

RESEARCH ARTICLE

Long-term musical training induces white matter plasticity in emotion and language networks

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Abstract

Numerous studies have reported that long-term musical training can affect brain functionality and induce structural alterations in the brain. Singing is a form of vocal musical expression with an unparalleled capacity for communicating emotion; however, there has been relatively little research on neuroplasticity at the network level in vocalists (i.e., noninstrumental musicians). Our objective in this study was to elucidate changes in the neural network architecture following long-term training in the musical arts. We employed a framework based on graph theory to depict the connectivity and efficiency of structural networks in the brain, based on diffusion-weighted images obtained from 35 vocalists, 27 pianists, and 33 nonmusicians. Our results revealed that musical training (both voice and piano) could enhance connectivity among emotion-related regions of the brain, such as the amygdala. We also discovered that voice training reshaped the architecture of experience-dependent networks, such as those involved in vocal motor control, sensory feedback, and language processing. It appears that vocal-related changes in areas such as the insula, paracentral lobule, supramarginal gyrus, and putamen are associated with functional segregation, multisensory integration, and enhanced network interconnectivity. These results

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suggest that long-term musical training can strengthen or prune white matter connectivity networks in an experience-dependent manner.

KEYWORDS

brain asymmetry, emotion, graph theory, language, structural connectivity, vocal training

1 | INTRODUCTION

Intensive musical training has been widely studied, due to its ability to induce structural neuroplasticity in brain regions associated with perception, motor control, and cognitive functions (Foster & Zatorre, 2010; Groussard et al., 2014; Habibi et al., 2018; Hyde et al., 2009; Miendlarzewska & Trost, 2013; Schmithorst & Wilke, 2002; Shenker et al., 2021; Wang et al., 2019). Emerging neuroimaging evidence has revealed a strong relationship between structural connectivity and long-term training in various instrumental musicians (Dhakal et al., 2021; Elmer et al., 2016; Jancke et al., 2012; Li et al., 2014). Most previous studies reported local changes in the architecture of white matter, such as microstructural changes in the fiber tract organization in various regions of the brain. However, little is known about how the topological properties of brain networks in noninstrumental musicians are changed after long-term training. In this work, we adopted graph theory measurements to characterize the architectures of structural brain networks in musicians after long-term vocal training (Leipold et al., 2021; Li et al., 2014).

The neuroplasticity patterns presented by musicians differ according to the specifics of their musical training (Barrett et al., 2013). Among the variety of musical training, singing is the most important form of musical expression, as it is an innate ability (Knight, 1999; Nettle, 2015) and universal human activity (Lomax, 2017). Singing is also distinct in that practitioners use their bodies as an instrument (Zarate, 2013). One previous brain imaging study reported that long-term vocal training enhances structural connectivity between widespread brain regions related to sound perception, sound production, and kinesthetic motor control (Halwani et al., 2011). They also reported increased leftward asymmetry in white matter tracts related to language learning (e.g., arcuate fasciculus) in singers. However, there has been relatively little research on structural network architectures altered by vocal training.

The means by which musicians convey emotion in music also vary, depending on the specifics of musical training. For example, instrumental musicians exploit a set of skills to translate their finger touches and body movements into emotional intentions. Singers manipulate acoustic parameters (e.g., tempo, pitch, and phonation) in the singing voice for emotion expression (Juslin & Laukka, 2003; Scherer, 2003). Professional singers express anger through the use of vibrato, sadness by the absence of vibrato at a slow tempo with low voice intensity, and fear by the presence of steep spectral slope (Jansens et al., 1997). One recent study using multiple discriminant analysis demonstrated robust vocal signatures in the interpretation and expression of emotional content by professional opera singers

(Scherer et al., 2017). The authors reported that the acoustic parameters of anger and joy can both be characterized by high levels of loudness, vocal dynamics, and perturbation variation. Singers might utilize a motor system that is intrinsically linked to innate emotional expression, and then develop volitional control over emotional vocalization in the context of speech motor control. In the current study, we hypothesized that the intensive musical practice that involves the interpretation of emotions could strengthen the connectivity between brain regions related to emotional expression and motor control. We also speculated that this connectivity would differ between professional singers and instrumental musicians.

Graph theory has been widely used to characterize the architecture of networks in human brains (Bassett & Bullmore, 2006; Loui et al., 2011; Rubinov & Sporns, 2010; Sporns, 2014, 2016). Graph theory metrics used to measure the organization of networks can be divided into local (regional) and global. Regional metrics included strength centrality (SC), betweenness centrality (BC), and local efficiency (LE). Strength centrality reflects the correlation between one region and the others. Betweenness centrality measures the importance of nodes to overall network integrity (Brandes, 2001; Kintali, 2008), which has been defined as the fraction of all shortest paths passing through a given node in the network (Rubinov & Sporns, 2010). Local efficiency measures the fault tolerance of a system, as an indication of communication efficiency between the direct neighbors of a node (Latora & Marchiori, 2001). Global metrics included density, global efficiency, mean local efficiency, mean clustering coefficient, characteristic path length, mean betweenness centrality, and transitivity (Rubinov & Sporns, 2010). Global efficiency measures network integration, indicating the ability to transmit information across the whole brain (Achard & Bullmore, 2007; Estrada & Hatano, 2008). Mean local efficiency measures the mean communication efficiency of the whole brain. These metrics describe the importance of brain regions, the efficiency of information transfer among brain regions, and the integration and segregation of specific brain networks.

In this study, we adopted the graph theory framework and diffusion-weighted images to identify changes in structural networks in the brain after long-term musical training. We recruited vocalists, instrumental musicians, and nonmusicians to elucidate the effects of long-term vocal training on the architecture of white matter networks. Note that most vocalists received long-term piano training before maturation of the voice during adolescence (Gackle, 2019; Williams & Harrison, 2019). Unlike vocalists, pianists are required to replay long motor sequences rapidly using both hands, which relies on the precise retrieval of motor memory functions (Heun et al., 2004; Landau &

D'Esposito, 2006). A functional activation study showed that pianists had greater rightward asymmetry activity in several regions related to motor sequence learning (Landau & D'Esposito, 2006). In contrast, singers exhibited left lateralization in the white matter tracts associated with language learning (Halwani et al., 2011). Here, we hypothesized that long-term vocal training would strengthen connectivity and network efficiency among brain regions related to auditory-motor control, sensory feedback, and emotion expression. We also speculated that vocalists would exhibit leftward asymmetry in language-related areas, as a result of intensive singing exercises.

