movement time between the pre- and post-test. One group *t*-test was applied in order to reveal differences in movement initiation and termination time between two arms.

Results

Movement kinematics

The limb movements proved to be predominantly planar, since the deviations of the markers (averaged across the markers, subjects, and trials) from the movement plane were about an order of magnitude smaller that the displacements of the same markers within the movement plane. There were no significant differences in these deviations among markers positioned on the elbows, wrists, and the pointer tip and target. When averaged across the trials and markers, the post-test (8.5±3.1% SD) demonstrated smaller deviations than the pre-test (11.1±2.1% SD; $F_{1, 134}=12.0$; $P<0.01$).

Time series of joint angles obtained within the pre- and post-test suggest a decrease in variability in all six

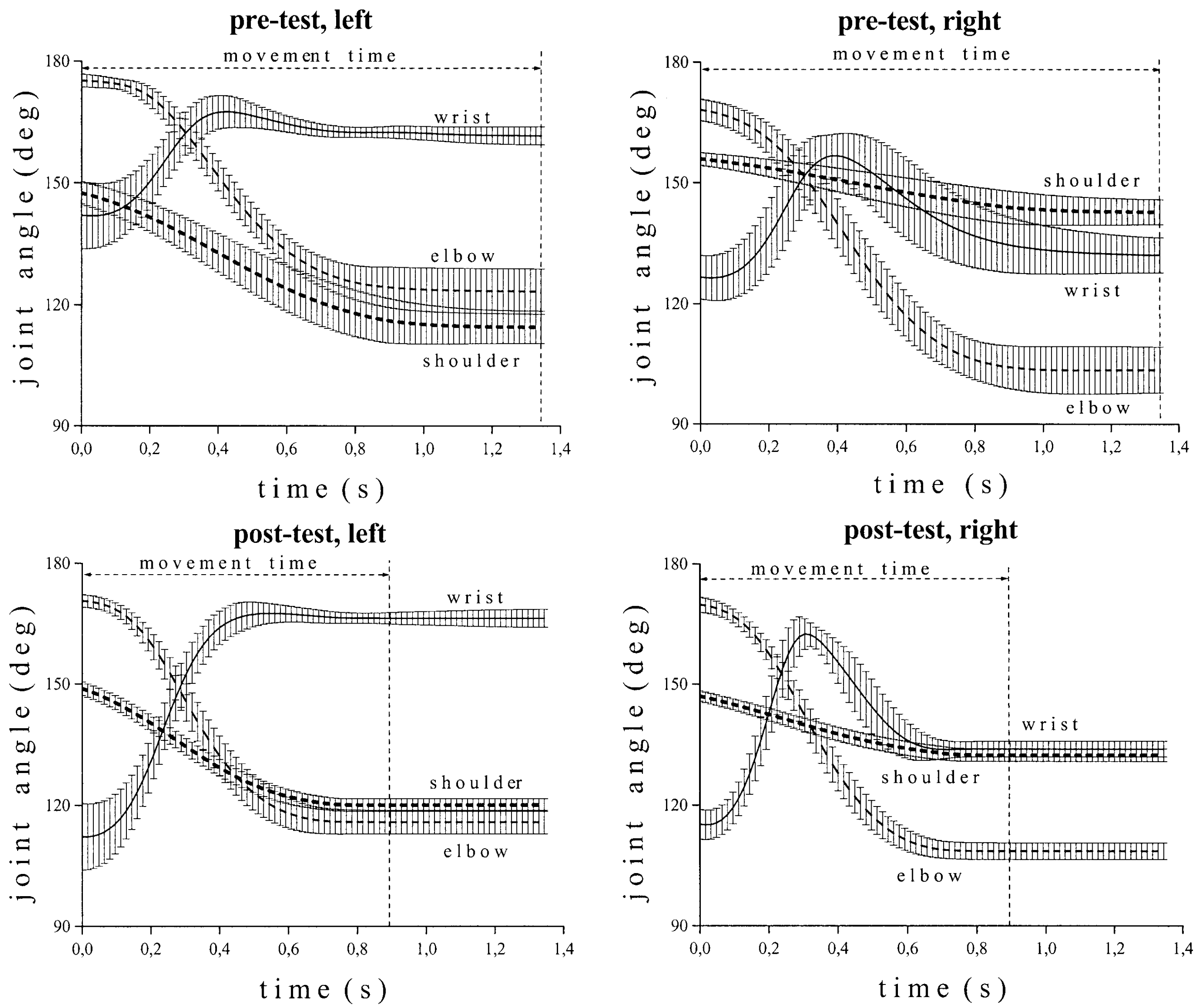

Fig. 3 Joint angles of the left (*left*) and right arm (*right*) obtained within the pre-test (*upper graphs*) and post-test (*lower graphs*) movement block in a representative subject. The *vertical bars* represent standard deviations

Table 1 The range of motion for each joint (degrees), averaged across the subjects

Joint	Shoulder		Elbow		Wrist	
Side	Left	Right	Left	Right	Left	Right
Pre-test						
Mean	37	18	39	52	48	44
SD	±14	±9	±20	±20	±14	±10
Post-test						
Mean	31	11	51	65	50	41
SD	±9	±4	±16	±13	±11	±12

