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Motor Abundance Supports Multitasking While Standing

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Abstract

Many activities require simultaneous performance of multiple tasks. Motor redundancy may provide a key mechanism for multitasking, ensuring minimal inter-task interference. This study investigated the effect of performing two supra-postural tasks on postural stability. The component of joint configuration variance (JCV) reflecting flexible joint combinations (V_{UCM}) that stabilize the center of mass (CoM) position, and the component of JCV leading to variability (V_{ORT}) of the CoM was determined using the Uncontrolled Manifold (UCM) approach. Subjects executed a targeting task alone or in combination with a ball-balancing task. UCM analysis revealed that the joints were coordinated such that their combined variance reflected primarily V_{UCM} , without a substantial effect on CoM position stability. Evidence for this flexible control strategy increased when the ball-balancing task was added to targeting, or when the index of difficulty of targeting increased, both without leading to substantial increases in V_{ORT} or CoM position variance. The increase in joint variance when performing additional tasks without affecting adversely CoM position stability supports the hypothesis that the nervous system takes advantage of available motor redundancy for the successful performance of multiple tasks concurrently. Future work is needed to investigate the limits of this control scheme.

Keywords

postural control; quiet stance; uncontrolled manifold; multitasking

1. Introduction

Many activities require simultaneous performance of multiple tasks. Motor redundancy may provide a key mechanism for multitasking, ensuring minimal inter-task interference. This study investigated the effect of performing two supra-postural tasks on postural stability. The component of joint configuration variance (JCV) reflecting flexible joint combinations (V_{UCM}) that stabilizes the center of mass (CoM) position, and the component of JCV leading to variability (V_{ORT}) of the CoM was determined using the Uncontrolled Manifold (UCM) approach. Subjects executed a targeting task alone or in combination with a ball-balancing task. UCM analysis revealed that the joints were coordinated such that their combined variance reflected primarily V_{UCM} , without a substantial effect on CoM position stability. Evidence for this flexible control strategy increased when the ball-balancing task

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was added to targeting, or when the index of difficulty of targeting increased, both without leading to substantial increases in V_{ORT} or CoM position variance. The increase in joint variance when performing additional tasks without affecting adversely CoM position stability supports the hypothesis that the nervous system takes advantage of available motor redundancy for the successful performance of multiple tasks concurrently. Future work is needed to investigate the limits of this control scheme.

Humans interact with the environment while executing tasks with the extremities without adversely affecting postural stability. Tasks performed while controlling upright posture are often referred to as supra-postural (Mitra & Fraizer, 2004; Oullier, Bardy, Stoffregen, & Bootsma, 2004), or focal movements (Pozzo, Stapley, & Papaxanthis, 2002; Robert, Blouin, Ruget, & Mouchnino, 2007; Weeks, Forget, Mouchnino, Gravel, & Bourbonnais, 2003). External forces, joint interaction torques and changes in the body geometry while performing supra-postural tasks can challenge postural equilibrium. How does the nervous system counteract these potentially disturbing effects on posture?

The motor system is known to have substantial redundancy at the joint, muscle and neural levels. For example, to position the hand at a particular location in external space with a given orientation requires six degrees of freedom (DOFs) of joint motion. While standing, substantially more DOFs are available than necessary to achieve a given hand position and orientation. Recent studies indicate that the nervous system takes advantage of motor redundancy, or more positively viewed, motor abundance (Latash, 2000). Motor abundance has been shown to provide for flexible control of a variety of motor tasks (Latash, 2000; Scholz & Brandt, 1997; Scholz, Kang, Patterson, & Latash, 2003; Scholz & Schöner, 1999; Scholz et al., 2007; Scholz, Schöner, & Latash, 2000; Zhang, Scholz, Zatsiorsky, & Latash, 2008). Several recent studies led to the conclusion that the postural control system uses available motor abundance to stabilize the CoM position and center of pressure excursions during external and self-generated challenges to upright posture (Freitas, Duarte, & Latash, 2006b; Freitas & Scholz, 2010; Scholz et al., 2007), as well as during quiet standing (Hsu, Scholz, Schöner, Jeka, & Kiemel, 2007). In quiet standing, ankle and hip joints, typically considered most important for postural control (Jeka, Kiemel, Creath, Horak, & Peterka, 2004; Nashner & McCollum, 1985; Nashner, Shupert, Horak, & Black, 1989; Winter, Patla, Ishac, & Gage, 2003), were shown to exhibit less variance over 5-min of quiet standing than several other joints (Hsu et al., 2007). Although it is tempting to suggest that this fact reflects greater control of the hip and ankle joints than other joints, most of joint variance proximal to the hip reflected flexible joint combinations consistent with the average CoM position over time. Significantly less joint variance led to CoM position variability.

A neural control scheme that makes use of motor abundance is predicted to facilitate the performance of multiple tasks simultaneously. That the nervous system takes advantage of motor abundance to provide for flexible coordination of motor elements was recently supported by a model-experiment study based on the Uncontrolled Manifold (UCM) hypothesis (Martin, Scholz, & Schöner, 2009). That hypothesis is that the nervous system decouples the space of motor elements such that combinations of those elements that do not affect important task-relevant variables are minimally resisted while combinations that produce unwanted changes in the values of such task variables are resisted selectively. Note that this decoupling refers to the space of the motor elements, not to the motor elements themselves; e.g., decoupling of joint space into V_{UCM} (combinations that allow for task flexibility) and V_{ORT} (combinations causing unwanted variability of the task variable) subspaces requires a high degree of joint coordination. This model has similarities with the minimal intervention principle derived from optimal control theory (Todorov & Jordan, 2002), but better accounted for experimental details of reaching experiments (Martin et al., 2009). One purpose of the current study was to investigate the effects of multitasking on

control of the CoM position and, in particular, whether measured changes in joint configuration variance reflected increased flexibility when supra-postural tasks were added (Latash, Scholz, & Schöner, 2007).

Most studies of multitasking have used the dual-task paradigm (Abernethy, 1988) to examine the effect of simultaneous performance of cognitive tasks on posture (Andersson, Hagman, Talianzadeh, Svedberg, & Larsen, 2002; Dault, Geurts, Mulder, & Duysens, 2001; Lajoie, Teasdale, Bard, & Fleury, 1993; O'Shea, Morris, & Iansek, 2002; Shumway-Cook & Woollacott, 2000; Siu & Woollacott, 2007; Wulf, Mercer, McNevin, & Guadagnoli, 2004). These studies have revealed variable findings (Andersson, Yardley, & Luxon, 1998; Dault et al., 2001; Hunter & Hoffman, 2001; Lajoie et al., 1993; Marsh & Geel, 2000; Shumway-Cook & Horak, 1986; Shumway-Cook & Woollacott, 2000) on the effect of a secondary cognitive task on posture, probably due to differences in the novelty and complexity of the tasks studied. Stoffregen and colleagues (2000) reported that cognitive activities during standing, e.g., reading text, can lead to a reduction of sway compared to staring at the blank target, supporting the notion that posture is functionally regulated by the constraints of the task. This group (2007) later showed that postural sway variability was not influenced by the cognitive difficulty of tasks when they controlled for perceptual difficulty, emphasizing the need to differentiate between perceptual and cognitive influences on posture. When the perceptual task's difficulty was increased, there was a tendency for postural sway to decrease. However, changes in joint or muscle coordination underlying these effects were not investigated.

There have been fewer studies of the effect of additional motor tasks on posture. Bardy et al. (1999) observed both in-phase and anti-phase coordination of the torso and legs when subjects performed a tracking task with the head, the coordination pattern observed depending on the constraints imposed by the tracking task. Once again, stability of the coordination pattern was found to be higher when subjects tracked an object on the wall of a moving room rather than simply looking at the wall, indicating an effect of the task constraints on the coordination pattern (Oullier, Bardy, Stoffregen, & Bootsma, 2002; Oullier et al., 2004). Similarly, Smart and colleagues (Smart, Mobley, Otten, Smith, & Amin, 2004) described differences in the coordination of leg and trunk when subjects stood on different surfaces while reading text placed at two distances in front of them or when no object was present. None of these studies attempted to formally link changes in the coordination pattern directly to task success, however. Nonetheless, many studies of anticipatory postural reactions fall under the topic of multitasking (Adkin, Frank, Carpenter, & Peysar, 2002; Aruin, Forrest, & Latash, 1998; Aruin & Latash, 1996; de Wolf, Slijper, & Latash, 1998; Freitas et al., 2006b; Latash, Aruin, Neyman, & Nicholas, 1995; Massion, Ioffe, Schmitz, Viallet, & Gantcheva, 1999; Patla, Ishac, & Winter, 2002; Shiratori & Latash, 2001), although they are frequently investigated from a different point of emphasis. The relevance of these studies will be discussed further in the Discussion.