2 | MATERIALS AND METHODS

2.1 | Participants

We initially recruited 100 right-handed participants (age range: 20–40); however, 5 participants were excluded due to signal loss in their diffusion-weighted images. This resulted in 95 participants overall, which included 35 vocalists (V; male = 5), 27 pianists (P; male = 6), and 33 nonmusician control participants (C; male = 6). The musicians were college students or graduates who majored in vocal or piano performance. Control participants were nonmusicians who were mainly college students majoring in liberal arts. In the vocalist group, the mean vocal training was 7.68 ± 3.1 years, involving 13.4 ± 7.1 training hours per week. In the pianist group, the mean piano training was 16.22 ± 2.2 years, involving 21.3 ± 7.5 training hours per week.

2.2 | MRI data acquisition

All MRI images were acquired using a 3-Tesla scanner (MAGNETOM Trio, A Tim System; Siemens Medical Solution, Erlangen, Germany) with a 32-channel head coil. Diffusion spectrum images (DSIs) were obtained using spin-echo diffusion echo-planar imaging sequence (EPI) with the following parameters: repetition time (TR) = 9700 ms, echo time (TE) = 136 ms, 56 axial slices, field of view (FOV) = 200×200 mm², matrix size = 80×80 , and slice thickness = 2.5 mm. The diffusion acquisition scheme comprised 102 diffusion-encoding directions (Chen et al., 2015). A diffusion spectrum imaging (DSI) dataset consisted of 101 DWIs with variable *b*-values ($b_{\max} = 4000$ s/mm²; 16 distinct *b*-values in the present study) and a *b*₀ volume image (Hsu et al., 2015). The acquisition scheme was modified from the DSI203 scheme (Kuo et al., 2008). The volume image in the DSI dataset corresponded to 102 isotopic grid points in *q*-space (Wedeen et al., 2005). High resolution T1-weighted images were acquired using three-dimensional magnetization-prepared rapid gradient echo (3D-MPRAGE) sequence with the following parameters: TR = 2530 ms, TE = 3.03 ms, 192 axial slices, flip angle = 7°, FOV = 224×256 mm², matrix size = 224×256 , and slice thickness = 1 mm.

2.3 | Image processing and analysis

To ensure image quality, diffusion-weighted images were inspected visually to verify that they were unaffected by significant signal dropout due to head motion, which is a common practice for DWI pretreatment (Chen et al., 2015). For the datasets with signal loss, the images that could not be recovered by subsequent image processing were discarded (Chen et al., 2015). Hence, each image in our data was visually scrutinized, and datasets with more than three axial slices of signal loss were discarded. DWIs also underwent denoising using MRtrix3 (<http://www.mrtrix.org/>) to improve the signal-to-noise ratio and reduce scanning artifacts (Veraart et al., 2016). The brain area was extracted from T1-weighted images and DWIs using BET package in FSL (<http://fsl.fmrib.ox.ac.uk>). Both the T1-weighted and DWIs were normalized to the standard Montreal Neurological Institute (MNI) space by the following steps: (1) The *b*₀ images were co-registered to individual T1-weighted images; (2) The T1-weighted image was normalized to the standard MNI space; (3) The deformation field from step (1) and (2) was applied to DWI data in the standard MNI space. For the measurement of network characteristics, the Automated Anatomical Labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002) was applied to individual DWIs using the same inverse deformation field.

Reconstruction of the orientation distribution function (ODF) and whole-brain fiber tracking were performed using DSI Studio with optimized parameter settings (Yeh et al., 2013). Generalized fractional anisotropy (GFA) was computed for each voxel. A maximum of 1,000,000 streamlines were reconstructed for each individual using deterministic tractography and the standard protocol with the following parameters: step size (1.1 mm), fiber length (range: 20–500 mm), quantitative anisotropy threshold (0.01–0.10), turning angle threshold (60°), and smoothing (20%). Redundant streamlines at a Hausdorff distance of less than 1 mm were then removed (Fernandez-Miranda et al., 2015; Yeh et al., 2010, 2013, 2018).

2.4 | Measurement of structural network characteristics

Brain networks were analyzed using graph-based information related to structural connectivity. This involved defining 90 nodes ($N = 90$) involving whole-brain structural connectivity using the AAL atlas without cerebellar regions. The weight of the edge between each pair of nodes was estimated by calculating the total number of end-to-end streamlines. Connectivity matrix measurements were calculated using the Brain Connectivity Toolbox (BCT) as indices of the topological properties of the networks (Rubinov & Sporns, 2010).

We constructed anatomical brain networks for each subject and calculated the properties using weighted networks. The number of streamlines was converted to edge weights, w_{ij} , for subsequent analysis using the following equation:

Edge weights (w_{ij}) = $m_{ij} \div \text{Max}(M_k) \times 100$,

where M_k is the $N \times N$ connectivity matrix of the k th participant and m_{ij} is the number of streamlines between node i and node j in M_k .

The degree of an individual node (indicating the importance of the node in the network) represents the number of edges connected to other nodes in this network (Rubinov & Sporns, 2010). Density was defined as the mean degree of the entire network.

The effects of musical training on structural connectivity were detected by computing the following local (regional) and global network metrics. The regional metrics included strength centrality, betweenness centrality, and local efficiency. Strength centrality of node i , S_i , was defined as the summation of all neighboring edge weights, as follows:

$$\text{Strength centrality } (S_i) = \sum_{j \in N, j \neq i} W_{ij}. \quad (1)$$

Betweenness centrality measures the importance of nodes to overall network integrity (Brandes, 2001; Kintali, 2008), which has been defined as the fraction of all shortest paths in the network passing through a given node (Rubinov & Sporns, 2010), written as follows:

$$\text{Betweenness centrality } (b_i) = \frac{1}{(N-1)(N-2)} \sum_{h,j \in N, h \neq i, j \neq i} \frac{\rho_{hj(i)}}{\rho_{hj}},$$

where $\rho_{hj(i)}$ is the number of shortest paths between node h and node j passing through node i , and ρ_{hj} is the shortest path number between node h and node j .