Table 2 Main effects of two-way ANOVA ("test" and "side" being main factors) applied to each right-left pair of joints separately. No interaction effects were observed

	Shoulder	Elbow	Wrist
Pre- vs post-test	$F_{1,8}$=4.0 P=0.054	$F_{1,8}$=4.5 P<0.05	$F_{1,8}$=0.5 P>0.05
Left vs right arm	$F_{1,8}$=36 P<0.0001	$F_{1,8}$=5.4 P<0.05	$F_{1,8}$=5.6 P<0.05

involved joints over most of the movement time (Fig. 3). The figure also indicates a prominent decrease in movement time. Finally, one can notice considerable differences in joint angle patterns between the left and right arms, suggesting an asymmetric bimanual movement.

Constant errors of the final pointer tip position with respect to the target averaged across the subjects were approximately 1 cm and scattered randomly in the vicinity of the target along both axes of the movement plane. No effects of test were found. Variable errors averaged across the subjects were 1.79±0.72 cm SD and 1.24±0.39 cm SD in the pre-test and post-test, respectively. This difference was slightly below the level of significance (P=0.077; paired t-test). The pre-test and post-test variability of the meeting point position calculated in the movement plane and averaged across the subjects was 3.1±0.7 cm SD and 2.3±0.5 cm SD, respectively. These results suggested a decrease in the variability of the meeting point position between two tests (P<0.01; paired t-test).

Although left arm movements were initiated and terminated 18 ms and 2 ms prior to the right arm movements, respectively (averaged across the subjects and tests), these differences were insignificant. Averaged across the subjects movement time decreased between the pre-test and post-test from 1.37±0.31 s SD to 1.04±0.46 s SD, respectively (P<0.05; paired t-test).

Tables 1 and 2 depict the ranges of motion for the three arm joints obtained within the pre-test and post-test. Only the elbow joints demonstrated a main effect of "test," suggesting a higher involvement of the elbows in the post-test than in the pre-test movements. However, all three joints demonstrated main effects of side, suggesting asymmetrical movements of the two arms while

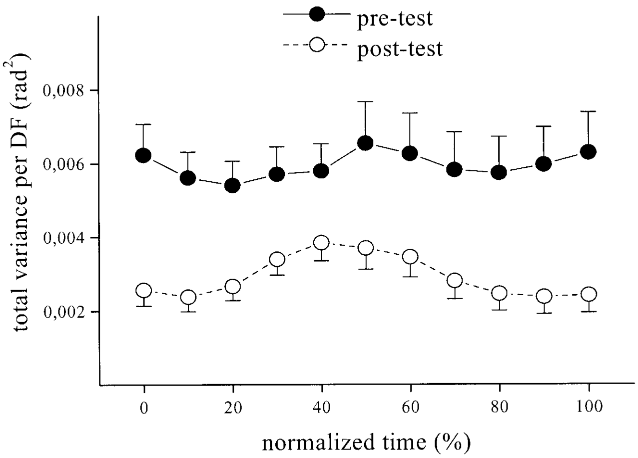

Fig. 4 Mean ± SE (averaged across the subjects) of total variance per degree of freedom (V_{TOT}) obtained in the pre-test (*filled circles*) and post-test (*open circles*) and represented for each of the 10% bins of the normalized movement time

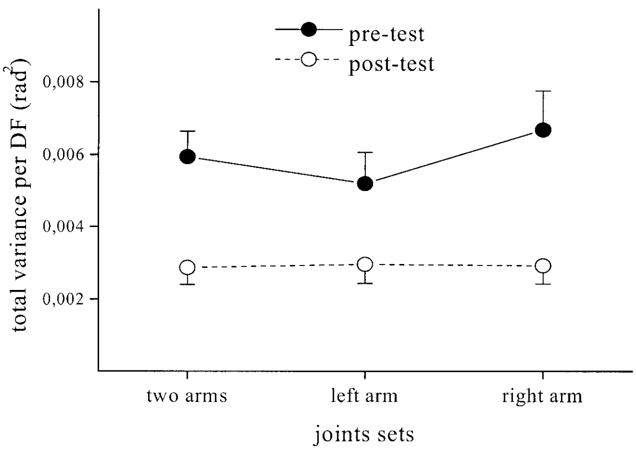

Fig. 5 Mean ± SE of variance per degree of freedom (V_{TOT}) averaged across the subjects and time bins and presented for two arms together (data from Fig. 4), and for left and right arm separately. *Filled circles* and *open circles* represent the pre- and post-test results, respectively

performing the task. Generally, the right shoulder and the right wrist moved less than the left joints, while the opposite was true for the elbows.