The current study investigates the role of motor abundance in the performance of multiple tasks simultaneously. Coordination was studied by evaluating the relationship between variance of the multi-joint configuration and variables more directly related to the tasks of postural control (Hsu et al., 2007) or to the supra-postural targeting tasks with the UCM approach (Scholz & Schöner, 1999). How joint configuration variance associated with (1) flexible combinations of the joints that produced a consistent CoM position (V_{UCM}) versus (2) variability of the CoM (V_{ORT}), was affected when an additional targeting task or a combined targeting and ball balancing were added to quiet standing was investigated. If motor abundance provides an advantage for multitask control, then increased joint configuration variance with the performance of an additional task was predicted to be primarily V_{UCM} (see Methods). Target size also was varied systematically to increase the

index of task difficulty (ID) (Fitts, 1954). Based on the studies of Stoffregen and colleagues (Bardy et al., 1999; Oullier et al., 2002; Stoffregen et al., 2007), increasing task difficulty might be expected to result in reduced CoM variability. This could result from by either limiting overall joint variance of more postural-related joints or by increased, but structured joint variance that reflects primarily motor abundance (V_{UCM}).

2. Methods

2.1. Participants

Eight each healthy male and female volunteers (mean age 26.81 ± 5.39 years old) participated, ranging in weight and height from 53.62–81.72 kg (mean = 67.33 ± 9.47 kg) and 1.56–1.82 m (mean = 1.73 ± 0.09 m), respectively. All subjects gave informed consent in compliance with ethical standards laid down by the Declaration of Helsinki.

2.2. Procedure

2.2.1. Apparatus—A VICON (Oxford metrics, UK) MX-13 motion measurement system sampled at 120-Hz the motion of 1.5-cm reflective markers placed on the right side of the body and trunk at approximate joint centers. Marker coordinates were filtered in MATLAB™ (Mathworks, Version 7.0.1) using a 5-Hz low-pass, bi-directional 2nd order Butterworth digital filter. Segment lengths of the body were computed from average marker positions over three seconds of static standing.

2.2.2. Equipment setup—A laser pointer was clamped on lightweight fiberboard that subjects held with both hands. A stand with a shallow indentation was mounted firmly on the top surface to hold a racket ball for the combined task. Total weight of the board and mounted objects was 196.65 g with and 155.10 g without the ball.

Two targets were mounted vertically on a wall partition, placed at a distance equal to subjects' height at the levels of the acromion and greater trochanter. The centers of the upper and lower targets were calibrated prior to data collection. Initial posture was controlled by a tripod-rod setup that was moved immediately before trial onset (Fig. 1).

2.2.3. Experimental tasks—Subjects performed (1) quiet standing holding the board still at 90° elbow flexion without the targets present (**QS**); (2) a targeting task requiring subjects to move the laser continuously between two 5.5 cm square targets, either (a) without (**Large Target No Ball**) or combined with (**Large Target With Ball**) ball balancing; (3) the same targeting task between two 2.5-cm square targets either (a) without (**Small Target No Ball**) or with (**Small Target With Ball**) ball balancing. Subjects were told to allow the body to sway naturally during all tasks but not to purposely move the legs and trunk around. Targeting tasks then were performed in random order across subjects after QS. The indices of difficulty (ID) for the large (5.5 cm) and small (2.5 cm) targets, calculated from Fitts' law (Fitts, 1954)

$$ID = \log_2(D/W) \quad (1)$$

where D = inter-target distance, and W = target width, averaged 3.31 ± 0.13 and 4.27 ± 0.13 , respectively.

Targeting tasks were paced by a metronome to control movement time (MTs), its speed based on the fastest speed with which a subject could successfully perform the targeting task to the small target without dropping the ball on after practice trials. Targeting conditions were performed in consecutive 2-min trials until subjects accumulated 80 consecutive

successful targeting cycles. For ball-balancing tasks, 10 consecutive successful cycles were required to count towards the 80 cycles. Two to seven trials were needed to acquire 80 successful cycles. Subjects were instructed to point continuously between the centers of the two targets with smooth motion, to use all arm joints and, when balancing the ball, to keep the ball from falling while following the metronome. The failure rate, defined as the ratio of the number of times that the ball was dropped to the total number of movement cycles needed before each subject reached 80 successful cycles, was 1.8% for the LTWB condition and 2% for the STWB condition (LTWB vs. STWB: $t = -0.832$, $p = .115$).

2.3. Data analysis

2.3.1. Time normalization of movement paths—After the onset and termination of upward arm movement was determined as when the pointer anterior marker on the board reached its minimum and maximum vertical positions (Fig. 2A) and confirmed from the vertical velocity profile (Fig. 2B), data were time-normalized to 100% (100 samples) with cubic spline interpolation in MATLAB™.

2.3.2. Computation of laser projection—Target locations were calibrated prior to the experiment with temporary reflective markers placed at their center. The laser pointer's orientation was determined from temporary markers at the front and back during target calibration, and reconstructed from the permanent markers on the board post-experiment (Spoor & Veldpaus, 1980). Projection of the laser onto the wall panel then was estimated geometrically at each point in the movement. The *Z*-coordinate (vertical direction) of the computed projection at the minimum and maximum laser projection was used to compute absolute and variable errors of targeting.

2.3.3. Trial selection—Trials with final laser positions within ± 2 standard deviations (*SD*) of the mean in the medial-lateral direction and within ± 1 *SD* of the median value in the vertical direction were included in the analysis, resulting in an average of 32 successful cycles per condition per subject.

2.3.4. Dependent variables

2.3.4.1. Target error: This report focuses on targeting to the higher target location because it required movement against gravity. Absolute error (*AE*) was computed as the absolute value of the across-cycles average deviation of the maximum vertical laser position from the calibrated target center. Variable error (*VE*) is the across-cycles standard deviation of the maximum vertical laser position (Schmidt, 1999). *AE* and *VE* were then averaged across subjects to obtain the mean and standard error of measurement (*SEM*).

2.3.4.2. Joint angle calculations: Reflective marker coordinates were used to calculate sagittal plane joint angles: (1) ankle, (2) knee, (3) hip, (4) lumbo–sacral junction (LSJ), (5) sternal-clavicular (6) shoulder, (7) elbow, (8) wrist, and (9) cervical-thoracic junction (CTJ), according to

$$\text{Angle} = \arccos(\text{dot}(V1, V2)) \quad (2)$$

where *V1* and *V2* are unit vectors representing the proximal segment and distal segment, respectively. Positive angles were defined as clockwise. The sterno-clavicular joint was added to increase accuracy of the geometric model used for UCM analysis. Without its inclusion, the difference between the actual hand position and that computed from the geometric model was 8.2 cm in the AP direction and 8.1 cm in the vertical direction, on average. Adding this motion reduced the discrepancies to approximately 0.5-cm.

2.3.4.3. Center of mass calculation: Location of the total body center of mass was estimated using measured body segment lengths, estimated locations of each segment's center of mass along those lengths, and their proportion to total body mass according to Winter (D. A. Winter, 1990):

$$\text{Whole body CoM position} = \frac{1}{M} \sum_{i=1}^n m_i d_i \quad (3)$$

where m_i = mass of segment 'i', d_i = distance from distal end of segment 'i' to its center of mass, and M = total body mass. Variability of the whole body CoM was calculated by computing its standard deviation across targeting cycles at each percentage of the normalized movement time and then averaged across the upward portion of the targeting cycle because the inter-cycle variability was relatively stable across the cycle. For QS, variability was computed across the 2-min of standing for each trial.

2.3.4.4. Uncontrolled Manifold (UCM) Analysis: The effect of different experimental conditions on CoM position stability and hand path consistency was addressed using the Uncontrolled Manifold (UCM) method. This method partitions variability of elemental variables, here joints, into two components (Scholz & Schöner, 1999), variance that reflects flexible combinations of the joints that are equivalent with respect to the value of a variable most clearly associated with task performance (V_{UCM} , e.g., COM position or instantaneous hand path), and variance that leads to performance variable variability (V_{ORT}). V_{UCM} occurs within the UCM, estimated linearly by the null space of the Jacobian matrix that relates small changes in joint motions to changes in the value of the performance variable. Mathematical details can be found in the Appendix. Variance of joint postures within the linearized UCM leads to a consistent CoM position across cycles or across time for QS. Joint variations lying in the complementary subspace leads to variations of the CoM position from its mean value, which is used to compute the null space. Questions about the degree of stabilization of the CoM position, then, can be addressed by comparing variances in the two subspaces, i.e., 'variance within the UCM (V_{UCM}) and variance within the orthogonal subspace (V_{ORT}). Given that the analysis is performed with respect to a UCM based on the mean joint configuration, this makes the analysis somewhat conservative because some amount of V_{ORT} is expected (Freitas, Duarte, & Latash, 2006a) and, therefore, not necessarily 'bad'. A finding of $V_{UCM} > V_{ORT}$, therefore, provides strong evidence in favor of the UCM hypothesis. For targeting tasks, V_{UCM} and V_{ORT} were computed at each percentage across time-normalized movement cycles and then averaged across the cycle for statistical analysis. For quiet standing condition, V_{UCM} and V_{ORT} were computed over the entire 2-min of relatively steady-state standing. Two different geometric models relating joint motions to COM position, from which the Jacobian is derived, were evaluated. The first included all relevant joints. The second included only the ankle, knee, hip and LSJ, with the mass proximal to the latter joint treated as a lumped sum (Winter, 1990).