Local efficiency of node i , $E_{loc,i}$, was defined as follows:

$$E_{loc,i} = \frac{1}{S_i(S_i-1)} \sum_{j,h \in N, j \neq i, h \neq i} (w_{ij}w_{jh} [d_{jh}(N_i)]^{-1})^{1/3},$$

where $d_{jh}(N_i)$ is the length of the shortest path between node j and node h containing only neighbors of node i . This metric measures the level of system fault tolerance, as an indication of communication efficiency between the first neighbors of node i , when node i is removed (Latora & Marchiori, 2001).

The global metrics included density, global efficiency, mean local efficiency, mean clustering coefficient, characteristic path length, mean betweenness centrality, and transitivity (for more details, see Rubinov & Sporns, 2010).

Global efficiency, E_{glob} , was the average of $E_{glob,i}$ (Latora & Marchiori, 2001):

$$E_{glob} = \frac{1}{N} \sum_{i \in N} E_{glob,i} = \frac{1}{N} \sum_{i \in N} \frac{\sum_{j \in N, j \neq i} (d_{ij})^{-1}}{N-1},$$

where $E_{glob,i}$ was the average of the value inversely proportional to d_{ij} , the shortest distance between node i and node j , $\forall i, j$. Global efficiency is a measurement of network integration, indicating the ability to transmit information across the whole brain (Achard & Bullmore, 2007; Estrada & Hatano, 2008).

Mean local efficiency of the whole brain, E_{loc} , was defined as follows:

$$E_{loc} = \frac{1}{N} \sum_{i \in N} E_{loc,i}.$$

The above-mentioned global network metrics were also calculated separately in the right and left hemispheres. We utilized the local (regional) lateralization measure with the strength asymmetry index to compare connectivity strength between the two hemispheres in each region of the brain (Catani et al., 2007):

$$\text{Strength asymmetry } (SA_j) = \frac{S_{j,LH} - S_{j,RH}}{S_{j,LH} + S_{j,RH}},$$

where $S_{j,LH}$ and $S_{j,RH}$, respectively, represent the strength centrality of the left and right hemispheres in brain region j , as defined in Equation (1).

2.5 | Statistical analysis

Statistical analyses were performed using SPSS 21 (IBM Corp., Armonk, NY; Version 21) and MATLAB (Mathworks, Natick, MA; version 9). In the demographic characteristics, two-sample t -tests were used to compare continuous variables and chi-square tests were used to compare nominal variables. The difference of connectivity matrices among the three groups was tested with network-based statistic (NBS; Zalesky et al., 2010) for the local changes before graph-theoretical measurement. NBS controls for the family-wise error rate (in a weak sense) when mass-univariate testing is performed on all the connections in the graph. Differences in the number of streamlines and network metrics among the three groups were assessed with one-way Kruskal-Wallis tests ($p < .05$) followed by post hoc independent sample permutation tests (iterations = 10,000 iterations) ($p < .05$, corrected) using the t_{\max} method (Blair & Karniski, 1993), which adjusts the p -values of each variable for multiple comparisons (i.e., the number of nodes [$n = 90$]) and strongly controls the family wise error-rate (FWE) (Blair & Karniski, 1993; Westfall & Young, 1993). Results were visualized with BrainNet Viewer (Xia et al., 2013). The Spearman correlation coefficient was used to estimate the association between accumulated vocal training duration and the network metrics, with the level of significance set at $\alpha = 0.05$.

3 | RESULTS

3.1 | Demographic characteristics

The pianists (P) in this study were significantly younger than the vocalists (V) and nonmusicians (C) (P, 21.7 ± 1.4 years; V, 23.0 ± 2.3 years; C, 23.0 ± 1.7 years; $p < .05$; Table 1). There were no significant differences among the three groups in terms of gender or

TABLE 1 Demographic characteristics among the three groups

	Vocalists (N = 35)	Pianists (N = 27)	Nonmusicians (N = 33)
Age (years)	23.0 (2.3)*	21.7 (1.4)##	23.0 (1.7)
Gender (F/M)	30/5	21/6	27/6
Education (years)	16.5 (1.6)	15.7 (1.0)	16.1 (1.1)
Vocal training duration (years)	7.68 (3.1)**	0.67 (1.4)	-
Piano training duration (years)	15.0 (4.2)	16.22 (2.1)	-
Right-handedness	74.3 (28.3)	83.3 (26.0)	80.1 (18.6)

Note: Values are presented as mean (SD). * $p < .05$, ** $p < .01$, vocalist vs. pianists; ## $p < .01$, pianist vs. nonmusicians; two-sample t-test.

Abbreviations: F, females; M, males; SD, standard deviation.

handedness. In terms of vocal training history, vocalists had undergone training significantly longer than pianists (V, 7.68 ± 3.1 years; P, 0.67 ± 1.4 ; $p < .01$). The duration of piano training was not different between musician groups (V, 15.0 ± 4.2 years; P, 16.22 ± 2.1 years).

3.2 | Local structural connectivity

The results of NBS analysis showed no significant differences in the connectivity matrices among the three groups.

3.3 | Global network metrics

There were no significant differences in the summation of whole-brain streamlines or network metrics among the three groups (Figure S1, Table S1, and Figure 1a).

Compared to nonmusicians, vocalists exhibited significantly higher network density in structural networks in the left hemisphere (Figure 1b and Table S2). Compared to pianists, vocalists exhibited significantly higher density in the left hemisphere and lower global efficiency in the right hemisphere (Figure 1b,c, and Table S2).