Structure of variance

Figure 4 shows a prominent decrease in total joint variance of joint configuration per degree of freedom (V_{TOT}) observed between the pre- and post-test over the entire movement time. The total variance calculated for each arm separately is depicted in Fig. 5 as V_{TOT} averaged across the subjects and time bins. Due to the method of calculation, V_{TOT} for the six joints of the two arms inevitably adds up to the mean of V_{TOT} obtained for the sets of three joints within each arm separately. Therefore, we

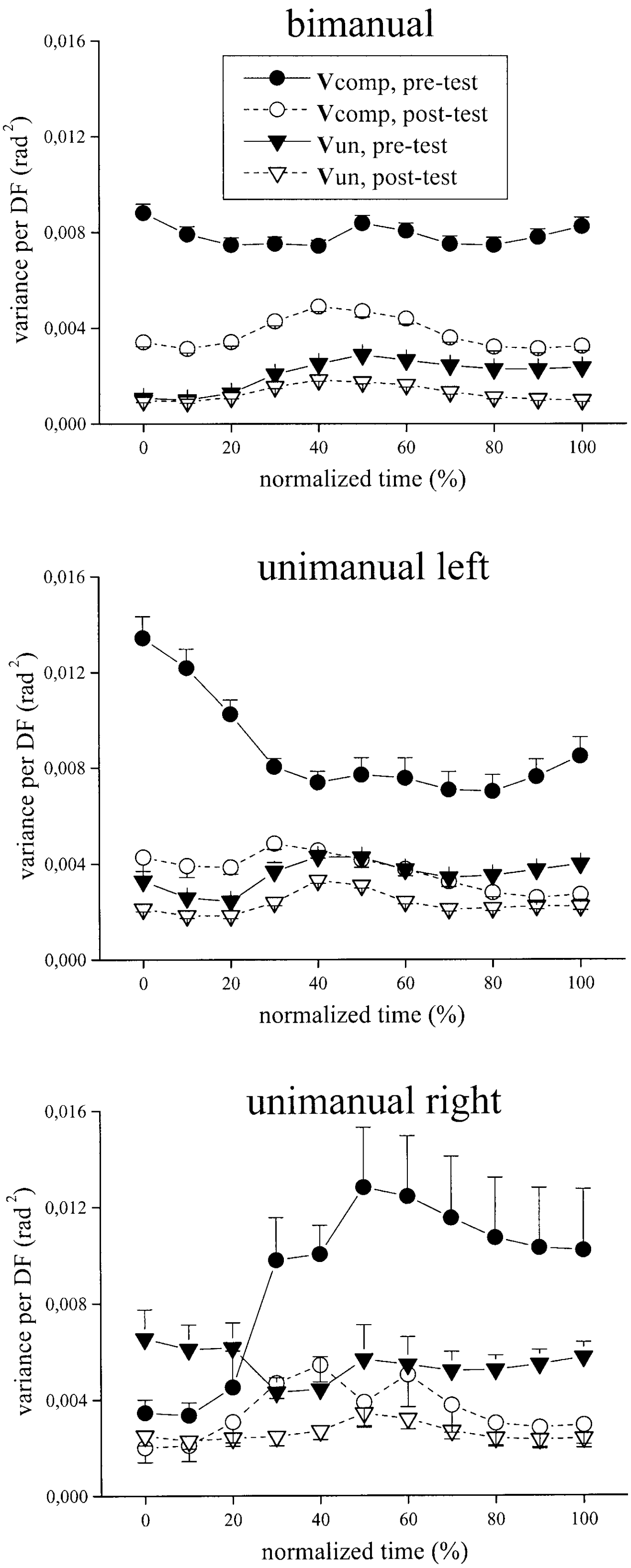

Fig. 6 Mean ± SE (averaged across the subjects) of V_{TOT} partitioned into the compensated (V_{COMP}) and uncompensated (V_{UN}) variance for three control hypotheses related to selective stabilization of the distance between the pointer tip and the target (bimanual hypothesis, *upper graph*), to the target separately (unimanual-left, *middle graph*), and pointer tip separately (unimanual right, *bottom graph*). *Circles* and *triangles* represent V_{COMP} and V_{UN}, while *filled symbols* and *open symbols* represent pre- and post-test results, respectively

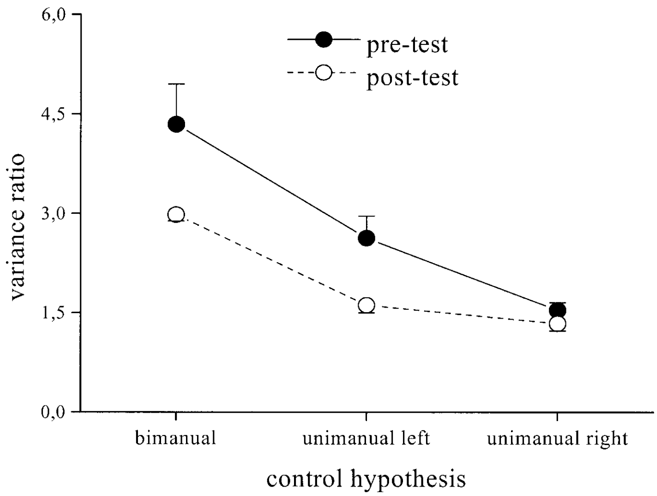

Fig. 7 Mean ± SE (averaged across the subjects and time bins) of the variance ratio (R_V=V_{COMP}/V_{UN}) obtained within the pre- (*filled circles*) and post-test (*open circles*) for the bimanual control hypothesis, and for the unimanual control hypotheses applied on the left and right arm separately. Depicted results are calculated from the data presented in Fig. 6 averaged across the time bins

performed a 2-way ANOVA ("test" vs "side") on V_{TOT} obtained only on each arm separately. The results demonstrated a significant decrease in V_{TOT} averaged across the subjects and time bins between the pre- and post-test ($F_{1, 134}$=182, P<0.01), while the right arm demonstrated higher V_{TOT} than the left arm ($F_{1, 134}$=10.7, P<0.01). The test × side interaction was also significant ($F_{1, 134}$=11.8, P<0.01), showing that the difference between two arms observed within the pre-test did not appear within the post-test.

