RESEARCH ARTICLE

Local and global effects of neck muscle vibration during stabilization of upright standing

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Abstract Neck muscle vibration (NMV) during upright standing is known to induce forward leaning, which has been explained as a global response to the (illusory) perception of a lengthening of the dorsal neck muscles. However, the effects of NMV both at the level of individual joints and on whole-body postural coordination, and its potential modulation by vision, have not yet been analyzed in detail. Eight healthy young adult participants completed a total of ten trials each, with a 10-s period of unperturbed standing followed by a 10-s period of NMV. Participants were instructed to stand "as still as possible". This postural task was executed under two visual conditions: eyes open (EO) and eyes closed (EC). Postural responses were measured in terms of center of pressure (CoP) and center of mass (CoM) profiles, and whole-body kinematics. Responses to NMV at the level of individual body segments and joints were assessed by decomposing the time series into linear trends and residual fluctuations. Inter-segmental coordination was analyzed using a decorrelation technique, assessing motor-equivalent stabilization of four task-related variables: CoM position, trunk orientation, as well as head position and orientation. NMV induced a general forward leaning response under both visual conditions, visible in CoP, CoM, segment positions and orientations. Locally, NMV induced a pronounced extension of the atlanto-occipital joint. Residual fluctuations were higher with EC and unaffected by NMV. Coordination analysis showed that stabilization of different body parts was differentially affected by NMV. Head orientation was consistently stabilized across all conditions, with weaker coordination in the EC condition. In contrast, motor-equivalent stabilization of CoM and head position, and trunk orientation was only observed during no-vibration periods. Taken together, our results demonstrate specific effects of vision and proprioception on different aspects of local and global postural control. While perturbed neck proprioception seemed to affect the postural "set point" (inducing forward leaning), vision appeared to mainly serve in noise reduction (residual fluctuations) and control of head orientation.

Introduction

Human erect posture is known to depend on the coordination of numerous biomechanical degrees of freedom (Creath et al. 2005; Hsu et al. 2007; Pinter et al. 2008), based on the integration of vestibular, visual and somatosensory information (Peterka 2002), to stabilize equilibrium and orientation (Horak and MacPherson 1996; Massion 1994). Here, equilibrium refers to the biomechanical requirements of upright stance (stabilizing the center of mass, CoM, within the base of support), while orientation refers to the relative or absolute positions of different body parts such as trunk and head. Proprioception of the neck may be particularly important to integrate

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vestibular and visual information with somatosensory information from the rest of the body to estimate the position and motion of different body parts in space (e.g., Cohen 1961; Mergner et al. 1997).

Perturbation of neck proprioception, by means of neck muscle vibration (NMV), is known to affect postural control during upright quiet standing (Eklund and Hagbarth 1966; Eklund 1971, 1972; Gregoric et al. 1978; Lund 1980). Symmetric NMV induces a forward leaning of the body, which can be detected both based on center of pressure (CoP) profiles (Kavounoudias et al. 1999) and kinematic measurements (Ivanenko et al. 1999; Gomez et al. 2009).

This effect has been explained as a corrective reaction to perceived *backward* leaning of the body (e.g., Kavounoudias et al. 1999; Lekhel et al. 1997), in the sense that neck muscle vibration induces the illusory perception of a lengthening of the neck muscles (Goodwin et al. 1972a, 1972b; Lackner and Levine 1979; Gilhodes et al. 1986), which may signify a distal movement (forward tilt of the head) or a proximal movement (forward movement of the body below the space-fixed head). Vestibular or visual information indicating constant head orientation provides sensory evidence against the former (distal) interpretation. Therefore, the NMV-induced perceived neck lengthening is hypothesized to be interpreted by the postural control system as a backward leaning that would lead to a corrective response, i.e., the observed forward leaning of the body.

To our knowledge, postural responses to neck muscle vibration at the level of individual joints along the central body axis and their coordination have not yet been investigated. We consider this issue relevant for two main reasons. On the one hand, analysis at the joint level allows assessing local effects of stimulation. In particular, the local effect of neck muscle vibration on neck and head orientation has not been explicitly addressed in previous research. On the other hand, global analysis of intersegmental coordination may reveal which specific aspects of posture (equilibrium vs. orientation) are affected by the perturbation of neck proprioception.

For most motor activities, the number of degrees of freedom (DOF) available to the motor system exceeds those specified by the performance requirements. For instance, in a simple (sagittal plane) postural model, the human body can be modeled with six DOF (ankle, knee, hip, lower back, upper back, neck), while important task-related variables, such as the anterior–posterior CoM position, are one dimensional. Analyzing the organization of variability across the DOF allows formally testing whether the motor system stabilizes specific task-related variables (Schöner 1995; Scholz and Schöner 1999; Latash et al. 2007). The rationale of this approach is that the structure of intrinsic fluctuations is informative about how the motor system deals with naturally occurring

perturbations. Stabilization of a task-related variable does not necessarily mean that variability is minimized in each DOF that affects this variable, but that variability is organized across DOF in a way that minimizes fluctuations in the task-related variable. Importantly, this notion of stabilization differs fundamentally from using raw variability scores as indicators of stability.

Several methods have been proposed to analyze task-specific organization of variability in multi-DOF effector systems (Cusumano and Cesari 2006; Müller and Sternad 2003; Scholz and Schöner 1999). The general idea in such an analysis is to relate variability at the level of the effector system (e.g., joint angles) to variability of specific task-related variables. Due to motor equivalence, the extent to which joint angle variability results in variability in task-related variables depends on the coordination among the joint angles. In the case of upright postural control, CoM and head position, as well as trunk and head orientation, have been proposed as relevant (Horak and MacPherson 1996; Hsu et al. 2007). Here, we follow the approach of Müller and Sternad (2003), in which joint angles time series are randomly permuted to produce "decorrelated" surrogate data. The difference between actual and decorrelated performance, measured at the level of task-related variables (e.g., variability of CoM position), is used to quantify coordination (see "Methods" for details). Using this method, it can be assessed whether and to what extent joint angles are organized in a way that they stabilize a specific task-related variable (compensatory organization among joint angles), are independent (no compensation) or "destabilize" (inducing a change in) the task-related variable. It has to be noted that this latter notion of "destabilization" is independent of a potential new stable point reached after the change.

