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Relation between postural sway magnitude and metabolic energy cost during upright standing on a compliant surface

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Houdijk H, Brown SE, van Dieën JH. Relation between postural sway magnitude and metabolic energy cost during upright standing on a compliant surface. *J Appl Physiol* 119: 696–703, 2015. First published July 9, 2015; doi:10.1152/jappphysiol.00907.2014.—Postural control performance is often described in terms of postural sway magnitude, assuming that lower sway magnitude reflects better performance. However, people do not typically minimize sway magnitude when performing a postural control task. Possibly, other criteria are satisfied when people select the amount of sway they do. Minimal metabolic cost has been suggested as such a criterion. The aim of this study was to experimentally test the relation between sway magnitude and metabolic cost to establish whether metabolic cost could be a potential optimization criterion in postural control. Nineteen healthy subjects engaged in two experiments in which different magnitudes of sway were evoked during upright standing on a foam surface while metabolic energy expenditure, center of pressure (CoP) excursion, and muscle activation were recorded. In one experiment, sway was manipulated by visual feedback of CoP excursion. The other experiment involved verbal instructions of standing still, natural or relaxed. In both experiments, metabolic cost changed with sway magnitude in an asymmetric parabolic fashion, with a minimum around self-selected sway magnitudes and a larger increase at small compared with large sway magnitudes. This metabolic response was paralleled by a change in tonic and phasic EMG activity in the major leg muscles. It is concluded that these results are in line with the notion that metabolic cost can be an optimization criterion used to set postural control and as such could account for the magnitude of naturally occurring postural sway in healthy individuals, although the pathway remains to be elucidated.

postural control; energy expenditure; optimal control

HUMAN MOTOR CONTROL IS CHARACTERIZED by motor variability (20). In postural control of upright standing, this becomes apparent as postural sway (38). The magnitude of body sway, or as a related measure the displacement of the center of pressure of the ground reaction force under the foot, is typically used to compare postural control performance between different populations (e.g., young vs. older people or patients vs. healthy controls) or between different conditions (e.g., with manipulated sensory information), often with the assumption that less sway indicates better control. Posturography, being the technique for assessing postural control performance, has been used abundantly in both research and clinical practice (24, 39).

Postural sway emerges from many sources. Sway magnitude depends on availability and accuracy of sensory information (10), sensory weighting (36), delays and gains of control loops

(31) and noise in the neuromotor system (8) or the environment. Differences in these sources, for instance, between groups or conditions, have been shown to account for differences in sway amplitude. However, postural sway reflects more than static properties of the neuromusculoskeletal system and environment. Ample evidence exists that postural sway can be modulated by the central commands from the central nervous system. People can voluntarily increase or decrease sway amplitude (4, 22, 40). Moreover, although postural control seems a highly automated process, dual-task studies have shown that postural control poses a demand on working memory (41). In addition, EEG studies also confirm that postural control involves specific cortical activity depending on sway magnitude and direction (33). Volitional modulation of sway can be the result of altered muscle (co)activation, through increased altered tonic drive to the motor neurons, or altered gains of the feedback loops in the servocontrol system (30). Both mechanisms are under subcortical and cortical control. Additionally, modulation of sway has been suggested to be obtained through predictive feedforward muscle control (2, 7, 22, 23).

The adaptive control of postural sway seems in line with the optimal control paradigm in sensorimotor control (34), which suggests that we organize our control system in such a way that a given performance criterion is optimized. This performance criterion could be minimizing sway amplitude. However, it has been shown that people can reduce sway amplitude below their naturally occurring values when requested to do so (4). Hence, other criteria probably play a role in setting the different elements of the servocontrol system and accounting for the resulting self-selected sway magnitude.

Metabolic cost has been suggested as such a potential optimization criterion (36). Postural control during upright standing has previously been shown to require a significant amount of metabolic energy, which varies with postural control conditions and with health status (12, 13). It can be hypothesized that minimizing sway might require increased tonic muscle (co)activation and high gains of short-latency responses, while large sway amplitudes might require increased phasic muscle activation for balance recovery using long-latency responses. Hence, minimal metabolic cost might occur at intermediate sway magnitudes. Metabolic energy demand has already been shown to be a potential optimization criterion in cyclic tasks like walking (1, 25, 26) and cyclic upper extremity activities (5, 14, 15). In addition, modeling studies previously revealed that parameters related to metabolic energy expenditure (i.e., minimizing torque or activation) can predict human behavior during upright standing (18, 21, 36). However, no experimental evidence yet exists on the relation between metabolic energy demand and postural sway.

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The aim of this study was to investigate the relation between postural sway magnitude and metabolic energy demand. The existence of such a relation is conditional for metabolic cost to be considered as a potential optimization criterion during postural control tasks, and might explain differences in control strategies between individuals and conditions. Two different experimental tasks were used in this study to evoke different magnitudes of sway in healthy subjects, and the related metabolic cost was recorded. In addition, muscle activation was recorded to support and explain the potential relation between sway magnitude and metabolic cost. We hypothesized that metabolic cost would vary with sway magnitude in such a way that minimal metabolic cost would occur at self-selected sway magnitude.

