# Experimental Brain Research

## Coordination of muscle torques stabilizes upright standing posture: an UCM analysis
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| **Abstract:** | The control of upright stance is commonly explained on the basis of the single-inverted pendulum model (ankle strategy), or the double inverted pendulum model (combination of ankle and hip strategy). Kinematic analysis using the Uncontrolled Manifold (UCM) approach suggests, however, that stability in upright standing results from coordinated movement of multiple joints. This is based on evidence that postural sway induces more variance in joint configurations that leave the body position in space invariant than in joint configurations that move the body in space. But does this UCM-structure of kinematic variance truly reflect coordination at the level of the neural control strategy or could it result from passive biomechanical factors? To address this question, we applied the UCM approach at the level of muscle torques rather than joint angles. Participants stood on the floor or on a narrow base of support. We estimated torques at the ankle, knee and hip joints using a model of the body dynamics. We then partitioned the joint torques into contributions from net, motion dependent, gravitational, and generalized muscle torques. A UCM analysis of the structure of variance of the muscle torque revealed that postural sway induced substantially more variance in directions in muscle torque space that leave the COM force invariant than in directions that affect the force acting on the COM. This difference decreased when we de-correlated the muscle torque data by randomizing across time. Our findings show that the UCM structure of variance exists at the level of muscle torques and is thus not merely a by-product of biomechanical coupling. Because muscle torques reflect neural control signals more directly than joint angles do, our results suggest that the control strategy for upright stance involves the task-specific coordination of multiple degrees of freedom. |

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# Coordination of muscle torques stabilizes upright standing posture: an UCM analysis

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**ABSTRACT**

The control of upright stance is commonly explained on the basis of the single-inverted pendulum model (ankle strategy), or the double inverted pendulum model (combination of ankle and hip strategy). Kinematic analysis using the Uncontrolled Manifold (UCM) approach suggests, however, that stability in upright standing results from coordinated movement of multiple joints. This is based on evidence that postural sway induces more variance in joint configurations that leave the body position in space invariant than in joint configurations that move the body in space. But does this UCM-structure of kinematic variance truly reflect coordination at the level of the neural control strategy or could it result from passive biomechanical factors? To address this question, we applied the UCM approach at the level of muscle torques rather than joint angles. Participants stood on the floor or on a narrow base of support. We estimated torques at the ankle, knee and hip joints using a model of the body dynamics. We then partitioned the joint torques into contributions from net, motion dependent, gravitational, and generalized muscle torques. A UCM analysis of the structure of variance of the muscle torque revealed that postural sway induced substantially more variance in directions in muscle torque space that leave the COM force invariant than in directions that affect the force acting on the COM. This difference decreased when we de-correlated the muscle torque data by randomizing across time. Our findings show that the UCM structure of variance exists at the level of muscle torques and is thus not merely a by-product of biomechanical coupling. Because muscle torques reflect neural control signals more directly than joint angles do, our results suggest that the control strategy for upright stance involves the task-specific coordination of multiple degrees of freedom.

## INTRODUCTION

Models of the control of upright stance have made simplifying assumptions. In the single inverted pendulum model (Horak, Nashner, & Diener, 1990; Jeka, Oie, Schoner, Dijkstra, & Henson, 1998; McCollum & Leen, 1989) upright standing posture is mainly controlled by activity at the ankle joint. In the double inverted pendulum model (Creath, Kiemel, Horak, Peterka, & Jeka, 2005; Loram & Lakie, 2002; Winter, Patla, Prince, Ishac, & Gielo-Perczak, 1998) upright standing postural control is achieved by the combination of ankle and hip joint activities. The ankle and hip control strategies are postulated to be always present, but one strategy may dominate depending on the difficulty of the task or the magnitude of a perturbation (Creath et al., 2005). These two control models may simplify the postural control system too much. While the contributions of the ankle and hip are important, there is evidence that other joints are recruited and coordinated to maintain upright standing posture (Hsu, Scholz, Schoner, Jeka, & Kiemel, 2007; S. Park, Horak, & Kuo, 2004; Schoner & Scholz, 2007).

One source of evidence is based on the idea that the variance of movement across repetitions or across time reflects the underlying control strategy (Schoner & Scholz, 2007). Variables that are stabilized by neural control mechanisms are assumed to be less variable than variables not relevant to the motor task. The uncontrolled manifold (UCM) captures those combinations of degrees of freedom that leave a hypothesized task variable invariant. In the UCM approach, for a given task variable, variance within the UCM is compared to variance orthogonal to the UCM. If variance per degree of freedom within the UCM is larger than variance orthogonal to the UCM then this is interpreted as evidence that a task variable is controlled (Scholz & Schoner, 1999). That the UCM structure of variance reveals coordination among the degrees of freedom can be determined by removing co-variance in a surrogate data set in which degrees of freedom are randomly reshuffled across time or trials (Verrel, 2011). If this destroys the UCM structure of variance, than that structure truly reflects coordination. Any remaining UCM structure of variance reflects inherent difference of variance across degrees of freedom.

The UCM approach has been applied to movements of the whole body from sit to stand (Scholz & Schoner, 1999; Reisman, Scholz, & Schoner, 2002). Hsu et al. (2007) applied this form of UCM analysis to the joint angles of the body during quiet stance. In a variety of conditions, they established that during quiet stance, the pattern of joint angle variance reflected the preferential stabilization of the horizontal COM or head position. Convergent evidence for such stabilization of the COM was obtained by Verrel, Lovden, and Lindenberger (2010) during walking.

Other evidence that multi-degree of freedom coordination is critical to upright stance comes from a study in which external mechanical perturbations are applied to a standing participant by abruptly shifting the support platform (Park et al., 2004). In an new analysis of this data, Scholz et al. (2007) showed that after a transient, postural stability was recovered in a new joint configuration which differed from the pre-perturbation configuration primarily within the UCM of the COM. In other words, following the perturbation, the mechanism of postural control reduced the deviation of the COM from its pre-perturbation position on the basis of a different, motor-equivalent joint configuration. To achieve this, the mechanism of postural control must, presumably, be sensitive to the multi-joint configuration of the upright body.