Availability of visual feedback generally has a stabilizing influence on postural control, providing additional information on position and orientation (e.g., Paulus et al. 1984; Redfern et al. 2001; Vuillerme et al. 2006). Indeed, withdrawal of visual information was found to increase the forward leaning induced by NMV, both in response to short (Bove et al. 2009) and prolonged (Gomez et al. 2009) stimulation intervals. Vision has also been found to influence postural coordination during unperturbed upright standing (Zhang et al. 2007). However, the combined effects of NMV and availability of visual information on segmental variability and intersegmental coordination stabilizing different balance-related variables (e.g., head orientation or CoM position) have not been investigated to our knowledge.

In the present study, we studied the immediate effects of short (10 s) neck muscle vibration on upright posture, under conditions with and without visual feedback (eyes open, eyes closed). Participants were instructed to stand as still as possible (Zok et al. 2008). Postural responses to the

proprioceptive perturbation were assessed in the sagittal plane, both using a force plate (measuring CoP profiles) and whole-body kinematics. Kinematic data were analyzed both "locally" (markers, segments, joints), and "globally", looking at whole-body coordination. Local variability was decomposed into (linear) trends and fluctuations (residual variability) to distinguish between vibration-induced postural shifts of set point (forward leaning) and fluctuations around this set point. The former are assumed to reflect changes in the internal reference for upright posture (Gurfinkel et al. 1995), while the latter are taken to be indicators of postural instability. Whole-body coordination was assessed using a decorrelation technique (Müller and Sternad 2003), with respect to motor-equivalent stabilization of anterior–posterior CoM and head position, as well as sagittal trunk and head orientation.

Methods

Subjects

Eight young male university students (mean age = 21.4 ± 2.4 years; body weight = 73.0 ± 5.2 kg; height = 179.6 ± 5.5 cm) voluntarily participated in the experiment. None of the subjects presented any history of motor problems, neurological diseases or other impairments that could have influenced their balance, and none of them had consumed alcohol or other drugs on the day prior to the experiment, according to self-report. Subjects gave written consent to the experimental procedure. The study was conducted in accordance with the Helsinki Declaration and was approved by the local ethics committee.

Muscle vibrator

A DC motor with an eccentric mass on the shaft, embedded in a plastic tube of 7-cm length and 2.5-cm wide (Techno-concept VB 115, France), produced vibration of an amplitude of 0.85 mm and a maximal force of 5 N at 100 Hz (Bove et al. 2009). Vibrators were secured by straps over the paravertebral muscles on either side of the neck by a custom-made collar (Gomez et al. 2009). The activation of the vibrators was computer controlled (ADwin-pro Keithley Instruments Inc., Cleveland, OH, US).

Data acquisition

A force platform (AMTI, Model 0R6-5-1) was used to measure the displacement of the center of foot pressure (CoP) by computation of the three orthogonal components of the ground reaction forces and their associated torque.

Signals from the force platform were sampled at 100 Hz (12 bit A/D conversion). An active opto-electronic motion capture system (Optotrak 3020, Northern Digital, Waterloo, ON, Canada) was used to record body movements. Eight infrared-emitting markers were placed at the head (os zygomaticum, ZYG, and orbit, ORB), shoulder (glenohumeral axis, SHLD), pelvis (anterior superior iliac spine, ASIS), femur (great trochanter, GTR), knee (lateral epicondyle of femur, KNEE), and feet (lateral malleolus, ANK, and fifth metatarsal head, TOE). The marker positions (reported 3D accuracy at 2.25-m distance: 0.1 mm) were sampled at a frequency of 100 Hz (12-bit A/D conversion).

Procedure

Subjects were asked to stand "as still as possible" (Zok et al. 2008), with the head facing forward, the hands at the back and their feet 10 cm apart. Each trial lasted 20 s and was divided into two intervals of 10 s: (1) no vibration (NOVIB) for the first 10 s, and (2) vibration (VIB) of the neck muscles for the second 10 s. This postural task was executed under two visual conditions: eyes open (EO) and eyes closed (EC). In the EC condition, subjects were asked to close their eyes, whereas in the EO condition they were asked to look at the intersection point of a black cross (20 × 25 cm) attached at eye level to the white wall at a distance of about 1 m in front of them. Between trials, 30 s of rest were provided. Before each trial started, subjects were given 3 s to stabilize their upright posture on the force platform, under the vision condition (EO or EC) of the subsequent trial. One practice trial and four experimental trials were performed in each vision condition, intermixed in pseudorandom order.

Data analysis: univariate variability

All the analyses were performed using custom-written Matlab routines. Kinematic and force place (CoP) data were low pass filtered using a forward and reverse second-order Butterworth filter with a cutoff frequency of 10 Hz. Data from the NOVIB and VIB intervals of each trial (first vs. last 10 s) were analyzed separately. Kinematic and force plate data were only analyzed in the sagittal plane, since symmetric neck tendon vibration had previously been found to affect posture mainly in this plane (e.g., Kavounoudias et al. 1999). Preliminary analyses showed that ankle and toe marker positions varied only minimally during trials (within-trial SD less than 1 mm for all participants, trials and spatial dimensions). Therefore, data of these markers were replaced by their within-trial means, allowing the use of the foot as a stable basis for the biomechanical model (see below).

