Cortical tracking of postural sways during standing balance

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Abstract

Maintaining an upright stance requires the integration of sensory inputs from the visual, vestibular and somatosensory-proprioceptive systems by the cortex to develop a corrective postural strategy. However, it is unclear whether and how the cerebral cortex monitors and controls postural sways. Here, we asked whether postural sways are encoded in ongoing cortical oscillations, giving rise to a form of corticokinematic coherence (CKC) in the context of standing balance. Center-of-pressure (CoP) and center of mass (CoM) fluctuations and electroencephalographic cortical activity were recorded as young healthy participants performed balance tasks during which sensory information was manipulated, by either removal or alteration. We found that postural sways are represented in ongoing SM1 cortical activity during challenging balance conditions, in the form of CKC at 1–6 Hz that was stronger for CoP compared with CoM fluctuations. Time delays between cortical activity and CoP features indicated that both afferent and efferent pathways contribute to CKC, wherein the brain would monitor the CoP velocity and control its position. Importantly, CKC was behaviorally relevant, as it predicted the increase in instability brought by alteration of sensory information. Our results demonstrate that human sensorimotor cortical areas take part in the closed-loop control of standing balance in challenging conditions. They demonstrate that CKC could serve as a neurophysiological marker of cortical involvement in maintaining balance.

Significance statement

Even a seemingly effortless task, like maintaining stable balance, requires the involvement of the cerebral cortex. The cortex monitors sensory inputs to develop corrective postural strategies. However, the fundamental questions of how the cerebral cortex integrates and leverages sensory information to maintain balance and when such an involvement becomes necessary have yet to be answered. We show that postural sways are encoded in ongoing cortical oscillations, as a result of bi-directional connections between the brain and the periphery. Compellingly, this encoding was strongest under conditions where sensory cues were altered, especially in individuals experiencing important difficulties in such conditions. Our results shed light on the neuronal mechanisms underlying balance maintenance, and open new avenues for their scientific and clinical assessment.

Introduction

Evolution has led humans to adopt an upright posture, thanks to—and fostering—the development of an exceptionally large brain as compared to other species. As a corollary, the cortical and subcortical network supporting motor control is complex, and even the simplest tasks, such as maintaining upright balance, require the involvement of the spinal cord and brainstem for reflexive control, and the cerebral cortex for adjustments to the environment (1–5). In this regard, sensory inputs from the visual, vestibular and somatosensory-proprioceptive systems to the cortex play a key role in the control of standing balance (6). The integration of this sensory information by the cortex is the basis of the development of a postural corrective strategy. But how does the cortex implement such a corrective strategy?

From the biomechanics perspective, the position of the center of mass (CoM) of the body can be controlled by adjusting the position of the center of pressure (CoP) on the support surface (7). This means that when the CoM is displaced from its neutral position, changes in CoP are made to redirect the CoM back toward the neutral axis. Indeed, previous studies have shown that the CoP regularly oscillates along the antero-posterior axis about the vertical projection of the CoM on the ground during quiet standing (8, 9). Whether and how the cerebral cortex monitors and controls CoP and CoM fluctuations is still unsettled.

Studies using electroencephalography (EEG) have identified changes in cortical oscillatory dynamics across several frequency bands during quiet stance compared with sitting (10). Hypothetically, these changes at the cortical level would reflect the engagement of mechanisms responsible for modulating muscle contractions over time, with the aim to adjust the body's CoM. Further supporting this view, the oscillatory dynamics was modulated by the quality of available visual and proprioceptive cues (3, 11, 12). Indeed, the manipulation of the sensory information during a balance task, by either removal or alteration, makes balance control significantly more challenging due to increased difficulty in estimating the dynamics of the body, leading to an increase in body sway (13, 14) and cortical involvement (15). However, it is still unclear whether and how CoP and CoM are integrated in the central nervous system. A promising means to gain insight into these integration processes is corticokinematic coherence (CKC). CKC, the coupling between brain activity and movement kinematics (16, 17), has been shown to specifically reflect the integration of proprioceptive input by the cortex during active and passive finger movements (18–21). Thus far it has been studied only for repetitive movements of the upper or lower extremity in a sitting position.

This study investigates postural maintenance through the lens of CKC, to determine if postural sways are encoded in ongoing cortical oscillations. Given that cortical involvement is expected to depend on the complexity of the balance task, we hypothesized that the extent of cortical sway encoding increases with the suppression or alteration of visual and proprioceptive input. In addition, we aimed to determine which aspects of the sways are encoded, focusing on excursion, velocity and acceleration of the CoP and CoM. We then tested the hypothesis that cortical sway encoding hinges on afferent signaling as commonly reported during voluntary movements. And finally, we asked whether such sway-driven CKC is relevant for postural stability.

Results

To study CKC during postural maintenance, a group of 36 young healthy adults maintained bipodal quiet standing on a solid surface or on a foam mat with eyes open or closed, leading to 4 conditions (*solid-eyes-open*, *foam-eyes-open*, *solid-eyes-closed*, and *foam-eyes-*

closed), each performed for a total of 10 minutes (Figure 1A-C). Cortical activity was recorded with EEG, along with the position of the CoP with a force plate. The vertical projection of the CoM on the support surface was computed using the zero-point-to-zero-point double integration technique (22). Both CoP and CoM traces were filtered though 0.1-10 Hz.