METHODS

Subjects. Nineteen healthy subjects (6 males, 13 females; age 22–52 yr, body mass index 24.4 ± 5.4) without a history of musculoskeletal impairments or neurological disorders participated in this study. All participants provided written informed consent in accordance with the declaration of Helsinki and regulations of the local research ethics committee, which approved this study.

Protocol. Two different experimental manipulations were used to provoke different magnitudes of sway during upright standing without changing sensory information or properties of the base of support within each manipulation. During both experimental manipulations, participants stood barefoot on a piece of foam ($60 \times 40 \times 11$ cm; width \times length \times thickness), which was taped on top of a force plate, with their arms along their sides and at a self-selected stance width. Foot positions were standardized between trials by marking the self-selected foot position at the start of the experiment. The foam support surface was used to enhance metabolic effect sizes compared with standing on a rigid surface (12). Experimental trials lasted 4 min to allow participants to accommodate to the imposed instruction and

reach metabolic steady state. Generally, the final 90 s of each trial were used for data analysis.

Experiment 1: Center of pressure position feedback. In the first experimental manipulation, participants were encouraged to alter postural sway by providing visual feedback on their center of pressure (CoP) position and requesting that they keep the CoP projection within an elliptical area of specified size. The visual feedback was projected on a wall 3.27 m in front of the participant at approximately eye height and amplified by a factor of 14 with respect to actual CoP displacement on the force plate. Five elliptical areas were provided in subsequent trials, representing a fraction of 0.5, 0.7, 1.0, 1.3, and 1.5 of subjects' self-selected sway area.

To determine the size and position of the self-selected sway area, at the start of the experiment, each participant was asked to stand naturally on two legs during four trials of 2 min (19) on the foam-covered force plate without feedback (looking at a white wall). From these trials, the average CoP position and the mediolateral (ML) and anteroposterior (AP) displacements around this average position were determined. The maximal ML and AP CoP displacements were estimated as three times the SD of CoP displacement in both directions. Both average CoP position and maximal displacements were averaged over the four reference trials. The average CoP position was used to determine the position of the center of the elliptical feedback area. The maximal CoP displacement in the AP and ML direction was used to set the radii of the elliptical feedback area and was scaled, depending on the desired target size.

After the size and position of the target area had been determined, participants performed five 4-min upright standing trials while being instructed to keep their CoP projection (a blue dot on the screen) within the elliptical area while standing "as relaxed as possible to use the entire feedback area" (Fig. 1). This instruction was repeated halfway through the 4-min trials. Each participant was allowed to practice this task for 30-s intervals starting with the largest area (1.5), then the middle area (1.0), and finally the smallest area (0.5). Subsequently, the five trials with varying target areas were offered randomly