3

110    Both sources of evidence for multi-joint mechanisms of postural control are indirect. The kinematic state of

111    the body is the result of both neural signals to the skeletal musculature and the biomechanical dynamics of the multi-

112    segement body or other passive biomechanical components around the joint (e.g., elastic components of ligament,

113    tendon and skins). Could the kinematic patterns consistent with multi-joint coordination emerge from the

114    biomechnics of the upright body rather than from coordinated neural control signals to the multiple degrees of

115    freedom? One line of work that has tried to get closer to the neural control signals has consisted of detecting

116    coordination within the patterns of muscular activation (Krishnamoorthy, Yang, & Scholz, 2005). In this work, sets

117    of muscles are recorded during quiet stance under various conditions. The relationship between patterns of muscle

118    activation and task variables such as the COM position or Center of Pressure (COP) was estimated indirectly using a

119    multiple regression approach (de Freitas & Scholz, 2010). Based on the estimated Jacobian, a UCM analysis in

120    muscle space (or muscle mode space) became possible. Patterns of muscle synergy were discovered, in which those

121    combinations of muscle activations that affected the COM or COP were less variable across trials than combinations

122    of muscle activations that left these task variables unchanged. Similar work has established structure of variance in

123    muscle space consistent with the control of COM for isometric tasks under various conditions (Krishnamoorthy,

124    Latash, Scholz, & Zatsiorsky, 2004; Krishnamoorthy, Scholz, & Latash, 2007).

125    This work on muscle UCM does not really address the question we raised above, however. This form of

126    analysis establishes a direct link between patterns of muscle activation and task variables such as COM. It does not

127    speak to whether the coordination among joints seen at the kinematic level is caused by coordinated neural

128    commands or is a side effect of biomechanics.

129    Because the neural commands underlying postural control activate the muscles, and muscle activation

130    produces torques on joints, joint torques are more directly a reflection of such neural commands than are the joint

131    kinematics, that depend also on other biomechanical factors. In the present study we aim to establish that joint

132    torques are coordinated to control task variables at the level of the COM. Specifically, we relate joint torques to the

133    force acting on the COM, a task variable relevant to postural control. If such a UCM analysis of variance shows that

134    muscle torques are coordinated to stabilize COM force, this provides support for the hypothesis that the coordination

135    underlying the stabilization of the COM originates from neural commands and is not due primarily to the

136    biomechanical properties of the system.

137    Yen, Auyang, and Chang (2009) have performed a related analysis of variance at the torque level using the

138    UCM approach. The task studied was hopping in place and the task variable considered was the ground reaction

139    force in the vertical direction. We will be using a similar method for estimating the Jacobian that links forces at the

140    end-effector level to joint torques (Khatib, 1987) . Our analysis employs joint angles rather than the segment angles

141    used in that earlier work. We believe, that is physiologically and biomechanically more appropriate (Scholz &

142    Schöner, 2014). We are studying upright stance, of course, rather than hopping, and horizontal COM force rather

143    than ground reaction forces.

144

145    ***METHODS***

146

4

147 *Participants:*

148     Twelve healthy young subjects (5 males and 7 females, mean age 24.0 ± 3.8 years old) volunteered to

149 participate in this study. They ranged from 51 to 88-kg in weight (67.2 ± 12.2 kg) and 1.52 to 1.84-m in height

150 (170.1 ± 8.7). Subjects were excluded if they had balance disorders, including dizziness, musculoskeletal injuries

151 and neurological disorders or uncorrected visual acuity deficits. Subjects signed an informed consent form according

152 to the procedures approved by the Institutional Review Board of the University of Delaware in compliance with

153 ethical standards specified by the 1964 Declaration of Helsinki.

154

155 ***Experimental Setup and Procedure:***

156   A single session of data collection was conducted for each subject. Each subject performed three 3-minute trials

157 each in two conditions: (1) Quiet standing on the normal floor (QS) and (2) Quiet standing on narrow wooden block

158 (9-cm and 10-cm depends on the foot size) (NB). Subjects were asked to stand comfortably and to allow the body to

159 sway naturally. Subjects were provided rest breaks as needed between trials. All trials were randomized.

160

161 **Motion capture data:**

162     Eight infrared cameras (VICON™ MX-13; Oxford Metrics) arranged in a circle around the subject were

163 used to track the reflective markers at a sampling rate at 120-Hz. All analysis for three experiments was performed

164 in the sagittal plane. Individual reflective markers were placed at estimated joint centers of the following locations:

165 Lateral of $5^{th}$ metatarsal bone, immediately inferior to the lateral malleolus, lateral condyle of femur, greater

166 trochanter of femur, L5-S1 junction of spine, C7-T1 junction of spine, acromion process, mastoid process, directly

167 anterior to the external auditory meatus.

168     The three-dimensional positions of the reflective markers were reconstructed with NEXUS (VICON™)

169 software. The position information of each marker was filtered in Matlab™ using $4^{th}$ order Butterworth low-pass

170 recursive filter with a 5-Hz cut-off frequency.

171

172 ***Data Processing:***

173 ***Reconstruction of reflective markers and kinematics:***

174     Segment lengths and joint angles on the sagittal plane were computed for further analysis. Segment lengths

175 ($l_i$) were calculated from the average of the marker positions, over the entire experimental trial. The reflective

176 marker coordinates at each data sample were used to calculate sagittal plane vectors for the shank, thigh and trunk

177 segments. The angles between linked segments was calculated using a link-segment model (Winter, 2009). The head

178 and arms were included in the trunk segment, which was defined by the acromion and greater trochanter markers.

179 The positive angle was defined as the upper (cranial) segment moving in anterior direction, based on the formula

$$\theta = \cos^{-1}(V_1^T \cdot V_2)$$

180 where $V_1$ and $V_2$ are unit vector for the proximal and distal segments of the joint.

181     After joint angle computation, joint velocities and accelerations were determined numerically by

182 differentiating the joint angles ($\theta_i$) using finite differences.

5

183

### *Calculation and grouping of the joint torques:*

184

185    We calculated the biomechanical equation of motion using the Lagrangian approach with the joint angles as

186    generalized coordinates:

$$M(\theta)\ddot{\theta} + C(\theta,\dot{\theta})\dot{\theta} + N(\theta) = \tau \ \in \ \mathbb{R}^3,$$

187    where $M(\theta)$ is the inertia matrix, $C(\theta,\dot{\theta})$ represents the motion-dependent torques, and $N(\theta)$ is the gravitational

188    torques. These terms were calculated using the screw theory of spatial manipulations (Murray, Li, & Sastry, 1994).