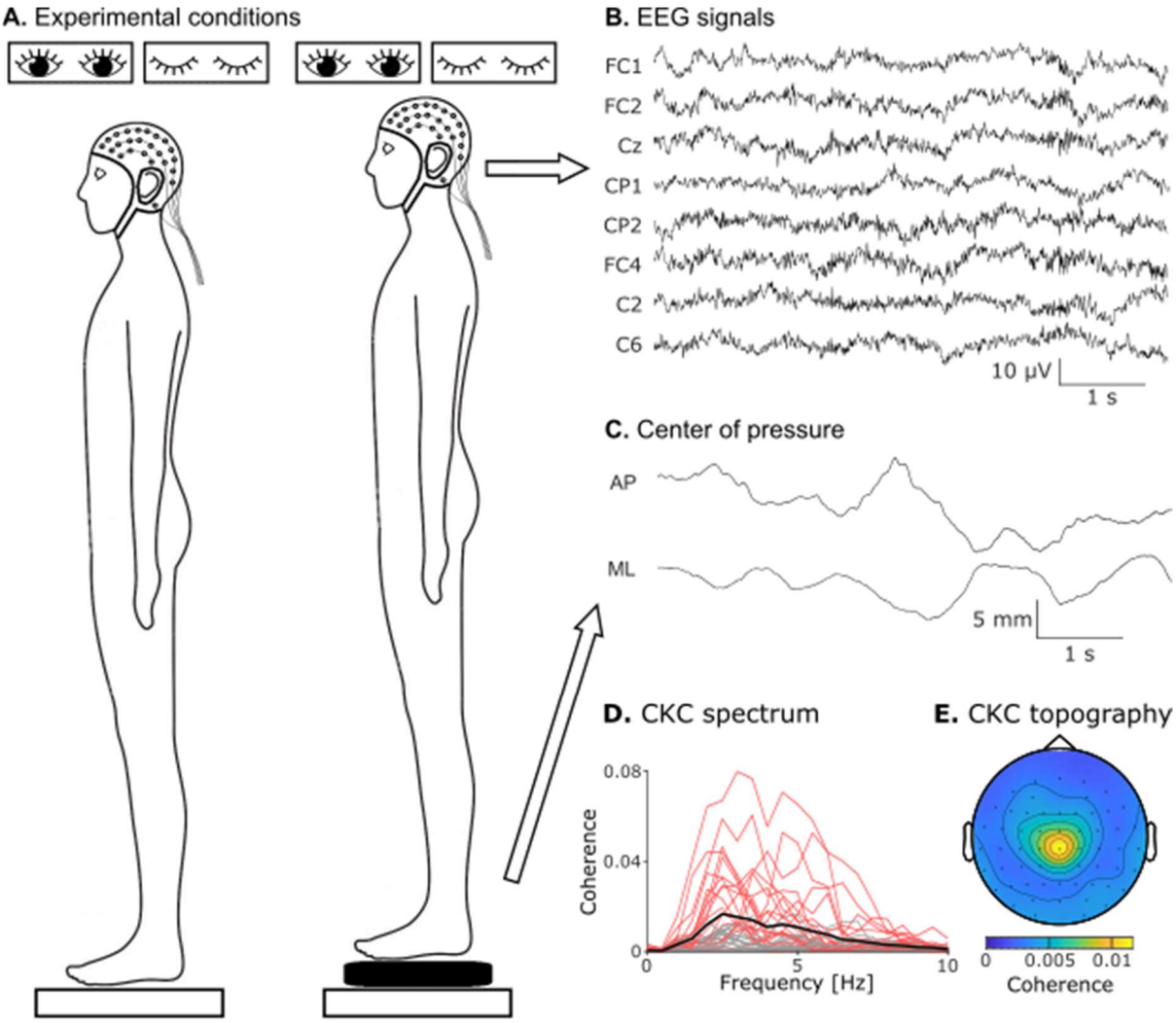

***Figure 1**. Experimental set-up and CKC estimation. A — Participants were equipped with a 63 channel EEG-cap and stood on a force plate in 4 experimental conditions: either on a hard surface or on foam pads, and with eyes open or closed. B — Six second excerpt of EEG collected during the foam-eyes-closed condition. C — CoP signals along the mediolateral (ML) and antero-posterior (AP) axes. D — CKC spectrum at the EEG_{SM1} electrode for CoP velocity when standing on foam eyes closed. There is one trace for each participant with (red traces) and without (gray traces) significant CKC and one for their group average (black traces). E — Topography of the CKC for CoP velocity in the band 1-6 Hz, averaged across the entire cohort and conditions.*

CoP and CoM variability

The inspection of CoP and CoM traces obtained in the four different balance conditions indicated that medio-lateral (ML) and antero-posterior (AP) sways were larger when standing on a foam surface compared with a solid surface, and when keeping the eyes closed compared to open (see Figure S1A). Overall, these observations were confirmed by statistical assessment

of three common instability parameters consisting of the mean speed and standard deviation (SD) of the position in the ML and AP direction (see Figure S1B and supporting text "effect of condition on instability parameters").

