Wang et al. Journal of NeuroEngineering and Rehabilitation (2025) 22:120
https://doi.org/10.1186/s12984-025-01650-8

Journal of NeuroEngineering and Rehabilitation

RESEARCH

Open Access

Cortical adaptations in Tai Chi practitioners during sensory conflict: an EEG-based effective connectivity analysis of postural control

Guozheng Wang[1,2,3†], Xiaoxia Liu[3†], Yiming Cai[2], Jian Wang[3,4], Ying Gao[3*] and Jun Liu[1,2*]

Abstract

Background Tai Chi (TC) is recognized for enhancing balance and postural control. However, studies on its effects on the central nervous system are limited and often involve static experiments despite the dynamic nature of TC. This study addressed that gap by examining cortical network activity during dynamic, multisensory conflict balance tasks. We aimed to determine whether long-term TC practice leads to neuroplastic changes in brain connectivity that improve sensory integration for postural control.

Methods Fifty-two young adult participants (long-term TC practitioners = 22; non-practitioners = 30) performed balance tasks under sensory congruent and conflict conditions using a virtual reality headset with a rotating supporting surface. EEG was performed, and generalized partial directed coherence was used to assess directed functional connectivity in the mu rhythm (8–13 Hz) between predefined regions of interest (ROIs) in the cortex implicated in sensory and motor integration. Graph-theoretic measures (in-strength and out-strength) indexed the total incoming and outgoing connection strengths for each region. Statistical analysis used mixed-design ANOVAs (Group × Condition) to compare balance and connectivity measures.

Results TC practitioners demonstrated significantly better postural stability under both sensory conditions, with a reduced sway area. EEG analysis revealed that increased sensory conflict decreased the global efficiency of the visual integration network but increased that of the somatosensory integration network. Furthermore, TC practitioners demonstrated enhanced out-strength of the somatosensory cortex and lower out-strength of the right posterior parietal cortex (PPC) compared to non-practitioners.

Conclusions Long-term TC practice is associated with quantifiable neuroplastic changes in mu-band cortical effective connectivity, specifically enhanced information outflow from somatosensory reduce parietal influence

†Guozheng Wang and Xiaoxia Liu have contributed equally to this work and share first authorship.

*Correspondence:
Ying Gao
yigao@zju.edu.cn
Jun Liu
liujun@zju.edu.cn

Full list of author information is available at the end of the article

regions. Our findings demonstrate central mechanisms by which TC practice may improve balance, providing neuroengineering evidence for TC as a neuroplasticity-driven balance intervention.

Keywords Tai chi, Postural control, EEG, Cortical connectivity, Sensory integration

Background

Postural control is an essential requirement for static and dynamic stability, integrating various sensory inputs from the visual, vestibular, and somatosensory systems to generate appropriate motor responses to maintain postural stability [1, 2]. Efficient postural control during most activities of daily living is important to prevent falls, which may lead to injuries. Tai Chi (TC) is a traditional Chinese martial art practiced worldwide for its health benefits, particularly in improving balance and postural control [3–5].

TC practice leads to substantial improvement in balance and proprioception, elements that form the basis of postural control [6]. Trials have shown that TC improves balance and prevents falls among older adults and individuals with neurological diseases because it involves slow and controlled movements [7, 8]. Li et al. also reported that TC significantly improves balance and reduces the risk of falls in older adults with a history of falls [9].

While many studies have examined the peripheral effects of TC, few studies have focused on central nervous system effects. Recent electroencephalography (EEG) studies have assessed the influence of TC on brain activity [10]. EEG offers high temporal resolution suitable for capturing the rapid neural dynamics involved in postural adjustments [11]. For example, enhanced alpha-wave activity has been found in TC practitioners, reflecting improvements in mental relaxation and reduced stress [12]. Liu et al. reported improved cognitive function and cortical connectivity in TC practitioners compared with that in non-practitioners [13].

However, most EEG-based TC studies have been conducted under static conditions despite the dynamic nature of TC. It is important to examine the cortical processing of multisensory information under dynamic and varied sensory input conditions. The prevailing static research paradigm may overlook or misrepresent the crucial neural adaptations that enable TC practitioners to excel in dynamic balance tasks, thereby limiting the translation of research findings into effective interventions for real-world balance challenges.

In recent years, there has been an increased focus on understanding cortical and muscular connectivity during balance control under sensory perturbations. Sensory-conflict paradigms based on virtual reality (VR) and moving platforms elicit substantial postural adjustments and neural responses without significant bodily movement interference. Multisensory conflicts, such as inconsistencies between visual and vestibular or proprioceptive information, challenge balance maintenance and test sensory adjustment capabilities. Peterson and Ferris (2019) conducted a study on group-level cortical and muscular connectivity during perturbations in walking and standing balance. Perturbations such as visual field rotations and physical pulls were found to significantly affect corticomuscular connectivity [14]. Our research group has also conducted a series of experiments based on brain network analysis under sensory conflict. We discovered that sensory conflicts induced through virtual reality and a rotating platform initially disrupt postural stability [15, 16]; however, over time, individuals show adaptation characterized by the dynamic reorganization of brain networks. These findings underscore the brain's capacity for rapid adaptation and suggest that investigating these dynamic reorganizational processes can inform the design of targeted balance training programs that specifically challenge and train these adaptive neural mechanisms.

Investigating brain function during such dynamic tasks necessitates analytical approaches that can capture the complex interplay within neural networks. Advances in network neuroscience, computational approaches [17, 18], particularly methods for estimating directed effective connectivity from EEG, offer new perspectives on cortical information interactions [19–21]. Effective connectivity quantifies the directed influence one neural population exerts over another, going beyond simple correlations (often termed functional connectivity) to infer information flow within brain networks. This shift from describing what brain areas are active to how they influence each other represents a fundamental advancement, allowing for the formulation of more mechanistic hypotheses about information processing in the brain, especially during complex behaviors like postural adaptation. One powerful approach for estimating effective connectivity from EEG time-series is Multivariate Autoregressive (MVAR) modeling. MVAR models capture the linear predictive relationships between multiple signals simultaneously. From fitted MVAR models, metrics like Generalized Partial Directed Coherence (GPDC) can be derived.

Furthermore, graph theory provides a quantitative framework for analyzing the topological properties of brain networks derived from connectivity data. Metrics such as node strength, specifically in-strength and out-strength for directed networks, can characterize the functional roles of different brain regions [22].

In-strength, the sum of weighted incoming connections to a node, reflects the total influence received by that region, potentially highlighting its role as an integration hub. Conversely, out-strength, the sum of weighted outgoing connections from a node, reflects the total influence exerted by that region on others, potentially indicating its role as an information source or driver within the network. Analyzing how these metrics change under sensory conflict, and whether they differ between TC practitioners and controls, can provide valuable insights into the adaptive neural strategies associated with TC training.

This study specifically focuses on the mu rhythm (8–13 Hz), an EEG oscillation originating predominantly from the sensorimotor cortex [23]. The mu rhythm is functionally relevant as it reflects the activation state (desynchronization) or idling/inhibition state (synchronization) of sensorimotor areas. Its power and connectivity are modulated during movement execution, preparation, imagery, observation, and crucially, during tasks requiring sensorimotor integration. Given that TC training involves extensive refinement of sensorimotor control and body awareness, we hypothesized that neuroplastic adaptations induced by TC would be particularly evident in the mu frequency band. Therefore, our a priori focus on mu-band effective connectivity represents a hypothesis-driven approach to investigate the specific sensorimotor network changes potentially underlying TC's postural benefits.

The primary aim of this study was to analyze cortical-directed information interactions within the mu frequency band in TC practitioners under sensory perturbations using effective brain network analysis via EEG technology. Using advanced EEG techniques, we sought to understand how TC practice influences the ability of the brain to process and integrate sensory information to maintain postural control. We hypothesized that: [1] TC practitioners would exhibit superior postural stability compared to controls, particularly under sensory conflict; [2] Sensory conflict would modulate mu-band effective connectivity networks in ways consistent with sensory re-weighting; and [3] Compared to controls, TC practitioners would demonstrate distinct patterns of mu-band effective connectivity during sensory conflict, specifically showing evidence of enhanced somatosensory processing (e.g., increased out-strength from somatosensory regions), reflecting adaptive neural strategies developed through extensive training.