189    This allowed determining the applied torques $T$ generated by both active muscle contractions and passive elastic

190    effects from tendons and ligaments.

191    These terms were grouped into torque components that are directly responsible for motions at a single joint

192    and torques that arise from the mechanical effects of the linkage between the different joints (Galloway & Koshland,

193    2002). Torques in the first group are proportional to the joint accelerations,

$$NET = M_{dia}(\theta)\ddot{\theta} \ \in \ \mathbb{R}^3,$$

194    where $M_{dia}$ is a matrix consisting of the diagonal elements of the inertia matrix. The second group consists of

195    motion-dependent torques (*MDP*), which comprises terms depending upon both joint velocities and accelerations.

$$MDP = -M_{off}(\theta)\ddot{\theta} \in \ \mathbb{R}^3 - C(\theta,\dot{\theta})\dot{\theta},$$

196    Where $M_{off} = M - M_{dia}$ contains the off-diagonal elements of the inertia matrix. The remaining two groups

197    $$GRA = -N \ , \quad MUS = \tau$$

198    are gravitational torques (*GRA*) and applied torques (MUS). Both correspond directly to the terms in the equation of

199    motion. Note that the sign for GRA and MDP was changed to make these terms directly comparable with MUS.

200

### **UCM analysis:**

201

202    To reveal coordination between elemental variables, we applied the UCM approach (Scholz and Schoner

203    1999) to analyze the structure of variance relative to hypothesized task variables. When people perform any task,

204    there is certain minimum of degrees of freedom (DOF) required to reliably solve the task. For example, 3 DOFs are

205    required to move the hand position in 3-dimensional space. However, even considering only movements of the arm

206    and keeping the rest of the body stationary, we have at least 7 DOF (three in the spherical shoulder, elbow flexion,

207    radio-ulnar rotation and wrist flexion/extension and ab/adduction) to move the hand position. Because of this

208    abundance of degrees of freedom, there are continuously many different combinations of joint angles that lead to the

209    same spatial position of the hand. The set of these configurations that leave the hand positions unchanged is called

210    Uncontrolled Manifold. Variance of elemental variables *within* this manifold is considered "good variance" (also

211    designated as $V_{UCM}$), because it does not interfere with the hypothetical task variable. Variance that does affect the

212    task variable, on the other hand, is called "bad variance" ($V_{ORT}$), because it interferes with the successful

213    performance of a motor task. Details of the analysis can also be found in other studies (Scholz and Schoner 1999,

214    Hsu et al. 2007, de Freitas and Scholz 2010).

215    In this study, we performed a UCM analysis using joint torques at the ankle, knee and hip in the sagittal plane

216  as the elemental variables, as first introduced by Yen and Chang (2009) and the force acting on the COM as task

217  variable. For comparison, we analyzed the same data using joint angles as elemental variables and the spatial COM

218  position as task variable. In both cases, UCM analysis was performed across all time frames, to determine the extent

219  to which each hypothetical task variable was stabilized by the CNS during postural sway.

220  1.  We first calculated the average position of the COM (Winter, 2009). From here on, the COM is understood

221  to be the position $c$ of this point, fixed to the trunk segment. While the actual COM position is not fixed but

222  moves relative to the trunk, the extent of this movement is negligible in quiet stance. Forces acting on this point

223  are not well-defined, however, which is why we used the fixed-point $c$ instead.

224  2.  We then calculated the kinematic Jacobian matrix J that relates changes of joint angles to changes of $c$. For

225  the joint torque analysis, we calculated the matrix

$$\bar{J} = M^{-1}J^T(JM^{-1}J^T)^{-1}$$

226  relating joint torques to forces acting on $c$ (see Appendix and Khatib (1987)). See Figure 2 for a visualization of

227  these relationships. Both Jacobians were calculated for the mean joint angle configuration across time.

228  3.  To approximate the UCM, we calculated the null space of these matrices and its orthogonal complement

229  using singular value decomposition in Matlab.

230  4.  The difference between the current elemental variable configuration and its mean was projected onto the

231  null-space (UCM) and the orthogonal subspace of the Jacobian. The average lengths of these differences within

232  each subspace were normalized to the dimensionality of the subspace to produce estimates $V_{UCM}$ and $V_{ORT}$ of

233  the variance per DOF within both subspaces.

234

235  A difference between these variance measures ($V_{UCM} > V_{ORT}$), called a "UCM-effect", has been interpreted as

236  an indication that the CNS actively controls the task variable. High stability implies low variance, so if the elemental

237  variables are actively coordinated to stabilize a relevant task variable, a UCM-effect is expected in the variance

238  structure of the elemental variables. While the actual observation of this UCM-effect is necessary, it is not, however,

239  a sufficient condition for active control, because the UCM-effect can also come from other sources. One such source

240  are intrinsic differences in the variability of the different elemental variables (Muller & Sternad, 2003; Verrel, 2011;

241  Yen & Chang, 2009). If an elemental variable that has relatively little effect on the task is intrinsically highly

242  variant, then it generates a contribution to the UCM effect that is not a result of coordination. To exclude this

243  possibility, we have decorrelated the data by removing the co-variation between elementary variables (Park,

244  Schoner, & Scholz, 2012; Yen & Chang, 2010). Any UCM-effect still present in the decorrelated data set cannot

245  result from coordination. So to determine the extent to which the observed UCM-effect result from active

246  coordination, we repeated the UCM analysis on the decorrelated data set. If $V_{UCM}$ remains higher than $V_{ORT}$ after

247  removal of the co-variation between the elemental variables, then the stabilization of the performance variable

248  originates from the coordination of the elemental variables.

249

250  ***Statistical Analysis:***

251  To test whether the magnitude of variance is different between the ankle, knee and hip joints, we performed

7

252 two-factor repeated measures ANOVAs with factors *joint* and *condition*. Significance was accepted at a level of

253 p<0.05. This analysis was carried out once each for joint angle variance and joint torque variance.

