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Two Kinematic Synergies in Voluntary Whole-Body Movements During Standing

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Freitas, Sandra M.S.F., Marcos Duarte, and Mark L. Latash. Two kinematic synergies in voluntary whole-body movements during standing. *J Neurophysiol* 95: 636–645, 2006. First published November 2, 2005; doi:10.1152/jn.00482.2005. We used a particular computational approach, the uncontrolled manifold hypothesis, to investigate joint angle covariation patterns during whole-body actions performed by standing persons. We hypothesized that two kinematic synergies accounted for the leg/trunk joint covariation across cycles during a rhythmic whole-body motion to stabilize two performance variables, the trunk orientation in the external space and the horizontal position of the center of mass (COM). Subjects stood on a force plate and performed whole-body rhythmic movements for 45 s under visual feedback on one of the four variables, the position of the center of pressure or the angle in one of the three joints (ankle, knee, or hip). The Fitts-like paradigm was used with two target amplitudes and six indices of difficulty (ID) for each of the four variables. This was done to explore the robustness of kinematic postural synergies. A speed-accuracy trade-off was observed in all feedback conditions such that the movement time scaled with ID and the scaling differed between the two movement amplitudes. Principal-component (PC) analysis showed the existence of a single PC in the joint space that accounted for over 95% of the joint angle variance. Analysis within the uncontrolled manifold hypothesis has shown that data distributions in the joint angle space were compatible with stabilization of both trunk orientation and COM location. We conclude that trunk orientation and the COM location are stabilized by co-varied changes of the major joint angles during whole-body movements. Despite the strong effects of movement amplitude and ID on performance, the structure of the joint variance showed only minor dependence on these task parameters. The two kinematic synergies (co-varied changes in the joint angles that stabilized the COM location and trunk orientation) have proven to be robust over a variety of tasks.

INTRODUCTION

The notion of synergies has been commonly used in studies of movement kinematics (Desmurget et al. 1995; Levin et al. 2003; Vereijken et al. 1992), in particular for coordinated joint motion during postural tasks (Alexandrov et al. 1998). Most studies have associated synergies with simultaneous motions in several joints that scaled together either over a realization of a task or over modifications in task parameters. Following the classical suggestion by Bernstein (1967), synergies have been assumed to contribute to solving the problem of motor redundancy. On the other hand, studies of kinematic patterns associated with postural tasks may be viewed as a window into the issues of postural control, particularly within the framework of the equilibrium-point hypothesis, which considers control of whole-body actions as the process of selection and modification of reference body configurations (Feldman and Levin 1995).

Recently, an operational definition of synergies has been offered that views synergies as flexible, task-specific neural organizations of elemental variables that stabilize certain performance characteristics of multi-element systems (reviewed in Latash et al. 2002). Elemental variables represent variables describing the system at a selected level of analysis. In the absence of a task-specific control strategy, elemental variables are expected to show independent variations across trials and potentially span the whole space of possible solutions. Synergies are reflected in co-varied changes in elemental variables. In previous studies of kinematic synergies, elemental variables were associated with individual joint angles (Scholz and Schöner 1999; Scholz et al. 2000). In studies of multi-finger synergies, hypothetical independent commands to fingers (finger modes) were viewed as elemental variables (Latash et al. 2001; Scholz et al. 2002). Studies of muscle synergies in postural tasks used muscle groups as elemental variables (muscle modes) (Krishnamoorthy et al. 2003). Each of these approaches assume that synergies are best defined through two major features: sharing patterns seen as invariant relationships among elemental variables (Desmurget et al. 1995; Li et al. 1998; Macpherson et al. 1986; Pelz et al. 2001) and error compensation, which manifests itself, in particular, through the correlations among elemental variables from trial to trial such that performance variables vary less than if elemental variables fluctuated independently (Abbs and Gracco 1984; Jaric and Latash 1999; Scholz and Schöner 1999).

The uncontrolled manifold (UCM) hypothesis has been developed to quantify synergies (Scholz and Schöner 1999). According to this hypothesis, the controller acts in the space of elemental variables and, for each moment of time, selects in this space a subspace (a UCM) corresponding to a certain value of a potentially important performance variable. Further, variability of the elemental variables is structured in such a way that most of it is confined to the UCM, i.e., its effect on the performance variable is reduced. This approach has been used in analysis of multi-joint actions such as sit-to-stand action (Scholz and Schöner 1999), two-arm pointing (Domkin et al. 2002, 2005) and quick-draw shooting (Scholz et al. 2000). In the original study by Scholz and Schöner (1999), the authors tested the hypotheses that co-varied changes in joint angles during sit-to-stand action stabilized such performance variables

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as the horizontal and vertical positions of the center of mass (COM).

In the current study, we used UCM analysis to investigate patterns of coordination of joint motion in a sagittal plane during whole-body actions performed by standing persons. A major question was what important performance variable(s) does the combined joint action stabilize during whole-body motion? Using an earlier study of the sit-to-stand action by Scholz and Schöner (1999) as a base, we hypothesized that the anterior-posterior position of the COM would be such a variable stabilized by co-varied changes in joint angle trajectories across trials. An earlier study of joint coordination patterns in a sagittal plane (Alexandrov et al. 1998) using the principal component analysis (PCA) has suggested the existence of a single PC in the three-dimensional space of the ankle, knee, and hip joints; that PC accounted for >95% of the total joint variance. A single PC corresponds to a unidimensional subspace in the three-dimensional joint angle space. Stabilization of the COM position in the anterior-posterior direction introduces a single constraint that can be satisfied within a two-dimensional subspace. Hence, we also hypothesized that there may be another constraint in the joint angle space corresponding to stabilization of another variable by the coordinated joint action. We considered trunk orientation with respect to the vertical as a candidate variable (cf. Gurfinkel et al. 1995).

To explore the robustness of kinematic postural synergies, we performed UCM and PCA analyses on modification of such task parameters as: amplitude of required body motion, accuracy constraint (target size), and type of feedback. Modifications of the amplitude of motion and target size were done using typical Fitts'-type tasks. Daily activities of humans frequently involve accurate "aiming" movements with the whole body while standing. Examples are leaning forward to reach for an object, sit-to-stand action, and stair walking. Clinical tests involving rapid aiming movements from one target to another with a global variable representing body sway (body COM or center of pressure position) have been used in the evaluation and rehabilitation of the control of balance (Hageman et al. 1995; Hamman et al. 1995; Nichols 1997). Hence, exploring the range of postural tasks that use particular kinematic multi-joint synergies has both practical and theoretical implications. Earlier studies (Danion et al. 1999; Duarte and Freitas 2005) have shown that when standing subjects try to shift their center of pressure (COP, the point of application of the resultant reactive force from the platform) under a typical "be fast and accurate" instruction, COP shifts show peculiarities in their patterns that deviate from those predicted by the classical speed-accuracy trade-off. Therefore we hypothesized that under such an instruction, joint coordination may change depending on the index of difficulty of the task. In addition, we have also explored the issue of whether patterns of joint coordination depend on sensory feedback, which is used to define the task. We did not manipulate the modality of the feedback, which has been shown to play a major role in postural stabilization (Buchanan and Horak 1999, 2003), but rather used different mechanical variables such as joint angle and COP location to provide visual feedback. To summarize, the main goal of the study has been to identify and quantify kinematic synergies that participate in whole-body motions performed by a standing person and to test their robustness with respect to manipulations of a range of task parameters.