Methods

Participants

The research included a total of 52 individuals, consisting of 22 TC practitioners and 30 controls who were matched in terms of age and sex. The TC practitioners were national first-class athletes and national master athletes with 6–15 years of TC experience. The TC practitioners reported currently practicing Tai Chi for a minimum of 30 min per session, at least three times per week, in addition to their years of experience. The control group, with no previous experience in TC practice, engaged in general aerobic exercises, such as walking, at least three times a week, with each session lasting 30 min or more.

The inclusion criteria for the participants were: age range of 18–35 years, good general health, normal or corrected vision, and right hand and right leg dominance confirmed through specific tests for hand and leg dominance. For the TC practitioners, a minimum of 6 years of TC practice was required. The following exclusion criteria were applied: any sensory, neurological, musculoskeletal, or cardiovascular disorders; recent surgery involving the lower extremities or the dominant arm; conditions such as motion sickness, dizziness, or vertigo; psychological problems such as fear of falling, anxiety, or depression; and a Montreal Cognitive Assessment (MoCA) score of < 26. While Tai Chi is often practiced by older adults, this study focused on young, highly experienced practitioners to isolate the long-term neuroplastic effects of extensive training itself, minimizing potential confounds from age-related changes in neural structure, function, and postural control mechanisms. Direct extrapolation of these specific findings to older populations requires caution.

Participants were adequately informed of the research protocols and gave signed permission before participating. The Zhejiang University Psychological Science Research Center Ethics Committee approved the research (2024.011). Ethical considerations included ensuring participant confidentiality, right to withdraw from the study at any time, and adherence to the principles of the Declaration of Helsinki.

Initially, 22 TC practitioners and 30 non-practitioners were recruited. However, EEG data were not collected from three non-practitioners because of equipment malfunction. Furthermore, excessive body movement during the sessions resulted in significant EEG data contamination for three TC practitioners and four non-practitioners. Consequently, the final analysis included center of pressure (COP) data from all 22 TC athletes and 30 non-athletes, while usable EEG data were available for 19 TC practitioners and 23 non-practitioners only.

Experimental design

This study examined the effect of TC training on posture control across multiple sensory conditions using a rotating platform (All Controller, Nanjing, China) to control actual motion and a virtual reality (VR) headset (VIVE PRO 2, HTC Corporation, New Taipei, Taiwan) to alter visual cues. Two balance disturbance conditions were set: "sensory congruent" and "sensory conflict." The "sensory congruent" condition aimed to present the participants with natural multisensory information during a clockwise rotation. The "sensory conflict" condition provided visual scenes expected during a counterclockwise rotation while the participants were rotating clockwise (Fig. 1).

Upon entering the laboratory, the participants were briefed on the experimental procedure and given a preliminary trial to familiarize themselves with the process (no data were collected). After the preliminary trial, the participants were asked to remove their shoes and socks and stand in the middle of the force plate with their feet shoulder-width apart and their hands crossed over the chest. They were then fitted with a VR headset that displayed a simulated laboratory environment created using Unity3D. Throughout the experiment, the participants were instructed to keep their eyes open and look straight ahead (normal blinking was allowed), and the eye-tracking systems within the VR headset ensured no prolonged intentional eye closure. Participants were required to maintain their posture while keeping their feet in the same position during the experiment.

Once their stance was stable, participants were exposed to the "sensory congruent" and "sensory conflict" balance disturbance conditions in random order, each lasting 36 s. Between these conditions, there were 5-minute breaks during which participants sat with their eyes closed to prevent any carryover effects. The "sensory congruent" condition simulated natural rotation movement in a stationary scene. Under this condition, the rotating platform was set to rotate clockwise at 30°/s, and the VR headset, following the internal sensors detecting the participant's movement, adjusted the scene to rotate counterclockwise at the same rate of 30°/s relative to the participant's eyes. The entire rotation process lasted 36 s, with the acceleration and deceleration phases completed within 2 s, maintaining a steady clockwise speed of 30°/s in the middle phase. This rotation speed was determined in preliminary trials to sufficiently stimulate neural activity without significantly interfering with the EEG data. The rotation speed of 30°/s was chosen based on previous studies investigating postural responses to platform rotations and sensory conflicts and pilot testing, representing a balance between inducing a measurable sensory conflict and postural challenge. The "sensory conflict" condition aimed to provide participants with a visual scene expected during a counterclockwise rotation while they were rotating clockwise. In this condition, the rotating platform also rotated clockwise at 30°/s; however, the VR headset, in addition to following the participant's movement, added an extra counterclockwise rotation speed twice that of the original, making the visual scene appear to rotate clockwise at 30°/s relative to the participant's motion, as if they were rotating counterclockwise at 30°/s. This condition lasted 36 s, with acceleration and deceleration phases within 2 s and a steady speed of 30°/s in the middle phase.

Data collection and preprocessing

The collection of COP data was conducted with a Wii Balance Board manufactured by Nintendo in Kyoto, Japan. The balance board was positioned at the midpoint of the rotating platform, and the data were sampled at a rate of 100 Hz. Prior research has confirmed the precision and dependability of the Wii Balance Board in measuring COP [24, 25]. EEG data were collected using a 64-channel EEG cap (EE-225, ANT Neuro, Hengelo, The Netherlands). A conductive gel was applied on every electrode after placement to prevent impedance from exceeding 20 kΩ to promote good signal quality in the recording.

The COP signals were initially processed with a fourth-order Butterworth low-pass filter with a cutoff frequency of 20 Hz to eliminate high-frequency noise beyond this threshold potentially due to equipment noise or other non-postural dynamics not relevant for postural stability. The sway area, which is a typical index of the overall postural stability, was estimated for the processed COP data. The sway area measure usually reflects overall postural stability and is achieved by estimating an ellipse for the COP data in the anteroposterior and mediolateral directions. The ellipse encloses 95% of the COP movement area, thereby providing a quantitative measure of the sway area [26].

The raw EEG data underwent several preprocessing steps using custom scripts incorporating functions from the EEGLAB toolbox (R2023b;) running in MATLAB (R2023b; The MathWorks, Inc., Natick, MA, USA) to attenuate artifacts and isolate neural activity. The data were band-pass filtered in the range of 2–48 Hz using a Finite Impulse Response filter to attenuate very low- and high-frequency noise. Although the recording environment included shielding, a 50 Hz notch filter (implemented via the Cleanline plugin in EEGLAB) was applied to remove any residual power line noise potentially introduced by the VR system, rotating platform motors, or other auxiliary equipment operating nearby [27].

Given that the experimental setup involving standing balance on a rotating platform within VR inevitably induced movement artifacts, further cleaning was performed using the Artifact Subspace Reconstruction (ASR) method [28]. ASR is an automated, component-based technique that effectively removes large and transient artifacts, such as artifacts related to body movements. We set the ASR threshold at 20 standard deviations in this study. This specific threshold, in conjunction with subsequent ICA, has demonstrated effectiveness

Fig. 1 Schematic diagram of the experimental setup and installation. The schematic diagram illustrates the experimental setup used to study the impact of Tai Chi on postural control under sensory perturbation conditions. Participants stood barefoot on a Wii Balance Board placed in the center of a rotating platform, with a virtual reality (VR) headset providing visual stimuli. Two conditions were tested: "sensory congruent" and "sensory conflict." In the sensory congruent condition, visual and actual rotational movements were aligned, whereas in the sensory conflict condition, the visual scene was counter-rotated to create a mismatch between visual and proprioceptive inputs. Electroencephalographic (EEG) data were recorded using a 64-channel EEG cap, and center of pressure (COP) data were collected to assess postural stability

in handling artifacts during standing balance and walking tasks in previous studies [14, 29, 30]. Accordingly, data points with a standard deviation over 20 times the overall data standard deviation were regarded as artifacts and removed, particularly in datasets most affected by artifacts, a minimum of 75% of the original data duration was preserved across all participants. On average, 93.3% (mean) ± 4.4% (SD) of the data was retained following ASR cleaning. This level of data cleaning was deemed essential due to the unavoidable presence of motion-related artifacts intrinsic to dynamic balance tasks performed within VR.