254     We performed statistical analysis of the UCM-measures of variance in joint angle and in muscle torque space,

255 before and after removing the co-variation between the elemental variables. For comparison of different UCM-

256 effects, we calculated the relative measure

$$T = \frac{V_{UCM} - V_{ORT}}{V_{UCM} + V_{ORT}}$$

257 (Verrel 2010). If $T$ is close to 1, then most variance of the elemental variables preserves the task variable (Gera et

258 al., 2010). When $T$ is close to 0 or negative, this indicates that the task variable is not particularly stable relatively to

259 other combinations of degrees of freedom. Also, using a relative value makes this measure dimension-less, allows us

260 to compare the magnitude of UCM-effects in different spaces regardless of units (e.g. radians for angles, Nm for

261 torques).

262     Statistical analysis was used to answer four consecutive questions. 1) Is there more "good variance ($V_{UCM}$)"

263 than "bad variance ($V_{ORT}$)"? This was tested both for joint angle space and muscle torque space using a one-tailed t-

264 test. Significance was accepted at a level of $p < 0.025$ after Bonferroni correction. 2) Is this UCM-effect a result of

265 co-variation between the elemental variables or the result of differences in the intrinsic variance of the elemental

266 variables? We tested whether the UCM-effect is still present after removing the co-variation by performing the same

267 t-test on the decorrelated data set. 3) Is the reduction of the UCM-effect by decorrelating the data statistically

268 significant? This was tested using a t-test comparing $T$ before and after removing the co-variation, both for angles

269 and torques. 4) Is the UCM-effect equally large in joint angle space and in muscle torque space? This was tested

270 using a t-test comparing $T$ computed for joint angles and for muscle torques.

271

272

273 **RESULTS**

274

275 **Joint angles and torques**

276     *Figure 1* provides an example of torques in one quiet standing trial from one representative subject. Overall,

277 the magnitude of muscle torque (MUS) is similar to the gravitational torque (GRA), these two components largely

278 cancelling each other out at all joints. As a result, the net joint torque (NET) is comparatively small, leading to a

279 stable posture. As there is little movement, the motion-dependent torques (MDP) are also very small.

280

281             *<Figure 1 about here>*

282

283     *Figure 2* shows the average variance of joint angles and muscle torques for each joint, in quiet stance (light

284 bars) and narrow support (dark bars). The joint angle variance is smallest in the ankle compared to the knee and hip

285 joints. The muscle torque variance, on the other hand, is largest for the ankle and smallest for the hip. These

286 differences are statistically significant. The two-way repeated measures ANOVA reveals a significant effect of joint

287     for both joint angle variances and muscle torque variances (Joint angle variances: $F_{2,22} = 4.15$, $p = 0.03$; muscle

288     torque variances: $F_{2,22} = 11.15$, $p < 0.001$). Post-hoc testing reveals that there is no difference between ankle, knee

289     and hip joint angle variance for the quiet stance condition, but for the narrow support condition, the knee and hip

290     variance is significantly higher compared to the ankle variance (ankle vs. knee: $F_{1,11} = 5.18$, $p = 0.044$; ankle vs. hip:

291     $F_{1,11} = 8.33$, $p = 0.015$). For muscle torque variances, however, the hip variance is significantly smaller compared to

292     the variance of the ankle and knee in quiet standing (ankle vs. hip: $F_{1,11} = 9.89$, $p = 0.009$; knee vs. hip: $F_{1,11} = 8.45$,

293     $p = 0.014$) and narrow support (ankle vs. hip: $F_{1,11} = 40.04$, $p < 0.001$; knee vs. hip: $F_{1,11} = 18.11$, $p = 0.001$)

294     conditions.

295

296                           *<Figure 2 about here>*

297

**Comparison of the Jacobian matrices for two UCM approaches**

299       *Figure 3* shows the mean across subjects of the Jacobian matrices used in the two UCM analyses for joint

300     angles and muscle torques. The pattern of these two matrices is strikingly different. In the kinematic Jacobian

301     relating joint angles to COM position, the ankle has the largest value and the hip the smallest. This is in stark

302     contrast to the pattern exhibited by the torque Jacobian. Here, the ankle shows the smallest (absolute) value, with a

303     larger value for the knee and an even larger value for the hip.

304

305                           *<Figure 3 about here>*

306

**Variance analysis in UCM-space**

308       *Figure 4* shows the UCM-measures of variance $V_{UCM}$ and $V_{ORT}$ in joint angle space and muscle torque space,

309     before and after decorrelation, in quiet stance and narrow support. T-tests showed that in both conditions, $V_{UCM}$ is

310     significantly larger than $V_{ORT}$ for the original data in both joint angle space (QS: $p = 0.002$, NB: $p = 0.028$) and

311     muscle torque space (QS: $p = 0.001$, NB: $p = 0.004$).

312       After removing the covariation, no significant differences are found in joint angle space (QS: $p = 0.705$, NB:

313     $p = 0.937$). In muscle torque space, there is still a significant difference between $V_{UCM}$ and $V_{ORT}$ for quiet stance ($p =$

314     $0.013$), but not for the narrow support condition ($p = 0.280$).

315

316                           *<Figure 4 about here>*

317

318       Figure 5 shows the UCM-effect measure *T* for QS and NB in joint angle and muscle torque space. *T* is

319     significantly higher for the original data compared with the decorrelated data in both conditions in joint angle space

320     (QS: $p = 0.001$, NB: $p < 0.001$) and muscle torque space (QS: $p < 0.001$, NB: $p < 0.001$), suggesting that the UCM

321     effect ($V_{UCM} > V_{ORT}$) originates from active coordination of joint angles and muscle torques and is not purely a

322     result of the biomechanical coupling between the body segments.

323       Another t-test was performed to test the difference of *T* between the joint angle space and the muscle

9

324 torque space. This difference is significant for the normal data in quiet stance (p = 0.04), but fails to reach

325 significance in all other cases (NB with normal data: p = 0.462; QS with decorrelated data: $p = 0.83$; NB with

326 decorrelated data: $p = 0.147$).

327

328 <p style="color:red"><strong><em>&lt;Figure 5 about here&gt;</em></strong></p>

329

330 **DISCUSSION**

331       The aim of this study was to determine whether muscle torques are coordinated to stabilize COM movement

332 during upright standing. Our data provide evidence that the muscle torques acting on the ankle, knee and hip joints

333 in the sagittal plane are coordinated to stabilize the force acting on the COM during upright stance. These results

334 support the hypothesis that the coordination underlying the stabilization of the COM position originates from neural

335 commands and is not primarily due to the biomechanical coupling between the interconnected body segments.