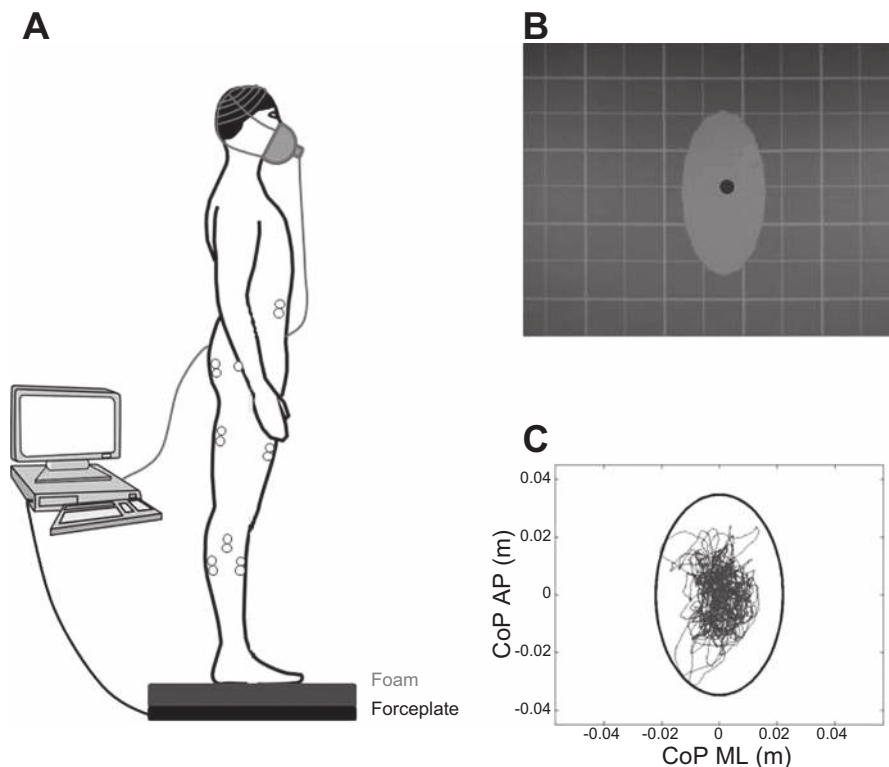


Fig. 1. Graphical representation of experimental setup. **A:** subjects stood on a foam surface mounted on top of a force plate looking forward with their arms alongside their body. They wore a face mask to collect breathing gases and EMG electrodes to record muscle activity. **B:** in the visual feedback condition, a feedback area and the actual center of pressure (CoP) position were projected on a screen in front of the subject. The feedback area consisted of an ellipse on a background raster. The dot indicates the actual CoP position that needed to be maintained within the elliptical area. **C:** the CoP stabilogram captured from the force plate showing a typical example of a subject's CoP behavior with respect to the elliptical feedback area. ML, mediolateral.

with 1-min seated rest periods in between. Subjects were not aware that one of the target areas represented their self-selected sway area.

Experiment 2: Verbal instruction. In the second experiment, participants were encouraged to alter postural sway by instructing them to “stand as still as possible,” “stand naturally,” or “stand as relaxed as possible” with roughly equal weight on each leg. All participants started out with the instruction of standing naturally. The next two conditions (still or relaxed) were performed in random order. For each instruction, a 4-min trial was performed in which the instruction to stand as naturally, still, or relaxed as possible was repeated every minute.

Data acquisition. CoP was derived from the ground reaction forces and moments, which were measured by a 60×40 cm force plate (Kistler) at a sample rate of 300 samples/s. CoP data were processed and projected online, after a 10-Hz second-order lowpass Butterworth filter was applied, using Dflow software (Motek Medical).

Metabolic energy expenditure was measured using standard breath-by-breath open-circuit respirometry (Cosmed K4). In and expired air was collected using a mask covering the mouth and nose (Hans Rudolph). This mask did not restrict breathing or vision. There is currently no available data demonstrating whether open-circuit respirometry alters postural sway or alters the relationship between sway and respiration. If any balance interference should occur, this was considered to be equal for all experimental conditions. Before the experiment, the system was calibrated with known gas concentrations and volumes.

Muscle activity was measured with surface EMG (TMSi) for the following muscles in a randomly selected leg: tibialis anterior (TA), gastrocnemius medialis, peroneus longus, rectus femoris (RF), semitendinosus (ST), gluteus maximus (GlutMax), gluteus medius (GlutMed), external oblique (EO), and erector spinae (ES). Electrode placement followed Seniam guidelines (9). A bandpass filter (10–500 Hz) was applied to the raw EMG signals before they were digitized at 1,000 samples/s.

Data analysis. Sway magnitude was quantified as the mean resultant distance of the CoP with respect to the average CoP position in each trial (28). The mean CoP distance was calculated over a 90-s time window at the end of each 4-min trial where metabolic steady state was reached (see below). Mean CoP distance was normalized to the mean CoP distance of the reference trials performed at the start of the experiment, to express mean CoP distance as a fraction of self-selected sway magnitude (CoP_{norm}).

Energy expenditure (in $\text{J} \cdot \text{kg}^{-1} \cdot \text{s}^{-1}$) was calculated from oxygen uptake and respiratory quotient (6) during steady state. Steady-state oxygen consumption was determined by performing a Mann-Kendall test to locate a 90-s continuous time window in which there was no rising or falling trend (32). The last 90 s were evaluated first, and, if a steady state was not found, the 90-s time window was backed up breath by breath from the end of the time series until a steady state window was confirmed.

The EMG amplitude probability distribution function (17) was used to derive the 10th (P10), 50th (P50), and 90th (P90) percentile of EMG amplitude probability distribution function (APDF). First, EMG signals were rectified and lowpass filtered (4th order, bidirectional

Butterworth, cutoff frequency 10 Hz). Subsequently, a cumulative frequency distribution of the EMG amplitudes over all samples was made. P10 of this cumulative probability function, i.e., the maximal EMG amplitude that was observed in the lowest 10% of the EMG samples, is considered to represent the level of tonic muscle activity related to static muscle contraction for generating required internal joint moments in the adopted position and coactivation. P50 represents the median activation, and P90 represents the magnitude of the phasic muscle responses in postural control, i.e., peak muscle responses.

Statistics. Normality of the data was checked with the Shapiro-Wilk test and residual plots. For normally distributed data (sway magnitude, energy consumption), the within-subject differences between conditions were determined using a repeated-measures ANOVA and were followed up with least-significant difference pairwise comparisons relative to the reference condition (1.0 or stand naturally) in case of a significant condition effect ($P < 0.05$). For nonnormally distributed data (EMG percentiles), differences were determined using a Friedman test with post hoc comparisons assessed by a Wilcoxon signed-rank test, with Bonferroni adjustment.