Following ASR, Independent Component Analysis (ICA) using the extended Infomax algorithm was performed to further refine the data. The sequential application of ASR followed by ICA was chosen to leverage their complementary strengths in artifact removal. ASR effectively addresses the large-amplitude, non-stationary artifacts (e.g., sudden movements, electrode pops) that can severely disrupt EEG signals and potentially violate the assumptions underlying ICA, thereby hindering its decomposition quality. Relying solely on ICA might fail to adequately remove these large-scale artifacts or could lead to their influence contaminating the estimation of other components. Conversely, attempting to use ASR to remove all types of artifacts, including lower-amplitude physiological ones like eye blinks or specific muscle activities that ICA excels at identifying, could necessitate overly aggressive thresholding and result in excessive data loss. By first using ASR to clean the most disruptive, high-variance artifacts, we create a dataset more amenable to robust ICA decomposition. ICA can then more effectively separate the remaining signal into maximally independent components (ICs), allowing for the precise identification and removal of residual physiological artifacts (e.g., eye blinks, lateral eye movements, tonic muscle activity) based on their characteristic spatial topographies and temporal features. ICs classified by ICLabel as having a high probability (> 0.8) of representing non-brain activity (muscle, eye, channel noise, etc.) were subsequently removed from the data before further analysis [31].

Table 1 Region of interest (ROI) definitions

ROI Abbreviation	Full Name	Included Brodmann Areas (BA)
LS1	Left Somatosensory Cortex	1, 2, 3
RS1	Right Somatosensory Cortex	1, 2, 3
LM1	Left Motor Cortex	4, 6
RM1	Right Motor Cortex	4, 6
LPPC	Left Posterior Parietal Cortex	5, 7
RPPC	Right Posterior Parietal Cortex	5, 7
LVC	Left Visual Cortex	17, 18, 19
RVC	Right Visual Cortex	17, 18, 19

EEG source analysis

To estimate the neural activity originating from specific cortical regions rather than scalp electrodes, which are affected by volume conduction, we performed EEG source localization. Source space analysis was performed in two stages: forward and inverse modeling. The ICBM-152 brain template was used to generate a forward model using the Boundary Element Method. This approach has been proven to simulate the EEG signal propagation properties on the scalp with high accuracy; thus, it provides sound underpinning for source reconstruction. In this study, the forward model was not generated using participant magnetic resonance imaging (MRI) data; instead, it was generated using a standardized head model. This is based on the assumption that the brain anatomy of all participants is similar to standardized brain anatomical structures. Although this approach does not account for anatomical differences among individuals, it is feasible and commonly used in cases where individual MRI data are not available [32].

The inverse model computed in this experiment used a well-known standardized low-resolution brain electromagnetic tomography (sLORETA) method [33]. sLORETA is a distributed source localization method that provides smooth and physiologically plausible solutions for EEG source imaging. It is used extensively because it can provide zero-error localization in the presence of measurement and model errors under ideal conditions [34].

The source reconstruction focused primarily on cortical regions, as the synchronous activity of cortical neurons is the predominant origin of EEG signals. The reconstructed source activity time-series were averaged within eight predefined Regions of Interest (ROIs) based on the Brodmann atlas template mapped onto the ICBM-152 standard brain [35]. These ROIs were selected a priori based on their known involvement in sensorimotor control and visual processing (see Table 1).

Directed functional connectivity computation

To investigate how TC practitioners integrate sensory information under perturbation, we employed generalized partial directed coherence (GPDC) to estimate directed effective connectivity among the eight ROIs within the mu frequency band (8–13 Hz). Effective connectivity analysis was performed using the Source Information Flow Toolbox (SIFT) (v1.0) implemented in EEGLAB/MATLAB [36]. GPDC is a powerful method for assessing directed functional connectivity [37]. It can discriminate between direct and indirect interactions among different structures. This feature makes it particularly well suited for analyzing complex brain network dynamics in the context of sensorimotor integration.

The computation of GPDC involves the following steps. First, a multivariable autoregressive (MVAR) model is fitted to preprocessed EEG data. The optimal model order 'p' was determined individually for each dataset by minimizing the Akaike Information Criterion (AIC) over a range of plausible orders (1 to 30). AIC balances model goodness-of-fit (likelihood) against model complexity (number of parameters), providing a standard criterion for model selection [38]. The median optimal order across participants was found to be $p = 20$, and this order was used consistently for all subsequent MVAR model fitting. The MVAR model was used to provide a frequency-domain representation of directed connectivity, which was applied to analyze the interactions within specific frequency bands. This study focused on the frequency band of the mu rhythm (8–13 Hz) because of its critical role in sensorimotor integration. The GPDC values for all the pairs of signal channels were then calculated to provide a directed connectivity matrix representing the causal dependencies of the various channels within the EEG network.

The validity of the fitted MVAR model for each participant's data was assessed using standard diagnostic tests implemented in SIFT: [1] Model Consistency [2], Model Stability, and [3] Residual Whiteness. To assess consistency, data simulation using the model was performed and then the Euclidean norm was calculated between the correlation matrix of the real and simulated data [39]. The statistic is measured on a scale of 0 to 100%, where greater percentages indicate a greater correlation between the model and the structure of the data. Stability was confirmed by analyzing the logarithm of the highest eigenvalue in the coefficient matrix of the model. A negative number indicates the stability of the model. In addition, the whiteness of the residuals was evaluated using an autocorrelation function test in conjunction with confidence intervals [40]. The result is represented as a numerical number ranging from zero to one, indicating the probability that the residuals exhibit a white noise pattern. A high value suggests that the residuals are free of correlation structures that are not captured by the model, thus increasing the confidence in the model's accuracy. These validation steps confirmed that our model provided a robust representation of the underlying EEG data, ensuring a reliable and meaningful interpretation of the GPDC results.

Based on the GPDC-derived directed connectivity matrix, we further analyzed both the global and local network characteristics. The global efficiency of the network was computed to assess the extent to which information was exchanged across the brain network. Given the potential independent roles of visual integration and sensorimotor integration, we divided the global efficiency calculation into three networks: the overall network, visual integration network (comprising four nodes: LPPC, RPPC, LVC, RVC), and sensory-motor integration network (comprising six nodes: LS1, RS1, LM1, RM1, LPPC, RPPC).

For local network properties, we calculated the strength of each node, which was further divided into in-strength and out-strength. In-strength, the sum of weighted incoming connections to a node, reflects the total influence received by that region. Out-strength, the sum of weighted outgoing connections from a node, reflects the total influence exerted by that region on others.

Statistical analysis

We used a 2 (Group: TC, Control) × 2 (Condition: Congruent, Conflict) mixed-design analysis of variance (ANOVA) to assess the impact of TC training (between-subject factor) and sensory information congruence (within-subject factor) on sway area, global efficiency, clustering coefficient, and the in-strength and out-strength of the cortical nodes. These metrics were calculated for the entire brain network, sensory-motor integration cortex, and visual integration cortex to assess overall and regional brain network efficiency and clustering, as well as local cortical interactions.

For each ANOVA, we reported the F-statistic, p-value, and partial eta-squared (η^2) as a measure of effect size. Partial eta-squared (ηp^2) values are interpreted with conventional thresholds of 0.01, 0.06, and 0.14 representing small, medium, and large effects, respectively. Significant main effects and interactions were further explored using post hoc pairwise comparisons with Bonferroni correction to account for multiple testing. A p-value of < 0.05 was considered statistically significant. All statistical analyses were performed using. Statistical results are reported consistently with two decimal places for F-values and effect sizes, and three decimal places for p-values.

Results

Analysis of COP

To examine the effects of long-term TC training (between-subject factor) and sensory information congruence (within-subject factor) on the sway area (an indicator of postural stability), we conducted a mixed-design ANOVA.