3.4 | Local (regional) metrics

3.4.1 | Strength centrality

SC in the left amygdala was significantly higher in both musician groups (vocalists and pianists) than in the nonmusician group (Figure 2 and Table S3). Comparing vocalists versus nonmusicians, vocalists exhibited significantly higher SC in the left amygdala and significantly lower SC in the left paracentral lobule (PCL). Comparing pianists versus nonmusicians, pianists exhibited significantly higher SC in the left amygdala. Comparing vocalists versus pianists, pianists exhibited significantly lower SC in the right pallidum. The upper panel in Figure S2 presents a map of mean whole-brain SC values from the entire study cohort.

3.4.2 | Betweenness centrality

Comparing vocalists versus nonmusicians, vocalists exhibited significantly lower BC in the left middle temporal gyrus (MTG) (Figure S3). There were no significant differences between pianists and nonmusicians. Comparing vocalists versus pianists, vocalists exhibited significantly lower BC in the left MTG while pianists exhibited significantly higher BC in the left inferior temporal gyrus (ITG), right precuneus, and cuneus. The lower panel in Figure S2 presents a map of mean whole-brain BC values from the entire study cohort.

3.4.3 | Local efficiency

Comparing vocalists versus nonmusicians, vocalists exhibited significantly lower LE in the left supramarginal gyrus (SMG), PCL, right middle frontal gyrus (MFG), and insula (Figure 3 and Table S4). There were no significant differences between pianists and nonmusicians. Comparing vocalists versus pianists, vocalists exhibited significantly lower LE in the left SMG and right MFG whereas pianists exhibited significantly higher LE in the right SMG.

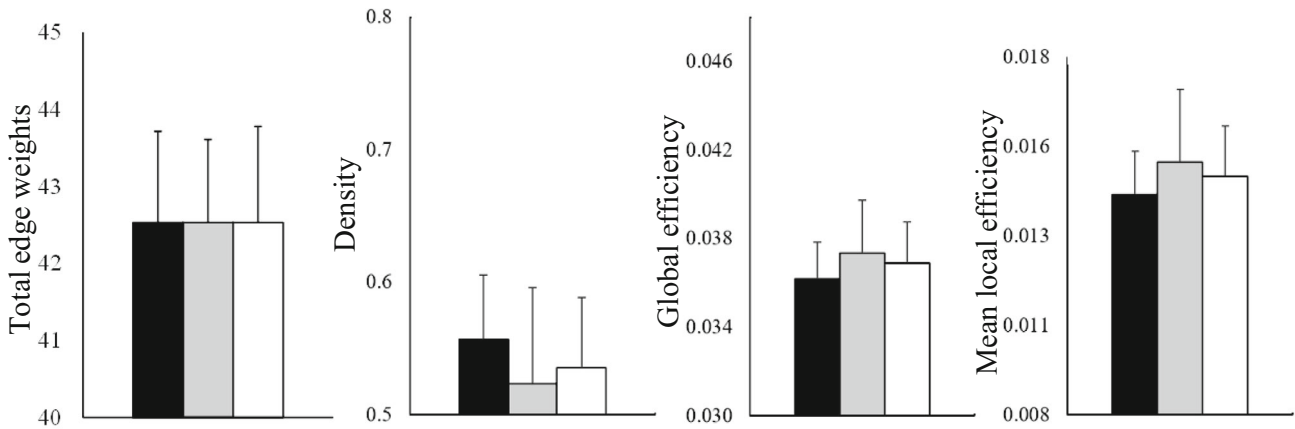
3.4.4 | Strength asymmetry

We observed significant differences between vocalists and pianists in terms of strength asymmetry (SA) scores in the putamen (Figure 4 and Table S5).

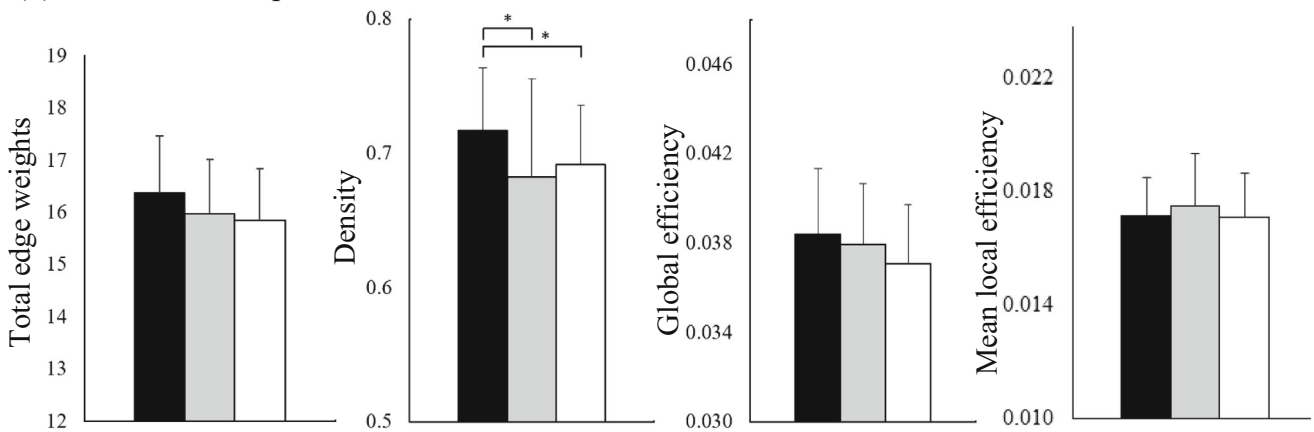
3.5 | Network metrics-behavior associations

Significant correlations were observed between the duration of vocal training and the network metrics (Table 2). In terms of global network metrics, we observed a significant positive correlation between the duration of vocal training and network density in the left hemisphere. Significantly negative correlations were observed between the duration of vocal training and the local efficiency of local metrics in the left SMG and right MFG.