Position data of consecutive markers along the kinematic chain from foot to head were used to compute

Fig. 1 Raw data (joint angles, segment angles, marker positions), illustrating the decomposition of variability into trend and fluctuations. The *dotted lines* show the linear fits (trends) for the time intervals 0–10 s (NOVIB) and 10–20 s (VIB) *vertical*. Residual fluctuations are defined as deviations from this trend
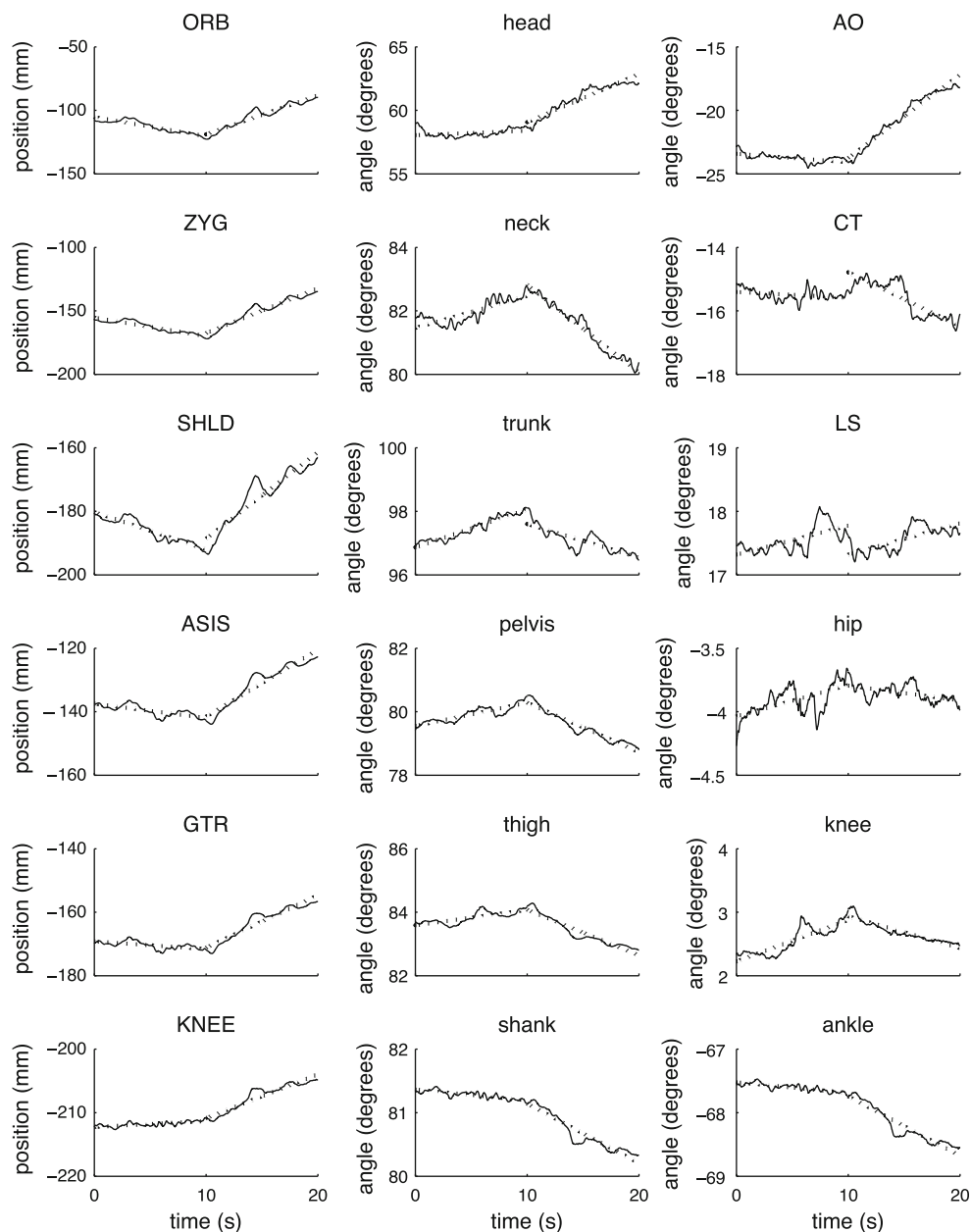
(absolute) segment positions and orientations. Whole-body CoM position was estimated from segment data by taking the relative mass-weighted sum of individual segments' CoM positions (Winter 2004, p. 63/64, Table 3.1). Segment elevation angles were computed for the following segments: foot, shank, thigh, pelvis, chest, neck and head (taking the markers SHLD and ZYG as approximations of the cervico-thoracic and atlanto-occipital joints in the sagittal plane). From these, relative orientations of neighboring segments were computed, yielding joint angles for the following joints: ankle, knee, hip, lumbosacral (LS), cervico-thoracic (CT) and atlanto-occipital (AO). Angle orientation followed the mathematical convention, i.e.,

positive values correspond to counterclockwise rotation. Therefore, for the knee joint, positive values correspond to flexion, for all other joints positive values correspond to extension (or plantar flexion for the ankle).

Positional (markers, CoM) and angular (segments, joints) time series frequently showed linear drifts, in particular during VIB (see raw data, Fig. 1). Therefore, their variability (within the two 10-s VIB and NOVIB intervals) was split into a linear component (*trend*) and residual variability (*fluctuations*). The trend was quantified as the difference between the start and end value in the interval, and fluctuations were quantified by means of the standard deviation of the residual variability.

Data analysis: motor-equivalent coordination

Whole-body postural coordination was analyzed using a decorrelation technique (Müller and Sternad 2003). Joint angles were randomly permuted ("decorrelated") across time (within VIB/NOVIB intervals of trials). Using a biomechanical forward model (see below), the effect of decorrelation on a specific task-related variable (e.g., CoM position) can be determined. The rationale of this approach is that coordination among the joints is destroyed by the decorrelation procedure. Therefore, coordination (with respect to the task-related variable) can be quantified as the normalized difference between empirically observed variance V_{emp} and decorrelated variance V_0 in the task-related variable. Specifically, a generalized correlation coefficient can be defined as $\rho = V_{emp}/V_0 - 1$. Coordination is indicated when, statistically, $V_{emp} < V_0$, or equivalently $\rho < 0$, with perfect coordination corresponding to $\rho = -1$. On the other hand, positive ρ indicates an organization of joint angles that destabilizes the task-related variable. It can be shown (Müller and Sternad 2003) that for the special case of the forward model $f(x,y) = x+y$, ρ equals the conventional correlation coefficient.