336       An essential step in the UCM analysis of a high-dimensional data set is forming a hypothesis about which

337 task variable the CNS might control and determining the Jacobian matrix of partial derivatives relating changes in

338 this hypothetical task variable to changes in the elemental variables (Scholz & Schoner, 1999). In the classical UCM

339 analysis, the task variable is a function of the kinematic state of the body and the Jacobian is given by the derivative

340 of the forward kinematic function (Hsu et al., 2007; E. Park et al., 2012; Scholz & Schoner, 1999; Scholz, Schoner,

341 & Latash, 2000). For example, if the hypothesized task variable is the whole-body COM, the forward kinematic

342 function can be formulated using a geometrical model depending on the joint angles, segment lengths and COM

343 position of each segment.

344       For other task variable hypotheses, however, the relationship to the elemental variables is less

345 straightforward. A geometrical model might be excessively difficult to formulate, or not even exist. In a finger force

346 production task, for instance, using the finger forces as elementary variables is problematic because enslaving

347 effects between fingers compromise the mutual independence of the finger forces. Estimating the magnitude of the

348 enslavement between fingers allows to correct for this effect and derive a set of independent control variables

349 (Scholz, Danion, Latash, & Schoner, 2002; Scholz, Kang, Patterson, & Latash, 2003; Shinohara, Scholz, Zatsiorsky,

350 & Latash, 2004). In another case, the relationship between the forces exerted by the activation of the arm muscles

351 measured by EMG is highly nonlinear and complicated. It is, however, possible to approximate this relationship

352 using multiple regression analysis between the recorded force and EMG data (Danna-Dos-Santos, Slomka,

353 Zatsiorsky, & Latash, 2007; Krishnamoorthy, Goodman, Zatsiorsky, & Latash, 2003; Krishnamoorthy et al., 2007).

354       In the current study, we assumed that the muscle torques at the ankle, knee and hip joints are a priori

355 independent elemental variables. The hypothetical task variable that depends upon the muscle torques was the force

356 exerted on a point at the COM of the whole body. The main research question was whether the so-called UCM-

357 effect would be observed under this hypothesis, i.e. whether the vector of muscle torques is more variable in

358 directions in torque space that leave the force at the COM invariant than in directions that do affect it. The Jacobian

359 relating changes in the task variable to changes in the elemental variable was derived using an analytical formula

360 obtained for the analysis and control of robotic manipulators with respect to the dynamic behavior of the end

10

361 effector (Khatib, 1987, 1995).

362        This UCM-analysis of variance in muscle torque space was compared to the established UCM-effect in joint

363 angle space, which shows that joint angle combinations affecting the COM position are more stable than

364 combinations that do not (Hsu et al., 2007). Figure 3, showing the two mean Jacobian matrices of the two

365 approaches, illustrate the difference between these two approaches. The magnitude of the effect a joint has on the

366 task variable is *decreasing* from ankle to hip in joint angle space, but *increasing* from ankle to hip in muscle torque

367 space. The underlying reason behind both patterns is the relative distance of the joints from the COM of the whole

368 body. Movements of the ankle have a bigger effect on the COM than movements of the hip, because the ankle is

369 further away from the COM than the hip. But this also means that the lever arm translating ankle torques into forces

370 at the COM is longer, so that the same torque induces less force at the COM location for the ankle than for the hip.

371 Furthermore, the sign of the COM force Jacobian for knee torque is negative, indicating that an extensor torque at

372 the knee joint corresponds to a force at the COM in *backward* direction. This effect is a result of the interaction

373 torques between the different body segments. For comparison, if the knees are extended while the ankle and hip

374 joints are fixed, the COM moves *forward* (Zajac & Gordon, 1989). For these reasons, the structure of the data in

375 muscle torque space is expected to be different from the well-known structure of the data in joint angle space.

376

377 **Muscle torques are coordinated to stabilize the COM force, just like joint angles are coordinated to stabilize**

378 **COM position**

379        We hypothesized that both the COM position and COM force are important task related variables for upright

380 standing posture. When the UCM analysis was performed in joint angle space, we observed a strong UCM effect

381 (i.e., $V_{UCM} > V_{ORT}$). The means that the joint angles are coordinated to stabilize COM position to maintain upright

382 standing posture and this result is consistent with previous studies (Hsu & Scholz, 2011; Hsu et al., 2007; Scholz et

383 al., 2007). A similar result was found when the UCM analysis was performed with muscle torques related to the

384 COM force. These results indicate that regardless of the elemental variable examined (e.g., joint angles or muscle

385 torques), both are coordinated to stabilize COM movement (i.e., position and force) to maintain upright standing

386 posture. This is further supported by comparing the relative magnitude (*T*) of the UCM effect between the two UCM

387 analyses. The variance measures $V_{UCM}$ and $V_{ORT}$ cannot be compared directly between the two UCM analyses,

388 because they are performed on elemental variables with different units (i.e., rad vs. Nm), thus necessitating a

389 comparison of the relative difference between $V_{UCM}$ and $V_{ORT}$ from the two analyses (*T*).

390        This similarity of the UCM-effects suggests that the structure of postural sway in quiet stance is not a result

391 of biomechanical coupling between different body segments. The joint angles are strongly affected by the

392 interaction torques between interconnected body segments (Zajac & Gordon, 1989). The muscle torques, on the

393 other hand, mostly depend upon activation from neural control (although this relationship is not straightforward and

394 there are some passive elements involved, see e.g. Latash, 2008). Taken together these results provide support for

395 the hypothesis that the coordination underlying the stabilization of important task variables in postural control

396 originates from neural commands and is not primarily due to the biomechanical properties of the system.