Neural encoding of CoP and CoM

CKC was assessed between each EEG signal and multiple CoP (see Figure S2) and CoM features (see Figure S3). For CoP, these features were the velocity along the ML ($vCoP_{ML}$) and AP directions ($vCoP_{AP}$), and the vector sum of position (rCoP), velocity (vCoP) and acceleration (aCoP). The same features were estimated for CoM. For further analyses, we retained only the electrode from among those typically overlying the lower limb primary sensorimotor cortex (SM1) (Cz, C1, C2, FCz, FC1, FC2, CP1, CP2) that yielded the highest CKC averaged across 0.5–10 Hz and balance conditions. From this point on, it is referred to as EEG_{SM1}.

Table 1. *Number and percentage of participants with significant CKC. Bold face indicates when the proportion was significantly higher than expected by chance.*

center	CoP				CoM			
eyes	open		closed		open		closed	
surface	solid	foam	solid	foam	solid	foam	solid	foam
$vCOP_{ML}$	1 (3%)	0	2 (6%)	1 (3%)	0	0	0	**5 (14%)**
$vCOP_{AP}$	0	3 (8%)	**4 (11%)**	**10 (28%)**	0	1 (3%)	1 (3%)	**7 (19%)**
vCOP	0	**7 (19%)**	3 (8%)	**19 (53%)**	0	0	1 (3%)	0
rCOP	0	3 (8%)	2 (6%)	**18 (50%)**	1 (3%)	1 (3%)	0	1 (3%)
aCOP	1 (3%)	2 (6%)	0	**7(19%)**	0	0	1 (3%)	**6 (17%)**

First of all, the balance condition did not affect the number of artifact-free epochs used in the analyses ($F_{3,105} = 0.88$, $p = 0.45$; mean ± SD epochs across conditions and participants, 1100 ± 20). This ensures CKC can be validly compared between conditions.

Table 1 presents the number and proportion of participants showing significant CKC for each condition, feature type and center type. Overall, the proportion of significant CKC was higher for CoP compared with CoM features and increased with the difficulty of the balance condition. The highest proportion of participants with significant CKC was reached for vCoP in the most challenging condition (*foam-eyes-closed*). We therefore concentrate first on the results for this specific feature, then assess the effect of condition on CKC for all CoP features, and finish by highlighting results for CoM features.

Figure 1D-E presents the spectra and topography of CKC for vCoP on foam eyes closed. Therein, CKC tended to peak in between 1 and 6 Hz. At the group level, the electrode showing the maximum level of CKC was Cz. This electrode was also the one where CKC was maximum in 79% of the participants with significant CKC.

More globally, significant CKC for CoP was uncovered in a significant proportion of participants (i.e., >10%) for 4 of the 5 features, vCoP, $vCoP_{AP}$, rCoP and aCoP. The highest proportion was in the most challenging condition (*foam-eyes-closed*), and the threshold of 10% was reached for none of the feature types in the easiest condition (*solid-eyes-open*). In all instances, group-averaged CKC magnitude tended to peak around Cz, and was well within our

sensor selection covering SM1 (see Figure S2). Across the participants, significant CKC tended to occur between 1 and 6 Hz, with 83% of the peak values being in that range.