The ANOVA revealed significant main effects of Group ($F(1,50) = 13.77$, $p < 0.001$, $\eta p^2 = 0.22$) and Condition ($F(1,50) = 26.48$, $p < 0.001$, $\eta p^2 = 0.35$). The Group × Condition interaction was not significant ($F(1,50) = 0.11$, $p = 0.738$, $\eta p^2 = 0.002$). Specifically, the TC group exhibited significantly smaller sway areas overall compared to the Control group. Independently, the sensory conflict

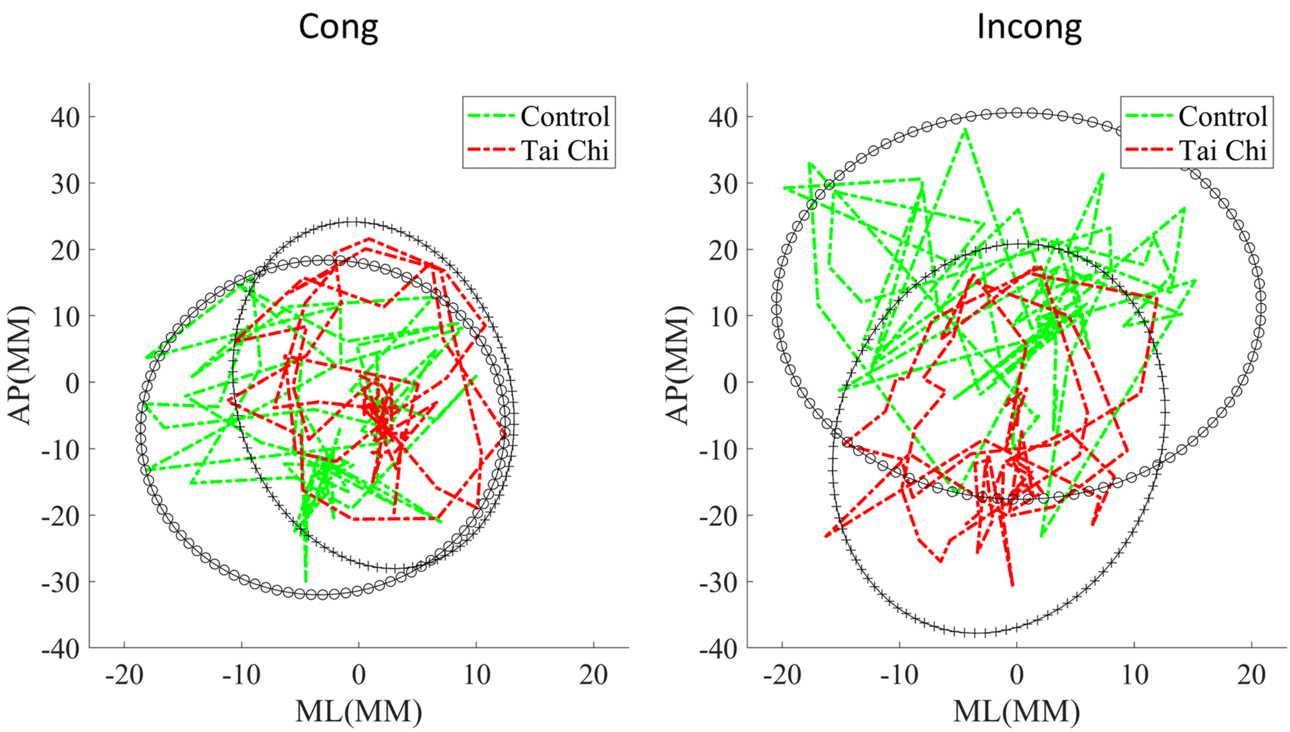

Fig. 2 Geometric sway measures. The figure displays geometric sway measures divided into left and right panels, representing sensory congruent and sensory conflict conditions, respectively. Each panel compares the center of pressure (COP) sway trajectories of Tai Chi practitioners and non-practitioners. The trajectories shown are from a representative participant whose sway areas closely approximate the average sway areas across all participants. The 95% ellipse profile illustrates the sway area under each condition

Table 2 Model fitting results ($n=38$)

Group	Control		Tai Chi	
Sensory	Congruent	Conflict	Congruent	Conflict
Residual Whiteness Likelihood	0.93 (0.031)	0.92 (0.033)	0.91 (0.036)	0.91 (0.039)
Stability Index	-0.23 (0.038)	-0.20 (0.079)	-0.23 (0.037)	-2.2 (0.0275)
Consistency (%)	95 (2.3)	94 (5.2)	93 (4.3)	92 (5.1)

Values are presented as Mean (SD)

condition resulted in significantly larger sway areas compared to the congruent condition across both groups (Fig. 2).

EEG model validation

To confirm the adequacy of the multivariate autoregressive (MVAR) models that form the basis of our generalized partial directed coherence (GPDC) analysis, we quantified three standard validation metrics: (i) percent consistency, (ii) residual whiteness probability (RWP), and (iii) stability index.

Percent consistency expresses the proportion of the empirical cross-spectra that the model can reproduce; values > 80% are generally interpreted as "good". RWP is the fraction of model windows in which the Ljung–Box portmanteau test fails to reject the null hypothesis of white residuals at $\alpha=0.05$ and ≥ 0.95 as ideal. The stability index is the maximum modulus of the MVAR companion-matrix eigenvalues; negative values indicate that all poles lie inside the unit circle, i.e., a stationary and hence stable solution.

Table 2 summarises the group means ± SD. All conditions exhibited high consistency (92–95%), confirming that the selected model order captured the bulk of temporal dependencies. The residual-whiteness probability averaged 0.916 ± 0.024. Although marginally below the ideal 0.95 threshold, a probability above 90% is generally considered acceptable in MVAR modeling. The stability index was negative for every subject (range −0.38 to −0.12), satisfying the requirement that all eigenvalues lie inside the unit circle.

Overall, these metrics demonstrate that the fitted MVAR models are stable, internally consistent, and free of substantial residual structure. The moderate (< 8%) departure from perfect whiteness is well within the range reported in previous EEG studies that adopted the same criteria and therefore does not compromise the reliability of the subsequent GPDC estimates.

Global network metrics of directed brain network analysis

We utilized GPDCderived from the validated MVAR models to estimate the directed brain networks between eight predefined cortical regions of interest (ROIs, see

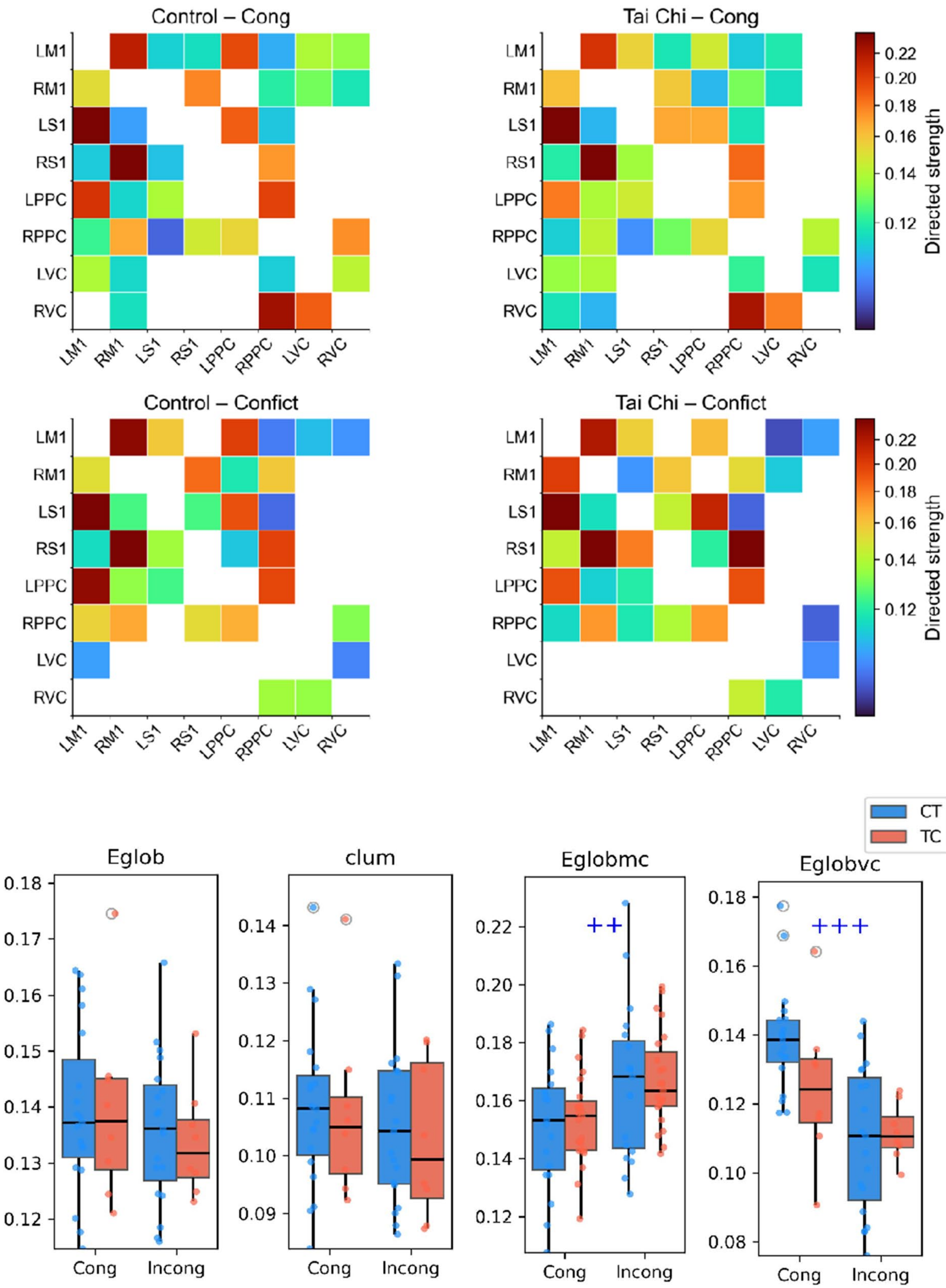

Fig. 3 (See legend on next page.)