In addition, the relation between sway magnitude and energy consumption within each experimental manipulation was quantified using generalized estimation equations (GEE). This regression technique allows the actual observed sway magnitude to be entered as the independent variable in the analysis, as opposed to the imposed sway magnitude that is used in the ANOVA. Moreover this technique takes into account the dependency of the within-subjects repeated measures in the dataset through modeling a random intercept over dependent data clusters. The regression model had the form:

$$\text{EG} (\text{J} \cdot \text{kg}^{-1} \cdot \text{s}^{-1}) = \beta_0 + \beta_1(1 - \text{CoP}_{\text{norm}}) + \beta_2 \cdot (1 - \text{CoP}_{\text{norm}})^2$$

This model takes into account a potential linear plus quadratic dependency of energy consumption (EC) on normalized sway magnitude (CoP_{norm}). An exchangeable working correlation matrix was chosen to define the dependency of the repeated measurements in this regression model.

Statistical analyses were performed using SPSS (version 21; SPSS, Chicago, IL). A P value < 0.05 was considered to indicate a significant effect.

RESULTS

The results for both experimental manipulations (visual feedback and verbal instruction) are presented below for each outcome measure. Data from two subjects for the visual feedback manipulation were excluded from analysis due to an error in size of the presented target area. Data from all 19 subjects for the verbal instruction manipulation were included in the analysis.

CoP sway magnitude. The sway responses to the visual feedback and verbal instruction manipulations are displayed in Fig. 2. Mean normalized CoP distance differed significantly between the imposed visual feedback conditions ($P < 0.001$).

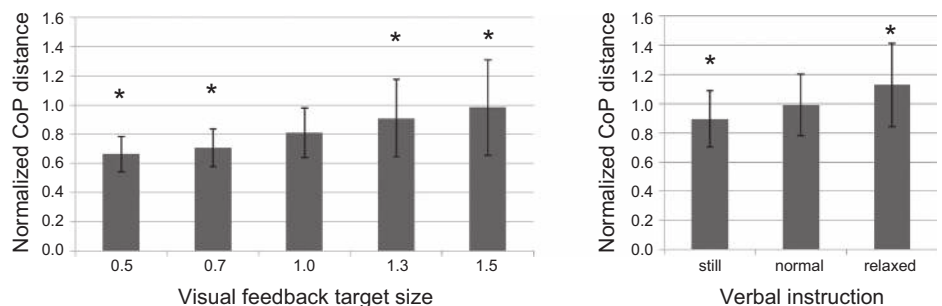


Fig. 2. Mean normalized CoP distance (mean and SD) during the visual feedback manipulations (left) and verbal instruction manipulations (right). *Sway magnitude was significantly (ANOVA, $P < 0.05$) different from the 1.0 visual feedback condition or from the “standing naturally” condition.

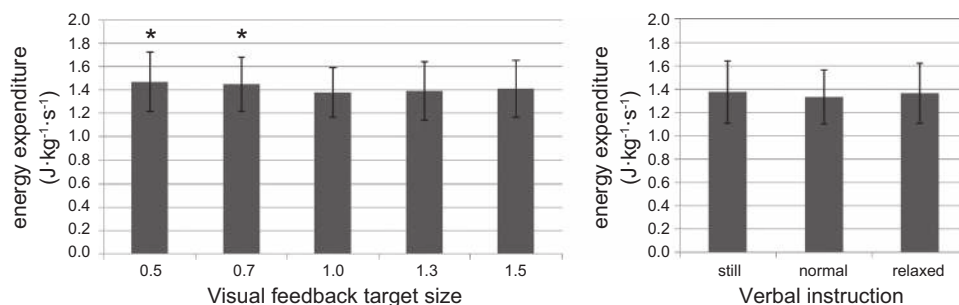


Fig. 3. Metabolic energy expenditure (mean and SD) during the visual feedback manipulation (*left*) and verbal instruction manipulation (*right*) SNR conditions. *Metabolic cost was significantly greater ($P < 0.05$) compared with the 1.0 visual feedback condition.

Pairwise comparisons showed a significant difference of all target areas with respect to the 1.0 area condition. The difference in sway magnitude between subsequent areas was on average 8%. Note that actually observed normalized sway magnitude was in general smaller than the imposed sway magnitude for the 1.0, 1.3, and 1.5 target areas and a little larger for the 0.5 target area.

In the verbal instruction experiment, also a significant effect of instruction on the mean normalized CoP distance was found ($P = 0.001$). Compared with standing naturally, standing still significantly reduced sway by 9.6%, and standing relaxed significantly increased sway by 13.7%. Note that on average the normalized sway magnitude during standing naturally was equal to the sway magnitude in the reference trials (i.e., normalized sway is close to 1).