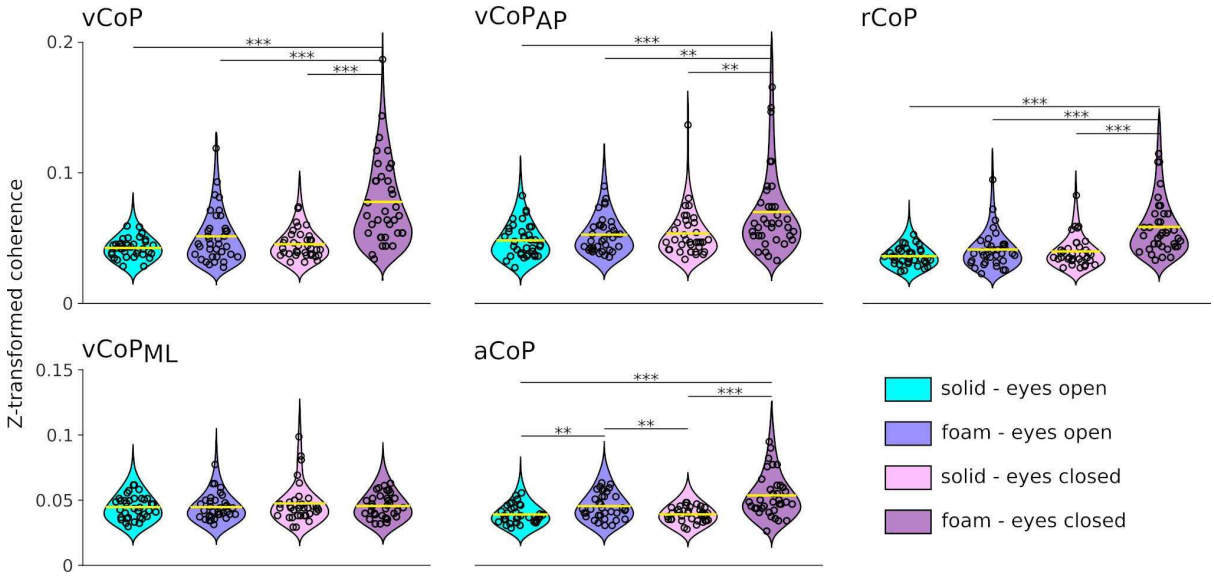

Figure 2. *Distribution of CKC values for CoP features in the four balance conditions. Displayed are the CKC values averaged across 0.5–10 Hz and z-transformed (by means of the arctangent of the square-root). Each individual subject's value is indicated with circles. Significant differences between conditions are indicated with stars (*, p < 0.05; **, p < 0.01; ***, p < 0.001).*

Figure 2 presents the distribution of individual CKC values (averaged across 0.5–10 Hz) for the 5 CoP features in all conditions. Visually, the pattern of variation across conditions of CKC for the 4 features highlighted in the previous paragraph (vCoP, $vCoP_{AP}$, rCoP and aCoP) followed that of CoP instability, being higher when standing on a foam surface compared with a hard surface, and when keeping the eyes closed compared to open. In support of that observation, one-way ANOVAs run for each CoP feature separately identified a significant effect of condition on CKC for these 4 features (vCoP, $F_{3,105} = 30.7$, $p < 0.0001$; $vCoP_{AP}$, $F_{3,105} = 10.3$, $p < 0.0001$; rCoP, $F_{3,105} = 29.9$, $p < 0.0001$; aCoP, $F_{3,105} = 17.3$, $p < 0.0001$), and not for the remaining one ($vCoP_{ML}$, $F_{3,105} = 0.22$, $p = 0.30$). However, unlike CoP instability, the effect of the foam surface or closing the eyes in isolation appeared rather small, and only their combination gave rise to a marked increase in CKC (see also Figure 2 for post-hoc comparisons).

The distribution of individual CKC values (averaged across 0.5–10 Hz) for the 5 CoM features was also analyzed with an ANOVA with condition as a factor (see Figure S4 for the distribution of CKC for CoM features). The impact of the condition was clearly less evident than in the case of CKC for CoP. Still one-way ANOVAs identified a significant effect of condition on CKC for rCoM ($F_{3,105} = 3.83$, $p = 0.01$), aCoM ($F_{3,105} = 11.9$, $p < 0.0001$) and $vCoM_{AP}$ ($F_{3,105} = 5.62$, $p = 0.001$). No effect was identified for the 2 other features (vCoM, $F_{3,105} = 0.57$, $p = 0.64$; $vCoM_{ML}$, $F_{3,105} = 0.32$, $p = 0.81$). Again, the significant effect of condition—on CKC for aCoM and $vCoM_{AP}$—was mainly explained by increased CKC in the most challenging condition compared with the 3 other conditions (see Figure S4 for post-hoc comparisons).

We had initially planned to compare CKC values between features (e.g., vCoP vs. aCoP), and between homologous CoP and CoM features (e.g., between vCoP and vCoM). The objective was to identify which aspects of body sways are most reliably encoded in cortical activity. However, such comparison led to results that were incompatible with the observed proportion of participants with significant CKC. For example, CKC for $vCoP_{ML}$ was significantly higher than CKC for aCoP ($p < 0.0001$ for all 4 conditions) despite the fact that $vCoP_{ML}$ was significant in less than 10% of the participants in each condition. This might be due to the specifics of the distribution of feature time-series. For example, $vCoP_{ML}$ tended to be characterized by the presence of transient events attributable to weight shifts between legs, thereby skewing the distribution of Fourier coefficient amplitude and biasing coherence towards higher values (23). Therefore, we did not further attempt to directly compare CKC between features and center types. Instead, a bootstrap analysis was used to compare the significance of the effect of condition on CKC between CoP and CoM features. This analysis revealed a significantly higher effect of condition on CKC for rCoP ($p < 0.001$) and vCoP ($p < 0.001$) compared with their CoM counterparts.

Delays.

The time delays between EEG_{SM1} and CoP or CoM features were estimated from the phase slope of their cross-spectral density at frequencies where significant coherence was found. A negative-phase slope corresponds to a positive delay whereby CoP variation precedes EEG_{SM1} activity. We performed these analyses only for CoP and CoM features yielding significant CKC in at least 10 participants. This led us to consider only rCoP, $vCoP_{AP}$ and vCoP in the most challenging condition (*foam-eyes-closed*).

The phase delays estimated with EEG_{SM1} were found statically different from 0 for rCoP ($p = 0.02$; Wilcoxon signed-rank test) and $vCoP_{AP}$ ($p = 0.03$) but not vCoP ($p = 0.13$; see Figure S5). The delays for $vCoP_{AP}$ were positive, with an average of 58 ± 57 ms (mean ± SD), indicating that fluctuations in $vCoP_{AP}$ led EEG_{SM1} activity. Contrastingly, the delays for rCoP were negative, with an average of -40 ± 56 ms (mean ± SD), indicating that EEG_{SM1} activity led fluctuations in rCoP.