METHODS

Subjects

Ten healthy volunteers, five males and five females, took part as subjects in the experiments. The mean (±SD) age of the subjects was 31 ± 6 yr, their mean (± SD) height was 172 ± 12 cm, and their mean (±SD) body mass was 67 ± 19 kg. All participants signed informed consent form according to the procedures approved by the Office for Research Protection of the Pennsylvania State University.

Apparatus

During the experiment, the subject stood in a comfortable position on a force platform (OR6-5, AMTI) with the feet at shoulder width and hands placed on the hips at all times. The position of the feet was marked and reproduced across trials. The subjects viewed the monitor located directly in front of them, ~1 m away at the eye level. The screen of the monitor showed two stationary targets and a cursor related to the current value of a selected mechanical variable (see later).

The force platform was used to record time patterns of three components of the force (F_x, F_y, and F_z) and three components of the moment (M_x, M_y, and M_z); x, y, and z are the anterior-posterior, mediolateral, and vertical directions, respectively. These force and moment components were used to calculate the COP location in the anterior-posterior direction as COP = $(M_y)/F_z$.

Joint angles in the sagittal plane were measured with three goniometers (Biometrics SG110 and SG150) placed on the right side of the subject's body. Goniometers were calibrated at the end of each experiment while they were still attached to the subject's body. The experiment was controlled by software written in LabView 6.1 (National Instruments). An IBM-compatible Dell PC was used for data acquisition and processing. The data were digitized at a sampling frequency of 100 Hz with a 12-bit resolution by an A/D card (National Instruments).

Procedures

There were four main conditions that differed by the visual feedback presented on the screen. Within each of the four feedback conditions, we manipulated other task parameters such as the amplitude and target size for the required actions (see later). The feedback could show either the instantaneous position in one of the joint angles in the sagittal plane (ankle: α_A, knee: α_K, or hip: α_H) or the instantaneous location of the COP. We will refer to the variable used for feedback in each condition as the *F* variable. The feedback was presented on the screen as a yellow dot moving on the black background between two target zones. Two horizontal red lines defined each target zone. The COP displacement in the anterior (posterior) direction or joint flexion (extension) produced motion of the cursor in the up (down) direction.

Within each feedback condition, the subjects performed 12 trials. In each trial, the task was presented as a combination of a particular amplitude of motion (*A*) of a *F* variable and a particular target size (*W*). For the tasks that required COP displacement, the amplitudes were 4.5 and 9 cm, and for the tasks that required joint displacement, the amplitudes were 4.5 and 9°. The magnitudes of the target width were selected to get indices of difficulty [ID = $\log_2(2A/W)$] equal to 1.4, 1.8, 2.2, 2.6, 3.0, and 3.4. The ID values were computed based on the classical formulation of the Fitts' law (Fitts 1954), which predicts movement time (MT) as a linear function of ID, MT = $a + b \cdot$ ID, where *a* and *b* are empirical constants. Correspondingly, the target width ranged from 0.85 to 6.82 (centimeters or degrees). The amplitude/ID combinations (tasks) were presented within each feedback condition in a pseudorandom (balanced) order. All the subjects performed the COP tasks first followed by the three joint feedback conditions with feedback on the α_A, α_K, and α_H position presented in a balanced order across the subjects. Subjects were specifically instructed to move in the sagittal plane. A training session was performed prior to the tasks within a feedback condition. It consisted of trials at six selected amplitude/ID combinations.

Each trial consisted of performing a cyclic body movement for 45 s without moving the feet in such a way that the cursor displayed on the monitor oscillated between the two targets. The subjects were asked to be as fast and as accurate as possible while they moved the cursor between the targets. Trials containing >20% of errors (over- or undershoots of the targets) were rejected and repeated at the end of each feedback condition. The subjects were free to select body-motion patterns to satisfy the task requirements and to adjust these patterns when the requirements were modified. The patterns differed across feedback conditions and *A*/*W* combinations (see also Duarte and Freitas 2005). In particular, during relatively slow motions, COP and ankle joint feedback conditions led to similar motion patterns; however, during faster movements (low ID), motion patterns under COP and hip feedback conditions were more similar.

The location of each target zone was determined based on the subject's limits of stability using a separate test. First, the subject was asked to stand in a comfortable posture (assumed to be the neutral COP location). Then the subject was asked to slowly move the body (maintaining the feet on the ground) forward and backward as far as possible to reach his or her limits of stability. The extreme positions of the COP in both forward and backward directions were considered as the limits of stability in these directions. The joint angles in these positions were used in a similar way to determine the joint ranges. The mean range of COP displacement across subjects in this test was 18 ± 2 cm with 67 ± 7% of the range anterior to the neutral position and 33 ± 7% of the range posterior to the neutral position. During this test, the mean α_A excursion across subjects in flexion-extension was 12 ± 6° with 58 ± 23% of this range into flexion. The mean α_K excursion was 17 ± 9° with 68 ± 10% of this range into flexion. The mean α_H excursion in flexion-extension was 20.8 ± 15° with 54 ± 22% of this range into flexion. The target zones were positioned proportionally to these ranges (linear or angular) with respect to the neutral position. For example, for the task of moving COP over 9 cm, the average location of the anterior target was 6 cm from the neutral position, whereas the average location of the posterior target was 3 cm from the neutral position.

Each subject performed at least one trial of 45-s duration per each combination of task parameters. The intervals between feedback conditions were 10 min, whereas the intervals between tasks within a feedback condition were 60 s. Fatigue was never reported by the subjects.

To summarize, the experimental design manipulated four described factors: *feedback* (*F* variable): four levels; amplitude (*A*): two levels; ID: six levels; and direction of movement: two levels.

Data processing

All the data were filtered with a fourth-order 10-Hz low-pass zero-lag Butterworth filter. The first 15 s of the 45-s COP time series was considered as an adaptation period and was discarded from the data analysis after the filtering process; all analyses were performed using the Matlab 6.5 (The Mathworks) software package. Peaks and valleys of the *F*-variable time series were detected for each trial, and the COP and joint angle data between successive valleys of the *F* variable were averaged to calculate the respective mean cycles of this trial (see Fig. 1 for an example). The movement time was computed as the time duration of a half-cycle: the time between a valley and the next peak, or between a peak and the next valley, of the *F*-variable time series. The COP and joint angle total displacements were calculated for each direction of motion. Further, they were averaged across the half-cycles within each direction and trial.