The decorrelation analysis requires a forward model, mapping elemental variables (joint angles) to the task-related variable at hand. This model was defined individually for each participant, estimating segment lengths by taking the mean across all trials of each participant. These were combined with joint angle data to compute segment orientations and positions, which were then used to compute the considered task-related variables: anterior–posterior CoM and head position, as well as sagittal trunk and head orientation (pitch). Thus, for each of these variables, V_{emp}, V_0 and ρ were determined, allowing to test the presence and amount of coordination with respect to these variables. To increase reliability of the generalized correlation estimate, V_0 was computed by taking the average over 100 repetitions of the decorrelation procedure. These measures were computed for each trial separately.

Statistical analysis

Statistical analysis was performed using R statistical software package (R Development Core Team 2008).

To correct for non-normal distribution, the fluctuations (but not trends) of CoP and marker positions, segment elevation and joint angles were log-transformed prior to statistical analysis. Since preliminary analyses did not show any systematic order effects, data from the four experimental trials of one Vision/Vibration condition were averaged for each participant.

Subsequently, dependent variables were submitted to separate repeated measures ANOVAs with Vision (EO, EC) and Vibration (NOVIB, VIB) as within-subject factors. Effect sizes are reported as Cohen's d (Cohen 1988), corresponding to the contrasts EC–EO (Vision), VIB–NOVIB (Vibration), and their interaction. In addition, generalized correlation with respect to each of the four task-related variables under consideration (CoM position, head position, trunk orientation, head orientation) were tested for being different from zero, separately for each Vision and Vibration condition, using two-tailed one-sample t tests.

The alpha level for statistical significance testing was set to 0.05.

Results

Sample data

Exemplary raw data from a single trial in the EO condition are shown in Fig. 1, illustrating the decomposition of univariate time series into trends and fluctuations. Neck muscle vibration started after 10 s. Note that the subject responded to the vibratory stimulation "locally" by extending the AO joint (right column) by about 7°. In contrast, head orientation is only shifted by about 4°, indicating compensatory coordination of the other joints stabilizing head orientation. Indeed, the CT, knee and ankle joints show clear trends in the opposite direction, partially compensating for the effect of neck extension on head orientation. Note also that this kind of whole-body strategy does affect body equilibrium (i.e., CoM position), as can be seen from the considerable forward shift of all markers plotted here (left column).

Center of pressure and center of mass

Figure 2 shows trends and fluctuations for CoP and CoM. Due to the high correlation between these variables, the patterns are very similar.

Statistical analysis of CoM *trend* showed a main effect of Vibration [$F(1,7) = 108.8$, $P < 0.0001$, $d = 3.41$] and a Vision-by-Vibration interaction [$F(1,7) = 9.56$, $P < 0.05$, $d = -1.86$]. CoM *fluctuations* showed a main effect of Vision [$F(1,7) = 40.0$, $P < 0.0005$, $d = 1.90$]. The effects for the CoP were similar: CoP *trend* showed a main effect of Vibration [$F(1,7) = 76.3$, $P < 0.0001$, $d = 3.48$] and a Vision-by-Vibration interaction [$F(1,7) = 10.24$, $P < 0.05$, $d = -1.69$]; CoP *fluctuations* showed a main effect of Vision [$F(1,7) = 55.0$, $P < 0.0005$, $d = 1.61$].

In sum, neck muscle vibration affected postural equilibrium, inducing a significant forward shift of CoM and CoP position trends. The Vibration-by-Vision interaction indicates that the difference in leaning trends between NOVIB and VIB periods tended to be larger in EO than in
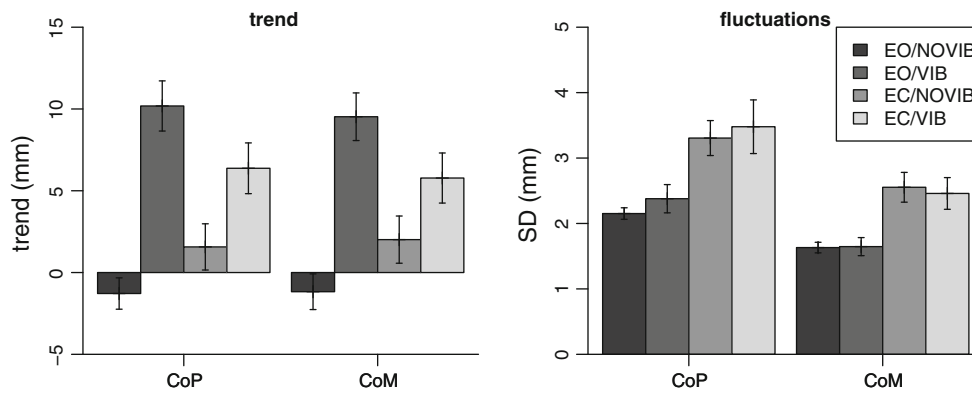
Fig. 2 Trend (*left*) and fluctuations (*right*) for center of mass and center of pressure positions. For the trend, *positive* values correpond to forward shifts. *Error bars* represent SEM
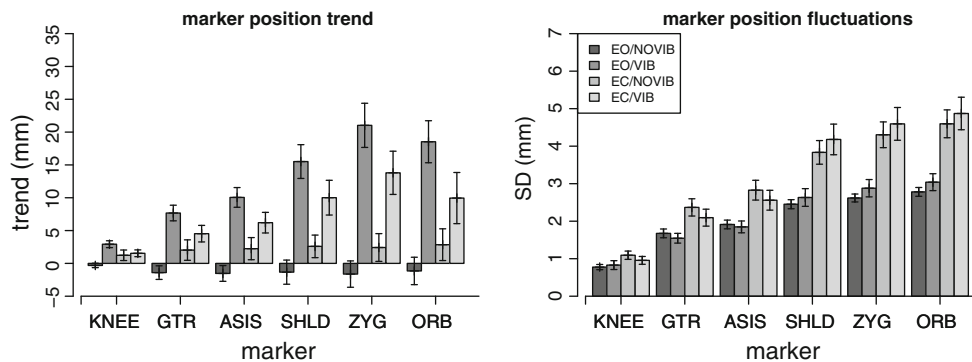

Fig. 3 Marker position trend (*left*) and fluctuations (*right*). For the trends, *positive* values correspond to forward shifts. *Error bars* indicate SEM

EC conditions. In contrast, CoM and CoP fluctuations were only affected by Vision, with higher fluctuations in the EC condition.