(See figure on previous page.)

Fig. 3 Group-level μ-band connectivity and graph-metric summary. (**A**) Directed-connectivity heat-maps. Each 8×8 matrix shows the grand-average GPDC value (row → column information flow) for the four experimental conditions: Control-Congruent, Control-Conflict, Tai Chi-Congruent and Tai Chi-Conflict (upper-left, lower-left, upper-right, lower-right, respectively). Abbreviations—LM1: left motor cortex; RM1: right motor cortex; LS1: left somatosensory cortex; RS1: right somatosensory cortex; LPPC/RPPC: left/right posterior parietal cortex; LVC/RVC: left/right visual cortex. Colour follows a power-normalised "turbo" scale (γ = 0.5): deep blue = weakest, red = strongest; connections below the group-wise 50 th percentile are masked white. Exact MNI coordinates of all ROIs are provided in Methods 2.4 and Table 1. (**B**) Graph-theoretical indices. Dual-axis box-and-whisker plots illustrate (i) whole-brain global efficiency (Eglob), (ii) whole-brain clustering coefficient (Clu), (iii) global efficiency of the sensorimotor-integration sub-network (Eglobmc; comprising six nodes: LS1, RS1, LM1, RM1, LPPC, RPPC), and (iv) global efficiency of the visual-integration sub-network (Eglobvc). B; comprising four nodes: LPPC, RPPC, LVC, RVCox centre = median; hinges = 25/75 th percentiles; whiskers = 1.5 × IQR. + indicates a significant main effect of Condition; * indicates a significant main effect of Group (two-way mixed ANOVA with Holm–Bonferroni correction). One, two and three symbols denote $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively

Methods 2.4 for definitions) under four conditions: TC practitioners with sensory congruence, TC practitioners with sensory conflict, control group with sensory congruence, and control group with sensory conflict. Figure 3A visualizes the average connectivity networks.

Mixed-design ANOVAs were performed on global network metrics (Fig. 3B). For global efficiency of the entire brain network (Eglob) and the clustering coefficient (Clum - analysis not shown as original results were non-significant), no significant main effects of Group or Condition, nor any significant interactions were found (all $p > 0.050$).

For the sensory-motor integration cortex, there was a significant main effect of sensory information congruence on global efficiency (F [1, 40] = 10.32, $p = 0.003$, $\eta p2 = 0.21$), indicating that global efficiency within this subnetwork was significantly higher during sensory conflict compared to the congruent condition. However, the main effect of TC training was not significant, (F [1, 40] = 0.11, $p = 0.742$, $\eta p2 = 0.00$), and the interaction effect was also non-significant (F [1, 40] = 0.01, $p = 0.919$, $\eta p2 = 0.00$).

For the global efficiency of the visual integration network (Eglobvc), a significant main effect of Condition was found (F [1, 40] = 37.64, $p < 0.001$, $\eta p^2 = 0.48$), with lower efficiency observed in the conflict condition compared to the congruent condition across both groups. The main effect of Group was not significant (F [1, 40] = 0.75, $p = 0.392$,$\eta p^2 = 0.02$), and the Group × Condition interaction approached significance (F [1, 40] = 3.00, $p = 0.091$, $\eta p^2 = 0.07$).

Local network metrics of directed brain network analysis

Mixed-design ANOVAs were used to analyze the in-strength and out-strength for each of the eight cortical ROIs. For in-strength, the ANOVAs revealed no significant main effects of Group or Condition, nor any significant Group × Condition interactions for any of the eight ROIs (all $p > 0.05$).

For out-strength (Fig. 4), the analysis revealed several significant effects. Significant main effects of Condition were found for the out-strength of LVC (F [1, 40] = 31.36,$p < 0.001$,$\eta p^2 = 0.44$) and RVC (F [1, 40] = 52.06,$p < 0.001$,$\eta p^2 = 0.57$). In both visual cortical regions, out-strength was significantly lower in the conflict condition compared to the congruent condition across both groups. The magnitude of this reduction appeared somewhat larger in the right hemisphere ($\eta p^2 = 0.57$) compared to the left hemisphere ($\eta p^{2=}0.44$), although this asymmetry was not directly tested.

For RS1, significant main effects were found for both Condition (F [1, 40] = 5.47, $p = 0.024$, $\eta p^2 = 0.12$) and Group (F [1, 40] = 7.78, $p = 0.008$, $\eta p^2 = 0.16$). The interaction was not significant (F [1, 40] = 0.22, $p = 0.64$, $\eta p^2 = 0.005$). Both the conflict condition and Tai Chi training led to an increase in RS1 out-strength.

For RPPC, a significant main effect of Group was found (F [1, 40] = 11.39, $p = 0.002$, $\eta p^2 = 0.22$), indicating that Tai Chi training significantly reduced RPPC out-strength, compared to the Control group. Neither the Condition nor the Interaction effects were significant (all $p > 0.05$).

Discussion

This study investigated the effects of long-term TC training on underlying cortical mu-band effective connectivity dynamics and postural control during sensory perturbation. Using EEG effective connectivity analysis, we sought to understand how long-term TC training influences the ability of the brain to integrate sensory information to maintain balance. The key statistically significant findings were (Table 3): [1] TC practitioners exhibited superior postural stability (reduced sway area) compared to controls under both conditions; [2] Sensory conflict induced changes in network efficiency across both groups, decreasing efficiency in the visual integration network while increasing efficiency in the sensorimotor integration network; [3] TC practitioners showed significantly increased the out-strength of the right primary somatosensory cortex (S1) and decreased that of the right posterior parietal cortex (PPC). These results provide novel insights into the potential neuroplastic adaptations associated with long-term TC practice that may contribute to enhanced postural control, particularly in challenging sensory environments.