We present an analysis of the temporal response function associated with CKC in the Supporting Information (Supporting text: Temporal dynamics**)**. Delays estimated therein were essentially compatible with those obtained with the phase slope of the cross-spectral density.

Behavioral relevance of CoP cortical encoding.

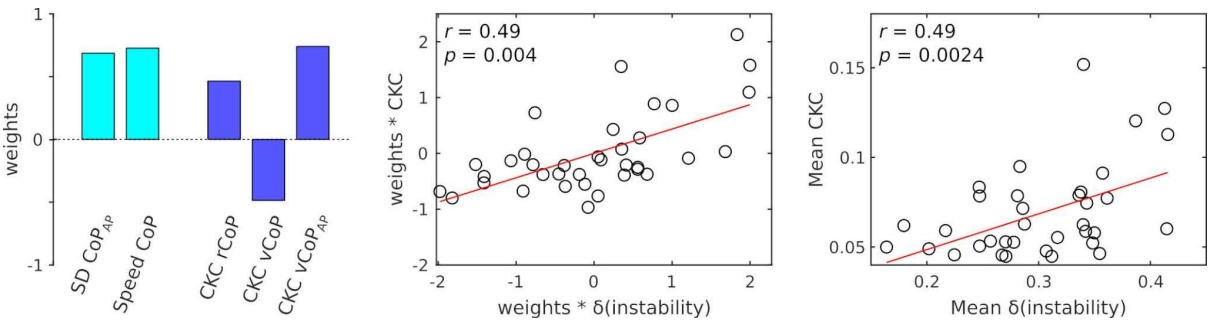

Figure 3. *Behavioral relevance of the cortical encoding of postural sways as assessed with a CCA between CKC values for the 3 dominant features and the relative increase in CoP instability parameters. The relative increases, indicated with a δ, represent a contrast between the foam-eyes-closed and solid-eyes-open conditions. From left to right are the*

weights for the instability and CKC variables, the scatter plot of CKC variables combined according to these weights as a function of the instability parameters combined likewise, and the scatter plot for the mean of CKC across the 3 features as a function of the mean of the two instability parameters.

Our results identified significant CKC, especially for rCoP, vCoP and $vCoP_{AP}$ in the most difficult condition. We therefore sought to determine the relevance of these couplings for balance maintenance, quantified with the SD of CoP_{AP} and CoP speed. Given the multivariate nature of the brain and balance data, we used regularized canonical correlation analysis (CCA). This analysis did not reveal a significant association between instability parameters and CKC values in the hardest condition ($p = 0.77$). Next, we assessed whether CKC could instead be associated with the degree of increase in instability induced by standing on foam eyes closed, with the rationale that such degree reflects that to which balance is compromised compared with an individual's typical reference point, begging for commitment of central resources to prevent falls.

Figure 3 presents the results of a regularized canonical correlation analysis evaluated between CKC and CoP variables, after each CoP variable in the most challenging condition were normalized by the value in the easiest condition as follows:

$$\delta CoP = (CoP_{\text{foam-eyes-closed}} - CoP_{\text{solid-eyes-open}})/(CoP_{\text{foam-eyes-closed}} + CoP_{\text{solid-eyes-open}}).$$

Such contrast was used because it is specific to changes induced by a reduction of sensory cues and factors out the inter-individual variability in the level of instability. It takes values between –1 and 1, with positive values indicating an increase due to reduction of sensory cues. It was not applied to CKC variables since these were mostly non-significant in the easiest condition. The CCA weights were all positive and of similar amplitude, except for CKC for vCoP. This indicates a positive association between overall increase in instability and a contrast involving positive weights for CKC for rCoP and $vCoP_{AP}$ and a negative weight for CKC for vCoP. However, CKC for vCoP was moderately and positively correlated with CKC for rCoP ($r = 0.55$, $p = 0.0006$) and CKC for $vCoP_{AP}$ ($r = 0.55$, $p = 0.0007$), the latter two showing an even stronger correlation ($r = 0.78$, $p < 0.0001$). In addition, the contrast for CKC identified by CCA largely correlated positively with a more intuitive average across the 3 features ($r = 0.84$, $p < 0.0001$). As a result, the relative increase in instability averaged across the 2 instability features was significantly correlated with the CKC averaged across the 3 retained CoP features (Figure 3, right graph).

Discussion

This study aimed at identifying and characterizing an electrophysiological signature of the cortical implication in regulating standing balance. It revealed that during challenging standing conditions, postural sways are represented in ongoing SM1 cortical activity, in the form of CKC at 1–6 Hz, with a stronger encoding of CoP than CoM fluctuations. Moreover, delay estimation indicated that CoP velocity drove cortical activity ~60 ms later, which itself drove CoP excursion by ~40-ms, indicating the existence of both afferent and efferent contributions to CKC in the context of balance regulation. Finally, the level of CKC correlated positively with the degree of increase in instability induced by task complexity. Overall, our results indicate that CKC reflects the closed-loop brain–peripheral interaction processes by which SM1 cortical areas intervene to maintain balance.