The effective ID (ID_e) was calculated as $ID_e = \log_2(2A_e/W_e)$, where A_e is the effective target amplitude and W_e is the effective target width. A_e was estimated as the actual average COP (or joint angle) total displacement. W_e was calculated as four times the SD of A_e over a trial [$W_e = 4{*}SD(A_e)$].

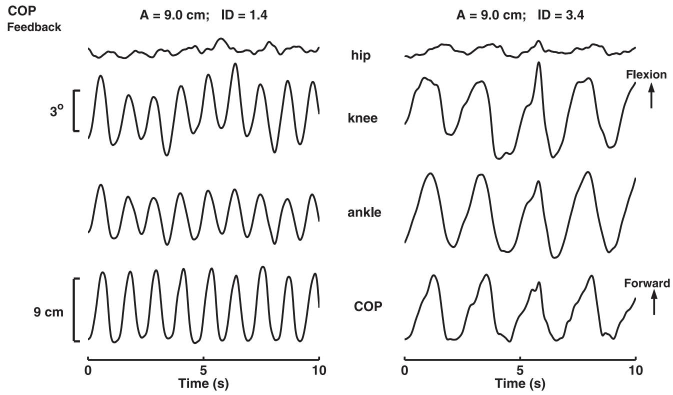

FIG. 1. Exemplary time series of the center of pressure (COP) and joint angle (hip, knee, and ankle) displacements during tasks with the 9-cm amplitude and the lowest and highest indexes of difficulty (ID = 1.4 and 3.4, respectively) when the COP was provided as the visual feedback.

ANALYSIS WITHIN THE UCM HYPOTHESIS. Trajectories representing half-cycles for each direction of motion of the *F* variable were time-normalized to 51 samples, each pair of samples separated by 2% of the half-cycle duration. The number of such half-cycle trajectories within a trial varied across tasks (amplitude and ID combinations) depending on the actual speed of performance of each subject. Variance analysis was performed at each 10% of the half-cycle (these 10% time interval will be referred to as movement phases). Calculation of the total variance of joint configuration in the sagittal plane was performed similarly to previous studies (Domkin et al. 2002; Scholz and Schöner 1999; Tseng et al. 2003). In the present study, the joint configuration in the sagittal plane is three dimensional (α_A, α_K, and α_H). By definition, the UCM represents combinations of joint angles that do not affect a particular selected performance variable. We performed UCM analysis with respect to two variables, the estimated location of the COM in the sagittal plane and the orientation of the trunk (α_{TR}) in the sagittal plane with respect to vertical. To test that joint angles co-varied across trials to stabilize the estimated average location of the COM, the following expression was used as an approximation for changes in the COM location as functions of small changes in the joint angles: $\Delta COM \approx \Delta\alpha_A(c_S m_S L_{AK} + c_T m_T L_{KH} + c_{TR} m_{TR} L_{HCOM}) - \Delta\alpha_K(c_T m_T L_{KH} + c_{TR} m_{TR} L_{HCOM}) + \Delta\,\alpha_H(c_{TR} m_{TR} L_{HCOM})$ where m_S, m_T, and m_{TR} and c_S, c_T, and c_{TR} stand for the masses and the positions of the COM of the shank, thigh, and trunk, respectively. The positions of the COM of segments (*c*) were defined as a percentage of body height, and the mass of segments (*m*) was defined as a percentage of total body mass. The letter *L* stands for the length of the segments between the ankle and knee joint (L_{AK}), between the knee and hip joints (L_{KH}), and between the hip joint and the estimated location of the COM (L_{HCOM}). During analysis, positive changes in joint angles were defined as those leading to joint flexion. The length of the segments was estimated as a percentage of body height as proposed by Drillis and Contini (Winter 1990).

For the latter hypothesis, the following equation was used to relate small changes in joint angles to changes in trunk orientation with respect to the vertical

$$\Delta\alpha_{TR} \approx \Delta\alpha_A - \Delta\alpha_K + \Delta\alpha_H$$

For each performance variable, the hypothesis was that joint angles co-varied from half-cycle to half-cycle to minimize deviations of this variable from its reference value assessed as its mean value across the half-cycles. The mean joint configuration (Θ^0) across all trajectories was computed at each 10% of the half-cycle. For a value of a performance variable, a two-dimensional null-space (a UCM) was computed. This null space is spanned by two basis vectors, ϵ_i. For each phase of the movement, the deviation (Δk) of the joint configuration (Θ) from Θ^0, computed for this particular phase of the movement, was assessed in its projections onto the UCM and onto its orthogonal complement

$$\Theta_{\parallel} = \sum_{i=1}^{2} \varepsilon i \cdot \Delta k$$

$$\Theta_{\perp} = (\Theta - \Theta^0) - \Theta_{\parallel}$$

The amount of variance per degree of freedom (DOF) within the UCM was estimated as

$$V_{UCM} = \sigma_{\parallel}^2 = \sum_{\text{trials}} |\Theta_{\parallel}^2|/(N_{\text{trials}})$$

and the variance perpendicular to the UCM was estimated as

$$V_{ORT} = \sigma_{\perp}^2 = \sum_{\text{trials}} |\Theta_{\perp}^2|/(N_{\text{trials}})$$

As in earlier studies (Domkin et al. 2002; Scholz et al. 2000), we used the ratio $R_V = V_{UCM}/V_{ORT}$ as an index of selective stabilization of the performance variable. Note that when this ratio is significantly over unity, a conclusion can be made that more variance per DOF is restricted to the UCM; hence, the performance variable is stabilized by a multi-joint kinematic synergy. For each feedback condition and each subject, the variance within the UCM (V_{UCM}) and the variance orthogonal to the UCM (V_{ORT}) were averaged over the phases of the movement for each of the two movement amplitudes and each of the six indices of difficulty separately. This was done because R_V did not change significantly within the half-cycle ($P > 0.1$).

In less precise but maybe more intuitive terms, the analyses produced two indices of joint angle variance, V_{UCM} and V_{ORT}. The former reflects the amount of joint angle variance that did not affect the average value of the selected performance variable ("good variance"). The latter reflected the amount of joint angle variance that changed the performance variable ("bad variance"). If the ratio R_V is significantly more than unity, a hypotheses that the performance variable is stabilized by a multi-joint kinematic synergy is confirmed.

PCA. For each task, each subject, and each movement phase (each 10% of the half-cycle), joint angle matrices were composed. The covariance matrices were subjected to principal component (PC) analysis using procedures from Matlab 6.5 (The Mathworks) software package. For each subject and each task, the obtained eigenvalues and PCs of the matrices were averaged across phases (half-cycles) and then analyzed across tasks and subjects. Based on the percentage of the total variance accounted by the first PC (>95% of the total variance in all cases, see later in RESULTS), we did not consider further PCs. Loading factors at individual joints were further analyzed.