Figure 6 shows V_{TOT} partitioned into compensated (V_{COMP}) and uncompensated variance components (V_{UN}) with respect to the linearized UCM and the subspace orthogonal to it, respectively. This partitioning was performed using task variables that correspond to the bimanual control hypothesis (i.e., the vectorial distance between the target and the pointer tip), as well as for the two unimanual control hypotheses (trajectories of the target and of the pointer tip). All three hypotheses lead to higher V_{COMP} than V_{UN}, while the post-test results demonstrate lower indices of both variance components than the pre-test results. The only apparent inconsistency was related to the trend of the pre-test V_{COMP} obtained on the left and right arm over the first couple of time bins.

After averaging across the time bins (the data in Fig. 6), the ratio R_V=V_{COMP}/V_{UN} proved to be more than unity for all three control hypotheses and both tests (Fig. 7). Two-way ANOVA has revealed that the 27% decrease in R_V obtained between the pre-test and post-test was significant ($F_{1, 134}$=14.7, P<0.01; see Fig. 7). The differences among the control hypotheses were also significant ($F_{2, 134}$=67, P<0.01). Tukey HSD post hoc tests confirmed higher R_V values for the bimanual control hypothesis than for either of the two unimanual hypotheses (P<0.01). Also, R_V for the unimanual control hypothesis applied to the right arm data was lower than for the unimanual control hypothesis applied to the left arm ($P<0.05$).

Discussion

The task used in the present study belongs to the group of motor tasks that emphasize both speed and accuracy and are commonly referred to as “Fitts’s type” tasks (Fitts 1954; Fitts and Peterson 1964). Such tasks are characterized by a well-known relation between movement time and the ratio of movement distance to target size, the speed-accuracy tradeoff (for reviews, see Keele 1986; Kim and Turvey 1996). Both unimanual and bimanual tasks have been used in studies of the speed-accuracy tradeoff. In particular, tasks when one arm was used to move a target while the other arm was moving a pointer presented on a computer screen were studied (Mottet et al., in press). All these studies have provided support for the robustness of the speed-accuracy tradeoff relation. The present study demonstrated the practice-associated changes that involved an improvement in indices of both movement speed and accuracy of landing the tip of the pointer inside the target. These findings by themselves contain relatively little novelty and mostly corroborate results of earlier studies of the effects of practice on the performance of Fitts’s-type tasks (Darling and Cooke 1987; Darling et al. 1988).

Due to the lack of an externally specified target, subjects could choose to perform the task by making symmetrical movements of the two arms. Specifically, such a movement would lead to a meeting point position shifted to the left approximately 8 cm from the center of the trunk, as well as the pointer oriented approximately along the *x*-axis. However, although two arms were synchronized in terms of movement initiation and termination, the patterns of joint involvement suggest that the subjects selected asymmetric movement patterns of the two arms both before and after practice (cf. Kelso et al. 1979).

The main purpose of the study was to analyze the structure of joint variability and its changes in the course of practice. The predictions (see Introduction) have been based on an assumption that the CNS organizes individual joint rotations within a redundant kinematic task such that particular important task variables are selectively stabilized (Scholz and Schoner 1999; Scholz et al. 2000). In other words, no kinematic degrees of freedom are “frozen” or “eliminated” (cf. Jaric and Latash 1999; Latash 2000), but they are all used to provide stable performance of a task despite the inherent variability in the patterns of rotation of each individual joint. Some of the formulated predictions have been supported by the findings, while others have been not.

Support for the UCM hypothesis

Many earlier studies have considered issues of coordinating two effectors as reflected in the relative timing of their performance. Such analyses were done based on different theoretical perspectives and computational methods (Kay et al. 1987; Heuer et al. 1995; Grossberg et al. 1997; Cattaert et al. 1999). The UCM approach rather addresses mutual coupling of effectors that affects their cooperative spatial or force performance by analyzing postures, without an explicit analysis of time series. The UCM hypothesis may be tested, in particular, by analyzing components of joint variance that do and do not affect a value of a selected task variable (Scholz et al. 2000). Within the present study, we performed analyses of joint configurations at particular percentages of the movement time across a series of trials. As such, this analysis may be viewed as “postural,” since time-dependent error compensation among individual joint rotations has not been explicitly addressed. Presently, this constitutes a major limitation of the method, which, however, has a potential to be resolved.