Interpretation of the coupling between CoP and cortical activity.

Maintaining an upright stance has long been known to be a highly dynamic task. Owing to its upright unstable position, the standing human body is in constant movement, known as postural sways, which are monitored by multiple senses for correction (6). Our study clarifies the nature and underlying mechanisms of the cortical contribution to these monitoring and correction processes. That is, we have found that fluctuations of the CoP are represented in sensorimotor cortical activity, at frequencies below 10 Hz, mainly between 1 and 6 Hz. Such cortical representation of movement kinematics, CKC, has been reported in a multitude of motor tasks, ranging from repetitive movements of the upper or lower limb (16, 17, 24), to isometric pinch contraction where a coupling is seen with below 3-Hz minute fluctuations in position (25). Our results therefore confirm that CKC reflects a general mechanism for motor control, also involved in maintaining balance.

In our study, CKC was essentially absent during regular standing and became visible in the most challenging condition consisting of standing on foam eyes closed. In unperturbed conditions, balance is thought to be regulated mainly by spinal and brainstem structures (5), with minimal implication of the cortex, in agreement with the absence of CKC in such conditions. When standing on a foam block, the ability to sense pressure distribution and body orientation decreases (26), while the effectiveness of ankle torque produced for postural stabilization is reduced (27, 28), leading to an increase in muscle activity (29). Closing the eyes further suppresses visual information, leaving only vestibular information intact to maintain balance. As a result, a greater degree of cortical involvement seems necessary (5), and this is precisely reflected in the appearance of significant CKC in our data. Altogether, the pattern of variation of CKC across conditions strongly indicates that it reflects the degree of cortical involvement in balance regulation.

Previous electrophysiological assessments of balance maintenance have focused on corticomuscular coherence with mixed results on its very existence in that context, and on whether it is modulated by condition complexity (2, 4, 30, 31). And although corticomuscular coherence and CKC can be considered as independent and complementary means to probe sensorimotor control (19), our data indicates that CKC possesses more desirable features. First, it appears to be relevant for balance maintenance as its amplitude correlated with the relative increase in instability. And second, significant CKC could be uncovered at the individual level, in 50% of our participants. Moreover, if CKC indeed scales with perceived task complexity, it is reasonable to think that it could be successfully recorded in an even larger proportion of individuals when balance is further challenged by task complexity (e.g., standing on one foot), pathology (e.g., vertigo), or aging. Therefore, CKC appears to be a highly promising neurophysiological marker of cortical involvement in balance maintenance, for use in future fundamental and clinical research endeavors.

With the advent of EEG technology and signal processing (32), a growing amount of EEG studies have moved to studying cortical activity during more natural settings, with a strong focus on gait. These studies have reported significant modulations of the beta rhythm and corticomuscular coherence along gait cycles (33, 34). And although some also reported significant coupling with muscle activity at lower, <8 Hz frequencies (19, 34), gait-induced artifacts make it challenging to tell to which extent this coupling arises from genuine brain signals. In that regard, EEG investigation of standing balance through CKC appears to strike the right balance between ecological validity and feasibility. That is, it nicely introduces the complexity of a full weight-bearing task requiring whole body coordination and moving away from well-controlled but too simplistic assessment of uniarticular movements (35, 36), while at the same time minimizing motion and related artifacts.

Our results fit well within the general framework of neural entrainment, whereby neuronal oscillations align to an external rhythm to optimize information processing. Indeed, because the phase of neuronal oscillations reflects a quasi-rhythmic fluctuation of neuronal excitability (37, 38), entrainment was suggested as a key mechanism to match periods of optimal cortical excitability with the most important periods of the incoming stimulus (37). Entrainment is seen across multiple modalities with neuronal oscillations entraining to flickering light (39) or speech temporal envelope (40). In the latter case, the entrainment occurs in the delta- and theta frequency ranges (41), with a benefit for speech comprehension (42). Likewise, CKC could reflect the mechanism by which sensorimotor cortical activity aligns its excitability with the most salient fluctuations of the CoP in the 1–6-Hz band to ensure swift delivery of optimal corrective motor command. Such mechanism could be under top-down attention control since (i) CKC occurs only in most challenging conditions and (ii) recent findings have linked the presence of theta oscillations (3-8 Hz) in behavioral and neural signals to top-down guided attention (37, 43).

Afferent and efferent contribution to CKC.

Our directionality results indicate that both afferent and efferent pathways contribute to CKC, with a ~60-ms delay from AP CoP velocity to cortical activity and from there, a ~40 ms delay back to CoP excursion. This is compatible with a closed-loop regulation of CoP, where CoP fluctuations are continuously estimated, monitored, and controlled by the brain. Following our results, the brain would monitor the CoP velocity and control its position.