2.4. Statistical analysis

All statistical analyses were performed using SPSS V.18.0 software (SPSS, Inc., Chicago, IL) with the α -level set at .05. Repeated measures analyses of variance (RM-ANOVA) were performed to evaluate the effects of factors target size (LT vs. ST) and ball condition (NB vs. WB) on the experimental variables of interest. For the UCM analyses, an additional factor was the variance type (V_{UCM} vs. V_{ORT}). Post-hoc investigations of significant effects from the RM-ANOVA were performed with Bonferroni corrections. Movement time was evaluated relative to the metronome half-period for each target size and condition using t -tests.

3. Results

3.1. Movement time (MT)

No significant differences in MT were found in the RM-ANOVA for the main effects of target size ($p = .26$) or ball condition ($p = .08$), and there were no significant interactions ($p > .07$). MT for the upward phase of the movement matched the half-period of the metronome for all conditions except LTNB (Table 1).

3.2. Targeting error

Absolute error (AE) and variable error (VE) are presented in Table 2. AE differed depending on the combination of target size and ball condition, $F(1, 15) = 6.74$, $p < .05$. AE decreased when performing the combined task compared to the targeting task alone (LTNB vs. LTWB: $F(1, 15) = 23.7$, $p < .001$; STNB vs. STWB: $F(1, 15) = 6.60$, $p < .05$). AE increased in the high ID compared to the low ID target size when performing ball balancing, $F(1, 15) = 5.1$, $p < .05$, but not for targeting alone ($p = .70$).

VE increased significantly when subjects targeted the low ID versus the high ID target size, $F(1, 15) = 21.4$, $p < .001$, likely due to the lower precision required when performing with the large target (low ID). VE did not differ significantly between WB and NB ($p = .84$). There also was no significant interaction between target size and ball condition ($p = .87$).

3.3. CoM variability

Fig. 3 presents the CoM_{AP} variability (mm) for each condition, averaged across the movement cycle. A small, but significant (ball condition: $F(1, 15) = 6.2$, $p < .05$) increase in CoM_{AP} variability occurred when adding ball-balancing (6.61 ± 0.76 mm) to targeting alone (5.16 ± 0.39 mm). This increase when performing the combined task did not differ between the low and high ID targets ($p = .045$). There was also no main effect of target size ($p = .57$). Comparisons of CoM_{AP} variability among all conditions including QS revealed a significant main effect, $F(4, 60) = 3.18$, $p < .05$. Post-hoc Bonferroni comparisons revealed that CoM_{AP} variability did not differ between any of the dynamic targeting conditions and QS (LTNB = 4.8 ± 0.35 mm vs. QS = 4.6 ± 0.42 mm: $p > .9$; LTWB = 6.62 ± 0.91 mm vs. QS: $p > 0.54$; STNB = 5.5 ± 0.59 mm vs. QS: $p > .9$; STWB = 6.6 ± 0.79 mm vs. QS: $p > .47$). The dynamic conditions also did not differ in CoM_{AP} variability from each other (minimum $p > .23$).

3.4. Joint variance

An RM-ANOVA was performed across all combinations of target size and ball condition, including QS (i.e., STNB, STWB, LTNB, LTWB vs. QS), and revealed a significant overall effect, $F(4, 60) = 22.8$, $p < .001$ (Fig. 4, top panel). Pairwise comparisons revealed, not surprisingly, that joint variance was significantly smaller for QS compared to all other target size – ball condition combinations (all comparisons, $p < .001$). Considering the targeting conditions alone, there was a significant effect of ball condition, joint variance increasing when adding the ball balancing task to tracking (NB: 34.3 ± 5.6 deg² vs. WB: 62.2 ± 9.4 deg²; $F(1, 15) = 19.2$, $p < .01$). There was also a significant interaction between target size and ball condition, $F(1, 15) = 4.5$, $p = .05$. This effect was because the increase in overall joint variance from targeting only to the combined task being greater for the high ID target (36.9 ± 6.6 deg² $\rightarrow$ 70.2 ± 9.1 deg²) compared to the low ID target (31.8 ± 5.7 deg² $\rightarrow$ 54.2 ± 10.5 deg²; Fig. 4, top panel). There was a trend for the high ID condition to have greater overall joint variance than the low ID condition ($p = .051$).

Joint configuration variance including only the ankle, knee, hip and lumbar spine (LSJ) joints (Fig. 4, bottom panel) was obtained to investigate joints not directly involved in the

targeting task. A significant overall effect was found, $F(4, 60) = 5.4, p < .01$. Except for the least difficult task (LTNB; $p = .051$), all other targeting tasks had significantly higher overall joint variance than did the QS condition (LTWB: $p < .01$; STNB: $p < .05$; STWB: $p < .05$). For the targeting tasks alone, there was no effect of target size on overall joint variance (high ID: $3.7 \pm 1.0 \text{ deg}^2$ vs. low ID: $2.8 \pm 0.54 \text{ deg}^2$; $p > .15$), nor did target size interact with the ball condition. However, adding the ball-balancing task to targeting ($4.4 \pm 1.1 \text{ deg}^2$) led to significantly higher overall joint variance compared to targeting alone ($2.1 \pm 0.52 \text{ deg}^2$; $F(1, 15) = 6.9, p < .05$).

3.5. Joint configuration variance related to CoM_{AP} position stability

3.5.1. Full, eight degree-of-freedom model—Fig. 5 shows continuous plots of across subjects, average $\pm$ SEM V_{UCM} and V_{ORT} for the upward portion of targeting cycles. Differences between these components were relatively consistent across the upward phase. Thus, the variance components were averaged across the phase (Fig. 6).

Regardless of the condition, V_{UCM} ($6.78 \pm 1.0 \text{ deg}^2$) was an order of magnitude larger than V_{ORT} ($0.83 \pm 0.14 \text{ deg}^2$), $F(1, 15) = 38.5, p < .0001$, for the targeting conditions. Our first question was whether differences between V_{UCM} and V_{ORT} observed for the targeting conditions differed from QS. We first compared the variance components for QS to the combination of all target size by ball condition combinations. The analysis resulted in a significant interaction effect of variance component by condition, $F(1, 15) = 35.8, p < .0001$. Further investigation revealed that both V_{UCM} (Targeting: $6.78 \pm 1.0 \text{ deg}^2$ vs. QS: $0.64 \pm 0.17 \text{ deg}^2$) and V_{ORT} (Targeting: 0.83 ± 0.14 vs. QS: $0.13 \pm 0.03 \text{ deg}^2$) were larger, $F(1, 15) = 46.3, p < .0001$, and $F(1, 15) = 37.7, p < .0001$, respectively, when combined across targeting conditions compared to QS. This is quite apparent in Fig. 6, top panel, for V_{UCM} . Because V_{ORT} for STNB was closest in value to that for QS, we next tested this comparison and found V_{ORT} for STNB significantly larger than for QS, $F(1, 15) = 8.4, p < .05$. Thus, both V_{UCM} and V_{ORT} increased when adding the targeting task compared to QS. The interaction of condition by variance component indicates that V_{UCM} increased more than V_{ORT} . This is evident in Fig. 6 by a greater slope of increase in V_{UCM} from QS to LTNB, which had the smallest difference from QS, compared to the slope of the increase in V_{ORT} from QS to LTWB, which had the largest difference from QS.