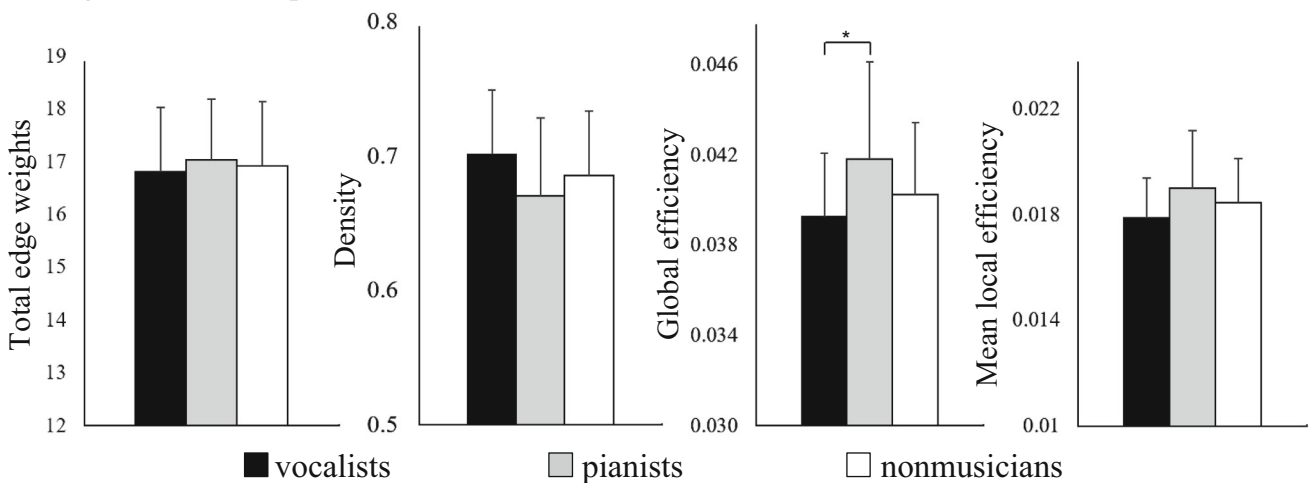
(a) whole brain



(b) left intra-hemisphere



(c) right intra-hemisphere



■ vocalists ■ pianists □ nonmusicians

FIGURE 1 Network measurement in the whole brain (a), left intra-hemisphere (b), and right intra-hemisphere (c). Kruskal-Wallis tests revealed significant group differences in terms of density in the left hemisphere ($H(2) = 8.116, p = .017$) and global efficiency in the right hemisphere ($H(2) = 6.686, p = .035$). (*FWE-corrected $p < .05$; post hoc permutation test using 10,000 iterations)

4 | DISCUSSION

In the current study, graph theory was used to explore the organization of white matter following long-term vocal training. Our results

revealed that long-term vocal training modified the organization of structural networks in both global and local (nodal) facets. Compared with nonmusicians, vocalists exhibited higher density in the left hemisphere (global network metrics). Compared with pianists, vocalists