11

To more completely understand whether the UCM effect (i.e., $V_{UCM} > V_{ORT}$) is due to the inter-elemental variable coordination rather than the body geometry or intrinsic differences in the variability of elemental variables, we artificially removed co-variation by decorrelating the data across time (Martin, Norris, Greger, & Thach, 2002; Muller & Sternad, 2003; Yen & Chang, 2010) and then repeated the UCM analysis. If the coordination between elemental variables plays a dominant role for the stabilization of a task variable, the UCM-effect found in the actual data is expected to disappear, or diminish, in the decorrelated data set. In the current study, the UCM-effect indeed largely disappeared in the decorrelated data set. This implies that the stabilization of the COM is a result of coordination between elemental variables (i.e. joint angles or joint torques), not independent differences in variability or body geometry. These results extend the results of previous studies, which found that the coordination of joint angles primarily originated from the active coordination among the elemental variables (Hsu et al., 2007; E. Park et al., 2012). For the UCM analysis in torque space a small UCM effect remained after decorrelation. This reflects the relatively large variance of the ankle torques (Figure 2), which loads strongly on the UCM (small entry in the Jacobian, Figure 3). The ankle torque is naturally large because the ankle faces the largest inertial moment.

**Conclusions**

We analyzed coordination between different joints in the control of quiet, upright stance using the uncontrolled manifold approach at the level of muscle torques. The results provide support for the hypothesis that muscle torques are coordinated to stabilize the force acting at the COM, analogous to the pattern of coordination observed at the joint level. Taken together, the results from the UCM analysis on normal and decorrelated data support the hypothesis that the geometrical structure of multi-joint postural sway in quiet stance is a result of active coordination between different joints achieved by neural control.

**Acknowledgments**

434 **APPENDIX**

435

436 **<u>The relationship between forces at the COM and joint torques</u>**

437

438 Let x be a point on the body given by the position of the COM in reference configuration.

439 The equation of motion of the full body is given by

440
$$M(\theta)\ddot{\theta} + C(\theta, \dot{\theta})\dot{\theta} + G(\theta) = \tau \qquad \textit{(Eq. 1)}$$

441 where $M(\theta)$ is the inertia or mass matrix of the full dynamical equations of motion, $C(\theta, \dot{\theta})\dot{\theta}$ are the centrifugal and

442 Coriolis joint torques, $G(\theta)$ is gravity torque vector and $\tau$ is the vector of muscle torques. $J$ is the kinematic

443 Jacobian relating displacement of the COM position $x$ to changes in joint angles.

444
$$\partial x = J \cdot \partial \theta \qquad \textit{(Eq. 2.1)}$$

445
$$\Rightarrow \quad J = \frac{\partial x}{\partial \theta} \qquad \textit{(Eq. 2.2)}$$

446 Our goal is to derive a matrix $\bar{J}$ that maps torques $\tau$ to the force F applied at $x$ via

447
$$F = \bar{J}^T \tau \qquad \textit{(Eq. 3)}$$

448 The general solution of this equation is

449
$$\tau = J^T F + [I - J^T \bar{J}^T]\tau_0 \qquad \textit{(Eq. 4)}$$

450 where $\tau_0$ is and arbitrary joint torque vector. Together with Equation 1 we get

451
$$[I - J^T \bar{J}^T]\tau_0 = M\ddot{\theta} + C + G \qquad \textit{(Eq. 5)}$$

452 In the dynamic case with gravity, torques $[I - J^T \bar{J}^T]\tau_0$ that do not affect the endpoint force in Eq. 4 must satisfy the

453 following dynamical constraint.

454
$$JM^{-1}[I - J^T \bar{J}^T]\tau_0 = 0 \qquad \textit{(Eq.6)}$$

455 We solve the Eq.6 for $\bar{J}^T$

$$JM^{-1}\tau_0 - JM^{-1}J^T \bar{J}^T \tau_0 = 0$$
$$JM^{-1}J^T \bar{J}^T = JM^{-1}$$

456
$$\bar{J}^T = [JM^{-1}J^T]^{-1}JM^{-1} \qquad \textit{(Eq. 7)}$$

457
$$\bar{J} = M^{-1}J^T(JM^{-1}J^T)^{-1} \qquad \textit{(Eq. 9)}$$

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**Figure Captions**

563

**Fig 1** Example of Torques (MUS, GRA, MDP and NET) with Lagarrangian approach. This example plotted based on one representative subject and condition, for three joints (ankle, knee and hip). MUS: torque due to the passive and active properties of muscle. GRA: Torque due to the gravity, MDP: torque due to motion of segments about other joints. NET: torque that is proportional to the joint acceleration.

568

**Fig 2** Variance of joints angles and muscles torques, Error bars represent standard deviation across subjects. QS: Quiet Standing on normal floor, NB: Standing on Narrow Base of Support. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

572

**Fig 3** The Jacobian matrixes derived from the geometrical model (left), and Jacobian derived based on the Khatib approach (right) (1987), QS: quiet standing, NB: narrow base standing.

575

**Fig 4** The UCM results for the stabilization of COM position with respect to the joint angles (left). The UCM results for the stabilization of COM Force with respect to the muscle torques (right). $V_{UCM}$: variance of elemental variable, which does not affect the task variable, $V_{ORT}$: Variance of elemental variable that does affect the task variable. QS: quiet standing, NB: narrow base standing. Norm: UCM analysis with normal data set, De-Corr: UCM analysis with decorrelated data by removing the covariation between elemental variables. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