The 60-ms delay in monitoring the velocity is similar to that of 50–100 ms previously reported for CKC in SM1 in response to rhythmic movements of the index finger (18, 24). In the context of upper limb continuous movement, CKC is thought to reflect cortical processing of proprioceptive afferent signaling (18–20). Therefore, our results demonstrate that similar cortical mechanisms are at play in regulating balance, especially in situations of high postural demands such as standing on foam. Accordingly, the brain would monitor CoP velocity, which should accurately reflect the rate of change in length of the muscle spindles within muscles acting across the ankle joint. However, it should be noted that any derivative of the CoP in the AP direction (position, velocity or acceleration) should lead to identical results, simply because coherence is not affected by a linear transformation, which time derivation is in the Fourier domain (23). A predominant monitoring of velocity would however be compatible with previous results on sensory reweighting, where perception thresholds for the visual, vestibular and proprioceptive systems depend on the velocity of sway (44). It would also be in line with modelization-based studies who have highlighted the role of velocity information rather than position or acceleration for the control of postural sway (45, 46). In any case, our results suggest that CKC derived from CoP velocity provides a marker of the integration of proprioceptive information to inform postural control.

The 40-ms delay in controlling CoP excursion is compatible with delays estimated between brain and lower limb muscle activity during isometric contractions (47). It is also partly in line with results reported during overground walking where cortical activity synchronizes (34) with the electromyographic activity of the tibialis anterior in the 4–7 Hz range. And from a biomechanics standpoint, the distance to a neutral CoP position, rCoP, directly scales with the motor correction that would be required from the muscles acting on the ankle and hip joints to align the CoM with the CoP (48). Therefore, supported by the predictions of biomechanics, our results indicate that CKC derived from rCoP reflects the efferent commands sent to muscles for postural control.

Behavioral interpretation.

Our results revealed an overall positive relationship between CKC strength in the most challenging condition (standing on foam eyes closed) and the relative increase in instability induced by this challenging condition, compared with unperturbed standing. Interestingly, such a relationship with CKC was not found when considering the uncontrasted instability in the challenging condition. This suggests that CKC does not reflect how much instability there is, but how much instability exceeds that commonly experienced.

Pragmatically, individuals with more unstable posture on foam with eyes closed should be those having more difficulties to leverage vestibular information. Being fully deprived of vision, they could have relied more on proprioceptive information, which was less reliable than usual when standing on foam (26). And indeed, standing on an unstable surface such as foam challenges the capacity of the central nervous system to shift the weight of individual sources of afferent information (49). Thus, a stronger impact of the hardest condition on balance could indicate inefficient weight shift of the cortex on proprioceptive integration instead of leveraging vestibular information. As a result, in a predictive coding framework (50), the discrepancy between perceived and expected proprioceptive input resulted in larger prediction errors for balance, as reflected by high CKC values.

Impact of COP and COM features on CKC strength.

Only a few participants displayed significant CKC derived from CoM features. This indicates that SM1 integrates information pertaining to the variation of CoP rather than CoM for maintaining upright balance.

CKC was higher for CoP features computed along the AP axis compared to the ML axis. This was expected considering the bipedal nature of the task known to mainly recruit lower limb flexor and extensor muscles, especially those acting across the ankle joint (51).

Limitations and perspectives.

CoM was estimated from a double-integration technique instead of a full-body model as this was not available in the lab. However, no significant differences between the two methods were reported for bipedal stance (52). This therefore gives confidence in the present estimation of CKC for CoM features.

More studies are warranted to explore the relationship between CKC strength, available afferent sources and motor performance. Such findings could help optimize the rehabilitation of neurologically impaired patients suffering from loss of balance.

Conclusion

Our results demonstrate that human sensorimotor cortical areas take part in the closed-loop control of standing balance in challenging conditions. In doing so, they preferentially integrate and control the—rate of change of—CoP rather than CoM. In clinical practice, CKC strength could serve as a predictor of postural instability, quantifying the degree of cortical implication in maintaining balance.

Material and methods

Participants.

Thirty-six young healthy participants (age: 25 ± 3.5 years; weight: 71.7 ± 18.9 kg; 21 women) participated in this study. Volunteers with a history of neurological, muscular, or vestibular disorders were excluded from the study. The study had prior approval by the ethics committee of Erasme university hospital (CCB: B4062021000323, Brussels, Belgium). The participants gave informed consent before participation.

Protocol.

Participants completed a total of 8 recordings, 2 for each of the 4 conditions. The foam mat used in the foam conditions (Domyos, Decathlon, Villeneuve-d'Ascq, France) measured 39 × 24 × 6 cm and weighed 0.2 kg. The order of the recordings was counterbalanced and each recording lasted 5 minutes. All conditions were performed barefoot, without speaking, arms straight alongside the body, looking straight ahead at a cross on the wall. The position of the feet was standardized to a narrow stance where heels were touching and the line from the heel to the big toe was set at a 20° angle outward for all conditions. Participants were guarded by an experimenter located just behind to prevent falls to the ground. No contact was made between the participants and the experimenter unless a fall would have occurred without assistance. No assistance was required for this cohort. Participants were monitored for self-reported fatigue and took mandatory breaks of at least 2 minutes between trials.

Data acquisition.

Cortical activity was recorded during the balance tasks with a 63-channel EEG headcap (Waveguard original, ANT Neuro, Hengelo, Netherlands). Electrodes, embedded in a cap, were arranged according to the 10/20 system. Impedances of the electrodes were kept below 50 kΩ using electrolyte gel, and the reference was set at CPz. EEG signals were amplified (Advanced Neuro Technology, Enschede, the Netherlands) and sampled at 1000 Hz. Additionally, ground reaction forces and moments were recorded at 1000 Hz during each condition with a force plate (AccuSway-O, AMTI, Watertown, MA, USA).