DESCRIPTIVE AND INFERENTIAL STATISTICS. Statistical tests were performed using the SPSS 10.0 (SPSS) statistical package. Repeated-measures ANOVA were used with factors feedback (COP, ankle: α_A, knee: α_K and hip: α_H), amplitude [small: 4.5 cm (degrees) and large: 9.0 cm (degrees)], ID (1.4, 1.8, 2.2, 2.6, 3.0 and 3.4), and direction (forward/flexion and backward/extension). Repeated-measures MANOVAs were used with same factors for joint displacements and PC loading factors. Significant effects were further analyzed using pairwise comparisons with Bonferroni corrections. The significance level was set at 0.05.

RESULTS

All the subjects were able to perform all the tasks successfully with the exception of one subject, who failed to meet the 20% error criterion for the task of moving the knee joint with the smaller amplitude and the highest ID. This subject's data were discarded only for that particular condition. In general, all three joints were involved over all the feedback conditions (Figs. 1 and 2). Figure 2 also illustrates a relatively symmetric pattern of COP and joint excursions when feedback was provided on these variables.

Data in Table 1 show that the ranges of COP and joint motion varied with the amplitude of motion and with the feedback condition [$F(3,24) > 11.0$, $P < 0.001$]. For all conditions, the COP displacements were larger for the larger amplitude of motion [$F(1,8) > 159$, $P < 0.001$]. The COP displacements were not significantly different across IDs when

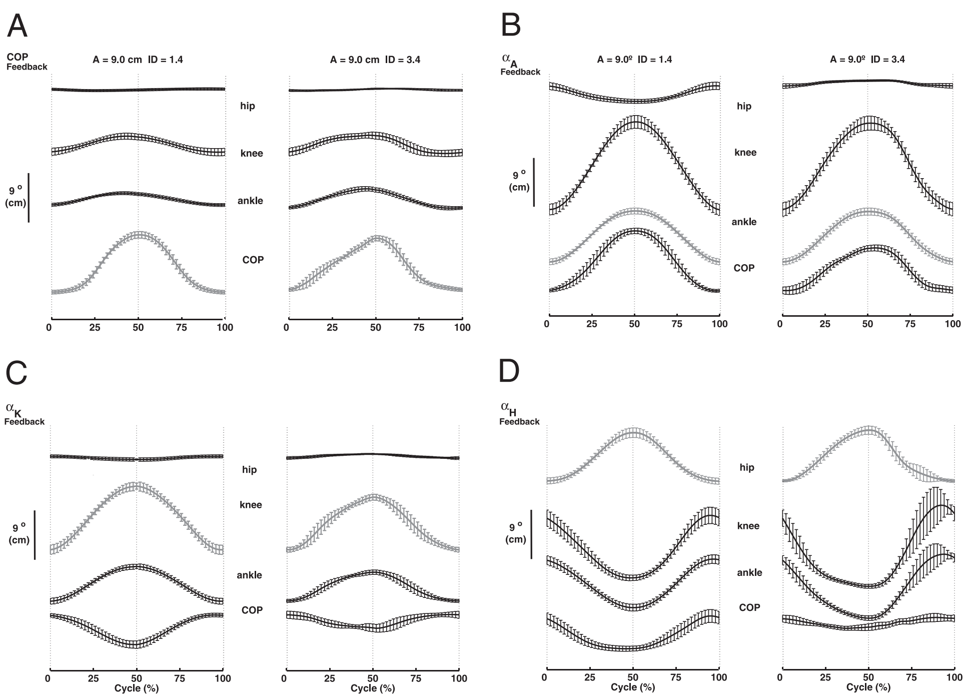

FIG. 2. Exemplary mean time series (with SDs) across cycles of the COP displacement and joint excursions. Tasks with 9.0 cm (or 9.0°) and 2 IDs (=1.4 and 3.4) when the COP (*A*), the ankle -α_A (*B*), knee - α_K (*C*), and hip - α_H (*D*) joint angles were provided as the visual feedback. The 1st half of the cycle (from 0 to 50%) represents the forward/flexion movement and the 2nd part of cycle (from 50 to 100%) represents the backward/extension movement.

TABLE 1. *Ranges of COP motion and joint excursion*

		Feedback Conditions			
Variables	Amplitude	COP	α_A	α_K	α_H
COP, cm	4.5	5.2 ± 0.3	4.8 ± 1.2	2.7 ± 0.9	2.7 ± 0.6
	9.0	10.0 ± 0.3	7.3 ± 1.0	4.2 ± 0.8	4.1 ± 1.1
Ankle, °	4.5	1.3 ± 0.3	4.7 ± 0.2	3.2 ± 0.2	4.0 ± 0.2
	9.0	2.9 ± 0.9	9.2 ± 0.1	5.17 ± 0.22	6.7 ± 0.6
Knee °	4.5	1.3 ± 0.5	7.4 ± 0.8	4.86 ± 0.21	5.15 ± 0.41
	9.0	3.4 ± 1.9	15.0 ± 0.9	9.77 ± 0.40	7.37 ± 1.03
Hip, °	4.5	0.6 ± 0.3	1.7 ± 0.3	1.1 ± 0.4	4.8 ± 0.2
	9.0	1.2 ± 0.4	3.6 ± 0.6	1.3 ± 0.2	9.3 ± 0.2

Means ± SD across indices of difficulty and subjects are shown for all feedback conditions. COP, center of pressure; ankle-α_A, knee-α_K, and hip-α_H.

COP location was the *F* variable [$F(5,45) = 2.21$, $P = 0.07$], but they decreased for higher ID magnitudes when feedback was provided on a joint angle. All joint displacements were larger for movements of the larger amplitude for all feedback condition [$F(1,8) = 73.3$, $P < 0.001$]. The ID did not affect α_A and α_H displacements [$F(5,40) < 1.1$, $P > 0.1$] for all feedback conditions. However, ID affected α_K displacement during α_A and α_K feedback conditions [$F(5,40) = 4.19$, $P < 0.01$] such that an increase in ID led to a decrease in the α_K displacement.