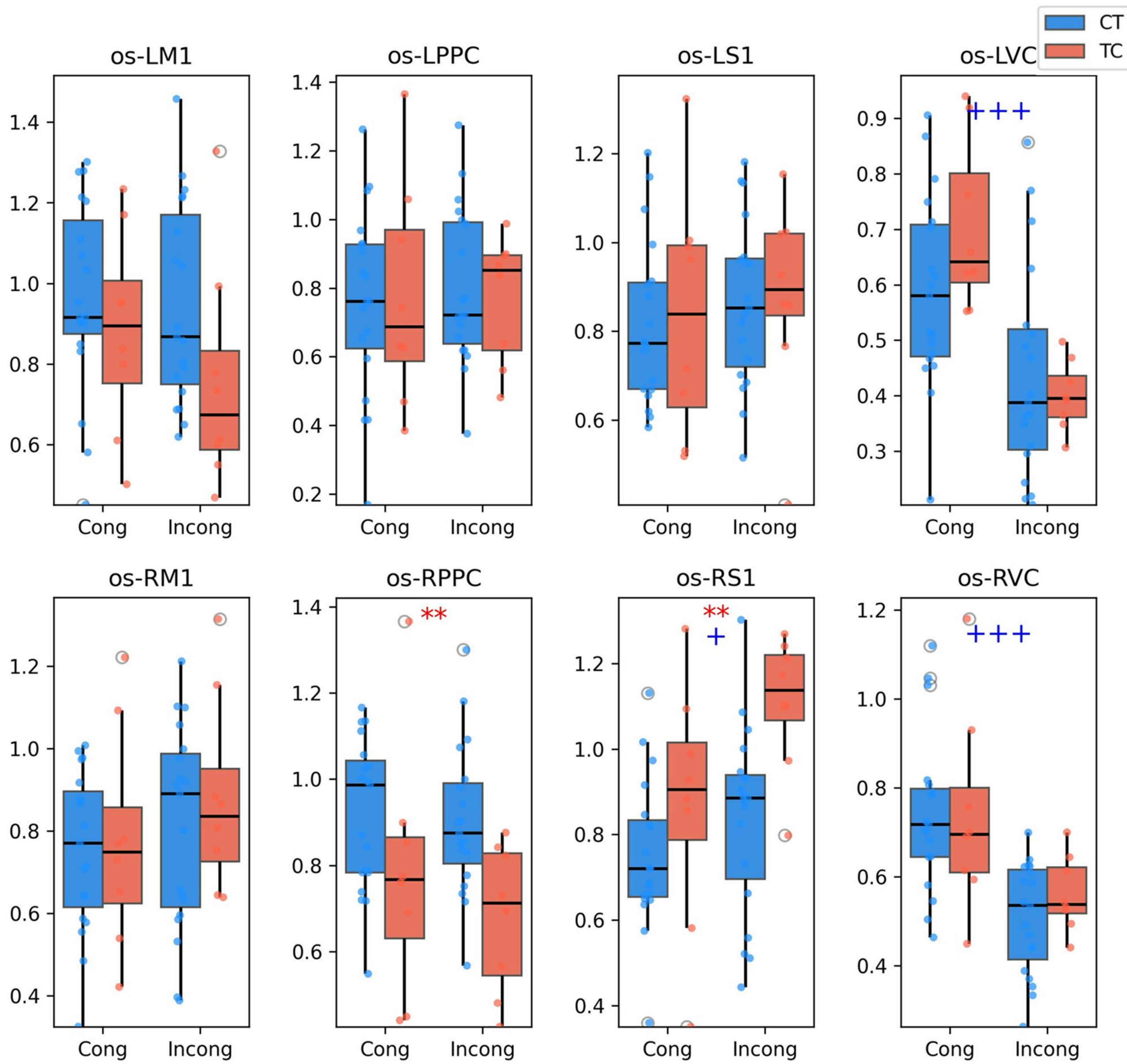

Fig. 4 Out-strength of cortical nodes under the sensory congruent and conflict conditions. The box plots illustrates the out-strength values for eight cortical nodes under sensory congruent (Cong) and sensory conflict (Incong) conditions for Tai Chi practitioners (TC) and the control group (CT). The cortical nodes are defined in Table 1. Each subplot is a dual-axis box plot showing the out-strength distribution under the specified conditions. Plus symbols (+) denote significant main effects of Condition; Asterisks (*) denote significant main effects of Group. Single symbols: $p < 0.05$; double symbols: $p < 0.01$; triple symbols: $p < 0.001$

Effects on sway areas and postural control

Our study revealed that TC practitioners demonstrated significantly better postural stability than did non-practitioners under both sensory congruent and conflict conditions. These findings underscore the effectiveness of TC in enhancing balance and stability even when sensory inputs are incongruent. These findings are consistent with those of earlier studies that have shown the benefits of TC in improving balance and reducing the risk of falls. For instance, Li et al. showed that TC practitioners had a much better balance ability and lower rate of falling than did controls [9]. Similarly, Wayne et al. concluded that TC improved postural control and stability in an older cohort [41].

While previous studies have primarily focused on static conditions, our study uniquely demonstrates the efficacy of TC under dynamic and challenging sensory perturbations. This further underlines the robustness of TC as an intervention for improving balance in complex environments.

Table 3 Summary of key statistical findings from 2 × 2 mixed ANOVAs

Dependent Variable	Main Effect: Group (TC vs. CT)	Main Effect: Condition (Conflict vs. Cong)	Interaction Group × Condition
Behavioral			
Sway Area	$F(1, 50) = 13.77$, $p < 0.001$, $\eta p^2 = 0.22$ *	$F(1, 50) = 26.48$, $p < 0.001$, $\eta p^2 = 0.35$ *	$F(1, 50) = 0.11$, $p = 0.738$, $\eta p^2 = 0.00$
EEG Network Metrics (μ-band)			
EglobSMC	$F(1, 40) = 0.11$, $p = 0.742$, $\eta p^2 = 0.00$	$F(1, 40) = 10.32$, $p = 0.003$, $\eta p^2 = 0.21$ *	$F(1, 40) = 0.01$, $p = 0.919$, $\eta p^2 = 0.00$
EglobVC	$F(1, 40) = 0.75$, $p = 0.392$, $\eta p^2 = 0.02$	$F(1, 40) = 37.64$, $p < 0.001$, $\eta p^2 = 0.48$ *	$F(1, 40) = 3.00$, $p = 0.091$, $\eta p^2 = 0.07$
Out-Strength			
LVC	$F(1, 40) = 0.01$, $p = 0.910$, $\eta p^2 = 0.00$	$F(1, 40) = 31.36$, $p < 0.001$, $\eta p^2 = 0.44$ *	$F(1, 40) = 2.16$, $p = 0.150$, $\eta p^2 = 0.05$
RVC	$F(1, 40) = 0.70$, $p = 0.407$, $\eta p^2 = 0.02$	$F(1, 40) = 52.06$, $p < 0.001$, $\eta p^2 = 0.57$ *	$F(1, 40) = 0.79$, $p = 0.379$, $\eta p^2 = 0.02$
RS1	$F(1, 40) = 7.78$, $p = 0.008$, $\eta p^2 = 0.16$ *	$F(1, 40) = 5.47$, $p = 0.024$, $\eta p^2 = 0.12$ *	$F(1, 40) = 0.22$, $p = 0.640$, $\eta p^2 = 0.01$
RPPC	$F(1, 40) = 11.39$, $p = 0.002$, $\eta p^2 = 0.22$ *	All $p > 0.05$	All $p > 0.05$
LM1, RM1, LPPC, LS1	All $p > 0.05$	All $p > 0.05$	All $p > 0.05$
In-Strength (all ROIs)	All $p > 0.05$	All $p > 0.05$	All $p > 0.05$

*** $p < 0.01$; Eglobsmc = Global Efficiency Sensorimotor Network; Eglobvc = Global Efficiency Visual Network; LVC/RVC = Left/Right Visual Cortex; LS1/RS1 = Left/Right Somatosensory Cortex

Cortical network efficiency changes and sensory Re-weighting

The analysis of global network efficiency revealed significant effects of the sensory condition across both groups (Table 3; Fig. 4). Our results further showed a clear decrease in the global efficiency of the visual information integration network under sensory conflict. This decrease indicates that the brain relies less on visual input when it is unreliable, and compensates by using more somatosensory information for stabilization. This adaptive mechanism is supported by the findings of previous studies showing that conflicting sensory inputs lead to decreased reliance on visual information and increased dependence on somatosensory stimuli [42].

In contrast, the global efficiency of the somatosensory information integration networks increased under sensory conflict. This enhancement indicates that the brain compensates for the increased processing of somatosensory information, thereby enhancing effective postural control despite the incongruence generated by visual inputs. Previous studies have shown that the brain can dynamically shift processing resources to utilize the most reliable sensory modality under conditions of sensory interference [43]. Our findings provide network-level evidence for such re-weighting occurring within the mu frequency band during sensory conflict, affecting both TC practitioners and controls.

Directed connectivity: enhanced somatosensory outflow in Tai Chi practitioner

The application of GPDC in the current study provides a fine-grained understanding of directed information interactions within the brain with respect to postural control during sensory perturbations. We distinguished the sources and destinations of in-strength and out-strength from different cortical nodes by analyzing the values of these parameters. Our results showed that chronic TC training changed the out-strength of the somatosensory cortices.

The key finding differentiating the groups was the significantly higher μband outstrength from the right somatosensory cortex (RS1) in TC practitioners compared with controls, along with an overall increase in RS1 outstrength during the conflict condition across both groups. Recalling that out-strength reflects the total weighted directed influence a region exerts on the network, this suggests that long-term TC training enhances the effective outflow of processed somatosensory information from these primary sensory regions to downstream areas potentially involved in postural control and motor planning, particularly within the mu frequency band linked to sensorimotor processing. This result supports those of previous studies suggesting that good somatosensory integration is important for balance and stability, particularly in difficult conditions [44, 45].