If individual joint rotations are indeed structured with respect to a UCM, the ratio $R_V=V_{COMP}/V_{UN}$ is expected to be more than unity. We tested three control hypotheses, i.e., hypotheses assuming that a particular task variable is selectively stabilized: the first hypothesis assumed that the vectorial distance between the target and pointer tip was selectively stabilized, while the additional two hypotheses corresponded to stabilization of the trajectories of the target and of the tip of the pointer separately. These hypotheses were tested using data sets obtained prior to and after the practice. In both pre- and post-practice tests and with respect to all three hypotheses, the ratio R_V was more than unity, suggesting that individual joint rotations were indeed coordinated to stabilize all three hypothesized variables at both tests. These findings are similar to those reported by Scholz and his colleagues (Scholz and Schoner 1999; Scholz et al. 2000) in their studies of sit-to-stand and quick-draw shooting. Taken together, these results provide support for the UCM hypothesis with respect to various motor tasks, involving a single multijoint extremity, two extremities, and a whole-body coordination.

There are two factors that make these findings nontrivial. First, the CNS could adopt a completely different strategy and stabilize the outputs of all the involved elements (joint rotations) to the same degree such that no particular direction or manifold in the joint state space is stabilized selectively. Second, success at some of these tasks depended crucially on the state of the system at a particular time. For example, during quick-draw shooting, success depended on the orientation of the pistol at the moment of pulling the trigger. In the present study, success was defined by the relative location of the pointer tip with respect to the target at movement termination. In both studies, stabilization of a particular trajectory by which the pistol achieves a required orientation or the pointer tip gets into the target were neither explicit nor implicit task components. Nevertheless, the angle between the pistol barrel and the direction from the pistol to the target in the shooting study, and the vectorial distance between the pointer tip and the target in the present study were stabilized throughout the whole movement time. Thus, the applied method of analysis of motor variability not only confirms the main assumption underlying the UCM hypothesis but also allows discerning particular strategies by which the CNS achieves stable, successful performance.

Differential stabilization of task variables

This study is the first to apply the UCM method to an analysis of joint coordination during a bimanual pointing task. The explicit involvement of two kinematically independent effectors allowed us to perform such analyses with respect to three control hypotheses. Although all three of them were confirmed by the data (R_V>1), there were significant differences among the R_V values computed for the three control hypotheses. These differences illustrate one more potential strength of the UCM approach.

Within the UCM hypothesis, control of a particular task variable is equated to its selective stabilization. The ratio R_V may be viewed as a reflection of the degree of selectivity: Higher values of R_V computed for a UCM corresponding to a particular task variable mean that the controller structures individual joint variability such that most of the variance is confined to the UCM. Lower R_V values for another variable (but still more than unity!) may be interpreted as a reflection of the controller stabilizing a value of this variable but not as strictly as in the case of the former variable.

Based on these considerations, one may conclude that, over the duration of the movement, the CNS stabilized instantaneous values of the vectorial distance between the pointer tip and the target to a larger degree than instantaneous positions of the pointer tip or of the target in the external space. Hence, within the traditions of Gelfand and Tsetlin (1966), the two effectors were indeed united into a synergy, which could not be reduced simply to two single-arm synergies underlying the trajectories of the target and of the pointer separately. Note that the hypothesized single synergy of the bimanual task was acquired despite both the asymmetric kinematic pattern and different variance scores obtained on two arms.

Although mutual coupling between movements of two extremities has been described in many studies (for reviews, see Turvey et al. 1988; Kelso 1998), these effects have mostly been limited to regularities in the phase relations between the two movements. In our experiments, mutual relations between the two arm trajectories were seen at a different level, at a level of uniting all six joints of the two effectors into a single synergy. This synergy reflected in the high degree of selective stabilization of a variable that depended on an interplay of individual joint rotations in both arms.

There were also modest but significant differences between the R_V values averaged over the movement time for the pointer tip trajectory (right arm) and the target trajectory (left arm). The ratio R_V for the target trajectory was higher, implying its better stabilization. This result looks counterintuitive, since the target was moved by the left arm of the right-handed subjects, i.e., by an arm which is not expected to demonstrate higher dexterity. This finding may reflect the fact that hand preference in fine motor behaviors can be independent of strength-related hand preference (Kimura and Vanderwolf 1970; Healey et al. 1986). On the other hand, the finding may represent a reflection of a genuine central strategy: During most pointing tasks, humans point at an external fixed target. Therefore, a strategy preferred by the CNS might have consisted of stabilizing the target position to a larger degree, thus making the rather unusual task more similar to common everyday tasks. For example, during putting a thread into the needle eye, humans commonly prefer to hold the needle steady in the nondominant hand and move the thread with the dominant hand. Since in the present study we did not ask subjects to move the target using the dominant hand, we cannot distinguish between these two possibilities.

Practice-related changes in the structure of joint variability

In the Introduction, we have suggested that one way to achieve a practice-associated improvement in both speed and accuracy would be to increase the degree of error compensation among the joints. This was expected to lead to an increase in the R_V ratio as shown in Fig. 1D. The results, however, demonstrated a modest, statistically significant drop in R_V with practice, more in line with Fig. 1E. This was true for R_V ratios calculated with respect to all three control hypotheses. Thus, changes in the structure of joint variability with practice defied our expectations. Namely, the improvement in traditional indices of performance such as movement time and accuracy obtained in the final position was not associated with an increase in the degree of stabilization (i.e., an increase in R_V) of either the distance between the endpoints or the trajectories of the endpoints in the external space calculated over the movement time.