Speed-accuracy trade-off

In general, subjects performed slower movements for the smaller target sizes as well as the smaller amplitudes. The relations between MT and ID averaged across all subjects are illustrated in Fig. 3*A*. Note that under all feedback conditions, the data points for the two movement amplitudes form two different regression lines, which "fan out" at different slopes. All regression lines were significant with the *r* values higher than 0.93 ($P < 0.01$, Table 2). Statistical analysis of MT using three-way ANOVA with factors feedback (COP, α_A, α_K, and α_H), amplitude (small and large), and ID (1.4, 1.8, 2.2, 2.6, 3.0,

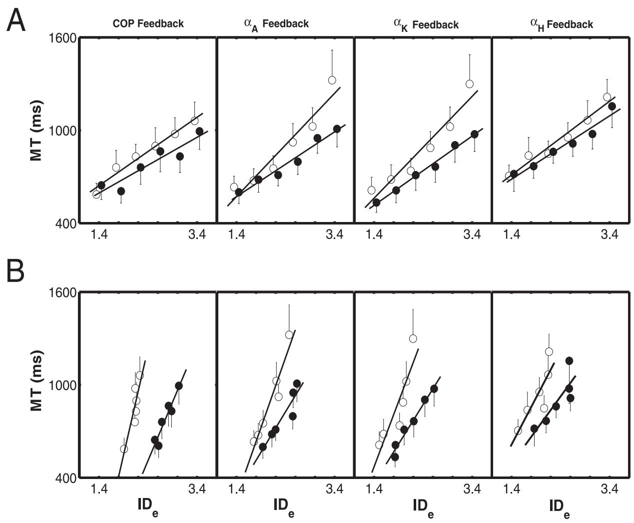

FIG. 3. *A*: movement time (MT) as the function of the ID for each feedback condition (COP, ankle -α_A, knee -α_K, and hip - α_H). *B*: same data are plotted as functions of the effective index of difficulty (ID_e). Means ± SE across subjects and movement directions are presented. Linear regression lines are shown. Note the different slopes of the regression lines for the 2 amplitudes of the movements. ○, 4.5° (cm) amplitude; ●, 9° (cm) amplitude.

TABLE 2. *Results for the fitting of movement time (MT) versus index of difficulty (ID) using the Fitts' equation*

		MT = a+b*ID			MT = a+b*ID_e		
Feedback Condition	Amplitude	*a,* ms	*b,* ms	*r*	*a,* ms	*b,* ms	*r*
COP	4.5 cm	321	221	0.98**	−2076	1379	0.89*
	9.0 cm	351	180	0.94*	−1304	756	0.95**
α_A	4.5°	88	333	0.96**	−990	902	0.96**
	9.0°	288	209	0.98**	−428	522	0.93*
α_K	4.5°	83	329	0.96**	−711	843	0.89*
	9.0°	212	224	0.99**	−352	510	0.98**
α_H	4.5°	365	238	0.98**	−237	607	0.84*
	9.0°	407	205	0.98**	−122	436	0.84*

Intercept (*a*), slope (*b*), and correlation coefficient (*r*) for the straight-line fits by least squares with Fitts' equation using index of difficulty (ID) and effective index of difficulty (ID_e) for each visual feedback condition (COP, ankle-α_A, knee-α_K, and hip-α_H).

and 3.4) showed no significant effects of feedback [$F(3,24) = 1.65$, $P = 0.2$]. Although MT was longer for the tasks with the smaller amplitude [$F(1,8) = 9.22$, $P < 0.05$] across all feedback conditions, the effect of amplitude was significant only for the COP and α_K conditions [$F(1,9) = 4.9$, $P < 0.05$ and $F(1,9) = 9.75$, $P < 0.01$, respectively]. The main effect of ID was observed for all feedback conditions [$F(5,40) = 27.57$, $P < 0.001$].

MT was also represented as a function of the ID_e, representing the actual performance of the subjects. The relation between MT and ID_e is illustrated in Fig. 3*B*. The difference in the slopes of the two regression lines is obvious for all conditions. These relations are also steeper for the task with the visual feedback on the COP motion. All regression lines were statistically significant with the *r* values ranging from 0.84 to 0.98 (all $P < 0.05$, Table 2).

PCA

PCA of joint angle excursions was performed over each data set for each movement phase, condition, direction, amplitude, ID, and subject separately (see METHODS). The obtained eigenvalues and PCs of the matrices were averaged across phases and then across subjects for each condition and each task (amplitude and ID combinations). The first PC accounted for ≥95% of the variance among the joint angles for all the feedback conditions.

Analysis of the loading factors at individual joints for the first PC revealed motion of the ankle and knee joint in the same direction, whereas the hip moved in the opposite direction. Of note, there was a relatively small loading factor at the hip joint when α_A and α_K were used as *F* variables.

Figure 4 illustrates the loading factors at individual joints for the first PC under different conditions. As described in METHODS, positive loadings correspond to flexion movement of α_A, α_K, and α_H. There were significant effects of direction [$F(1,8) > 8.5$, $P < 0.05$] and feedback [$F(3,24) > 8$, $P < 0.001$] on all the joint loadings and no significant effect of amplitude [$F(1,8) < 4.6$, $P > 0.05$]. Effects of ID were significant for the α_K and α_H loadings [$F(5,40) > 2.9$, $P < 0.05$] but not for the α_A loadings.

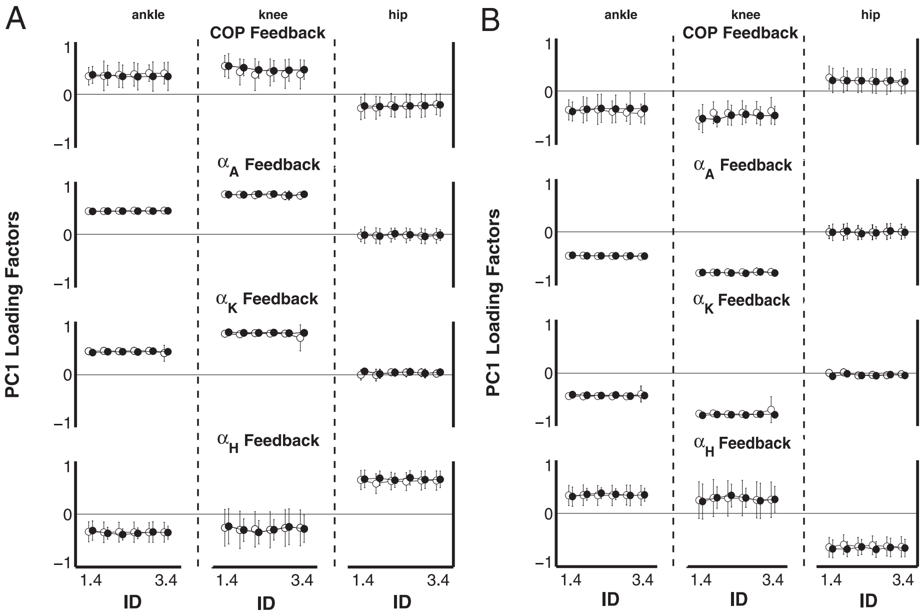

FIG. 4. Means ± SD across subjects of the 1st principal component (PC1) loading factors for each combination of movement amplitude and ID for the forward/flexion movements (*A*) and backward/extension movements (*B*) for each feedback condition (COP, ankle - α_A, knee -α_K, and hip - α_H). Positive values correspond to joint flexion. ○, 4.5° (cm) amplitude; ●, 9° (cm) amplitude.

UCM analysis

The results of the PCA suggest the existence of two constraints in the three-dimensional joint space resulting in a single PC that accounted for most of the joint variance. We ran UCM analysis to test hypotheses on two candidate performance variables forming the core of the two constraints, namely position of the COM and trunk orientation (α_{TR}) with respect to vertical.