Focusing now on comparisons between the different targeting tasks, significant ball condition by variance component, $F(1, 15) = 19.85, p < .001$, target size by variance component, $F(1, 15) = 5.11, p < .05$, and three-way, $F(1, 15) = 5.36, p < .05$, interactions were found. Given the three-way interaction, simple interaction effects were evaluated. When considering each target size independently, the ball condition by variance component interaction was significant for both the large, $F(1, 15) = 5.95, p < .05$, and small, $F(1, 15) = 29.8, p < .0001$, target sizes. This is evident in Fig. 6, upper panel: adding the ball-balancing task to the targeting task led to a significant, 1.7 (LTNB $\rightarrow$ LTWB: $p < .01$) and 1.9 (STNB $\rightarrow$ STWB, $p < .0001$) times increase in V_{UCM} , but no significant increase in V_{ORT} (LTNB vs. LTWB, $p = .06$; STNB vs. STWB, $p = .15$). Considering each ball condition independently, the target size by variance component interaction was significant only for the WB conditions, $F(1, 15) = 6.95, p < .05$, but not for the NB conditions ($p = .32$). That is, neither V_{UCM} nor V_{ORT} were substantially different between the large (LTNB) and small (STNB) targets for targeting alone. For combined targeting and ball balancing, V_{UCM} increased significantly, from $7.55 \pm 1.49 \text{ deg}^2$ to $10.0 \pm 1.3 \text{ deg}^2$, from the low ID to the high ID target condition ($p < .05$), whereas V_{ORT} did not differ significantly between these conditions ($p = .27$).

3.5.2. Reduced, four degree-of-freedom model—Because of the segment masses, variability of joint motions of the lower extremities and trunk has more impact on changes in the CoM location than does variability of upper extremity and cervical joints, especially in the AP direction. Therefore, the effect of ankle, knee, hip and LSJ variance alone on stability of the CoM_{AP} position was investigated. Similar to the full model, the condition by variance component interaction was significant, $F(1, 15) = 4.8, p < .05$ (Fig. 6, lower panel), when comparing the combination of all targeting conditions (i.e., LTNB+LTWB+STNB+STWB) to QS. Further investigation revealed that only V_{UCM} differed (targeting: $1.06 \pm 0.24 \text{ deg}^2$ vs. QS: $0.64 \pm 0.17 \text{ deg}^2, F(1, 15) = 23.0, p < .001$), but not V_{ORT} (targeting: $0.09 \pm 0.17 \text{ deg}^2$ vs. QS: $0.13 \pm 0.03 \text{ deg}^2, p = .08$). STNB, the targeting condition with the smallest increase in V_{UCM} over QS, was significantly larger, $F(1, 15) = 5.8, p < .05$. V_{ORT} for STWB, which had the largest difference compared to QS, was also significantly larger, $F(1, 15) = 4.7, p < .05$ (Fig. 6, lower panel). This result is consistent with the larger CM_{AP} variability in this condition compared to QS (see above). However, none of the other targeting conditions had significantly higher V_{ORT} than during QS (LTNB: $p = .8$; LTWB: $p = .12$; STNB: $p = .2$). Thus, overall, adding an additional task to quiet standing led to substantial increases in V_{UCM} in this 4-DOF model, but a smaller or no increase in V_{ORT} (Fig. 6B).

Focusing now on comparisons involving the targeting conditions, significance was found only for main effects of ball condition, $F(1, 15) = 6.96, p < .05$, and variance component, $F(1, 15) = 17.8, p < .001$, and their interaction, $F(1, 15) = 6.6, p < .05$. Target size had no effect in the reduced model results ($p = .17$). The significant interaction is apparent in Fig. 6, lower panel. Regardless of the target's ID, adding ball balancing to targeting led to a significantly greater increase in V_{UCM} (WB: $1.43 \pm 0.4 \text{ deg}^2 > \text{NB: } 0.68 \pm 0.19 \text{ deg}^2$) than in V_{ORT} (WB: $0.12 \pm 0.03 \text{ deg}^2 > \text{NB: } 0.07 \pm 0.01 \text{ deg}^2$).

3.6. Joint configuration variance related to stability of the 2D hand path

Adding the ball-balancing task (i.e., LTWB and STWB) to targeting alone (i.e., LTNB and STNB) led to increases in both V_{UCM} and V_{ORT} (Fig. 7). However, there was a significant interaction between ball condition and variance component, $F(1, 15) = 19.6, p < .000$, which held whether the target size was large, $F(1, 15) = 10.3, p < .01$, or small, $F(1, 15) = 24.9, p < .0001$. In both cases, V_{UCM} increased significantly when adding the ball-balancing task (low ID; LTNB: $4.0 \pm 0.79 \text{ deg}^2 \rightarrow \text{LTWB: } 7.35 \pm 1.48 \text{ deg}^2, F_{1,15} = 12.3, p < .01$ and high ID; STNB: $5.2 \pm 0.94 \text{ deg}^2 \rightarrow \text{STWB: } 9.97 \pm 1.3 \text{ deg}^2, F(1, 15) = 27.0, p < .0001$. V_{ORT} increased in the combined task compared to targeting alone for the low ID target (LTNB: $0.72 \pm 0.13 \text{ deg}^2 \rightarrow \text{LTWB: } 1.12 \pm 0.18 \text{ deg}^2, F(1, 15) = 5.0, p < .05$, and approached significance for the high ID target (STNB: $0.47 \pm 0.09 \text{ deg}^2 \rightarrow \text{STWB: } 0.71 \pm 0.10 \text{ deg}^2, F(1, 15) = 4.4, p = .054$). Thus, while both V_{UCM} and V_{ORT} increased when adding the additional ball-balancing task to targeting, the increase in V_{UCM} , the component reflecting flexible joint combinations that produce a consistent hand path, was larger.

To further investigate this difference, the relative change of both V_{UCM} and V_{ORT} between either the ball conditions or between the two target IDs were computed (Table 3). The increase in V_{UCM} when going from the targeting condition alone to the combined task was larger than for V_{ORT} , $F(1, 15) = 19.6, p < .001$, and this effect was stronger for the high ID target condition, $F(1, 15) = 5.2, p < .05$. However, if expressing the change between targeting alone to the combined task as a ratio of the targeting alone value (e.g., (LTWB-LTNB)/LTNB), then no difference between the changes in V_{UCM} compared to V_{ORT} was found ($p > .62$). Comparing the change in V_{UCM} and V_{ORT} between the low and high ID targets also revealed a significantly greater increase in V_{UCM} compared to V_{ORT} , $F(1, 15) = 14.3, p < .01$, and this difference was greatest when combining targeting with ball balancing

than for targeting alone, $F(1, 15) = 5.2, p < .05$. In fact, while V_{UCM} increased when targeting the high ID target compared to the low ID target, V_{ORT} actually decreased when the task became more difficult. This difference remained after normalizing the change in each component by the value for the low ID condition (e.g., $(STNB-LTNB)/LTNB$; $F(1, 15) = 19.7, p < .001$).

4. Discussion

This study investigated the hypothesis that motor abundance plays an important role in enabling multitasking without adversely affecting postural control. Although much of the joint configuration variance of the ankle, knee, hip and LSJ joints is likely related to stabilizing the CoM from disturbances caused by arm movement during targeting, some of that joint movement also may assist with the targeting behavior. Moreover, some combinations of joint movements that would assist the targeting behavior could also act to disturb the CoM. A control system that takes advantage of motor abundance could largely resolve this problem by allowing flexible combinations of joint motions to assist the targeting behavior as long as they preserve CoM stability. This requires restricting other joint combinations that would lead to postural instability. This assumes that the CNS plans for a family of coordination solutions that occur in time, rather than a sequence of fixed solutions. If true, then one should see a stronger signature of the supra-postural tasks within the subspace of joint space referred to as the UCM and a minimal effect in the complementary subspace that leads to changes in the CoM position. The results of the current investigation largely support this hypothesis.

4.1. Multitasking led to changes in joint configuration variance related primarily to the use of motor abundance

The focus of the current study is on stability of the anterior-posterior excursion of the center of mass (CoM_{AP}) position because of its importance to postural stability. When subjects stood quietly, variance of joint combinations equivalent with respect to the task of stabilizing the CoM_{AP} position, i.e., V_{UCM} , was significantly larger than V_{ORT} , consistent with results of previous studies (Hsu et al., 2007; Krishnamoorthy, Yang, & Scholz, 2005). We will refer to this difference, $V_{UCM} > V_{ORT}$, in what follows as the “UCM effect”. When adding the performance of the targeting task alone to upright standing, a significant increase in overall joint variability was observed but without a concomitant increase in CoM_{AP} position variability. Hence, the increased overall joint variability was structured selectively such that V_{UCM} increased substantially while V_{ORT} increased much less than its value during quiet standing.

When ball balancing was added to produce an additional constraint on performance, overall joint variance increased further. CoM_{AP} variability did increase somewhat when performing the combined task in the low ID (5.5-cm target) condition due to an increase in V_{ORT} . However, the increase in V_{ORT} was small and only the difference between the LTNB and LTWB conditions approached significance, consistent with the significant increase in CoM_{AP} variability for the low ID condition. Nevertheless, the greatest increase in joint configuration variance was due to the increase in V_{UCM} . This was true for the full geometric model as well as a 4-joint model.