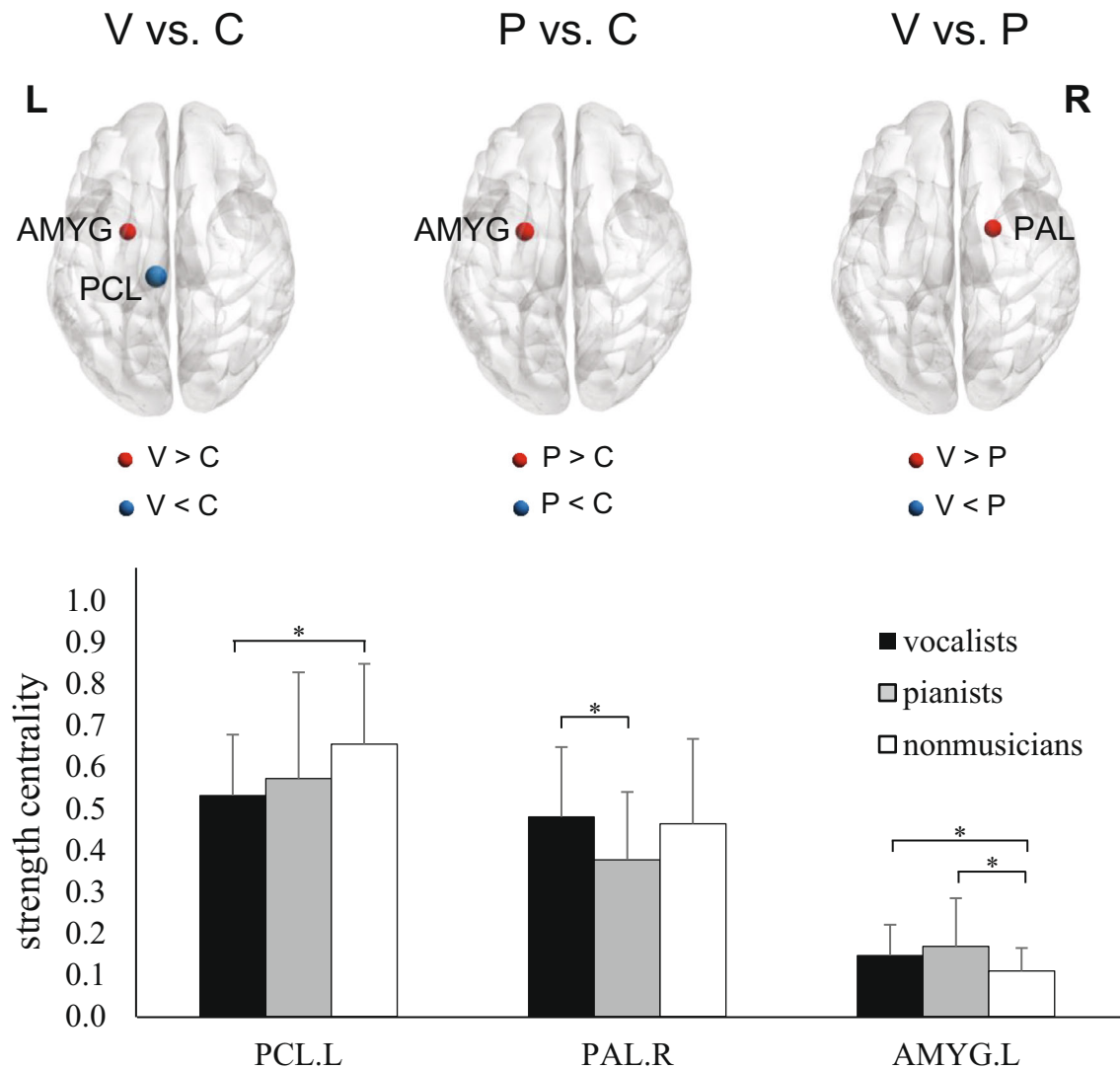


FIGURE 2 Comparison of strength centrality among the three groups. Note that the size of the sphere indicates the degree of statistical significance between the results from the two groups. The Kruskal-Wallis tests revealed significant group differences in the left paracentral lobule (PCL; $H(2) = 10.135, p = .006$), right pallidum (PAL; $H(2) = 6.23, p = .044$), and left amygdala (AMYG; $H(2) = 6.699, p = .035$). P, pianists; V, vocalists; C, nonmusicians; L, left; R, right (*FWE-corrected $p < .05$; post hoc permutation test using 10,000 iterations)

exhibited higher density in the left hemispheres, but lower global efficiency in the right hemisphere. Compared with nonmusicians, both vocalists and pianists showed enhanced strength centrality in emotion-related regions of the brain (local network metrics). These findings provided neuroimaging evidence of the piano- and vocal-related effects of long-term musical training on brain networks related to emotion processing, singing performance, and language functions.

4.1 | Changes in global network organization

4.1.1 | Vocalists versus nonmusicians

Compared to nonmusicians, vocalists presented higher network density in structural networks in the left hemisphere. Prior

research in vocalists reported changes in the microstructure of white matter related to language and semantic memory (Ashtari et al., 2007; Halwani et al., 2011). Of note, singing requires proficiency in language processing, which is lateralized to the left hemisphere, particularly in the right-handed (Knecht et al., 2000). Moreover, previous studies found that long-term musical training significantly enhances not only verbal function but also visual-spatial and mathematical performance (Schlaug et al., 2005). Our results of higher network density in vocalists are indications of enhanced interconnectivity between brain regions in the left hemisphere. Our results also revealed an association between the duration of vocal training and network density in the left hemisphere, suggesting that the characteristics of long-term vocal training may play a role in shaping the architecture of structural networks in the left hemisphere.

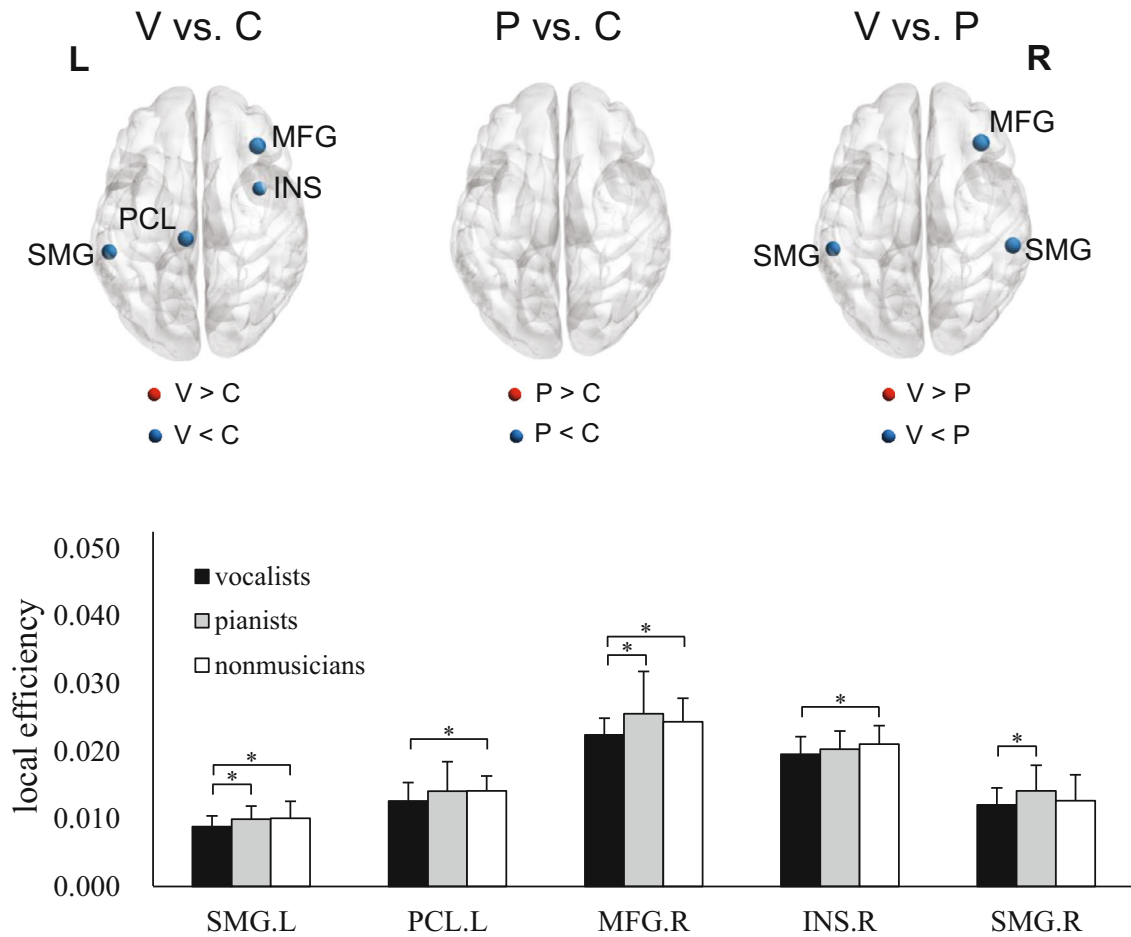


FIGURE 3 Comparison of local efficiency among the three groups. Note that the size of the sphere indicates the degree of statistical significance between the results from the two groups. Kruskal-Wallis tests exhibited significant group differences in the left supramarginal gyrus (SMG; $H(2) = 6.596, p = .037$), left paracentral lobule (PCL; $H(2) = 7.309, p = .026$), right middle frontal gyrus (MFG; $H(2) = 6.565, p = .038$), right insula (INS; $H(2) = 6.144, p = .046$), and right supramarginal gyrus ($H(2) = 7.873, p = .020$). P, pianists; V, vocalists; C, nonmusicians; L, left; R, right (*FWE-corrected $p < .05$; post hoc permutation test using 10,000 iterations)