This analysis tests the hypothesis that deviations of joint angles from their average pattern in different movement cycles co-varied to stabilize average trajectories of a performance variable. Such analysis produced two indices of joint angle variance, V_{UCM} and V_{ORT}, reflecting the amount of joint angle variance that did not affect the average value of the selected performance variable ("good variance") and the amount of joint angle variance that changed the performance variable ("bad variance"). The ratio of these two components of variance ($R_V = V_{UCM}/V_{ORT}$) was used as an index of stabilization of a performance variable (COM and α_{TR}). If this ratio is significantly more than unity, a hypothesis that the performance variable is stabilized by a multi-joint kinematic synergy is confirmed. Analysis was performed across series of movement half-cycles for each subject, each feedback condition, each direction, each movement amplitude, and each ID separately.

ANALYSIS WITH RESPECT TO THE COM LOCATION HYPOTHESIS. The amount of joint angle variance that did not affect the average value of the selected performance variable (V_{UCM}) was greater than the amount of joint angle variance that changed the performance variable (V_{ORT}). This result is particularly obvious in Fig. 5*A*, which shows the ratio $R_V = V_{UCM}/V_{ORT}$ for all conditions, averaged across subjects, for each 10% of the half-cycle (movement phase) and direction of movement (forward/flexion and backward/extension). R_V values were over unity for all feedback conditions. Also, the R_V values did not change with the task parameters, i.e., the index of COM

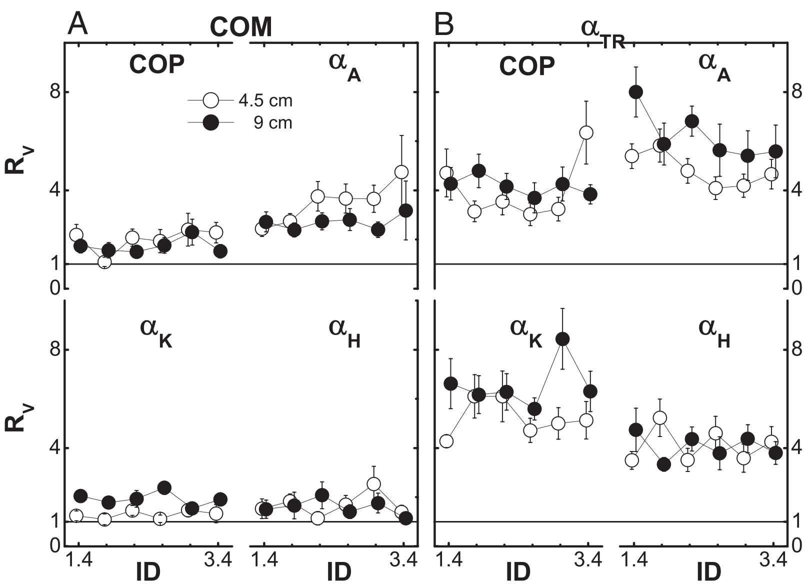

FIG. 5. Means ± SE across subjects and movement directions of the ratio ($R_V = V_{UCM}/V_{ORT}$), where V_{UCM} and V_{ORT} are the variance components computed with respect to the hypothesis on stabilization of the center of mass (COM) location (*A, left*) or of the trunk orientation (α_{TR}) with respect to the vertical (*B, right*). The data are shown for each combination of movement amplitude and ID for each feedback condition (COP, ankle - α_A, knee -α_K, and hip -α_H). ○, 4.5° (cm) amplitude; ●, 9° (cm) amplitude.

stabilization was independent of the amplitude and ID. ANOVA results showed no effect of feedback [$F(3,24) = 0.99$, $P > 0.05$] and revealed a significant effect of direction on R_V [$F(1,8) = 10.2$, $P < 0.05$]. In general, no difference was found in the R_V values across conditions, however, there were effects of task parameters on components of the joint angle variance (V_{UCM} and V_{ORT}).

Figure 6*A* illustrates the results for the two components of the joint angle variance computed with respect to COM stabilization and averaged across subjects for each 10% of the half-cycle (movement phase) and direction of movement (forward/flexion and backward/extension). Note that both components of the joint angle variance (V_{UCM} and V_{ORT}) increased for the higher movement amplitude and dropped with an increase in ID. There were significant effects of feedback on V_{UCM} [$F(3,24) = 3$, $P < 0.05$] but not on V_{ORT} [$F(3,24) = 2.9$, $P > 0.05$]. Post hoc tests showed that this effect of feedback on V_{UCM} was due to differences in V_{UCM} between α_A and α_K conditions. ANOVA results confirmed significant effects of amplitude on V_{UCM} [$F(1,8) = 10.22$, $P < 0.05$] and on V_{ORT} [$F(1,9) = 23.9$, $P < 0.01$] and a significant effect of ID on V_{UCM} [$F(5,40) = 3.85$, $P < 0.01$] and on V_{ORT} [$F(5,40) = 5.3$, $P < 0.01$]. ANOVA results revealed no significant effects of direction on V_{UCM} and V_{ORT} [$F(1,8) < 1.3$, $P > 0.05$].

ANALYSIS WITH RESPECT TO THE TRUNK ORIENTATION HYPOTHESIS. Overall, the V_{UCM} component of joint configuration was typically much larger than V_{ORT}, regardless of the information used for visual feedback, movement direction, amplitude, and size of target. The differences between V_{UCM} and V_{ORT} components were larger than those described in the previous section for the COM hypothesis. This is illustrated in Fig. 5*B* by the R_V values for all conditions averaged across subjects for each 10% of the half-cycle (movement phase), and direction of movement (forward/flexion and backward/extension). R_V values were similar between the two movement amplitudes and across the IDs for all feedback conditions. ANOVA results showed no significant differences among conditions for the factors feedback, amplitude, ID, and direction; with the exception of the α_A visual feedback condition there was a significant effect of ID on R_V [$F(5,35) = 3.75$ $P < 0.01$] as can be seen in Fig. 5*B*.

The two components of the joint angle variance, V_{UCM} and V_{ORT}, related to stabilization of α_{TR} averaged across subjects for each 10% of the half-cycle (movement phase) and direction of movement (forward/flexion and backward/extension), are illustrated in Fig. 6*B*. V_{UCM} and V_{ORT} increased for the higher amplitude of movement and decreased with an increase in ID. Neither V_{UCM} nor V_{ORT} differed between movement directions ($P > 0.05$). ANOVA results revealed significant effects of feedback on V_{UCM} [$F(3,27) = 3.87$, $P < 0.05$] and V_{ORT} [$F(3,27) = 6.25$, $P < 0.01$]. Post hoc tests demonstrated that these effects were due to the difference between the α_A and α_K feedback conditions. V_{ORT} values were also different between the α_K and α_H feedback conditions. ANOVA results confirmed significant effects of amplitude and ID on V_{UCM} [$F(1,9) = 17.64$, $P < 0.01$; and $F(5,45) = 5.24$, $P < 0.05$, correspondingly] and on V_{ORT} [$F(1,9) = 14.11$, $P < 0.01$; and $F(5,45) = 5.02$, $P < 0.05$, correspondingly].