One interpretation of this result is that the original task was not sufficiently novel, despite its asymmetrical nature, so that the subjects quickly adopted an optimal bimanual coordination strategy. Note that bimanual coupling/cooperation has been demonstrated in a number of studies involving asymmetrical actions by the two arms (Kelso et al. 1979; Mottet et al., in press). Hence, it is possible that practice could lead in our experiments only to a scaling of an existing two-hand multijoint synergy rather than to a creation of a new, more efficient synergy that was expected to lead to a larger R_V ratio. Prior to practice, R_V values were already more than unity, meaning that the components of joint angle variance within the corresponding UCMs (V_{COMP}) were larger than those orthogonal to the UCMs (i.e., V_{UN}) and hence had more room for improvement. We would like to emphasize that this finding could only be detected using the UCM method, since the component of variance within a UCM by definition is not reflected in the overall variance of the task variable. We do not know why the controller might choose to decrease a component of variance that is not affecting important task variables. Such a strategy may be related to features of the task that were not explicitly analyzed in our essentially kinematic study such as the dynamic stability of the trajectory or other optimization criteria. We also do not know whether the role of visual and proprioceptive feedback modifies over the learning course, consequently causing a change in control of the practiced task (Sergio and Scott 1998; Hirata and Yoshida 2000).

One could also speculate on possible learning stages and learning processes while interpreting a decrease in R_V ratio associated with practice. For example, automatization usually concerns one limb, and the transfer to the other one is expected to be weak (Jeka and Lackner 1995; Hikosaka et al. 1999). Therefore, since the amount of practice was by far insufficient for task automatization (Karni and Sagi 1993), it remains possible that a prolonged training would lead to a further decrease in R_V, particularly with respect to the bimanual hypothesis.

Conclusions

The UCM hypothesis provides a viable alternative to a view that the CNS controls redundant systems by eliminating or “freezing” redundant degrees of freedom (Vereijken et al. 1992). Rather, all the degrees of freedom are used to assure stability of selected task variables reflected in the structure of the variability in the state space of the elements. Within this approach, the apparent motor “redundancy” does not pose a computational problem but offers a powerful “abundant” apparatus that may be structured to stabilize a set of functionally important task variables. When compared with the concept of motor equivalence (see Introduction), the UCM approach provides the opportunity to study variability through the entire movement rather than only at the movement endpoint, while different hypotheses concerning controlled variables can also be tested.

The present study has provided support for the general principle of the UCM approach. Besides, it has demonstrated that during a bimanual pointing task several functional variables can be stabilized at the same time, but to different degrees. Changes in the structure of the joint angle variability with practice have raised more questions than they answered. Discovering the purpose of the observed counterintuitive changes in the structure of joint angle variability is a challenge to be met in future studies.

The UCM approach is promising not only for basic research in the area of motor control but also in its potential clinical applications. Patients with motor disorders are likely to organize their multijoint movements differently, possibly paying more attention to components of everyday tasks related to safety and comfort than to efficacy and esthetics (cf. Latash and Anson 1996). As demonstrated in the present study, the UCM method may be able to detect and quantify changes in the relative stabilization of different variables related to components of motor tasks. It may ultimately turn into a powerful tool for understanding atypical motor patterns of patients and helping development of new approaches to motor rehabilitation.

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Appendix

Computation of variance within the uncontrolled manifold and within the orthogonal manifold

A selected task variable defines an uncontrolled manifold (UCM) in the approriate joint space. Here we describe how the studied task variables define the corresponding UCMs at each percentage of movement time. Thereafter, we show how the two components of the joint configuration vectors within the UCM and within the subspace orthogonal to it (ORT) were obtained and how the variances of these components were computed (V_{COMP} and V_{UN}, respectivly).

Forward kinematics was applied to compute the task variable associated to the mean joint configuration across trials (**M**). Let r_0 be the value of the task variable for the mean joint configuration and $\mathbf{r_k}$ be the value of the task variable for the *k*th trial. If the joint configuration vectors ($\mathbf{A}_k$) of a particular trial remain in the vicinity of **M**, than the deviation of the task variable $\Delta\mathbf{r_k}=\mathbf{r_k}-\mathbf{r_0}$ relates to the deviation of joint configuration $\mathbf{k}=\mathbf{M}-\mathbf{A}_k$ approximately as:

$$\Delta\mathbf{r_k} = \mathbf{J} * \Delta\mathbf{k} \tag{3}$$

where **J** is the Jacobian matrix; its elements are the partial derivatives of the task variable’s coordinates with respect to the joint angles in the mean joint configuration. The nullspace of **J** contains those changes of joint configurations that result in zero change in the task variable. The UCM is linearly approximated by this subspace, which was identified by finding independent vectors (**e1**,...,**em**) that are spanning it.