In contrast, Tai Chi training was associated with a significant reduction in μ band out-strength from the right posterior parietal cortex (RPPC). Given the RPPC's role in multisensory integration and attentional re-allocation, this decrease might reflect a more efficient reliance on proprioceptive cues, with less need for parietal-mediated compensatory processes when visual information is unreliable [46]. Together, the heightened RS1 outstrength and reduced RPPC outstrength may represent complementary neural adaptations whereby TC practitioners prioritize accurate somatosensory inflow while streamlining parietal processing.

Previous studies have suggested that TC practice enhances sensory reweighting capabilities, particularly increasing reliance on proprioceptive input [47, 48]. Our findings provide a potential neural correlate for this phenomenon at the level of cortical effective connectivity within the mu frequency band. The increased somatosensory out-strength in TC practitioners suggests a more robust or efficient channeling of relevant sensory information within the cortical network, facilitating adaptive postural responses.

Limitations and future research directions

Although our study provides significant insights into the effects of long-term TC training on cortical connectivity and postural control under sensory perturbation, it is important to acknowledge some limitations that may influence the interpretation and generalizability of our findings.

First, the study focused exclusively on young, healthy, highly experienced TC practitioners. While this allowed us to isolate the effects of extensive training while minimizing age-related confounds, it limits the direct generalizability of these specific findings to older adults, who represent a primary population for TC balance interventions. The patterns of cortical adaptation might differ in older individuals due to age-related changes in brain structure, function, and baseline postural control mechanisms. Future research should specifically investigate mu-band and other frequency band connectivity adaptations in middle-aged and older TC practitioners, potentially using longitudinal designs to track changes with training initiation.

Second, we used a highly controlled VR and rotating platform setup to create one specific type of sensory conflict (continuous yaw rotation mismatch). This is a somewhat artificial scenario compared to everyday balance challenges, which can involve translational perturbations, slips, trips, uneven surfaces, or cognitive distractions. The ecological validity of our findings is thus limited – they apply to a sustained visual-vestibular conflict. It would be erroneous to assume the same neural adjustments happen for, say, a sudden push or a vestibular loss scenario. Moreover, our perturbation was relatively short-term; we don't know how sustained exposure (minutes rather than seconds) would influence connectivity (maybe some habituation occurs).

Third, this study focused solely on cortical dynamics recorded via EEG. The absence of concurrent electromyography (EMG) recordings prevented the analysis of corticomuscular coherence (CMC) or directed corticomuscular connectivity. CMC provides insights into the direct functional coupling between the motor cortex and active muscles during postural tasks. Investigating how TC practice modulates CMC, particularly in lower limb muscles crucial for balance, would complement the current findings on cortico-cortical interactions and provide a more complete picture of the neuromuscular adaptations. Future studies integrating simultaneous EEG and EMG are warranted.

Fourth, the use of a standard head model for EEG source localization rather than individual MRI data may have introduced inaccuracies in identifying the exact neural sources of the observed EEG signals. Individual anatomical differences can influence the precision of source localization, and future studies should consider incorporating personalized head models to improve accuracy.

Finally, although the sample size was relatively small, it was adequate for detecting significant effects. Larger sample sizes would increase the generalizability of the findings and provide greater statistical power for detecting subtle effects. Additionally, the cross-sectional design limits causal inferences; longitudinal studies tracking individuals as they undertake TC training would be necessary to definitively establish that the observed differences in brain connectivity are caused by the practice itself.

Future research should aim to address these limitations by studying older populations, employing more varied and ecologically valid paradigms, analyzing multiple frequency bands and corticomuscular coupling, utilizing individual head models, and incorporating longitudinal designs.

Conclusions

This study demonstrated that long-term TC practice enhanced postural stability and reorganized cortical connectivity under sensory perturbation. Crucially, this behavioral advantage was accompanied by specific, quantifiable differences in mu-band (8–13 Hz) cortical effective connectivity patterns compared to non-practicing controls. While sensory conflict induced adaptive changes in network efficiency (decreased visual, increased sensorimotor) across both groups, TC practitioners exhibited significantly greater information outflow from the right somatosensory cortex (RS1) and, simultaneously, reduced outflow from the right posterior parietal cortex (RPPC). These complementary adaptations suggest that extensive TC training may foster neuroplastic changes that amplify the utilization of somatosensory information while streamlining parietal integration processes for postural control. The enhanced somatosensory out-strength observed in TC practitioners provides a potential neural substrate underlying their superior balance performance in challenging environments. These results elucidate possible neural mechanisms contributing to the well-documented balance benefits of TC and highlight its potential as an intervention that may promote beneficial central neuroplasticity.

Abbreviations

ANOVA	Analysis of variance
ASR	Artifact subspace reconstruction
COP	Center of pressure
EEG	Electroencephalography
MVAR	Multivariate autoregression
GPDC	Generalized partial directed coherence

MRI	Magnetic resonance imaging
ROIs	Regions of interest
sLORETA	Standardized low-resolution brain electromagnetic tomography
TC	Tai chi
VR	Virtual reality

Acknowledgements
The authors would like to thank the participants for supporting our study and the students for helping with data collection.

Author contributions
GZW: Writing–original draft, Writing–review & editing, Conceptualization, Data curation, Methodology, and Visualization. XXL: Writing–original draft, Writing–review & editing, Software, Methodology, Formal analysis, and Visualization. YMC: Writing–review & editing, Investigation, and Data curation. JW: Writing–review & editing and Resources. YG: Writing–review & editing, Conceptualization, Investigation, Methodology, and Resources. JL: Writing–review & editing, Conceptualization, Investigation, Methodology, Supervision, Project.

Funding
This research was funded by the Zhejiang Provincial Medical and Health Science Research Fund Committee, grant number WKJ-ZJ-2334. Funding was also provided by the National Defense Foundation Strengthening Program Technology Field Fund Project of China (2021-JCJQ-JJ-1029) and the Key Research and Development Program of Zhejiang Province (Grant No. 2025C01135).

Data availability
The datasets used and/or analyzed during the current study available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
The study was approved by the Ethics Committee of Zhejiang University Psychological Science Research Center (2024.011). The study procedures were thoroughly explained to all individuals, and written informed consent was obtained prior to participation.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

Author details
[1]Taizhou Key Laboratory of Medical Devices and Advanced Materials, Taizhou Institute of Zhejiang University, Taizhou 318000, China
[2]Key Laboratory for Biomedical Engineering of Ministry of Education, College of Biomedical Engineering & Instrument Science, Zhejiang University, 866 Yuhangtang Road, Hangzhou 310058, China
[3]Department of Sports Science, College of Education, Zhejiang University, Hangzhou 310058, China
[4]Center for Psychological Science, Zhejiang University, Hangzhou 310058, China