DISCUSSION

In the INTRODUCTION, we formulated two hypotheses. The first hypothesis was that joint angles would co-vary across repetitive trials (cycles) to stabilize time profiles of two performance variables, the location of the COM and the orientation of the trunk (α_{TR}) with respect to vertical. This hypothesis has been confirmed. Statistically, more variance in the joint angle space was confined to manifolds consistent with stable values of the two performance variables. The second hypothesis was that patterns of joint coordination would change with changes in ID and possibly also with changes in the variables used for visual feedback. This hypothesis was not confirmed. The structure of the joint variance (assessed with the R_V index) showed only minor dependence on the mentioned task parameters. This happened despite the fact that the subjects were free to select their preferred patterns of joint motion and modify them with changes in task parameters. This particular result suggests that the multi-joint synergies stabilizing the two

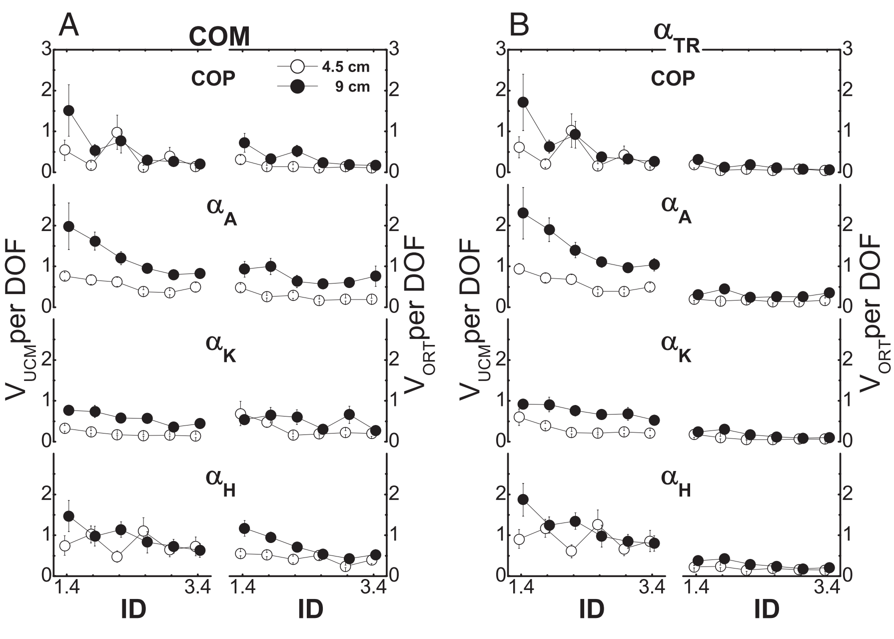

FIG. 6. Means ± SE across subjects and movement directions of the 2 components of the joint angle variance, V_{UCM} (*left y* axes) and V_{ORT} (*right y* axes) computed with respect to the hypothesis on stabilization of the COM location (*A, left*) or of the trunk orientation (α_{TR}) with respect to the vertical (*B, right*). The data are shown for each combination of movement amplitude and ID for each feedback condition (COP, ankle - α_A, knee -α_K, and hip -α_H). ○, 4.5° (cm) amplitude; ●, 9° (cm) amplitude.

performance variables are robust over manipulations of task amplitude, accuracy constraints, and type of visual feedback.

Kinematic joint synergies

Many studies have analyzed regularities in joint displacements over a wide variety of tasks including arm movement (Scholz et al. 2000; Tseng et al. 2003), two-arm pointing (Domkin et al. 2002, 2005), and whole-body actions (Krishnamoorthy et al. 2005; Scholz and Schöner 1999). In many studies, the term "synergy" referred to conjoint scaling of joint trajectories over movement repetition, changes in movement parameters, or over the realization of a single trial. PCA has been commonly used to study such regularities (Alexandrov et al. 1998, 2001a,b). In particular, Alexandrov and collaborators (2001a,b) introduced three eigenmovements (3 PCs) that could be used in combinations over a variety of whole-body tasks. In our experiments, PCA has shown the existence of a single PC that accounted for >95% of the total joint variance (similar to findings of Alexandrov et al. 2001b). However, our interpretation of this finding differs from those offered earlier such that we do not consider the first PC a synergy.

This interpretation follows a line of studies based on the UCM hypothesis (Latash et al. 2002; Scholz and Schöner 1999). According to this hypothesis, a synergy stabilizes an important performance variable. It has been applied, in particular, to kinematic analysis of multi-joint actions (Domkin et al. 2002; Scholz et al. 2000) and to analysis of muscle synergies associated with postural tasks (Krishnamoorthy et al. 2005; Scholz and Schöner 1999). Let us assume that a synergy is based on a set of n elemental variables (joint angles in our study). If a performance variable corresponds to a single equation that links elemental variables of the system, a value of the variable is expected to be associated with a subspace with the dimensionality of $(n - 1)$. In our experiments, $n = 3$, and a single synergy is expected to correspond to variance limited to a two-dimensional subspace, not to a single-dimensional PC. This logic led us to presume that the existence of a single PC accounting for nearly all the variance in the joint space reflected two synergies implemented simultaneously.

Many studies have suggested that the location of the COM should be an important performance variable stabilized by the CNS to avoid falling down during whole-body movements (Krishnamoorthy et al. 2005; Peterka 2003). Indeed, COM is located ~1 m above the level of support, while typical dimensions of the support area are of the order of 0.3×0.3 m. This imposes rather strict constraints on possible COM motion in the anterior-posterior direction. Our analysis of the structure of the joint variance with respect to the location of COM has supported the hypothesis that this was one of the two performance variables stabilized by the coordinated joint action. The variance was structured such that most of it was "good" in a sense that it did not affect COM location, reflected in R_V values significantly higher than unity. Similar findings have been described by Scholz and Schöner (1999) in their study of the sit-to-stand action and in a recent study of postural sway by Krishnamoorthy and colleagues (2005). Note that different joint covariation patterns could achieve this synergy thus leaving space for stabilization of another performance variable.

We selected another candidate performance variable, trunk orientation with respect to vertical, based on the following considerations. First, the notion of a reference vertical has been commonly used in studies of postural control (Gurfinkel et al. 1995) and stabilization of trunk orientation has been reported in studies with oscillation of the supporting surface (Buchanan and Horak 1999). Second, keeping the trunk orientation relatively unchanged allows relatively small predictable changes in signals of two major sensory modalities, those coming from the visual and vestibular systems. Analysis of the structure of joint variance has supported the hypothesis that joint angles co-varies across cycles to stabilize trunk orientation.

Taken together, the results of the analysis of the structure of joint variance with respect to the two performance variables allow us to offer the following interpretation of the PCA findings. The single PC accounting for most joint space variance reflects two synergies with different functions. One of them may be more directly related to the mechanical constraints associated with vertical posture (COM stabilization). The other may be associated with preserving stable sensory environment for the controller (trunk orientation stabilization).