That component of $\Delta\mathbf{k}$ which is parallel to the UCM is obtained by its projection onto this nullspace. If DV is the dimension of the task variable and DF is the number of degrees of freedom, then m=DF–DV, and the projection of $\Delta\mathbf{k}$ into the nullspace is:

$$\Delta\mathbf{k}^{UCM} = \sum_{i=1}^{m} ZZZ38; lt; \Delta\mathbf{k}, \mathbf{ei} > *\mathbf{ei} \tag{4}$$

where <,> denotes scalar product.

The component that is orthogonal to the null space is:

$$\Delta\mathbf{k}^{ORT} = \Delta\mathbf{k} - \Delta\mathbf{k}^{UCM} \tag{5}$$

The variance per DF of those components of the joint configuration vectors which confine to the UCM is computed as:

$$V_{COMP} = \sum_{k=1}^{N} \left(\Delta\mathbf{k}^{UCM}\right)^2 / ((DF - DV) * N) \tag{6}$$

where N is the number of trials.

The variance per DF of the orthogonal components is:

$$V_{UN} = \sum_{k=1}^{N} \left(\Delta\mathbf{k}^{ORT}\right)^2 / (DV * N) \tag{7}$$

We formulize the forward kinematics and the Jacobians for the described bimanual task and for the two arms separately and we define the variances for these cases.

Bimanual control hypothesis

The hypothetized task variable for a bimanual control hypothesis is the 2D vectorial distance between the pointer and target position within the movement plane. Using forward kinematics, the coordinates of the target position (Tx, Ty) and the pointer position (Px, Py) were computed from the mean joint configuration M given by joint angles (αj; j=1,...,6) and from segment lengths (l1, left upper arm; l2, left forearm; l3, the distance between the left wrist and the target; l4, right upper arm; l5, right forearm; l6, distance of the right wrist and the pointer tip; Fig. 2B). Let (SLx, SLy) and (SRx, SRy) be the coordinates of the left and right shoulders, respectively: The following equations were employed to compute the target and pointer positions:

$$\begin{aligned} Tx &= \sum_{i=1}^{3} \left(li * \cos\left(\sum_{j=1}^{i} \alpha j \right) \right) + SLx \\ Ty &= \sum_{i=1}^{3} \left(li * \sin\left(\sum_{j=1}^{i} \alpha j \right) \right) + SLy \\ Px &= \sum_{i=4}^{6} \left(li * \cos\left(\sum_{j=4}^{i} \alpha j \right) \right) + SRx \\ Py &= \sum_{i=4}^{6} \left(li * \sin\left(\sum_{j=4}^{i} \alpha j \right) \right) + SRy \end{aligned} \tag{8}$$

The assumed task variable (the vectorial distance of the target and the pointer tip) is:

$$(rx, ry) = (Tx, Ty) - (Px, Py); \tag{9}$$

Using equation (8), (rx, ry) are expressed by joint angles:

$$\begin{aligned} rx &= \sum_{i=1}^{3} \left(li * \cos\left(\sum_{j=1}^{i} \alpha j \right) \right) \\ &\quad - \sum_{i=4}^{6} \left(li * \cos\left(\sum_{j=1}^{i} \alpha j \right) \right) + SLx - SRx \\ ry &= \sum_{i=1}^{3} \left(li * \sin\left(\sum_{j=1}^{i} \alpha j \right) \right) \\ &\quad - \sum_{i=4}^{6} \left(li * \sin\left(\sum_{j=1}^{i} \alpha j \right) \right) + SLy - SRy \end{aligned} \tag{10}$$

Let J_{xi} denote the derivative of rx with respect to αi (J_{xi}=rx/αi, i=1,...6). Let J_{yi} denote the derivative of ry with respect to αi (J_{yi}=ry/αi, i=1,...6). The UCM is approximated with the nullspace of the following Jacobain matrix:

$$\mathbf{J} = \begin{bmatrix} J_{x1} & J_{x2} & J_{x3} & J_{x4} & J_{x5} & J_{x6} \\ J_{y1} & J_{y2} & J_{y3} & J_{y4} & J_{y5} & J_{y6} \end{bmatrix} \tag{11}$$

The elements of the Jacobians are:

$$\begin{aligned} J_{x1} &= -l1 * \sin(\alpha 1) - l2 * \sin(\alpha 1 + \alpha 2) \\ &\quad - l3 * \sin(\alpha 1 + \alpha 2 + \alpha 3) \\ J_{x2} &= -l2 * \sin(\alpha 1 + \alpha 2) - l3 * \sin(\alpha 1 + \alpha 2 + \alpha 3) \\ J_{x3} &= -l3 * \sin(\alpha 1 + \alpha 2 + \alpha 3) \\ J_{x4} &= -l4 * \sin(\alpha 4) + 15 * \sin(\alpha 4 + \alpha 5) \\ &\quad + 13 * \sin(\alpha 4 + \alpha 5 + \alpha 6) \\ J_{x5} &= -l5 * \sin(\alpha 4 + \alpha 5) + 13 * \sin(\alpha 4 + \alpha 5 + \alpha 6) \\ J_{x6} &= -l6 * \sin(\alpha 4 + \alpha 5 + \alpha 6) \\ J_{y1} &= l1 * \cos(\alpha 1) + l2 * \cos(\alpha 1 + \alpha 2) \\ &\quad + l3 * \cos(\alpha 1 + \alpha 2 + \alpha 3) \\ J_{y2} &= l2 * \cos(\alpha 1 + \alpha 2) + l3 * \cos(\alpha 1 + \alpha 2 + \alpha 3) \\ J_{y3} &= l3 * \cos(\alpha 1 + \alpha 2 + \alpha 3) \\ J_{y4} &= -l4 * \cos(\alpha 4) - 15 * \cos(\alpha 4 + \alpha 5) \\ &\quad - 13 * \cos(\alpha 4 + \alpha 5 + \alpha 6) \\ J_{y5} &= -l5 * \cos(\alpha 4 + \alpha 5) - 13 * \cos(\alpha 4 + \alpha 5 + \alpha 6) \\ J_{y6} &= -l6 * \cos(\alpha 4 + \alpha 5 + \alpha 6) \end{aligned} \tag{12}$$