The Vision-by-Vibration interaction observed for CoM and CoP trends was unexpected and has not been reported in previous research, to our knowledge. Since it may be partly due to differences in leaning behavior during EO/NOVIB and EC/NOVIB periods, we conducted an additional statistical analysis of Vision within the EC condition. Directly comparing CoM and CoP trends in EO/VIB and EC/VIB did not reveal a significant effect for either measure [CoM: $F(1,7) = 2.06$, $P = 0.19$; CoP: $F(1,7) = 2.13$, $P = 0.19$]. This issue will be discussed in more detail below.

Marker, segment and joint variability

Trends and fluctuations of marker positions, segment elevation and joint angles are plotted in Figs. 3, 4, 5. Results of the statistical analysis are reported in Tables 1, 2 and 3 and discussed below.

Marker position (Fig. 3, Table 1) *trends* for all markers showed main effects of Vibration and Vision-by-Vibration interactions. This indicates an NMV-induced forward shift

of all markers ,which tended to be more pronounced in the EO condition. Marker position *fluctuations* for all markers showed main effects of Vision, with higher fluctuations in the EC condition.

Segment elevation (Fig. 4, Table 2) *trends* showed main effects of Vibration for all segments, and significant Vision-by-Vibration interactions for all segments except for the pelvis and the trunk. However, the direction of the effects was opposite for the head (backward leaning) compared to all other segments (forward leaning). According to the interaction effects, the Vibration effect for the shank, thigh, pelvis and neck was more pronounced in the EO condition, while the Vibration effect for the head was more pronounced in the EC condition. Segment elevation *fluctuations* showed effects of Vision for all segments except the neck, with higher fluctuations in the EC condition. Head fluctuations were also increased during NMV (main effect of Vibration). For the trunk and the neck, the Vision-by-Vibration interaction indicates a stronger perturbing effect of neck muscle vibration in the EC compared to the EO condition.

The pattern for the joint angles (Fig. 5, Table 3) was less uniform. Joint angle *trends* showed significant effects for the ankle (main effect of Vibration, Vision-by-Vibration
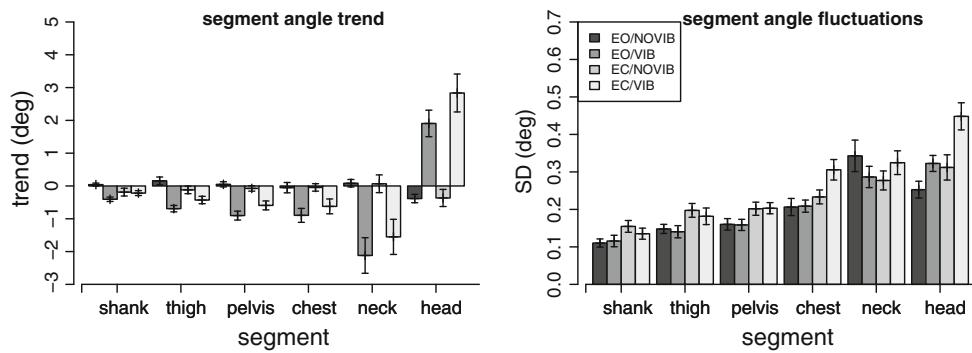
Fig. 4 Segment elevation angle trends (*left*) and fluctuations (*right*). For the trends, *positive* values correpond to backward leaning. *Error bars* indicate SEM
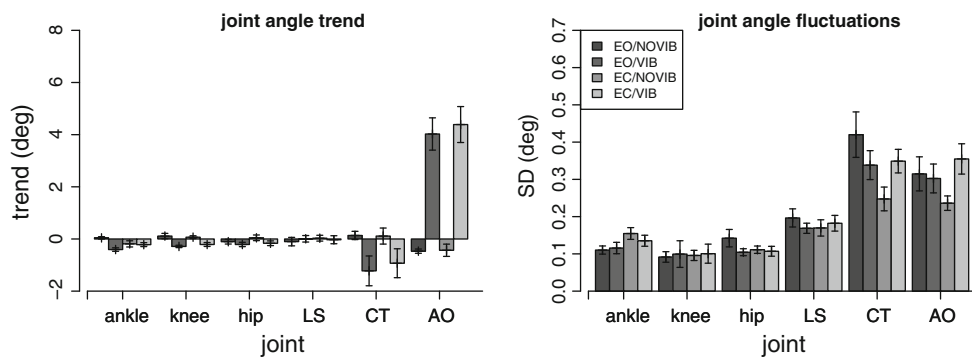

Fig. 5 Joint angle trends (*left*) and fluctuations (*right*). For the trends, *positive* values correspond to extension (except for the knee joint, where *positive* values correspond to flexion). *Error bars* indicate SEM

Table 1 T values ($t(7)$) and effect sizes (Cohen's d) for marker position trends and fluctuations

Measure	Vision	Vibration	Vision × vibration
KNEE trend	$t = 0.10, d = 0.06$	$t = 4.26, d = 1.79**$	$t = -3.91, d = -1.85**$
GTR trend	$t = 0.08, d = 0.05$	$t = 8.17, d = 2.59***$	$t = -3.19, d = -1.86*$
ASI trend	$t = -0.02, d = -0.01$	$t = 10.57, d = 3.09***$	$t = -3.08, d = -1.87*$
SHLD trend	$t = -0.24, d = -0.15$	$t = 7.95, d = 3.68***$	$t = -2.57, d = -1.40*$
ZYG trend	$t = -0.41, d = -0.24$	$t = 7.14, d = 3.55***$	$t = -2.90, d = -1.30*$
ORB trend	$t = -0.52, d = -0.32$	$t = 5.47, d = 2.73***$	$t = -3.07, d = -1.39*$
KNEE fluctuations	$t = 4.18, d = 0.98**$	$t = -0.98, d = -0.20$	$t = -1.36, d = -0.54$
GTR fluctuations	$t = 4.54, d = 1.29**$	$t = -1.79, d = -0.46$	$t = -0.20, d = -0.08$
ASI fluctuations	$t = 5.43, d = 1.53***$	$t = -1.20, d = -0.38$	$t = -0.36, d = -0.12$
SHLD fluctuations	$t = 6.72, d = 2.19***$	$t = 0.53, d = 0.21$	$t = 0.74, d = 0.17$
ZYG fluctuations	$t = 6.49, d = 2.63***$	$t = 0.56, d = 0.24$	$t = -0.08, d = -0.02$
ORB fluctuations	$t = 6.85, d = 2.82***$	$t = 0.52, d = 0.23$	$t = -0.12, d = -0.04$