582

**Fig 5** Relative difference ($T$) between two variance components from UCM in joint angle space and muscle torque space. QS: quiet standing, NB: narrow base standing. Norm: UCM analysis with normal data set, De-Corr: UCM analysis with decorrelated data by removing the covariation between elemental variables.
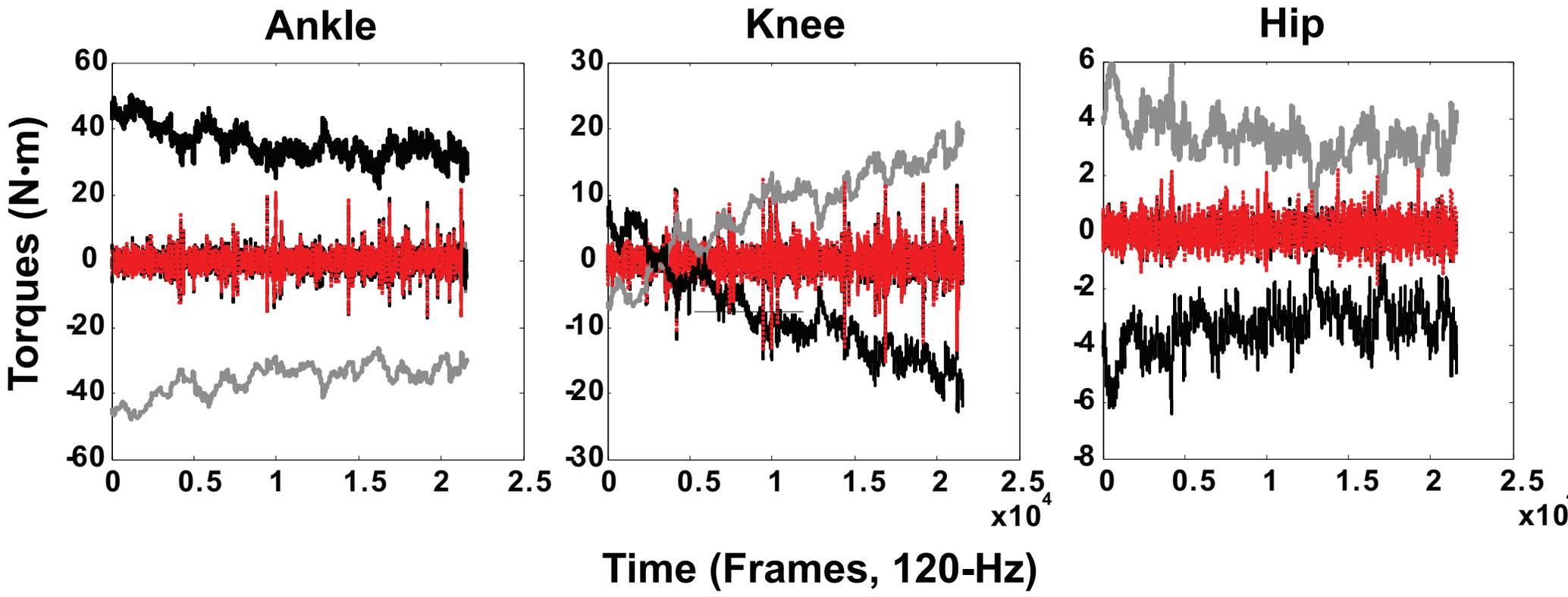
Figure 1

Figure 2
Click here to download Figure: Fig2.eps

Figure 3
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Jacobian from Khatib approach for UCM in Torque space