The nullspace of $\mathbf{J}$ is four-dimensional. Finally, the variance within the UCM for the bimanual control hypothesis is computed as the particular form of Eq. 6, with DF=6, DV=2, N=15:

$$V_{COMP} = \sum_{k=1}^{15} \left(\Delta\mathbf{k}^{UCM}\right)^2 / 60 \tag{13}$$

The variance within the ORT is computed from Eq. 7:

$$V_{UN} = \sum_{k=1}^{15} \left(\Delta\mathbf{k}^{ORT}\right)^2 / 30 \tag{14}$$

Unimanual control hypothesis applied on left and right arm

If the two arms are considered separately, than the joint space is three-dimensional. For the unimanual control hypothesis applied on the movements of the left arm, the task variable is target position (Tx, Ty). Therefore, the corresponding UCM_{left} is approximated by the nullspace of a 2×3 matrix ($\mathbf{J}_{left}$) that is a part (the first three columns) of **J** defined above, since $\partial Tx/\partial \alpha I = \partial rx/\partial \alpha i$ and $\partial Ty/\partial \alpha i = \partial ry/\partial \alpha i$ for i=1,2,3.

Using notation of the bimanual control hypothesis calculation, it gives:

$$\mathbf{J}_{left} = \begin{bmatrix} J_{x1} J_{x2} J_{x3} \\ J_{y1} J_{y2} J_{y3} \end{bmatrix}$$

The nullspace of $\mathbf{J}_{left}$ and thus UCM_{left} is one-dimensional. ORT_{left} is two-dimensional. The deviation vector ($\Delta\mathbf{k}_{left}$) is the difference of the joint configuration of the left arm in the kth trial ($\alpha 1_k, \alpha 2_k, \alpha 3_k$) from the mean configuration of the left arm calculated for all 15 trials ($\alpha 1_0, \alpha 2_0, \alpha 3_0$).The variance per DF and trial within UCM_{left} is denoted by $V_{COMP,\ left}$ and obtained from equation (6) with DF=3, DV=2, N=15:

$$V_{COMP,left} = \sum_{k=1}^{15} \left(\Delta\mathbf{k}_{left}^{UCM} \right)^2 / 15 \qquad (15)$$

where k_{left}^{UCM} is the projection of k_{left} to UCM_{left}.

The variance within ORT_{left} is computed from Eq. 7 with DV=2, N=15:

$$V_{UN,left} = \sum_{k=1}^{15} \left(\Delta\mathbf{k}_{left}^{ORT} \right)^2 / 30 \qquad (16)$$

For the unimanual control hypothesis applied on the right arm, the task variable is the position of the pointer-tip (Px, Py). UCM_{right} is defined as the nullspace of a 2×3 matrix taken from the last three coloumns of **J**, since $\partial Px/\partial \alpha i = -\partial rx/\partial \alpha i$ and $\partial Py/\partial \alpha i = -\partial ry/\partial \alpha i$ for i=4,5,6. Thus, with the notation used for the bimanual approach:

$$\mathbf{J}_{right} = -\begin{bmatrix} J_{x1} J_{x2} J_{x3} \\ J_{y1} J_{y2} J_{y3} \end{bmatrix}$$

The nullspace of $\mathbf{J}_{right}$ and thus UCM_{right} is one-dimensional.

The deviation vector $\Delta\mathbf{k}_{right}$ represents the difference between the joint configuration measured in the kth trial ($\alpha 4_k, \alpha 5_k, \alpha 6_k$) and the mean configuration of the right arm ($\alpha 4_0, \alpha 5_0, \alpha 6_0$). The variance per DF in the UCM_{right} is denoted by $V_{COMP,\ right}$:

$$V_{COMP,right} = \sum_{k=1}^{15} \left(\Delta\mathbf{k}_{right}^{UCM} \right)^2 / 15 \qquad (17)$$

where $\Delta\mathbf{k}_{right}^{UCM}$ is the projection of $\Delta\mathbf{k}_{right}$ onto UCM_{right}.

The variance within ORT_{right} is a particular form of Eq. 7:

$$V_{UN,right} = \sum_{k=1}^{15} \left(\Delta\mathbf{k}_{right}^{ORT} \right)^2 / 30 \qquad (18)$$

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