The finding of increased joint variance with each additional supra-postural task that was primarily V_{UCM} indicates enhanced coordination among the component DOFs to preserve CoM stability in the face of the need to perform additional tasks. Otherwise, we would expect to see similar or at least substantial increases in V_{ORT} , with associated increases in CoM_{AP} variability. The observed increase in the range of joint combinations used, i.e., increased V_{UCM} , when performing the combined task even with the 4-DOF model, may

represent compensations for joint motions related to the arm tasks that would otherwise lead to CoM variability. Our results are in line with those of a recent study of a multi-digit coordination that required concurrent stabilization of total force and total moment of force (Zhang et al., 2008).

The current results also are consistent with studies of anticipatory postural adjustments where the effect of a focal task such as dropping a load on changes in the center of pressure or CoM have been considered (Krishnamoorthy, Latash, Scholz, & Zatsiorsky, 2003, 2004). Recent studies have examined flexibility of postural synergies with the UCM approach when subjects performed task requiring explicit or implicit changes in posture, such as actively moving the center of pressure (Freitas et al., 2006a; Klous, Danna-dos-Santos, & Latash, 2010). For example, Klous and colleagues (Klous et al., 2010) found postural muscles to be organized into muscle modes that co-varied to produce consistent changes in the targeted moment of force about the foot as well as the shear force that was not specified. Although these authors investigated the effects of different applied loads on the stabilization of the moment of force, they did not directly examine synergies related to stabilizing the CoM or alternative measures of postural stability. Danna-Dos-Santos and colleagues (Danna-Dos Santos, Degani, & Latash, 2008) had subjects perform voluntary whole-body sway under different challenging conditions where the supra-postural task was more directly related to the postural control system than in the current study. Differences in flexibility of muscle synergies used to control center of pressure excursion, the performance variable, across levels of task difficulty were not found. The effect of the task on postural stability per se was not examined. Freitas et al. (2006a) did investigate CoM stability in subjects who performed a targeting task where the controlled variable was either CoP or individual leg joint excursions. Flexible kinematic synergies among ankle, knee and hip joint motion were found that stabilized (i.e., $V_{UCM} > V_{ORT}$) both the CoM position and trunk orientation. The reported structure of joint variance was not found to differ substantially between the tasks, which also included a Fitts' type manipulation (Fitts, 1954). Thus, the results reported in the current article are novel in that they examined supra-postural tasks that were relatively distinct from the postural control system, and compared performance with the dynamic tasks to quiet standing as well as across supra-postural tasks presenting different levels of difficulty.

What can account for the increased use of motor abundance to stabilize the CoM when additional tasks were performed? One possible mechanism is an increase in the gains of feedback loops. It has been proposed that the nervous system utilizes back-coupling that is tunable via feedback loops to compensate for errors among movement components in a task-specific way (Latash, Shim, Smilga, & Zatsiorsky, 2005; Martin, Scholz, & Schöner, 2005). Back-coupling plays a prominent role in recent model of motor control based on the UCM hypothesis (Martin et al., 2009). The presence of back-coupling from movement-related sensory feedback to the motor plan, transformed into appropriate joint combinations, was shown to be necessary in model simulations to account for the well-known movement phenomena of motor-equivalence (Martin et al., 2005). Although that analysis did not provide an account of joint variance, Martin et al. (2009) showed that four joint planar reaching tasks were associated with a substantial amount of self-motion, a component of the joint velocity vector that does not affect the velocity of the hand. A dynamic model of neural control was developed to account for reaching. Simulations of that model corroborated experimental findings of substantial self-motion during reaching (Scholz et al., 2011). A similar control model developed to account for supra-postural tasks is possible, although it likely would not involve a specific plan for the postural component as is the case for voluntary movement. Also, a postural control model must consider stabilization against both buckling and falling over, where the effects of gravity become more complicated than for reaching. A preliminary model of postural control based on the UCM concept was recently

reported (Reimann, Schöner, & Scholz, 2010, 2011), based in part on the model of Martin et al. (2009). Recent simulations of a model (Reimann et al., 2011) that includes both segmental motor control and passive mechanisms nicely accounts for many previously identified features of upright standing (Hsu et al., 2007).

This postural model proposes to treat each joint as a damped mass-spring system, controlled by the CNS via specification of the system's equilibrium point (λ -model) (Feldman, 1986; Feldman & Latash, 2005; Feldman & Levin, 1995; Latash, 2010a, 2010b; Latash & Goodman, 1994). Using proprioceptive feedback of each joint angle, the equilibrium points are shifted to counteract deviations from a preset value for each joint, which are defined relative to stability of the task variable, e.g., CoM or head position. This allows the destabilizing effects of gravity to be neutralized without having to estimate those effects explicitly by an internal model. Adding a control mechanism similar to the Martin et al. (2009) model that exploits the redundancy of the task by selectively controlling those directions in joint space affecting the CoM position leads to a variance structure similar to that reported in the studies reviewed above (i.e., $V_{UCM} > V_{ORT}$). Further development of this model may allow us to better understand mechanisms underlying the use of motor abundance for multitasking as in the current study.

Results of the current study suggest a control strategy in which changes of joint configuration that are irrelevant for stabilizing the CoM_{AP} are selectively released from control when other tasks are performed simultaneously. This is in line with the “task-dynamic approach” proposed by Saltzman and Kelso (Saltzman & Kelso, 1987). In this theoretical account, the control of task-relevant variables such as the position of the CoM in the current study is specified by an appropriate abstract dynamical system (i.e., a point-attractor). Action units (muscles, joints) are related to the task-relevant variables by nonlinear dynamics. Thus, phenomena such as motor-equivalence and the related selective changes in joint variance observed in the present study are viewed in the task-dynamic approach as implicit consequences of a task's underlying dynamics. The modeling of Martin et al. (2009) captures the spirit of that approach.

4.2. Hand position variability increased when performing targeting and ball balancing simultaneously, although effects on target-error were mixed

Because hand movement during the targeting task occurred primarily in the sagittal plane, our analysis focused on the two-dimensional, sagittal plane hand position ($Hand_{2D}$). Regardless of the targeting condition, V_{UCM} related to producing a consistent $Hand_{2D}$ path was substantially and significantly larger than V_{ORT} . When subjects performed either the targeting task alone or in combination with ball balancing, V_{UCM} increased while V_{ORT} actually decreased, leading to less hand path variance when performing with the high ID target (Fig. 7). Adding ball balancing to targeting resulted in increases of both variance components. However, this increase was relatively greater for V_{UCM} and the increase in V_{ORT} was only significant for the large target, low ID condition, leading to slightly increased variability of the $Hand_{2D}$ position. Thus, adding the additional ball-balancing task challenged control of the $Hand_{2D}$ position. However, as noted, V_{UCM} increased proportionally more than V_{ORT} in all cases, indicating that the variance was structured in a similar manner as for CoM position but just not as selectively. Apparently, therefore, priority was given compensating for joint variations that would otherwise disturb the CoM position over hand path control. This finding is in line with the results of other studies using dual-task paradigms to study postural control in standing (Brauer, Woollacott, & Shumway-Cook, 2002; Siu & Woollacott, 2007). In those studies, participants prioritized balance over the secondary task, so that postural stability was not influenced by a concurrent cognitive task.

Although V_{ORT} increased when subjects performed the combined task compared to targeting alone, this increase did not impact significantly the consistency of targeting. Absolute error was actually lower when adding ball balancing to targeting without a significant difference in movement time. And variable error did not differ between the two tasks. Absolute error was significantly higher when targeting the high ID target compared to the low ID target, however. Increased V_{ORT} leads to higher hand path variance. However, this apparently was limited and adequately constrained near the target to attain relatively accurate performance.

5. Conclusions

The results of this study provide support for the hypothesis that successful performance of multiple tasks simultaneously can be accomplished because the nervous system is designed to take advantage of the available abundance of the neuromuscular system. Rather than motor abundance being a problem, therefore, it provides for flexible solutions to joint and muscle coordination that can accommodate both increasing task difficulty (i.e., when targeting is performed with a high ID target) and the need to perform multiple tasks simultaneously. Together, these findings indicate that the motor system is capable of deriving numerous and equally effective methods to ensure the successful completion of tasks. The results suggest that complex dual-task paradigms provide a valuable means by which to gain insight into how motor coordination changes to meet task demands. Moreover, the results of this study provide important constraints on the development of future models of multi-DOF postural control and the sensory estimation underlying that control.