Significant effects are indicated (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, uncorrected)

interaction, dorsiflexion in EO/NOVIB compared to the other conditions), knee (Vibration, extension in VIB condition) and AO joint (Vibration, extension in VIB condition). Joint angle *fluctuations* showed significant effects for the ankle (Vision, higher fluctuations in EC), pelvis (lower fluctuations in VIB), CT joint (Vision, lower fluctuations in EC; Vibration by Vision, stronger perturbing effect of

vibration in EC condition) and AO joint (Vibration-by-Vision interaction: stronger perturbing effect of vibration in EC condition).

As for CoM and CoP, a Vision-by-Vibration interaction was found in the *trends* of several variables (in particular, marker positions, but also some shank elevation and ankle joint angles), indicating that, unexpectedly, the forward

Table 2 T values ($t(7)$) and effect sizes (Cohen's d) for segment elevation trends and fluctuations

Measure	Vision	Vibration	Vision × vibration
Shank trend	$t = -0.18, d = -0.10$	$t = -4.38, d = -1.71**$	$t = 3.91, d = 1.94**$
Thigh trend	$t = -0.04, d = -0.02$	$t = -9.64, d = -2.83***$	$t = 2.58, d = 1.58*$
Pelvis trend	$t = 0.67, d = 0.35$	$t = -9.50, d = -3.47***$	$t = 2.34, d = 1.27$
Trunk trend	$t = 0.67, d = 0.39$	$t = -3.16, d = -1.90*$	$t = 0.96, d = 0.36$
Neck trend	$t = 0.88, d = 0.34$	$t = -3.28, d = -1.80*$	$t = 3.61, d = 0.35**$
Head trend	$t = 1.17, d = 0.58$	$t = 6.00, d = 3.14***$	$t = 2.40, d = 0.65*$
Shank fluctuations	$t = 4.21, d = 1.05**$	$t = -0.96, d = -0.21$	$t = -1.10, d = -0.46$
Thigh fluctuations	$t = 4.28, d = 1.24**$	$t = -1.48, d = -0.49$	$t = 0.33, d = 0.12$
Pelvis fluctuations	$t = 3.00, d = 1.58*$	$t = -0.20, d = -0.12$	$t = 0.25, d = 0.07$
Trunk fluctuations	$t = 8.86, d = 1.28***$	$t = 1.74, d = 0.62$	$t = 3.41, d = 0.88*$
Neck fluctuations	$t = -0.22, d = -0.04$	$t = -0.10, d = -0.03$	$t = 3.56, d = 1.04**$
Head fluctuations	$t = 4.92, d = 1.16**$	$t = 3.68, d = 1.32**$	$t = 1.51, d = 0.54$

Significant effects are indicated (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, uncorrected)

Table 3 T values ($t(7)$) and effect sizes (Cohen's d) for joint angle trends and fluctuations

Measure	Vision	Vibration	Vision × vibration
Ankle trend	$t = -0.18, d = -0.10$	$t = -4.38, d = -1.71**$	$t = 3.91, d = 1.94**$
Knee trend	$t = 0.28, d = 0.10$	$t = -4.62, d = -1.96**$	$t = 1.03, d = 0.45$
Hip trend	$t = 1.66, d = 0.46$	$t = -2.19, d = -0.72$	$t = -0.58, d = -0.32$
LS trend	$t = 0.34, d = 0.19$	$t = 0.13, d = 0.08$	$t = -0.93, d = -0.28$
CT trend	$t = 0.46, d = 0.16$	$t = -1.95, d = -1.05$	$t = 1.39, d = 0.18$
AO trend	$t = 0.78, d = 0.21$	$t = 7.12, d = 3.61***$	$t = 1.02, d = 0.17$
Ankle fluctuations	$t = 4.21, d = 1.05**$	$t = -0.96, d = -0.21$	$t = -1.10, d = -0.46$
Knee fluctuations	$t = 1.60, d = 0.32$	$t = -1.11, d = -0.32$	$t = 1.39, d = 0.32$
Hip fluctuations	$t = -1.02, d = -0.18$	$t = -3.46, d = -0.50*$	$t = 0.93, d = 0.59$
LS fluctuations	$t = -0.78, d = -0.07$	$t = -0.14, d = -0.05$	$t = 2.13, d = 0.73$
CT fluctuations	$t = -4.81, d = -0.69**$	$t = 0.93, d = 0.30$	$t = 2.90, d = 1.29*$
AO fluctuations	$t = -0.16, d = -0.04$	$t = 1.89, d = 0.56$	$t = 4.08, d = 1.19**$

Significant effects are indicated (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, uncorrected)

leaning was more pronounced in the EC condition. A direct comparison of the forward trend in EO/VIB and EC/VIB did not reach significance ($P > 0.1$) for any of these variables.

In summary, the effects on marker position trends and fluctuations parallel the effects observed for CoM and CoP, with a general forward leaning of the body and generally increased fluctuations in the EC condition. The analysis of segment elevation angles reveals differences along the central body axis: in contrast to all other segments (that showed a forward leaning trend upon vibration), the head tended to lean backward. This is explained by a pronounced extension of the AO joint, the joint most directly affected by neck tendon vibration, presumably due to the tonic vibration response (e.g., Eklund and Hagbarth 1966).

Note that the vibration-induced extension of the AO joint was larger [mean ± SD, EO: $4.20° ± 2.06°$, EC: $4.39° ± 2.38°$] than the resulting backward leaning of the head [EO: $1.91° ± 1.55°$, EC: $2.84° ± 2.03°$], suggesting that the rest of the body compensated for the local effect of the neck vibration to stabilize head orientation.