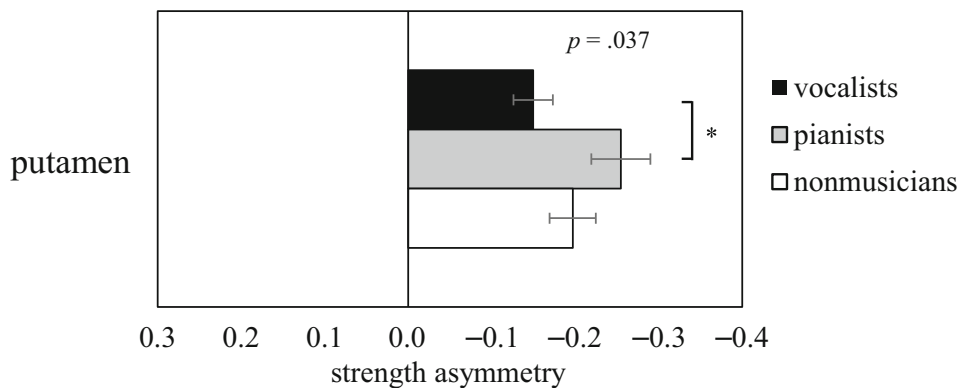


FIGURE 4 Comparison of regional strength asymmetry $(L - R)/(L + R)$ among the three groups ($H(2) = 6.59, p = .037$ for one-way Kruskal-Wallis test; *FWE-corrected $p < .05$; post hoc permutation test using 10,000 iterations)

4.1.2 | Vocalists versus pianists

Different types of musical training may differ in the way that they shape cognitive and sensory functions, in accordance with the specific demands imposed by practice (Pantev et al., 2001; Slater et al., 2017). One recent study reported that the ability to

discriminate between auditory acoustic features varies according to the type of musical training (Slater et al., 2017). Compared with pianists, vocalists exhibited higher density in the left hemisphere and lower global efficiency in the right hemisphere. In comparison to piano performance, singing requires more language processing, which may cause the enhancement of network density in the left

TABLE 2 Correlation between the duration of vocal training and network metrics

Network metrics	Region	Correlation coefficient	p-value
Global metric			
Density	Left hemisphere	0.287	.005
Local metric			
Local efficiency	Left supramarginal gyrus	−0.247	.016
	Right middle frontal gyrus	−0.209	.042

hemisphere, as stated above. Our findings in which vocalists have higher density in the left hemisphere than nonmusician and pianists indicate that the topological organization of brain networks could be shaped in a vocal-specific manner. Unlike singers, pianists exhibited higher global efficiency only in the right hemisphere. Thus, it appears that in terms of brain networks, the main difference between pianists and singers may lie in the motor control of the muscle groups used for performing. Piano playing requires precise control of finger muscles, whereas singing requires fine motor control of phonatory muscles (e.g., vocalization, respiration, swallowing, and airway protection). The fact that pianists use left-hand motor control in the right hemisphere far more frequently than do singers may explain the higher global efficiency in the right hemisphere (Bangert & Schlaug, 2006). Note that most vocalists underwent training in piano prior to their vocal training; however, they did not exhibit rightward asymmetry. We therefore speculate that this asymmetry may undergo a reversal after they take up vocal training. Thus, it is reasonable to expect that long-term piano training could enhance the transfer of information within the right hemisphere. Taken together, our findings indicate that the specific characteristics of musical training (e.g., noninstrumental vs. instrumental) result in different topological characteristics in the subnetwork organization. This is a clear indication of neuroplastic network organization following long-term training in specific musical disciplines.

4.2 | Changes in local network metrics

Different types of musical training differ in the way they affect changes in the organization of local networks related to specific musical skills. For example, vocalists exhibit low local efficiency in the vocal motor control network and left asymmetry in the linguistic network. Furthermore, the rostral SMG contributes significantly to singing performance in trained singers (Kort et al., 2016). Our comparison of vocalists and pianists in terms of local efficiency suggests that professional training reshapes the network organization of the SMG and MFG. Researchers have reported a correlation between SMG activation and speech production (Bilodeau-Mercure et al., 2015; Tremblay & Deschamps, 2016), and changes in the SMG volume can be predicted based on the age at which formal vocal training began (Kort et al., 2016). Taken together, it appears that vocalists and pianists differ in terms of the structure and function of SMG networks. It also appears that the effects of musical training could conceivably be investigated using network metrics.

4.2.1 | Enhanced strength centrality in the emotion-processing networks of musicians

Musical training (instrumental and noninstrumental) involves learning how to evaluate and comprehend the emotions behind music and lyrics, which may promote interactions between brain regions related to the processing of emotion-related information (Fruhholz et al., 2014). The intensive practice required to achieve proficiency would help strengthen and reorganize connections among the relevant neural networks. The amygdala, a core region of the limbic network, plays a key role in the processing of affective information obtained from external stimuli (Wiethoff et al., 2009) and the formation of experience-dependent emotional memory (Vaquero et al., 2016). Our discovery of enhanced strength centrality in the left amygdala of vocalists and pianists indicates a high degree of interconnectivity between the left amygdala and other brain regions. We speculate that frequent practice in extracting the emotional value from music sculpts the local neuronal organization of limbic structures and emotion processing. This suggests that musical training, at least piano training, has effects on experience-dependent neuroplasticity in amygdala-centered networks, which is a generic function while performing musical arts.