Mean CoP positions were compared between trials to check for differences in body orientation between trials. In the visual feedback experiment, a small though significant systematic posterior shift in COP position was observed from the smallest to the largest target area. Mean AP CoP positions (relative to the mean CoP position in the 1.0 target area) were 1.4, 1.1, -1.2, and -1.2 mm for the 0.5, 0.7, 1.3, and 1.5 target areas, respectively ($P = 0.005$). No differences in mean CoP position were found for the ML direction, nor for any direction in the verbal instruction experiment.

Metabolic energy expenditure. For the visual feedback manipulations, a significant condition effect of target area on energy expenditure was found ($P = 0.016$) (Fig. 3). The energy expenditure for the 0.5 and 0.7 target area conditions was significantly higher compared with the 1.0 target area condition (9 and 7%, respectively). Although energy expenditure for the 1.3 and 1.5 target areas tended to be higher than for the 1.0 target area condition, these increases were not significant.

Although the verbal instruction seemed to cause a small increase in energy expenditure with both the standing still and relaxed condition (Fig. 3), the effect of verbal instruction on energy expenditure was not significant ($P = 0.549$).

In general, the energy expenditure was higher with the visual feedback manipulation compared with the verbal instruction manipulation.

Relation between CoP sway magnitude and energy expenditure. GEE analysis was used to quantify the relation between the actual observed mean normalized CoP distance and energy expenditure for both experimental manipulations separately. Figure 4 shows a scatterplot of normalized energy expenditure vs. mean normalized CoP distance vs. with superimposed regression curves derived from GEE analysis. Table 1 provides the regression coefficients of the regression curves obtained. For the visual feedback manipulation, GEE analysis revealed that the regression equation between mean normalized CoP distance and energy expenditure included a significant quadric component (β_2) but no linear component (β_1), indicating that a minimum energy expenditure existed around self-selected sway. For the verbal instruction manipulation, the GEE analysis revealed both a linear (β_1) and quadratic (β_2) dependency of energy expenditure on mean normalized CoP distance, indicating an asymmetric effect of sway magnitude on energy expenditure with a larger increase in energy expenditure with small sway magnitudes than with larger sway magnitudes.

EMG. In general, muscle activation was greatest in the conditions with the smallest sway magnitude (Fig. 5). In the visual feedback manipulation conditions, target area size had a significant effect on the P10 EMG amplitude of all muscles. For P50 the effect of target size was significant for TA, RF, ST, GlutMax, and GlutMed. For P90 this was significant for ST,

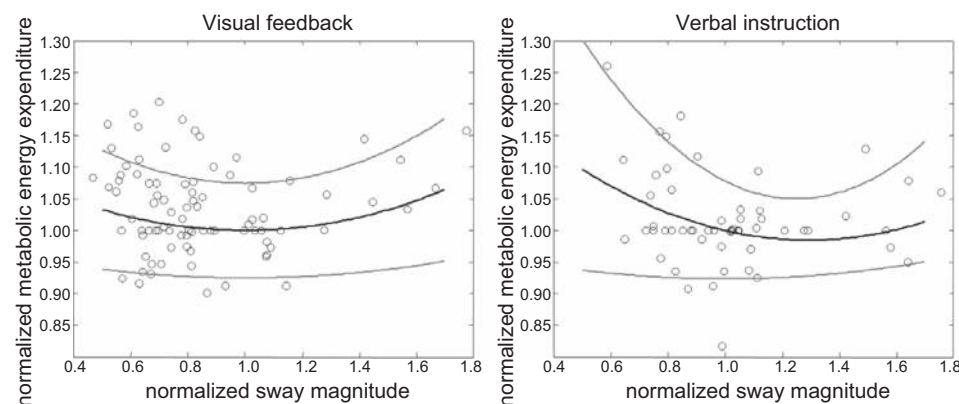


Fig. 4. Scatter plot of normalized energy expenditure vs. mean normalized CoP distance. Energy expenditure was normalized to the energy expenditure during the 1.0 target area condition in the visual feedback experiment (*left*) and to the standing natural condition in the verbal instruction experiment (*right*). Regression curves (black lines) with 95% confidence intervals (gray lines) are superimposed. Note that the data presented in this graph contain repeated measures within individuals, which is not explicitly shown in these graphs but is taken into account in the generalized estimation equations (GEE) analysis.

Table 1. GEE regression coefficients for the relation between mean normalized CoP distance and metabolic energy expenditure

	β_0 Intercept	β_1 (1 - CoP _{norm})	β_2 (1 - CoP _{norm}) ²
Visual feedback			
Initial model	1.402 ($P < 0.001$)	0.006 ($P = 0.894$)	0.186 ($P = 0.007$)
Final model*	1.403 ($P < 0.001$)		0.182 ($P = 0.001$)
Verbal instruction			
Final model	1.337 ($P < 0.001$)	0.138 ($P = 0.003$)	0.236 ($P = 0.012$)

GEE, generalized estimation equation; CoP, center of pressure; β_0 , intercept of the GEE regression model; β_1 , linear component; β_2 , quadric component. *Because β_1 was not significant in the initial model, a final model was determined without a linear term.