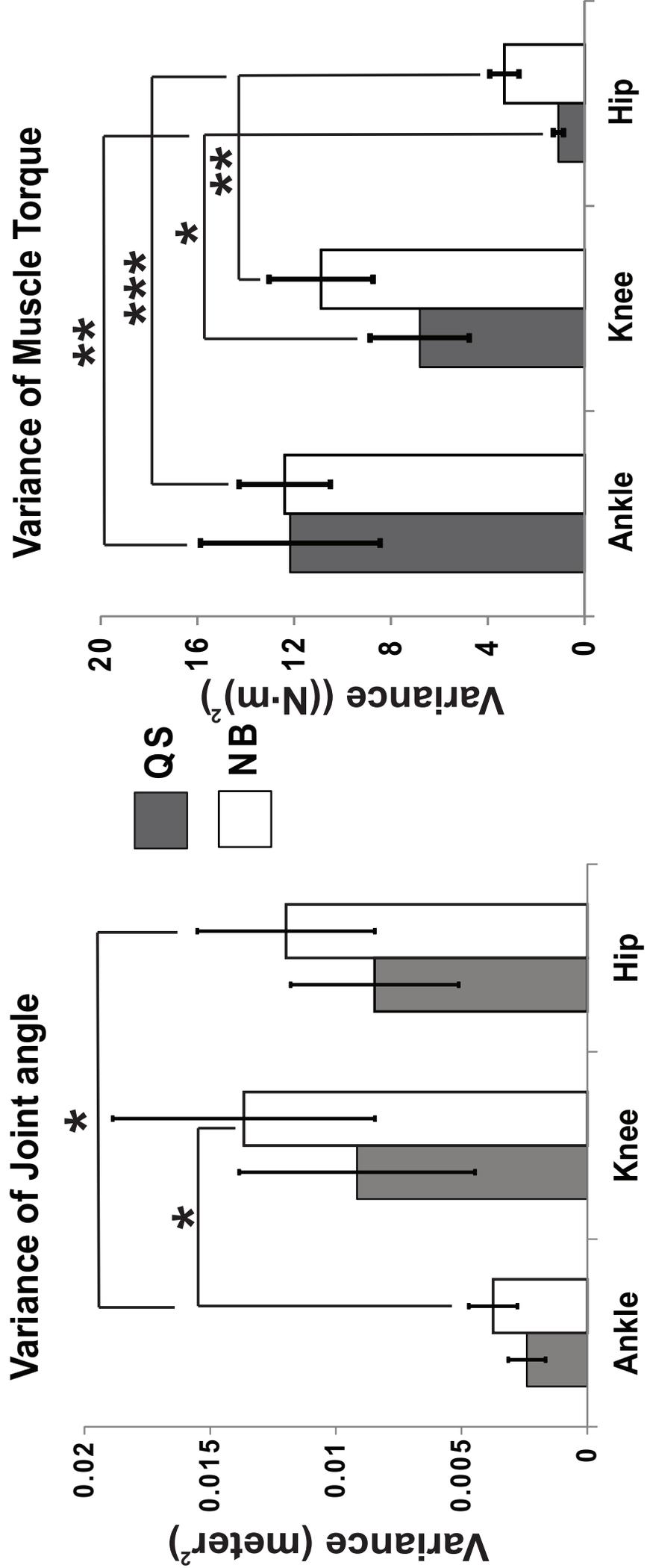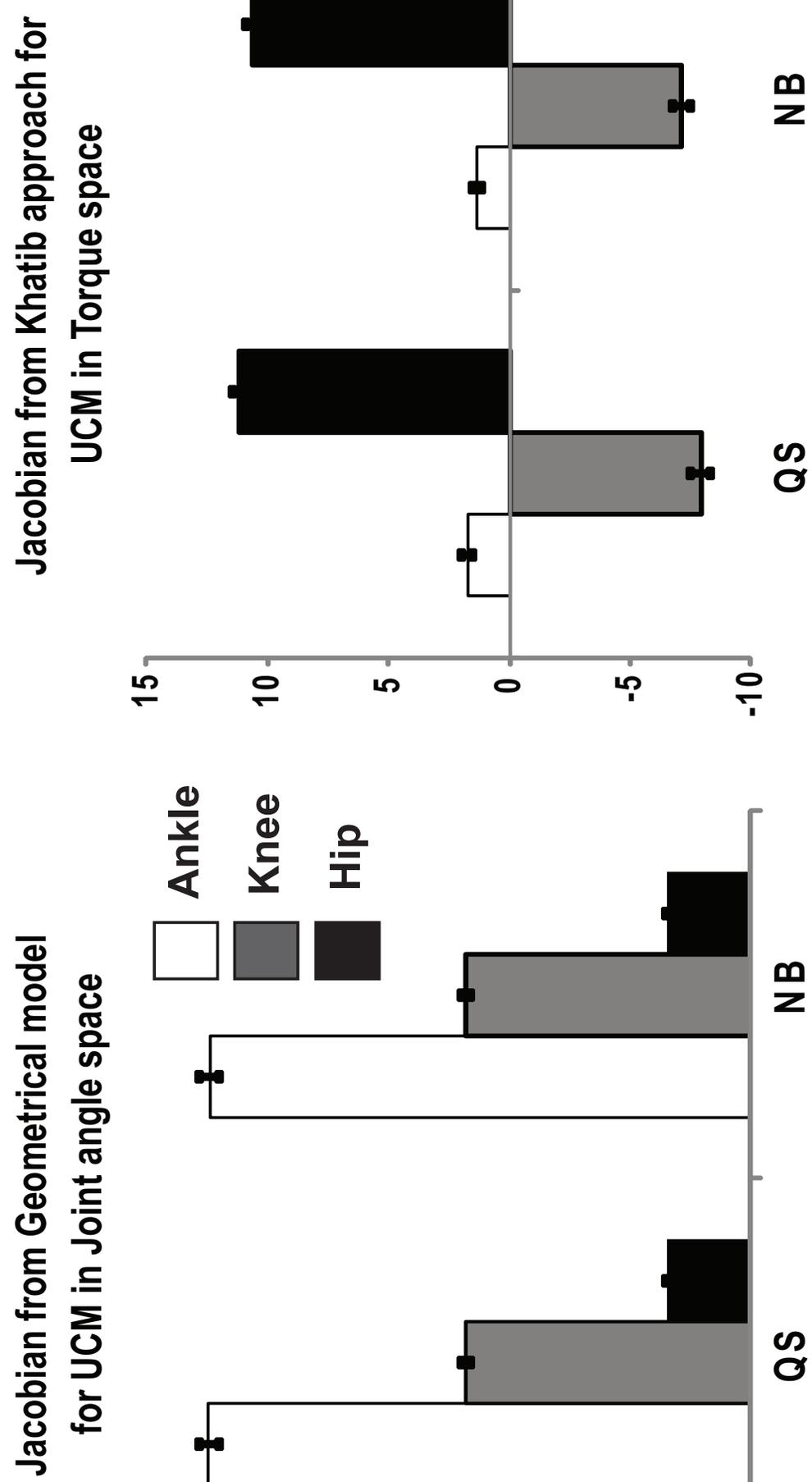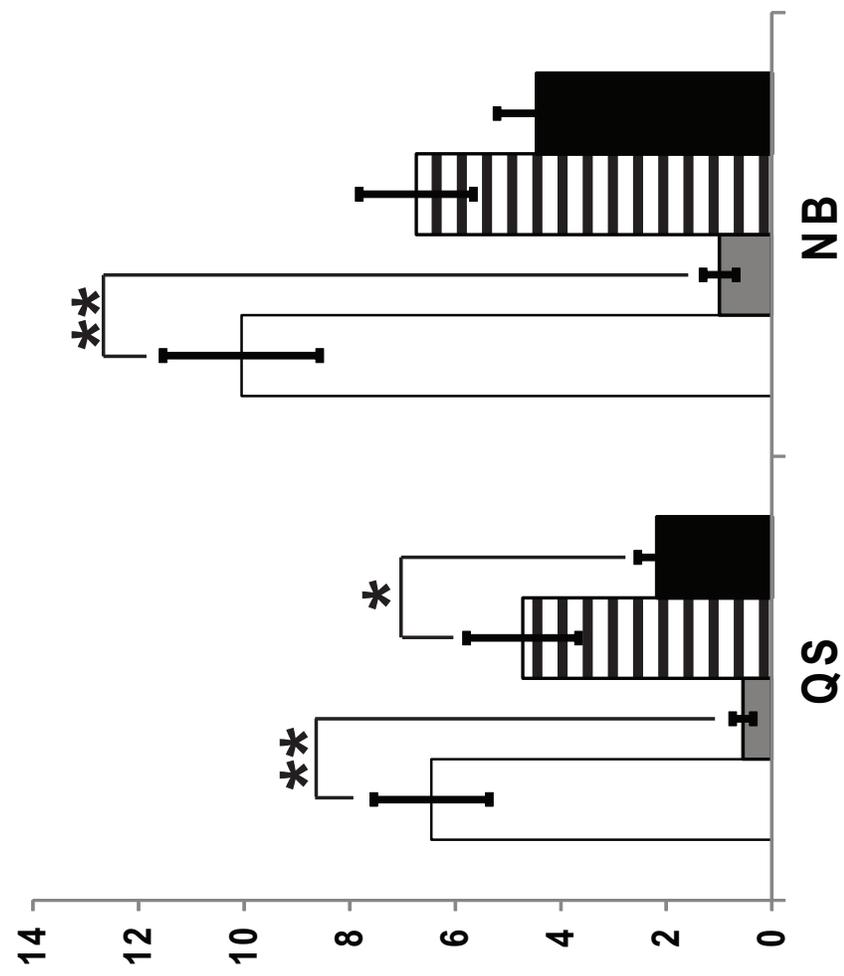Jacobian from Geometrical model for UCM in Joint angle space

Figure 4
Click here to download Figure: Fig4.eps



UCM Analysis in torque Space (3DoF)

UCM Analysis in joint angle space (3DoF)