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6. Appendix

The question of whether a selective increase in the number of joint combinations that were equivalent with respect to the average value of a performance variable (e.g., CoM), occurs when subjects performed additional motor tasks was addressed using the Uncontrolled Manifold (UCM) method of analysis (Scholz & Schöner, 1999), as follows:

1. The geometric model relating either the CoM_{AP} or hand position to the joint angle configuration and segment lengths was determined. The model for the CoM_{AP} position was composed of nine joint angles: (1) ankle, (2) knee, (3) hip, (4) LSJ, (5) sterno-clavicular, (6) shoulder, (7) elbow, (8) wrist, and (9) CTJ. The number of dimensions of the joint configuration space are thus $n = 9$ for hypotheses about control of the anterior-posterior center of mass (CoM_{AP}) position. For the 2D hand position, $n = 8$ (CTJ angle does not play a role). The geometric model for CoM_{AP} position spans a $d = 1$ dimensional task space, and with respect to control of the hand's sagittal plane movement, a $d = 2$ dimensional task space. Thus, the system is redundant ($n > d$) with respect to the motion of either task variable. The geometric model relating the CoM_{AP} position to the joint configuration, with the origin at the 5th metatarsal of the foot, is:

$$\begin{aligned}
\text{CoM}_{AP} = & M_{\text{foot}} * (d_{\text{foot}} * l_{\text{foot}}) + \dots \\
& M_{\text{shank}} * [d_{\text{shank}} * l_{\text{shank}} * \cos(\pi - \theta_{\text{ankle}})] + \dots \\
& M_{\text{thigh}} * [d_{\text{thigh}} * l_{\text{thigh}} * \cos(\pi - \theta_{\text{ankle}} + \theta_{\text{knee}})] + \dots \\
& M_{\text{pelvis}} * [d_{\text{pelvis}} * l_{\text{pelvis}} * \cos(\pi - \theta_{\text{ankle}} + \theta_{\text{knee}} + \theta_{\text{hip}})] + \dots \\
& M_{\text{trunk}} * [d_{\text{trunk}} * l_{\text{trunk}} * \cos(\pi - \theta_{\text{ankle}} + \theta_{\text{knee}} + \theta_{\text{hip}} + \theta_{\text{LSJ}})] + \dots \\
M_{\text{sterno-clavicular}} * & [d_{\text{sterno-clavicular}} * l_{\text{sterno-clavicular}} * \cos(\pi - \theta_{\text{ankle}} + \theta_{\text{knee}} + \theta_{\text{hip}} + \theta_{\text{LSJ}} + \theta_{\text{sterno-clavicular}})] + \dots \\
M_{\text{UpperArm}} * & [d_{\text{UpperArm}} * l_{\text{UpperArm}} * \cos(\pi - \theta_{\text{ankle}} + \theta_{\text{knee}} + \theta_{\text{hip}} + \theta_{\text{LSJ}} + \theta_{\text{sterno-clavicular}} + \theta_{\text{shoulder}})] + \dots \\
M_{\text{ForeArm}} * & [d_{\text{ForeArm}} * l_{\text{ForeArm}} * \cos(\pi - \theta_{\text{ankle}} + \theta_{\text{knee}} + \theta_{\text{hip}} + \theta_{\text{LSJ}} + \theta_{\text{sterno-clavicular}} + \theta_{\text{shoulder}} + \theta_{\text{elbow}})] + \dots \\
M_{\text{hand}} * & [d_{\text{hand}} * l_{\text{hand}} * \cos(\pi - \theta_{\text{ankle}} + \theta_{\text{knee}} + \theta_{\text{hip}} + \theta_{\text{LSJ}} + \theta_{\text{scapular}} + \theta_{\text{sterno-clavicular}} + \theta_{\text{elbow}} + \theta_{\text{wrist}})] + \dots \\
& M_{\text{head}} * [d_{\text{head}} * l_{\text{head}} * \cos(\pi - \theta_{\text{ankle}} + \theta_{\text{knee}} + \theta_{\text{hip}} + \theta_{\text{LSJ}} + \theta_{\text{CTJ}})]
\end{aligned} \tag{A1}$$

where $\{\theta_{\text{ankle}} \dots \theta_{\text{CTJ}}\}$ are the externally defined joint angles; $\{l_{\text{Foot}} \dots l_{\text{Head}}\}$ are the lengths of the respective segments calculated from the static calibration trial; $\{d_{\text{Foot}} \dots d_{\text{Head}}\}$ are the percentages of the segment lengths from the distal end where the mass of that segment lies; and; $\{M_{\text{Foot}} \dots M_{\text{Head}}\}$ are the proportion of total body mass for each of these segments (D. A. Winter, 1990).

2. Small changes in a performance variable are related to $\Delta\theta$ through the Jacobian, J , of the geometric model. J_i is a matrix (vector for $d = 1$) of partial derivatives of the task variable, i.e., CoM_{AP} and Hand_{2D} relative to θ_i at sample 'i'. For the CoM_{AP} position,

$$J_i = \left[\frac{\partial \text{CoM}_{AP}}{\partial \theta_{\text{ankle}}} \quad \frac{\partial \text{CoM}_{AP}}{\partial \theta_{\text{knee}}} \quad \dots \quad \frac{\partial \text{CoM}_{AP}}{\partial \theta_{\text{wrist}}} \quad \frac{\partial \text{CoM}_{AP}}{\partial \theta_{\text{CTJ}}} \right] \tag{A2}$$

3. The UCM subspace of joint space is approximated linearly by computing the nullspace of J_i at sample 'i' based on the mean joint configuration across targeting cycles at each time-normalized sample.

$$J_i \cdot (\bar{\theta}_i) \cdot \varepsilon_i = 0 \tag{A3}$$

where, $\bar{\theta}_i$ is the mean joint configuration at sample 'i' and ε_i are the unit vectors spanning the nullspace.

4. The mean-free joint configuration $s(\theta_{i,j} - \bar{\theta}_i)$ at each sample 'i' for trial 'j' was then projected into the nullspace (A4) and its complement (A5):

$$\theta_{\parallel} = (\theta_{i,j} - \bar{\theta}_i) \cdot \varepsilon_i \tag{A4}$$

$$\theta_{\perp} = (\theta_{i,j} - \bar{\theta}_i) - \theta_{\parallel} \tag{A5}$$

where $\theta_{\parallel}$ is the component the joint configuration vector after projection into the nullspace, and $\theta_{\perp}$ is the component after projection into the complementary subspace.

5. Variance across trials of the magnitudes of the projections at each sample 'i' were then computed and divided by the number of dimensions in each space:

$$V_{UCM} = \sigma_{\parallel}^2 = \frac{\sum_{\parallel}^{n-d} \sum_{j=1}^N \theta_{\parallel}^2}{(n-d) \cdot N} \quad (A6)$$

$$V_{ORT} = \sigma_{\perp}^2 = \frac{\sum_{\perp}^d \sum_{j=1}^N \theta_{\perp}^2}{d \cdot N} \quad (A7)$$

where $\theta_{\parallel}^2$ is variance within the UCM (V_{UCM}) and $\theta_{\perp}^2$ is variance in the joint space orthogonal to the UCM (V_{ORT}). N is the number of repetitions (cycles), n is the total number of DOFs (joints), and d is the number of DOFs describing the task. Because the dimensions of the UCM and orthogonal spaces differ, the variance components computed for each subspace were normalized to the number of dimensions of the respective subspace. Thus, the measures of V_{UCM} and V_{ORT} reported here are the variances per DOF. For CoM_{AP} , variance of the nullspace projections was divided by 8, while variance of the complementary subspace projections was divided by 1.

References

- Abernethy B. Dual-task methodology and motor skills research: Some applications and methodological constraints. *Journal of Human Movement Studies*. 1988; 14:101.
- Adkin AL, Frank JS, Carpenter MG, Peysar GW. Fear of falling modifies anticipatory postural control. *Experimental Brain Research*. 2002; 143:160–170.
- Andersson G, Hagman J, Talianzadeh R, Svedberg A, Larsen HC. Effect of cognitive load on postural control. *Brain Research Bulletin*. 2002; 58:135–139. [PubMed: 12121823]
- Andersson G, Yardley L, Luxon L. A dual-task study of interference between mental activity and control of balance. *American Journal of Otology*. 1998; 19:632–637. [PubMed: 9752972]
- Aruin AS, Forrest WR, Latash ML. Anticipatory postural adjustments in conditions of postural instability. *Electroencephalography and Clinical Neurophysiology*. 1998; 109:350–359. [PubMed: 9751298]
- Aruin AS, Latash ML. Anticipatory postural adjustments during self-initiated perturbations of different magnitude triggered by a standard motor action. *Electroencephalography and Clinical Neurophysiology*. 1996; 101:497–503. [PubMed: 9020822]
- Bardy BG, Marin L, Stoffregen TA, Bootsma RJ. Postural coordination modes considered as emergent phenomena. *Journal of Experimental Psychology: Human Perception and Performance*. 1999; 25:1284–1301. [PubMed: 10531664]
- Brauer SG, Woollacott M, Shumway-Cook A. The influence of a concurrent cognitive task on the compensatory stepping response to a perturbation in balance-impaired and healthy elders. *Gait & Posture*. 2002; 15:83. [PubMed: 11809584]
- Danna-Dos Santos A, Degani AM, Latash ML. Flexible muscle modes and synergies in challenging whole-body tasks. *Experimental Brain Research*. 2008; 189:171–187.
- Dault MC, Geurts AC, Mulder TW, Duysens J. Postural control and cognitive task performance in healthy participants while balancing on different support-surface configurations. *Gait & Posture*. 2001; 14:248–255. [PubMed: 11600328]
- De Wolf S, Slijper H, Latash ML. Anticipatory postural adjustments during self-paced and reaction-time movements. *Experimental Brain Research*. 1998; 121:7–19.
- Feldman AG. Once more on the equilibrium-point hypothesis (lambda model) for motor control. *Journal of Motor Behavior*. 1986; 18:17–54. [PubMed: 15136283]
- Feldman AG, Latash ML. Testing hypotheses and the advancement of science: Recent attempts to falsify the equilibrium point hypothesis. *Experimental Brain Research*. 2005; 161:91–103.