GlutMax, and GlutMed. Post hoc tests demonstrated significantly higher EMG amplitudes for the 0.5 and 0.7 target sizes relative to the 1.0 target area condition for these muscles.

In the verbal instruction manipulation, a significant effect was found in RF, ST, GlutMax, EO, and ES on P10 EMG amplitude. For P50 this trend was only significant for RF and for P90 for RF and GlutMed. Post hoc follow up of these effects showed that EMG amplitudes were higher in the standing still condition compared with standing natural.

DISCUSSION

The interpretation of postural sway has been debated extensively in postural control research. Given the fact that people can voluntarily vary the magnitude of sway during upright standing, it can be questioned whether small or large sway magnitudes would indicate superior or inferior postural control and why people select the magnitude of sway they do in natural standing conditions. The aim of this study was to investigate the relation between sway magnitude and metabolic cost during upright standing, to determine whether metabolic cost could be a potential optimization criterion in the postural control during upright standing. Two different experimental manipulations were used to elicit different magnitudes of sway during upright standing and to assess the metabolic cost in-

involved. Both experiments demonstrate a relation between sway magnitude and metabolic cost in which decreasing and, to a smaller extent, increasing sway relative to self-selected sway magnitude evokes a higher metabolic cost. This observation is conditional for the hypothesis that metabolic cost could be an optimization criterion for setting postural control.

We used two manipulations to evoke different magnitudes of sway without changing sensory or environmental properties within each manipulation. The verbal instruction task adequately increased and decreased sway as evidenced by a significant difference in sway magnitude between conditions of this task. Moreover, the standing natural instruction resulted in an average sway magnitude similar to the self-selected sway in the reference measurement (i.e., normalized sway was close to 1). The total range over which sway magnitude varied in this task was, however, relatively small, which might have prevented us from detecting a statistically significant effect on metabolic cost. The visual feedback manipulation resulted in a larger range of sway magnitudes, in agreement with previous studies (22). This manipulation did demonstrate significant effects on metabolic cost, especially for the low sway amplitude conditions. It should be noted, however, that the sway magnitude observed during the visual feedback task differed systematically from the imposed sway size. Especially, for condition 1.0 and larger, CoP_{norm} was lower than imposed. Apparently, eliciting a large sway size (exceeding self-selected sway) was more difficult with this manipulation. In addition, the individual responses to imposed sway varied between subjects, as can be derived from the relatively large SDs in observed sway magnitude in each experimental task (Fig. 2).

Using imposed sway amount as a fixed variable to analyze the relation between sway amount and metabolic cost (cf., Fig. 3) might obscure this relation because of the systematically lower observed sway in the visual feedback task and individual variation in responses to the imposed sway. To take this into account we used GEE analysis to quantify the relation between actually observed sway magnitude and metabolic cost. The regression models obtained for each task (visual feedback,

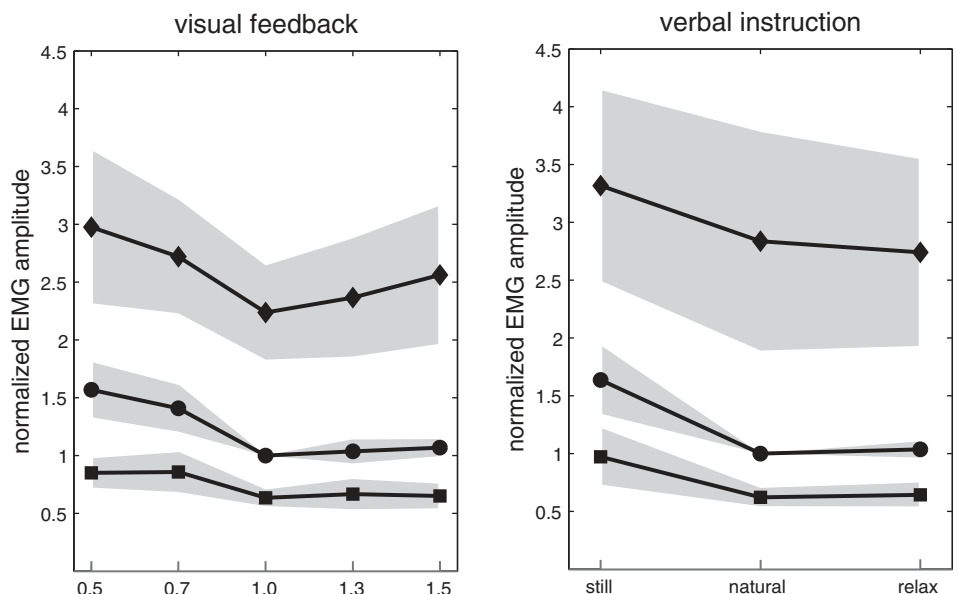


Fig. 5. The EMG amplitude at the 10th (P10), 50th (P50), and 90th (P90) percentile of the EMG amplitude probability distribution function averaged over all muscles as a function of imposed sway magnitude. EMG amplitude was normalized to the EMG amplitude at P50 in the reference condition (area size 1.0 or instruction to stand natural) in each muscle before averaging over all muscles. P10 represents the level of tonic activation, P50 represents average activation, and P90 represents the level of maximal phasic activation. Shaded area represents SD around the average over all muscles. *Left*, visual feedback manipulation; *right*, verbal instruction manipulation.