Motor-equivalent coordination

The results of the decorrelation analysis are shown in Fig. 6. Generalized correlations were first tested for deviating from zero (at the group level) with a one-sample t test, separately for each of the four Vision and Vibration conditions and for each the four task-related variables. Coordination stabilizing the task-related variable under consideration is indicated by *negative* generalized correlation, while a positive correlation indicates a postural organization that destabilizes the task-related variable.

Generalized correlations deviating from zero were found for CoM position control in the EO/NOVIB condition [$t(7) = -4.05$, $P < 0.005$; negative], for head position in both NOVIB conditions [EO: $t(7) = -10.44$, $P < 0.0005$; EC: $t(7) = -4.12$, $P < 0.01$; both negative], and for trunk orientation control in both NOVIB conditions [EO: $t(7) = -3.39$, $P < 0.05$, EC: $t(7) = -4.11$, $P < 0.005$; both negative] and in the EC/VIB condition [$t(7) = 2.59$, $P < 0.05$, positive]. In contrast, regarding head orientation control, generalized correlations deviated from zero in all
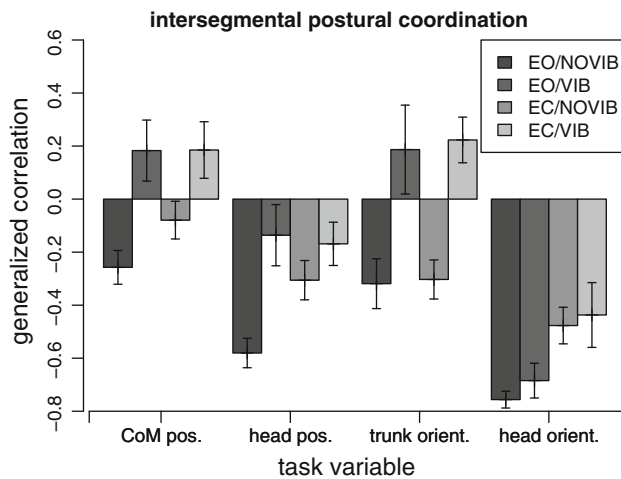
Fig. 6 Generalized correlation, with respect to center of mass position, head position, trunk orientation and head orientation. Coordination is indicated when the generalized correlation is *negative*, with perfect coordination corresponding to a value of −1. *Error bars* represent SEM

conditions [EO/NOVIB: $t(7) = -23.87$, $P < 0.0001$; EO/VIB: $t(7) = -10.43$, $P < 0.0001$; EC/NOVIB: $t(7) = -6.92$, $P < 0.0005$; EC/VIB: $t(7) = -3.58$, $P < 0.01$; all negative].

Analysis of variance regarding the influence of the Vision and Vibration manipulations yielded the following results. For CoM control, there was a main effect of Vibration [$F(1,7) = 31.44$, $P < 0.001$, $d = 1.69$], reflecting a weaker (less negative) generalized correlation in the VIB condition compared to the NOVIB condition. For head position control, a main effect of Vibration [$F(1,7) = 13.4$, $P < 0.01$, $d = 1.68$] and a Vision-by-Vibration interaction [$F(1,7) = 8.11$, $P < 0.05$, $d = -1.13$] were found, showing weaker coordination in the VIB condition and a weaker effect of vibration in the EC condition. For trunk orientation control, a main effect of Vibration [$F(1,7) = 24.2$, $P < 0.005$, $d = 1.92$] was found, indicating weaker coordination in the VIB condition. Regarding head orientation control, a main effect of Vision was present [$F(1.7) = 29.35$, $P < 0.001$, $d = 1.48$], with less negative generalized correlation in the EC condition.

In summary, sagittal head orientation was the only task-related variable for which generalized correlations were consistently negative. This shows that, across all conditions, all joints considered here were coordinated in a way stabilizing head pitch. This coordination was weaker (less negative generalized correlation) in the EC condition, consistent with the role of vision for head stabilization, but was not affected by NMV. In contrast, CoM and head position only showed negative generalized correlations in the EO/NOVIB (CoM position) or in both NOVIB (head

position, trunk orientation) conditions. As shown by the ANOVA, whole-body coordination stabilizing these variables was compromised by NMV.

Discussion

We studied the immediate effects of symmetric vibratory stimulation of the dorsal neck muscles on postural control, as well as their potential interaction with vision. Postural effects were analyzed locally (position and orientation of individual body parts) and globally (whole-body coordination). Besides replicating previously observed effects of NMV, i.e., a general forward learning of the body, the present analysis allows refining previous accounts of this phenomenon, as discussed below.

Postural trends and fluctuations are differentially affected by NMV and vision

Postural variability was decomposed into (linear) trends and (residual) fluctuations, based on the assumption that the former capture NMV-induced changes in the internal reference for upright posture (Gurfinkel et al. 1995), while the latter are taken to be indicators of postural instability. This decomposition showed differential effects of vibration and vision. Consistent with previous research (Eklund and Hagbarth 1966; Eklund 1971, 1972; Gregoric et al. 1978; Lund 1980), NMV induced a forward leaning of the body. This forward leaning was evident in *trends* of center of pressure and center of mass positions, marker positions, body segment orientations, and ankle and knee joint angles. In contrast, NMV did not affect residual *fluctuations* of the variables considered here, suggesting that the induced forward leaning did not lead to a breakdown of posture-stabilizing processes. On the other hand, in agreement with previous findings on the posture-stabilizing role of vision (e.g., Paulus et al. 1984; Redfern et al. 2001; Vuillerme et al. 2006), postural *fluctuations* were higher in the EC compared to the EO condition.

In addition, postural *trends* showed a Vision-by-Vibration interaction, indicating that the effect of NMV was stronger with EO compared to EC. This was unexpected and opposite to the typically observed stabilizing effect of vision on posture (Paulus et al. 1984; Redfern et al. 2001), as well as a recent analysis of modulation of NMV-induced postural effects by vision (Bove et al. 2009). However, a direct comparison of EO/VIB and EC/VIB in the present study did not show a significant difference for any of the forward leaning measures. This suggests that the observed interaction effect may be at least partly explained by vision-related differences in postural trend during the pre-vibration interval.