- Feldman AG, Levin MF. The origin and use of positional frames of reference in motor control. *Behavioral and Brain Science*. 1995; 18:723–806.
- Fitts PM. The information capacity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology*. 1954; 47:381–391.
- Freitas SM, Duarte M, Latash ML. Two kinematic synergies in voluntary whole-body movements during standing. *Journal of Neurophysiology*. 2006a; 95:636–645. 00482.2005 [pii] 10.1152/jn.00482.2005. [PubMed: 16267118]
- Freitas SM, Duarte M, Latash ML. Two kinematic synergies in voluntary whole-body movements during standing. *Journal of Neurophysiology*. 2006b; 95:636–645. [PubMed: 16267118]
- Freitas SM, Scholz JP. A comparison of methods for identifying the Jacobian for uncontrolled manifold variance analysis. *Journal of Biomechanics*. 2010; 43:775–777. S0021-9290(09)00607-1 [pii] 10.1016/j.jbiomech.2009.10.033. [PubMed: 19922938]
- Hsu WL, Scholz JP, Schöner G, Jeka JJ, Kiemel T. Control and estimation of posture during quiet stance depends on multijoint coordination. *Journal of Neurophysiology*. 2007; 97:3024–3035. [PubMed: 17314243]
- Hunter MC, Hoffman MA. Postural control: visual and cognitive manipulations. *Gait & Posture*. 2001; 13:41–48. [PubMed: 11166553]
- Jeka JJ, Kiemel T, Creath R, Horak FB, Peterka R. Controlling human upright posture: Velocity information is more accurate than position or acceleration. *Journal of Neurophysiology*. 2004; 92:2368–2379. 10.1152/jn.00983.2003 [PubMed: 15140910]
- Klous M, Danna-dos-Santos A, Latash ML. Multi-muscle synergies in a dual postural task: evidence for the principle of superposition. *Experimental Brain Research*. 2010; 202:457–471. 10.1007/s00221-009-2153-2
- Krishnamoorthy V, Latash ML, Scholz JP, Zatsiorsky VM. Muscle synergies during shifts of the center of pressure by standing persons. *Experimental Brain Research*. 2003; 152:281–292.
- Krishnamoorthy V, Latash ML, Scholz JP, Zatsiorsky VM. Muscle modes during shifts of the center of pressure by standing persons: Effect of instability and additional support. *Experimental Brain Research*. 2004; 157:18–31.
- Krishnamoorthy V, Yang JF, Scholz JP. Joint coordination during quiet stance: Effects of vision. *Experimental Brain Research*. 2005; 164:1–17.
- Lajoie Y, Teasdale N, Bard C, Fleury M. Attentional demands for static and dynamic equilibrium. *Experimental Brain Research*. 1993; 97:139–144.
- Latash M. There is no motor redundancy in human movements. There is motor abundance. *Motor Control*. 2000; 4:259–261. [PubMed: 10970151]
- Latash ML. The organization of quick corrections within a two-joint synergy in conditions of unexpected blocking and release of a fast movement. *Clinical Neurophysiology*. 2000; 111:975–987. [PubMed: 10825703]
- Latash ML. Motor synergies and the equilibrium-point hypothesis. *Motor Control*. 2010a; 14:294–322. [PubMed: 20702893]
- Latash ML. Stages in learning motor synergies: A view based on the equilibrium-point hypothesis. *Human Movement Science*. 2010b; 29:642–654. [PubMed: 20060610]
- Latash ML, Aruin AS, Neyman I, Nicholas JJ. Anticipatory postural adjustments during self inflicted and predictable perturbations in Parkinson's disease. *Journal of Neurology, Neurosurgery and Psychiatry*. 1995; 58:326–334.
- Latash ML, Goodman SR. An equilibrium-point model of electromyographic patterns during single-joint movements based on experimentally reconstructed control signals. *Journal of Electromyography and Kinesiology*. 1994; 4:230–241. [PubMed: 20870562]
- Latash ML, Scholz JP, Schöner G. Toward a new theory of motor synergies. *Motor Control*. 2007; 11:276–308. [PubMed: 17715460]
- Latash ML, Shim JK, Smilga AV, Zatsiorsky VM. A central back-coupling hypothesis on the organization of motor synergies: a physical metaphor and a neural model. *Biological Cybernetics*. 2005; 92:186–191. [PubMed: 15739110]
- Marsh AP, Geel SE. The effect of age on the attentional demands of postural control. *Gait & Posture*. 2000; 12:105–113. [PubMed: 10998606]

- Martin V, Scholz JP, Schöner G. Redundancy, self-motion, and motor control. *Neural Computation*. 2009; 21:1371–1414. [PubMed: 19718817]
- Martin, V.; Scholz, JP.; Schöner, G. A theoretical account for the uncontrolled manifold and motor equivalence in pointing movements; Paper presented at the Progress in Motor Control V; University Park. Pennsylvania State University; 2005 Aug 17-20.
- Massion J, Ioffe M, Schmitz C, Viallet F, Gantcheva R. Acquisition of anticipatory postural adjustments in a bimanual load-lifting task: Normal and pathological aspects. *Experimental Brain Research*. 1999; 128:229–235.
- Mitra S, Fraizer EV. Effects of explicit sway-minimization on postural--suprapostural dual-task performance. *Human Movement Science*. 2004; 23:1–20. [PubMed: 15201038]
- Nashner LM, McCollum G. The organization of human postural movements: A formal basis and experimental synthesis. *Behavioral and Brain Science*. 1985; 8:135–172.
- Nashner LM, Shupert CL, Horak FB, Black FO. Organization of posture controls: an analysis of sensory and mechanical constraints. *Progress in Brain Research*. 1989; 80:411–418. [PubMed: 2699375]
- O'Shea S, Morris ME, Iansek R. Dual task interference during gait in people with Parkinson disease: Effects of motor versus cognitive secondary tasks. *Physical Therapy*. 2002; 82:888. [PubMed: 12201803]
- Oullier O, Bardy BG, Stoffregen TA, Bootsma RJ. Postural coordination in looking and tracking tasks. *Human Movement Science*. 2002; 21:147–167. [PubMed: 12167296]
- Oullier O, Bardy BG, Stoffregen TA, Bootsma RJ. Task-specific stabilization of postural coordination during stance on a beam. *Motor Control*. 2004; 8:174–187. [PubMed: 15118201]
- Patla AE, Ishac MG, Winter DA. Anticipatory control of center of mass and joint stability during voluntary arm movement from a standing posture: Interplay between active and passive control. *Experimental Brain Research*. 2002; 143:318–327.
- Pozzo T, Stapley PJ, Papaxanthis C. Coordination between equilibrium and hand trajectories during whole body pointing movements. *Experimental Brain Research*. 2002; 144:343–350.
- Reimann, H.; Schöner, G.; Scholz, JP. Exploiting redundancy for maintaining upright stance - a model of human posture; Paper presented at the Bernstein Conference on Computational Neuroscience; Berlin, Germany. 2010.
- Reimann, H.; Schöner, G.; Scholz, JP. Passive effects in the control of upright stance; Paper presented at the Progress in Motor Control VIII; Cincinnati, OH. 2011.
- Robert G, Blouin J, Ruget H, Mouchnino L. Coordination between postural and movement controls: effect of changes in body mass distribution on postural and focal component characteristics. *Experimental Brain Research*. 2007; 181:159–171.
- Saltzman E, Kelso JA. Skilled actions: A task-dynamic approach. *Psychological Review*. 1987; 94:84–106. [PubMed: 3823306]
- Schmidt, RA. Motor control and learning: A behavioral emphasis. Champon, IL: Human Kinetics; 1999.
- Scholz JP, Brandt L. Trajectory formation and development of the control of standing up from sitting. *Motor Control*. 1997; 1:314–339.
- Scholz JP, Dwight-Higgin T, Lynch JE, Tseng YW, Martin V, Schöner G. Motor equivalence and self-motion induced by different movement speeds. *Experimental Brain Research*. 2011; 209:319–332.
- Scholz JP, Kang N, Patterson D, Latash ML. Uncontrolled manifold analysis of single trials during multi-finger force production by persons with and without Down syndrome. *Experimental Brain Research*. 2003; 153:45–58.10.1007/s00221-003-1580-8
- Scholz JP, Schöner G. The uncontrolled manifold concept: Identifying control variables for a functional task. *Experimental Brain Research*. 1999; 126:289–306.
- Scholz JP, Schöner G, Hsu WL, Jeka JJ, Horak FB, Martin V. Motor equivalent control of the center of mass in response to support surface perturbations. *Experimental Brain Research*. 2007; 180:163–179.
- Scholz JP, Schöner G, Latash ML. Identifying the control structure of multijoint coordination during pistol shooting. *Experimental Brain Research*. 2000; 135:382–404.