verbal instruction) support the hypothesis (and observed trends in Fig. 3) that increasing or decreasing sway relative to self-selected sway magnitude is accompanied by an increase in metabolic cost, as evidenced by a significant quadratic component in both regression models. Only for the verbal instruction condition, this analysis demonstrated a negative linear trend in this relation, indicating that the increase in metabolic cost is larger at low sway magnitudes and is attenuated at larger sway magnitudes. It should be noted, however, that both in the visual feedback and verbal instruction task participants only increased sway above self-selected sway to a limited extent, despite the instructions, as evidenced by a limited number of data points above self-selected normalized sway size ($\text{CoP}_{\text{norm}} > 1$, Fig. 4). Although the data at large sway magnitudes are consistently indicating an increase in metabolic cost with increased sway, the limited amount of data points on this side of the spectrum might warrant some caution in the interpretation of the nature of this relation for magnitudes larger than self-selected sway. Alternative curve fits such as an exponential decay model might also fit the data.

Although a significant quadratic relation was found between sway magnitude and metabolic cost, and although self-selected sway on average occurred around minimal metabolic cost, the current data do not automatically allow the conclusion that metabolic energy cost drives postural control. Two considerations should be made. First, parameters that covary with energy cost (e.g., muscle force or activation) could be the actual control parameters that drive postural control. It could also be possible that a second criterion exists that is weighted in ensemble with energy expenditure, to select postural control settings. Sway minimization or minimization of cognitive or attentional demand could be such additional criteria (3). Weighted minimization of sway magnitude might be especially realistic when the relation between sway magnitude and metabolic cost should be considered as an exponential decay function rather than a quadratic function. In such case, people might choose to minimize sway (and enhance stability) down to a limit beyond which minimizing sway would excessively increase metabolic cost.

Second, one may ask through which pathway metabolic energy expenditure could be used as a driving factor of postural control. The increment in metabolic cost with changing sway is rather small relative to the total cost of upright standing and its inherent variability. Moreover, time delays of metabolic processes are relatively long. Consequently the resolution and responsiveness of this control parameter might be low. It has previously been suggested that energy optimization could be a two-step process, which consists of a fast process relying on detection of more easily sensed (but less functionally relevant) control parameters, that predicts metabolic requirements (for instance, muscle force or activation) and a slower process that shapes the predictive value of these parameters with respect to metabolic cost from experience acquired over longer time courses (25, 26). Although the relation between sway magnitude and metabolic cost observed in this study provides a base for the notion that metabolic cost could be an optimization criterion in postural control, the two concerns above need to be elucidated in the future.

EMG recordings were made in this study to support and explain the relation between postural sway and metabolic cost. In general, average muscle activation paralleled the observed

responses in metabolic cost in both tasks (Fig. 5), showing increases in activation at sway magnitudes below self-selected sway and, to a lesser extent, at sway magnitudes above self-selected sway. This was most consistently apparent in the tonic muscle activity (quantified by P10 of the EMG-ADPF), which was significantly greater at low sway magnitudes in all muscles for the visual feedback task and in most muscles for the verbal instruction task. Hence, increasing joint stiffness by increasing agonistic muscle tone and/or coactivation levels seems an important mechanism to reduce sway (4, 22), but apparently it comes with a greater metabolic cost. Phasic muscle activity (quantified by P90 of the EMG-APDF), related to short and long latency responses, generally showed the same trend. However, this was only significant for selected muscles, primarily those crossing the hip joint (i.e., RF, ST, GlutMax, and GlutMed). This indicates that corrective postural responses were primarily initiated at the level of the hip. This is consistent with the use of the hip strategy, which has been observed to occur in more demanding postural control conditions (11, 18). It should be noted, however, that a hip strategy might have been preferred in this study, since the contribution of the ankle torque to balance control is reduced by standing on the foam surface (10). In contrast to small sway amplitudes, at sway amplitudes higher than naturally occurring sway, no significant increase in muscle activity levels was found, although the average P90 EMG amplitude showed an increasing trend (Fig. 5). Such a response would be in line with previous observations that at larger sway amplitudes muscles are recruited in a more phasic manner (4, 22). However, this could not be supported statistically in this study.