Differences in instruction may play a role as well. We instructed participants to stand as still as possible. In contrast, Bove et al. (2009) gave no specific instruction about postural stabilization (Marco Schieppati, January 2010, personal communication). The considerably larger forward leaning in this latter study (more than 40 mm in some conditions, for a 5-s vibration) compared to the present experiment (7–10 mm on average, for a 10-s vibration) may be related to this difference in instructions. Experimental instructions may also lead to a top–down modulated reweighting of sensory information and task priorities. In vestibular-loss patients, NMV-induced forward leaning was found to be reduced or absent (Lekhel et al. 1998). Thus, degraded information about head orientation may actually (and somewhat counter-intuitively) reduce the whole-body postural effects of NMV. Theoretically, the availability of vision, providing additional information about head orientation, may modulate NMV effects in a similar way as the availability of vestibular input. It remains to be investigated, in detail, how stabilizing and (potential) destabilizing mechanisms of visual feedback interact with experimental instruction.

Neck muscle vibration-induced extension of the upper neck

Locally, NMV induced a pronounced extension of the atlanto-occipital (AO) joint, leading to a backward leaning of the head. Such local responses to muscle or tendon vibration have previously been found for a number of stimulation sites across the body and are typically interpreted as a corrective response to the perceived (illusory) lengthening muscle induced by the vibration (Goodwin et al. 1972a, b; Lackner and Levine 1979; Gilhodes et al. 1986). Our findings show that the effect of NMV on upright postural control has a local component, besides the previously hypothesized global effect on the 'proprioceptive chain' (Roll and Roll 1988).

To our knowledge, this local effect has not previously been reported in unrestrained standing in healthy subjects. Clinical studies found such a local response in vestibular loss patients (Lekhel et al. 1998) and patients with torticollis (Lekhel et al. 1997), who in return showed no or reduced forward leaning of the body. Lekhel et al. (1998) report (without reference) that head backward tilt had been observed in healthy individuals only when the trunk was artificially restrained.

A simple and suitable reason why this effect was not previously reported may be that postural data were not acquired or analyzed accordingly. Numerous studies have analyzed NMV effects on posture only using force plates (Kavounoudias et al. 1999; Lekhel et al. 1998), while others have measured body kinematics but not analyzed movement in individual joints (Gomez et al. 2009). In the study by (Lekhel et al. 1997), head orientation was measured in patients with torticollis, but only visually assessed in control subjects.

More interestingly, another possible reason why previous studies did not find the local effect of neck extension might be that its influence on sagittal head orientation (pitch) was partially compensated by the forward leaning of the body. For instance, in the EO condition, average AO extension was about 4°, while the backward leaning of the head was less than half as large. Therefore, neck extension may go unnoticed when it is assessed by visual inspection or even on measurement of absolute (but not relative) head orientation.

Motor-equivalent coordination: differential effects of NMV and vision

Whole-body coordination was analyzed using a decorrelation technique (Müller and Sternad 2003). In this method, coordination with respect to variables in which stabilization is assumed to be task relevant (here: CoM and head position, trunk and head orientation) is quantified as a generalized correlation coefficient. This measure is defined by comparing variability in actual task performance to surrogate data, obtained by decorrelating (reshuffling) joint angle time series. The analysis is possible because the human motor system exhibits motor equivalence with respect to these task-related variables, since it has more DOF available (six joint angles, in the present model) than are specified at the task level (here, one DOF for each of the four variables).

Negative generalized correlations indicate coordinated stabilization of the studied variable, with −1 corresponding to perfect coordination, i.e., full compensation among the joint angles stabilizing the task-related variable. It has to be noted that, with this operationalization, a postural change that leads to a shift in the task-related variable (as observed in particular for the CoM) may be considered destabilizing (positive generalized correlation), even if the body reaches a new stable equilibrium after the shift.

Coordination analysis revealed that, of the variables under consideration, only head orientation was consistently stabilized across all vision and vibration conditions. Notably, coordination with respect to head orientation was affected by vision (poorer stabilization in EC condition) but not by NMV, indicating that participants coordinated all joints along the central body axis to stabilize head orientation even under conditions of proprioceptive perturbation. Note that this does not mean that head pitch was as stable during VIB and NOVIB conditions (this was actually not the case, as shown by the analysis of segment elevation angles), but that under all conditions, the joints

included in the present analysis were coordinated to a similar extent in a way that stabilized head orientation. In contrast, coordination underlying stabilization of CoM and head position, as well as trunk orientation, was compromised by the NMV.

Thus, NMV did not disrupt whole-body coordination stabilizing head orientation, despite the fact that the neck is most directly affected by NMV. In contrast, it *did* lead to a destabilization of whole-body equilibrium. This indicates that, probably within certain stability margins, orientation may be prioritized over equilibrium by the postural control system. This finding also suggests an alternative (or complementary) explanation of NMV-induced forward leaning, namely to compensate for the effect of neck extension (i.e., the local response to NMV) on head orientation, in contrast (or in addition) to a response to illusory backward leaning as suggested in previous accounts (e.g., Kavounoudias et al. 1999; Lekhel et al. 1997). The present study does not allow discrimination between these two hypotheses. A way to address this question may be to experimentally vary task requirements, either by instruction or by introducing different postural constraints concerning head stabilization (e.g., balancing an object on the top of the head).

Conclusions and outlook

In conclusion, our study amends and extends previous accounts of NMV-induced forward leaning in several ways. First, the decomposition of univariate variability (in CoM, CoP, markers, segments and joints) into linear trends and residual fluctuations revealed differential effects of Vision and NMV. Second, NMV also induced local postural responses, resulting in an extension of the upper neck (backward leaning of the head). Finally, analysis of whole-body coordination showed that, out of four analyzed task-related variables (CoM and head position, trunk and head orientation), only head orientation was consistently stabilized by motor-equivalent coordination across Vision and Vibration conditions. Future research should investigate how explicit instructions or additional task constraints may affect postural stabilization under conditions of perturbed proprioception introduced by NMV.

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