- Shiratori T, Latash ML. Anticipatory postural adjustments during load catching by standing subjects. *Clinical Neurophysiol.* 2001; 112:1250–1265.
- Shumway-Cook A, Horak FB. Assessing the influence of sensory interaction on balance. *Physical Therapy.* 1986; 66:1548. [PubMed: 3763708]
- Shumway-Cook A, Woollacott M. Attentional demands and postural control: The effect of sensory context. *Journal of Gerontology A Medical Sciences.* 2000; 55(1):M10–16.
- Siu KC, Woollacott MH. Attentional demands of postural control: the ability to selectively allocate information-processing resources. *Gait & Posture.* 2007; 25:121–126. [PubMed: 16554158]
- Smart LJ, Mobley BS, Otten EW, Smith DL, Amin MR. Not just standing there: the use of postural coordination to aid visual tasks. *Human Movement Science.* 2004; 22:769–780. [PubMed: 15063053]
- Spoor CW, Veldpaus FE. Rigid body motion calculated from spatial co-ordinates of markers. *Journal of Biomechanics.* 1980; 13:391–393. [PubMed: 7400168]
- Stoffregen TA, Hove P, Bardy BG, Riley M, Bonnet CT. Postural stabilization of perceptual but not cognitive performance. *Journal of Motor Behavior.* 2007; 39:126–138. [PubMed: 17428758]
- Stoffregen TA, Pagulayan RJ, Bardy BG, Hettinger LJ. Modulating postural control to facilitate visual performance. *Human Movement Science.* 2000; 19:203–220.
- Todorov E, Jordan MI. Optimal feedback control as a theory of motor coordination. *Nature Neuroscience.* 2002; 5:1226.
- Weeks DL, Forget R, Mouchnino L, Gravel D, Bourbonnais D. Interaction between attention demanding motor and cognitive tasks and static postural stability. *Gerontology.* 2003; 49:225–232. [PubMed: 12792157]
- Winter, DA. *Biomechanics and motor control of human movement.* New York: Wiley; 1990.
- Winter DA, Patla AE, Ishac M, Gage WH. Motor mechanisms of balance during quiet standing. *Journal of Electromyography and Kinesiology.* 2003; 13:49. [PubMed: 12488086]
- Wulf G, Mercer J, McNevin N, Guadagnoli MA. Reciprocal influences of attentional focus on postural and suprapostural task performance. *Journal of Motor Behavior.* 2004; 36:189–199. [PubMed: 15130869]
- Zhang W, Scholz JP, Zatsiorsky VM, Latash ML. What do synergies do? Effects of secondary constraints on multidigit synergies in accurate force-production tasks. *Journal of Neurophysiology.* 2008; 99:500–513. [PubMed: 18046000]

Fig. 1.

Subject set up for the experiment. (A) Posterior-lateral view showing subject in the initial position with laser and ball mounted on the tray. Two 2.5-cm targets are mounted on the panel in front, between which the subject moved the laser during the dynamic targeting trials. (B) Anterior-lateral view of the same subject in the starting position. Ball is sitting in a shallow indentation on the object mounted on the tray.

Fig. 2.

Illustration of the method used to compute the onset and cessation of the targeting movement. Top panel: Vertical position of the tray marker. Bottom panel: Vertical velocity of the tray marker.

Fig. 3. Mean ($\pm$ standard error of the mean) variability of CM_{AP} excursion for the dynamic targeting tasks alone (LTNB and STNB), the combined tasks (STNB and STWB), and quiet standing (QS)s.

Fig. 4.

Mean across subjects $\pm$ standard error of overall joint configuration variability for quiet standing (QS) and the dynamic tasks, targeting alone to the 5.5-cm (LTNB) and 2.5-cm targets, and targeting combined with ball balancing to the 5.5-cm (LTWB) and 2.5-cm (STWB) targets; Top panel: Joint variance computed across all 9 joints, Bottom Panel: Joint variance computed across the 4 joints (ankle, knee, hip and LSJ) used in the reduced model for computing CM variance.

Fig. 5.

Continuous plots of V_{UCM} (solid thick lines) and V_{ORT} (dashed thinner lines) with respect to stabilization of the CoM_{AP} position control during targeting to a 5.5-cm (left panels) and 2.5-cm target (right panels) alone (top panels) or combined with ball balancing (bottom panels) averaged across subjects $\pm$ standard error of the means. Note that the V_{ORT} values are plotted on a separate y-axis because of the much smaller values than V_{UCM} .

Fig. 6.

Mean across subjects $\pm$ standard error of components of joint configuration variability for the control of the anterior-posterior CoM position (CoM_{AP}). Adjacent pairs of bars represent V_{UCM} (left, stripped bars) and V_{ORT} (right, black filled bars) for quiet standing (QS), and for the dynamic targeting task alone to the 5.5-cm (LTNB) and 2.5-cm (STNB) targets, and with ball balancing to those same targets (LTWB and STWB, respectively). Top panel: Results for the full joint model. Dashed lines show slope of change between smallest targeting condition and QS for V_{UCM} and between largest targeting condition and QS for V_{ORT} ; Bottom panel: Results for the reduced 4-DOF Model.

Fig. 7.

Mean across subjects $\pm$ standard error of components of joint configuration variability for the control of the 2D hand position. Adjacent pairs of bars represent V_{UCM} (left, stripped bars) and V_{ORT} (right, black filled bars) for the dynamic targeting tasks alone to the 5.5-cm (LTNB) and 2.5-cm (STNB) targets, and with ball balancing to those same targets (LTWB and STWB, respectively).

Table 1

Mean $\pm$ SEM across subjects (N=16) movement time (MT) for the upward phase of the four targeting conditions compared to the metronome beat.

Condition	MT $\pm$ SEM (seconds)	t	p
Metronome	0.96 $\pm$ 0.05		
LTNB	0.93 $\pm$ 0.05	3.32	<0.01
LTWB	0.96 $\pm$ 0.06	0.13	0.89
STNB	0.94 $\pm$ 0.06	0.18	0.42
STWB	0.99 $\pm$ 0.07	-0.81	0.43

Table 2

Mean $\pm$ SEM (N=16) of absolute error and variable error of the laser's landing-point location when targeting the 5.5-cm target (low ID) without (LTNB) and with (LTWB) added ball balancing, and targeting the 2.5-cm target (high ID) without (STNB), and with (STWB) added ball balancing.

Condition	Absolute error (cm)	Variable error (cm)
LTNB	10.37 $\pm$ 0.60	1.02 $\pm$ 0.10
LTWB	8.75 $\pm$ 0.57	1.02 $\pm$ 0.10
STNB	10.54 $\pm$ 0.53	0.74 $\pm$ 0.06
STWB	9.88 $\pm$ 0.53	0.71 $\pm$ 0.06

Table 3

Difference in the value of each variance component (deg^2) between the combined task and targeting alone (left two columns) and between the two target sizes (right two columns).

	$V_{\text{Combined Task}} - V_{\text{Targeting alone}}$		$V_{\text{High ID}} - V_{\text{Low ID}}$	
	Low ID (LT)	High ID (ST)	Targeting Alone	Combined Task
V_{UCM}	3.28 ± 0.98	4.92 ± 0.99	1.31 ± 0.657	2.63 ± 0.657
V_{ORT}	0.328 ± 0.197	0.230 ± 0.131	-0.328 ± 0.098	-0.394 ± 0.328