In addition to alterations in EMG responses, we observed changes in the mean CoP position with sway size in the AP direction in the visual feedback experiment. This might be indicative of a change in body orientation with changing sway magnitude and can potentially contribute to differences in metabolic cost. The observed systematic forward shift of the mean CoP with decreasing target size was only 1.4 mm between the smallest (0.5) and self-selected (1.0) target area. This is approximately equivalent to a change in forward lean angle of ~ 0.1 degree (assuming center of mass height of 1 m) and an increase in net ankle torque of ~ 1 Nm (assuming body mass of 70 kg). Such a torque increase can be estimated at $\sim 3.5\%$ of the ankle torque in normal standing (22). Although being small, such a change in body orientation might be relevant in terms of metabolic energy expenditure, but is unlikely to explain the full 9% increase in metabolic cost between the 1.0 and 0.5 target area condition. Furthermore, the mean CoP position shifted further backward from the 1.0 to 1.5 target area condition without a reduction in metabolic cost, which demonstrates that the relation between mean lean angle and metabolic cost is not straightforward. Finally, it could be argued that changing body orientation (leaning more forward) is one strategy to reduce sway, and hence that the potential increase in metabolic cost related to this forward lean could be considered as metabolic cost related to sway.

It has previously been postulated that changes in sway size are not only subject to changes in stiffness or reflex gains, but might also rely on the accuracy of feedforward control (22). In such a case, sway size could be reduced through a more accurate muscle control, which would not involve an increase in metabolic cost and even could result in a reduced metabolic

cost with reducing sway. This is, however, not in agreement with the general trend in our data, which indicates the metabolic cost increases when sway is reduced. Nevertheless, this mechanism might be responsible for some variation between subjects in our data.

The analysis of muscle activation in this study grossly reflects changes in tonic and phasic muscle activation of the different muscle groups involved. It can, however, not provide detailed insight in the underlying control strategies nor elucidate the energy efficiency of these different control mechanisms. More advanced experimental manipulations will be required to differentiate between the contribution of coactivation, feedback, and feedforward control to sway magnitude (37). Additionally, existing feedback control models should be extended to musculoskeletal models incorporating the bioenergetics of muscle contraction (35) to estimate the metabolic cost associated with different control strategies and explain the metabolic cost of balance control.

Two methodological issues should finally be considered in relation to the generalization of the current results to normal standing. First, the experiments in this study were executed on a foam surface to increase metabolic responses and therewith effect size and statistical power of the study. It can be debated to what extent the foam surface has affected the results and to what extent these results can be generalized to standing on more rigid surfaces. Standing on foam has been shown to affect the somatosensory input of the mechanoreceptors of the foot (1a), which delays medium- and long-latency responses of the plantar flexors. Furthermore, foam affects the transfer of ankle torque to external ground reaction forces, thereby reducing the efficacy of the ankle strategy (27, 29). Because of these properties, spontaneous sway magnitude has been shown to increase when standing on foam relative to a firm surface, and this is accompanied by an increase in metabolic cost (12). It could be speculated that reducing sway, relative to spontaneously occurring sway, will be more difficult on foam than on a rigid surface. This might have amplified the relation between sway and metabolic cost at small sway magnitudes in this study. There seems less reason to assume that standing with increased sway magnitude would be more or less difficult on foam compared with rigid surfaces. The observed relation between large sway magnitude and metabolic cost is therefore not likely to change between surface conditions. Although differences in balance control strategies and effort exist between surfaces, we believe that qualitatively our findings can be extrapolated to different support surfaces, although quantitatively the energy cost and rate of change of energy cost in relation to sway magnitude will differ.

Second, on average metabolic cost was somewhat higher for the visual feedback task compared with the verbal instruction task. It is likely that the visual feedback, and concomitant precision task of maintaining the CoP projection within the limits of the target, imposed an additional constraint on postural control. This could confound our results when this constraint depends on the size of the imposed target, for instance, when this constraint would be less for the larger target sizes. The absence of a linear component in the regression model for the visual feedback task, however, suggests that this was not the case and that the potentially enhanced central control and precision demands could be considered as a systematic effect within this experiment.

In conclusion, the experimental data revealed that metabolic cost of upright standing increases at small and, to a lesser extent, large sway magnitudes and that people naturally select a magnitude of sway that resides at the bottom of the observed energy-sway relationship. These results are in line with the notion that metabolic cost could be an optimization criterion used for selecting motor control strategies in postural control tasks. Although the underlying pathway through which metabolic cost could drive postural control remains to be elucidated, these results contribute to our understanding of self-selected sway magnitude during upright standing in healthy people and might account for differences in sway magnitudes and underlying postural control strategies among individuals and conditions.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

Author contributions: H.H., S.E.B., and J.H.v.D. conception and design of research; H.H. and S.E.B. performed experiments; H.H. and S.E.B. analyzed data; H.H., S.E.B., and J.H.v.D. interpreted results of experiments; H.H. and S.E.B. prepared figures; H.H. and S.E.B. drafted manuscript; H.H., S.E.B., and J.H.v.D. edited and revised manuscript; H.H., S.E.B., and J.H.v.D. approved final version of manuscript.

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