The two performance variables, trunk orientation and COM position, are not perfectly independent (Buchanan and Horak 2003), although one can bend the trunk and avoid major changes in COM location or move the COM while keeping the trunk orientation relatively unchanged. These intuitive observations suggested to us that the two variables could be analyzed separately. However, it is certainly possible that the relatively weak synergy of COM stabilization is a reflection of the much stronger synergy stabilizing the trunk, i.e., that the two manifolds corresponding to stabilization of the two performance variables are not orthogonal.

The finding of stabilization of the COM location and trunk orientation fits well the reference configuration hypothesis (Feldman and Levin 1995) introduced as an extension of the equilibrium-point hypothesis for the control of voluntary movement (Feldman 1986). According to the reference configuration hypothesis, the controller specifies reference configurations for the body leading to equilibrium states, defined also by the external force field. Signals to muscles (and resulting joint rotations) are expected to reflect the tendency of the body to move toward the equilibrium states. If one assumes that control of such complex tasks as whole-body motion is based on a multi-level hierarchy (Gelfand and Tsetlin 1966), equilibrium states of the whole body (characterized, in particular, by COM location and trunk orientation) may be expected to be produced by coordinated action of elements (e.g., joint angles) at a lower level of the hierarchy that are driven by their own reference configurations. At this time, we do not feel confident to speculate about possible neurophysiological mechanisms involved in the hypothetical kinematic synergies. Commonly, the cerebellum has been invoked as a structure potentially responsible for synergy assembly (Houk and Gibson 1987; Thach and Bastian 2004), although cortical and spinal contributions to multi-element synergies have been hypothesized as well (Berkinblit et al. 1986; Lemon et al. 1998; Mussa-Ivaldi et al. 1994; Schieber 2001).

Note that two perfect synergies in the three-dimensional joint angle space correspond to two manifolds, and their intersection should have reduced the space of joint angles to a one-dimensional subspace across the feedback conditions. However, PCA showed different joint angle loadings in different feedback conditions (Fig. 4). This seeming contradiction may result from the following situations. Reduction of the joint angle space to a one-dimensional subspace is expected only if the two synergies are perfect ($R_V \gg 1$). In our subjects, one of the synergies (stabilization of the trunk orientation) was rather strong with the index of synergy corresponding to a strongly nonspherical data distribution (R_V ~4–5), whereas the other synergy (stabilization of the COM position) was relatively weak with data distributions differing significantly from a spherical distribution, but the index of synergy being just over the unity value (R_V ~ 1.5). This allows data in different conditions to satisfy both criteria but still differ in patterns of joint covariation and, consequently, in the results of the PCA. Another consideration is that our analysis is performed in a linear approximation, whereas the manifolds in the joint angle space are generally nonlinear. This means that the data may locally satisfy requirements for both synergies but correspond to different directions in the joint space.

Our selection of elemental variables (individual joint rotations in the sagittal plane) was based on an intuitive consideration that humans can move one joint independently of other joints as well as on previous studies using similar sets of elemental variables (Scholz and Schöner 1999; Scholz et al. 2000). However, it is possible that this choice was not optimal. Recent studies (Alexandrov et al. 1998, 2001a,b) have suggested that whole-body motion may be based on another set of elemental variables based on the same three major joint angles. These variables, termed eigenmovements correspond to parallel, proportional changes in all three joint angles. It would take another study to compare indices of synergies in the space of joint angles and in the space of eigenmovements.

Joint coordination and the speed-accuracy trade-off

Numerous studies have shown that humans slow down when they need to achieve a small distant target. These findings were formalized by Fitts (1954) into an equation that has been confirmed in studies of a variety of actions (Plamondon and Alimi 1997). According to Fitts' law, movement time is a monotonic function of the ID computed as a log-transformed ratio of movement amplitude to target size. Recent studies of whole-body actions have shown that this law may need to be reformulated (Danion et al. 1999; Duarte and Freitas 2005): such that changes in ID induced by manipulations of movement distance have different effects on movement time as compared with those induced by manipulations of target size.

Our studies confirmed such observations and extended them to tasks with different mechanical variables, joint angles, and COP location, the accurate motion of which was produced by the subjects. In contrast to predictions of the Fitts' law, the data for different movement amplitudes corresponded to different relations between movement time and ID. Such "fanning" of regression lines can be seen clearly in Fig. 3, *A* and *B*, for conditions with visual feedback on COP location and on joint position. Even though each of the regression lines indeed obeys the Fitts' law but the coefficients in the equation describing the Fitts' law differ, this may mean that effects of manipulations of movement amplitude and target width on movement time in our study cannot be reduced to a single parameter, ID. Changes in the slope of the relation between ID and movement time have been reported in a study of tasks performed by different effectors (Langolf et al. 1976). Changes in movement amplitude in our experiments could be associated with changes in relative joint involvement (see the data in Table 1); this could by itself contribute to the different slopes of the regression lines between movement time and ID.

Earlier, we offered an interpretation for the finding of fanning regression lines based on an idea that postural sway interfered with the task and changed the effective size of the target (Duarte and Freitas 2005). This interpretation may be used for the current studies with feedback on COP location because of the relatively large amplitude of the spontaneous COP migration during both posture and whole-body movement (Duarte and Freitas 2005; Duarte and Zatsiorsky 2002). However, we did not expect joint angles to show similar effects because leg and trunk joint angles are relatively motionless during quite standing (Gatev et al. 1999). However, our findings show similar degrees of the regression line "fanning" for the COP- and joint-based feedback conditions. These rather unexpected findings contrast earlier reports on Fitts' law being robust for accurate joint motion tasks across joints, movement amplitudes, and target sizes (Plamondon and Alimi 1997). Currently, we may only speculate that the specificity of the whole-body tasks is reflected, in particular, in relatively large, poorly reproducible joint deviations from a desired trajectory. This "joint sway" may be analogous to "movement sway" quantified as spontaneous deviations of the center of pressure during whole-body motion tasks (Latash et al. 2003). A direct comparison of tasks used in the current study to similar tasks involving only one joint at a time, e.g., performed by a sitting subject, may help test this hypothesis.

Changes in ID and in the feedback conditions had strong effects on both movement time and the total amount of variance in the joint space. These strong effects contrast the virtual lack of changes in the index of joint variance structure, R_V, used in analysis of stabilization of the COM location and trunk orientation. These findings suggest that joint synergies stabilizing these performance variables are robust across feedback conditions and accuracy constraints.

To summarize, our experiments illustrate a new facet of applying the UCM hypothesis to analysis of motor synergies. They show how PCA and analysis of structure of variance within the UCM hypothesis complement each other and allow to get insights into the origins of experimentally observed pattern of joint angle covariation. They show the robustness of such synergies and their possible relation to the reference configuration hypothesis.

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