4.2.2 | Lower local efficiency in vocal motor control network of vocalists

The networks involved in vocal motor control and the processing of sensory feedback are crucial to maintaining precise control over the muscles used for singing (Kleber et al., 2007; Zarate, 2013). The right anterior insula, a key node in the “singing network”, regulates the integration of saliency signals and somatosensory signals during vocal production, and could therefore be modulated by vocal training (Kleber et al., 2017). The SMA, another core node in the singing network, integrates motor, visuospatial, semantic, and socio-emotional information required for ongoing music performance (Tanaka & Kirino, 2017), which is essential for singing. In the current study, vocalists presented significantly lower local efficiency in the right insula and weak-significantly lower efficiency in the left SMA ($p = .083$). A decrease in local efficiency such as this may indicate a systematic pruning of task-irrelevant connections to strengthen functional segregation while performing cognitively demanding tasks under limited resources (Cohen & D'Esposito, 2016; Sporns, 2013). Microstructural and morphological changes in white matter occurred during professional training and brain development. Decreased local

efficiency may be associated with the pruning of small white matter fibers and the enhancement of major tracts during development (Huang et al., 2015). Our discovery of lower local efficiency in the insula and SMA of vocalists suggests that specific musical training (i.e., vocal training) may reshape structural connectivity and the organization of experience-dependent networks (i.e., the singing network) by promoting functional segregation and multisensory integration for the performance of vocal-related skills.

Singing heavily relies on the control of breathing, regulation of air-flow, and maintenance of posture. The muscles of the pelvic floor play an essential role in generating intra-abdominal pressure, supporting breathing, maintaining the optimal posture of singing, and modulating subglottal pressure; thus, all of which affect phonation and singing (Emerich Gordon & Reed, 2020). Previous reports have shown that the paracentral lobule is associated with the muscle control of toes, feet, and pelvic floor (Asavasopon et al., 2014; Patra et al., 2021). In our study, we found lower local efficiency and strength centrality in the left paracentral lobule in vocalists compared with nonmusicians. Lower local efficiency denotes lower connections among neighboring brain regions, and lower strength centrality represents a lower degree of interconnectivity between the left paracentral lobule and all other brain regions. Taken together, these findings suggest that the paracentral lobule might lose connections with neighboring brain regions, implying that the control of pelvic floor muscles might be centralized in the paracentral lobule without synergistic work with other brain regions.

The regulation of vocal pitch is another crucial skill in singing, particularly when demonstrating examples of skillful phonation and conveying affective information in experienced singers (Zarate & Zatorre, 2008). Vocal pitch control is conducted in three stages: detecting prediction error, coordinating motor changes, and detecting sensory consequences of that action (Kort et al., 2016). Multiple brain regions, including the left auditory cortex, right inferior parietal cortex, and inferior/middle frontal gyrus, are involved in the auditory error detection and auditory feedback control of pitch production (Kort et al., 2016). In line with previous research, the local efficiency of vocalists in this study was lower than that of pianists in multiple brain regions, including the right MFG, SMG, and left Heschl gyrus (lower but not statistically significant; $p = .065$). Lower local efficiency is an indication of network pruning to promote functional segregation. One previous animal study reported that the learning of novel motor experiences can mediate the structural adaptation of selective neural populations associated with a specific function (Wang et al., 2011). Thus, our findings suggest that the intensive practice of singing skills may increase resource usage in brain regions related to vocal pitch control and shape the architecture of circuits involved in the regulation of vocal pitch by strengthening functional segregation for error detection and feedback control.

4.2.3 | Hemispheric asymmetry changes—leftward asymmetry of strength centrality in language network of vocalists

Singers may develop expertise in linguistic expression due to not only musical training but also language training. The repertoire of nearly all

singers includes lyrics in a foreign language, the learning of which may promote the development of language skills via cross-domain transfer effects (Larrouy-Maestri et al., 2013). Previous evidence has shown that musical training can have positive effects on foreign language processing (Kolinsky et al., 2009) and linguistic tonal processing (Marie et al., 2011). This suggests that the linguistic expression of singers may benefit from vocal training and language courses. The left thalamus has been reported to be involved in the motor-sensory processing of human vocalization for music and language (Brown et al., 2006). Furthermore, the left putamen is related to the articulation and motor planning of multilingual speech (Abutalebi et al., 2013). Our discovery that vocalists present leftward asymmetry in strength centrality in the subcortical regions of the brain (putamen and thalamus, though not statistically significant in the thalamus; $p = .054$) indicates that intensive practice of multilingual pronunciation may enhance the efficiency of information transfer among related brain regions. This also suggests that multilingual pronunciation exercises may help to develop subcortical brain networks involved in monitoring articulatory processes.

4.3 | Limitations

The present study has some limitations that should be considered. First, our nodal connectivity analysis focused on how vocal experiences sculpt the connectivity strength and efficiency of information transfer. We did not exploit all graph theory measurements in our derivation of nodal measurements. Second, we were unable to determine whether changes in the organization of structural networks in musicians were experience-dependent or genetic-dependent. Longitudinal research would be required to clarify the causal relationship between long-term musical training and structural changes. Third, gender was an uncontrolled factor that could potentially bias our results, due to the ecology of female-dominant art student population in Taiwan. Further studies taking these factors into account will be required.

5 | CONCLUSIONS

To the best of our knowledge, this is the first study to assert that the sustained practice of musical skills can strengthen or prune white matter connectivity networks in an experience-dependent manner. Our use of graph theory analysis made it possible to measure changes in network metrics and thereby reveal instances of neuroplasticity in global and local architectures following extended musical training (vocal and piano). Overall, our results suggest that both types of musical training strengthen connections among emotion-related regions of the brain. We also discovered that training specific music-related skills may reshape the structural organization of experience-dependent networks. Vocal training appears to alter the networks related to vocal motor control, sensory feedback, and language processing by promoting functional segregation, facilitating multisensory integration, and enhancing network interconnectivity. This work provides a comprehensive assessment of brain plasticity following long-term and

complex musical learning. Our findings provide evidence on the underlying neural mechanisms of musical training and substantial insights into the neuroscientific perspective on art education and aesthetics.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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