Received: 26 August 2024 / Accepted: 13 May 2025
Published online: 28 May 2025

References

1. Kandel ER, Schwartz JH, Jessell TM, Siegelbaum S, Hudspeth AJ, Mack S. Principles of neural science: McGraw-hill New York 2000.
2. Horak FB. Postural orientation and equilibrium: what do we need to know about neural control of balance to prevent falls? Age Ageing. 2006;35(suppl2):ii7–11.
3. Li F. Transforming traditional Tai Ji Quan techniques into integrative movement therapy—Tai Ji Quan: moving for better balance. J Sport Health Sci. 2014;3(1):9–15.
4. Wayne PM, Kaptchuk TJ. Challenges inherent to T'ai Chi research: part II—defining the intervention and optimal study design. J Altern Complement Med. 2008;14(2):191–7.
5. Wang C, Schmid CH, Rones R, Kalish R, Yinh J, Goldenberg DL, et al. A randomized trial of Tai Chi for fibromyalgia. New Engl J Med. 2010;363(8):743–54.
6. Hu X, Lai Z, Wang L. Effects of Taichi exercise on knee and ankle proprioception among individuals with knee osteoarthritis. Res Sports Med. 2020;28(2):268–78.
7. Courel-Ibáñez J, Buendía-Romero Á, Pallarés JG, García-Conesa S, Martínez-Cava A, Izquierdo M. Impact of tailored multicomponent exercise for preventing weakness and falls on nursing home residents' functional capacity. J Am Med Dir Assoc. 2022;23(1):98–104. e3.
8. Li G, Huang P, Cui S-S, Tan Y-Y, He Y-C, Shen X, et al. Mechanisms of motor symptom improvement by long-term Tai Chi training in Parkinson's disease patients. Translational Neurodegeneration. 2022;11(1):6.
9. Li F, Harmer P, Fitzgerald K, Eckstrom E, Akers L, Chou L-S, et al. Effectiveness of a therapeutic Tai Ji Quan intervention vs a multimodal exercise intervention to prevent falls among older adults at high risk of falling: a randomized clinical trial. JAMA Intern Med. 2018;178(10):1301–10.
10. He T, Hu Z. Effects of Tai Chi Chuan on cortical sources of EEG rhythms in the resting state in elderly individuals: a cross-sectional study. NeuroReport. 2022;33(4):180.
11. Hua A, Wang G, Bai J, Hao Z, Liu J, Meng J, et al. Nonlinear dynamics of postural control system under visual-vestibular habituation balance practice: evidence from EEG, EMG and center of pressure signals. Front Hum Neurosci. 2024;18:1371648.
12. Wei GX, Xu T, Fan FM, Dong HM, Zuo XN. Can Taichi reshape the brain?? A brain? morphometry study. PLoS ONE. 2013;8(4):e61038.
13. Lu X, Siu KC, Fu SN, Hui-Chan CWY, Tsang WWN. Effects of Tai Chi training on postural control and cognitive performance while dual tasking– a randomized clinical trial. J Complement Integr Med. 2016;13(2):181–7.
14. Peterson SM, Ferris DP. Group-level cortical and muscular connectivity during perturbations to walking and standing balance. NeuroImage. 2019;198:93–103.
15. Wang G, Yang Y, Wang J, Hao Z, Luo X, Liu J. Dynamic changes of brain networks during standing balance control under visual conflict. Front Neurosci-Switz. 2022;16.
16. Wang G, Yang Y, Dong K, Hua A, Wang J, Liu J. Multisensory conflict impairs Cortico-Muscular network connectivity and postural stability: insights from partial directed coherence analysis. Neurosci Bull. 2024;40(1):79–89.
17. Li L, Zhang M, Chen Y, Wang K, Zhou G, Huang Q. TAGL: Temporal-Guided adaptive graph learning network for coordinated movement classification. IEEE Trans Industr Inf. 2024;20(11):12554–64.
18. Wang X, Li W, Song R, Ao D, Hu H, Li L. Corticomuscular coupling alterations during elbow isometric contraction correlated with clinical scores: an fNIRS-sEMG study in stroke survivors. IEEE Trans Neural Syst Rehabil Eng. 2025;33:696–704.
19. Dong K, Zhang D, Wei Q, Wang G, Chen X, Zhang L et al. An integrated information theory index using multichannel EEG for evaluating various States of consciousness under anesthesia. Comput Biol Med. 2023;153.
20. Liu J, Dong K, Sun Y, Kakkos I, Huang F, Wang G, et al. Progress of brain network studies on anesthesia and consciousness: framework and clinical applications. Engineering. 2021;20:77–95.
21. Friston KJ. Functional and effective connectivity: a review. Brain Connect. 2011;1(1):13–36.
22. Fallani FDV, Costa LF, Rodriguez FA, Astolfi L, Vecchiato G, Toppi J et al. A graph-theoretical approach in brain functional networks. Possible implications in EEG studies. Nonlinear Biomedical Phys. 2010;4(S1).
23. Sabate M, Llanos C, Enriquez E, Rodriguez M. Mu rhythm, visual processing and motor control. Clin Neurophysiol. 2012;123(3):550–7.
24. Huurnink A, Fransz DP, Kingma I, van Dieën JH. Comparison of a laboratory grade force platform with a Nintendo Wii balance board on measurement of postural control in single-leg stance balance tasks. J Biomech. 2013;46(7):1392–5.
25. Leach JM, Mancini M, Peterka RJ, Hayes TL, Horak FB. Validating and calibrating the Nintendo Wii balance board to derive reliable center of pressure measures. Sensors-Basel. 2014;14(10):18244–67.
26. Paillard T, Noe F. Techniques and methods for testing the postural function in healthy and pathological subjects. Biomed Res Int. 2015;2015.
27. Delorme A, Makeig S. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J Neurosci Methods. 2004;134(1):9–21.

28. Chang CY, Hsu SH, Pion-Tonachini L, Jung TP. Evaluation of artifact subspace reconstruction for automatic artifact components removal in Multi-Channel EEG recordings. IEEE Trans Biomed Eng. 2020;67(4):1114–21.
29. Shenoy Handiru V, Alivar A, Hoxha A, Saleh S, Suviseshamuthu ES, Yue GH, et al. Graph-theoretical analysis of EEG functional connectivity during balance perturbation in traumatic brain injury: A pilot study. Hum Brain Mapp. 2021;42(14):4427–47.
30. Artoni F, Fanciullacci C, Bertolucci F, Panarese A, Makeig S, Micera S, et al. Unidirectional brain to muscle connectivity reveals motor cortex control of leg muscles during stereotyped walking. NeuroImage. 2017;159:403–16.
31. Pion-Tonachini L, Kreutz-Delgado K, Makeig S. ICLabel: an automated electroencephalographic independent component classifier, dataset, and website. NeuroImage. 2019;198:181–97.
32. Huang Y, Parra LC, Haufe S. The new York Head—A precise standardized volume conductor model for EEG source localization and tES targeting. NeuroImage. 2016;140:150–62.
33. Pascual-Marqui RD. Standardized low-resolution brain electromagnetic tomography (sLORETA): technical details. Methods Find Exp Clin Pharmacol. 2002;24:5–12. Suppl D(Suppl D).
34. Grech R, Cassar T, Muscat J, Camilleri KP, Vanrumste B. Review on solving the inverse problem in EEG source analysis. J Neuroeng Rehabilitation. 2008;5(1):25.
35. Zilles K, Amunts K. Centenary of Brodmann's map—conception and fate. Nat Rev Neurosci. 2010;11(2):139–45.
36. Delorme A, Mullen T, Kothe C, Acar ZA, Makeig S. EEGLAB, SIFT, NFT, BCILAB, and ERICA: new tools for advanced EEG processing. Comput Intell Neurosci. 2011;2011:1687–5265.
37. Baccala LA, Sameshima K, Takahashi DY, editors. Generalized partial directed coherence. 2007 15th International conference on digital signal processing 2007. Ieee.
38. Akaike H. Citation Classic - a new look at the Statistical-Model identification. Cc/Eng Tech Appl Sci. 1981;51:22.
39. Ding MZ, Bressler SL, Yang WM, Liang HL. Short-window spectral analysis of cortical event-related potentials by adaptive multivariate autoregressive modeling: data preprocessing, model validation, and variability assessment. Biol Cybern. 2000;83(1):35–45.
40. Taylor R. New introduction to multiple time series analysis. Int J Forecast. 2007;23(1):153.
41. Wayne PM, Gow BJ, Costa MD, Peng C-K, Lipsitz LA, Hausdorff JM, et al. Complexity-based measures inform effects of Tai Chi training on standing postural control: cross-sectional and randomized trial studies. PLoS ONE. 2014;9(12):e114731.
42. Domingos C, Pêgo J, Santos N. Effects of physical activity on brain function and structure in older adults: A systematic review. Behav Brain Res. 2021;402:113061.
43. Taubert M, Draganski B, Anwander A, Müller K, Horstmann A, Villringer A, et al. Dynamic properties of human brain structure: learning-related changes in cortical areas and associated fiber connections. J Neurosci. 2010;30(35):11670–7.
44. Song Q, Zhang X, Mao M, Sun W, Zhang C, Chen Y, et al. Relationship of proprioception, cutaneous sensitivity, and muscle strength with the balance control among older adults. Ournal Sport Health Sci. 2021;10(5):585–93.
45. Fetsch CR, Pouget A, DeAngelis GC, Angelaki DE. Neural correlates of reliability-based cue weighting during multisensory integration. Nat Neurosci. 2011;15(1):146–54.
46. Tsang WW, Wong VS, Fu SN, Hui-Chan CW. Tai Chi improves standing balance control under reduced or conflicting sensory conditions. Archives Phys Med Rehabilitation. 2004;85(1):129–37.
47. Tsang WW, Hui-Chan CW. Standing balance after vestibular stimulation in Tai Chi–practicing and nonpracticing healthy older adults. Archives Phys Med Rehabilitation. 2006;87(4):546–53.
48. Cui J, Hao Z, Tian H, Yang Y, Wang J, Lin X. The effects of Tai Chi on standing balance control in older adults May be attributed to the improvement of sensory reweighting and complexity rather than reduced sway velocity or amplitude. Front Aging Neurosci. 2024;16:1330063.

Publisher's note