Data pre-processing.

EEG and force plate data were imported in Matlab (Mathworks, Natick, MA, USA). After examination of the raw data in all participants, EEG electrodes on the mastoids (M1 and M2) were removed because they featured high amplitude artifacts caused by poor or unstable skin-electrode contact. Thus, signals from the 61 remaining electrodes were kept for further analyses.

EEG data were band-pass filtered between 1 and 90 Hz and notched filtered at 50 Hz using a zero-lag FFT-based filter. Bad channels were identified and interpolated based on the signals of the surrounding electrodes (53). EEG signals were then re-referenced to their common average. Time-points at which EEG amplitude exceeded 10 SD above the mean were discarded from further analyses. In addition, 20 independent components were evaluated from the data with Fast ICA (54) to identify and suppress further physiological artifacts. Independent components corresponding to heartbeat, eye-blink, and eye movement artifacts were visually identified and corresponding signals reconstructed by means of the mixing matrix were removed from the full-rank data.

Force plate data were band-pass filtered between 0.1 and 150 Hz with a fourth order Butterworth filter.

Data analysis

CoP and CoM computation.

CoP time-series along the AP (CoP_{AP}) and ML (CoP_{ML}) axes were filtered between 0.1 and 10 Hz. Their single and double derivative yielded the velocity ($vCoP_{AP,ML}$) and acceleration of the CoP ($aCoP_{AP,ML}$). The vector sum at every time step of CoP_{AP} and CoP_{ML} yielded the excursion (CoP), that of $vCoP_{AP}$ and $vCoP_{ML}$ yielded the velocity (vCoP), and that of $aCoP_{AP}$ and $aCoP_{ML}$ yielded the acceleration (aCoP).

We also estimated the mean speed as the mean of vCoP and the standard deviation of displacement in the AP and ML directions. These 3 quantities are commonly referred to as the instability parameters.

These features and instability parameters were also estimated for the CoM reconstructed with the zero-point-to-zero-point double integration technique (22).

CKC computation.

CKC was assessed using coherence analysis. Coherence is an extension of Pearson correlation coefficient to the frequency domain, which quantifies the degree of coupling between two signals, i.e. CKC strength, by providing a number between 0 (no linear dependency) and 1 (perfect linear dependency) for each frequency (23). In practice, EEG, CoP and CoM data were divided into overlapping 2-s epochs with 1.6-s epoch overlap (leading to a frequency resolution of 0.5 Hz). The epochs were then Fourier-transformed to derive a spectrum of coherence between the CoP and CoM features (position, velocity, acceleration and their vector sum) and each EEG signal, following standard methods (23).

Time delay estimation.

Time delays were estimated from the phase slope of the cross-spectral density between the identified maximal electrode (EEG_{SM1}) and CoP or CoM feature on frequencies where significant coherence was found in the range 0.5–10 Hz. A minimum of 3 consecutive significant frequency bins were required to compute a linear regression. A negative-phase slope indicated that the cortical activity was led by the CoP or CoM variation.

Statistical analysis.

Statistical analyses were performed using Matlab (Mathworks, Natick, MA, USA).

A threshold for statistical significance of the coherence ($p < 0.05$ corrected for multiple comparisons) was obtained as the 95th percentile of the distribution of the maximum coherence (across 0.5 – 10 Hz, and across SM1) evaluated between EEG and Fourier transform surrogate reference signals (1000 repetitions) (44). The Fourier transform surrogate of a signal is obtained by computing its Fourier transform, replacing the phase of the Fourier coefficients by random numbers in the range [$-\pi$; π], and then computing the inverse Fourier transform (55).

Normality of the data was assessed using the Kolmogorov-Smirnov test. When the data was found to not be normally distributed, a Box-Cox transformation was applied prior to subsequent analyses.

Possible effects of the balance condition on the number of available epochs used to compute CKC and on CKC at EEG_{SM1} averaged across 0.5–10 Hz were assessed using one-way analyses of variance (ANOVA). Post-hoc t-tests were performed when significant differences were uncovered.

The difference in significance of the effect of condition on CKC between CoP and CoM features (rCoP, $vCoP_{ML}$, $vCoP_{AP}$, vCoP, aCoP) was assessed using a bootstrap analysis (1000 resamplings).

To assess the behavioral relevance of CKC in the *foam-eyes-closed* condition, we applied a CCA between standardized CoP instability parameters (or their contrast between *foam-eyes-closed* and *solid-eyes-open* conditions) and peak CKC values for rCoP, $vCoP_{AP}$ and vCoP in the range 0.5–10 Hz. Regularization was used to deal with the limited sample size at our disposition (56), with regularization parameters selected through leave-one-out cross-validation. The statistical significance of the final regression model was assessed with permutation statistics, by comparing the correlation value to its permutation distribution (1,000 permutations) obtained after having shuffled instability—but not CKC—values across participants

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