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Training-induced brain activation and functional connectivity differentiate multi-talker and single-talker speech training

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Abstract

In second language acquisition studies, the high talker variability training approach has been frequently used to train participants to learn new speech patterns. However, the neuroplasticity induced by training is poorly understood. In the present study, native English speakers were trained on non-native pitch patterns (linguistic tones from Mandarin Chinese) in multi-talker ($N=16$) or single-talker ($N=16$) training conditions. We focused on two aspects of multi-talker

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training, voice processing and lexical phonology accessing, and used functional magnetic resonance imaging (fMRI) to measure brain activation and functional connectivity (FC) of two regions of interest in a tone identification task conducted before and after training, namely the anterior part of the right superior temporal gyrus (aRSTG) and the posterior left superior temporal gyrus (pLSTG). The results showed distinct patterns of associations between neural signals and learning success for multi-talker training. Specifically, post-training brain activation in the aRSTG and FC strength between the aRSTG and pLSTG were correlated with learning success in multi-talker training group but not in the single-talker group. These results suggest that talker variability in training procedure may enhance neural efficiency in these brain areas and strengthen the cooperation between them. Our findings highlight the brain processing of newly learned speech patterns is influenced by the given training approach.

Keywords

talker variability; speech learning; fMRI; individual differences; functional connectivity; voice

Introduction

One of the most difficult learning tasks for many adults is second language learning, which requires great effort to acquire foreign sounds (e.g., Goto, 1971). A number of studies have used natural speech stimuli with high talker variability (spoken by more than one native speaker) to improve learning (e.g., Lively, Logan, and Pisoni, 1993; Lively, Pisoni, Yamada, Tohkura, and Yamada, 1994; Logan, Lively, and Pisoni, 1991). Because learners are exposed to multiple talkers, learners retain a high variety of long-term memory representations of phonetic features to be learned, resulting in a more robust representation of learned features, thus facilitating generalization from a trained set to a new set. However, not all learners benefit from multi-talker training. For example, Perrachione et al. (2011) found that compared with single-talker training, multi-talker training impaired lexical pitch learning for learners with low perceptual abilities for pitch patterns. Similar results have been observed by another laboratory (Sadakata and McQueen, 2014). These results suggest that effectiveness of high variability (e.g., multi-talker) training may depend on the individual predisposition, such as perceptual aptitude.

The neural sources of the individual predisposition in speech learning have been identified by a number of fMRI studies (e.g., Deng, Chandrasekaran, Wang, and Wong, 2016; Golestani and Zatorre, 2004; Ventura-Campos, Sanjuan, Gonzalez, Palomar-Garcia, Rodriguez-Pujadas, Sebastian-Galles, Deco, and Avila, 2013; Wong, Perrachione, and Parrish, 2007). However, the training-related plasticity in multi-talker training is largely unknown. At least two different neural substrates may underlie this plasticity. The first one may be responsible for accessing lexical phonology, which is crucial for learning new speech in a word context (Wong et al., 2007) regardless of talker variability. For example, using a sound-to-word paradigm with a single-talker approach that required learners to map foreign pitch patterns to word meanings, Wong et al. (2007) observed that brain activation in the posterior part of the left superior temporal gyrus (pLSTG), which supports the access of lexical phonology (Graves, Grabowski, Mehta, and Gupta, 2008), could discriminate

successful learners from less successful learners after training. Additionally, a later diffusion tensor imaging (DTI) study found that the inferior longitudinal fasciculus branch that runs along the pLSTG was related to learning success in a similar paradigm using a multi-talker training approach (Wong, Chandrasekaran, Garibaldi, and Wong, 2011). These results suggest that the neural signal of the pLSTG may be a marker for successfully establishing a map between foreign speech features (e.g., pitch patterns) and high level representations (e.g., word). The second neural substrate may reflect the neural signal induced by processing different voices. Speech perception in multi-talker environments has been consistently observed in the anterior part of the right superior temporal gyrus (aRSTG; Belin and Zatorre, 2003; Schelinski, Borowiak, and von Kriegstein, 2016; but see Chandrasekaran, Chan, and Wong, 2011 for bilateral aSTG), a region argued to be specialized for processing vocal features. Activation of the aRSTG was observed in both explicit talker-voice processing, such as performing voice identity tasks (Bonte, Hausfeld, Scharke, Valente, and Formisano, 2014; Schelinski et al., 2016), and implicit voice-change detection during speech perception, such as making a loudness judgment in an environment of changing talkers (Chandrasekaran et al., 2011). Additionally, aRSTG activation was correlated with performance in a voice identity task, and this correlation was absent for adults with autism spectrum disorder who showed less behavioral sensitivity to human voices (Schelinski et al., 2016). These results suggest that the neural signal of the aRSTG may be a neural indicator of the degree of involvement in voice processing.

Here, we used functional magnetic resonance imaging (fMRI) to investigate the neural plasticity involved in multi-talker training and its distinction from single-talker training. We applied a sound-to-word training paradigm (Wong & Perrachione, 2007), which included talker variability (multi-talker vs single talker), to train learners to acquire non-native pitch patterns. Participants with matching pre-training perceptual ability were assigned to receive either multi-talker or single-talker training. As mentioned above, the pLSTG and the aRSTG may be two critical regions in multi-talker training. We selected these two regions as regions of interest (ROIs) and examined their brain activation and the functional connectivity (FC) between them during a tone identification task conducted before and after training. We predicted that multi-talker training would induce “neural reallocation” (Golestani and Zatorre, 2004), thus showing stronger pLSTG and aRSTG activity and a stronger connection between them after training.

Materials and Methods

Participants

Thirty-two right-handed adults (17 males; 25.63 ± 4.36 years old) participated in this study. None of the participants reported a history of any neurological or language disorder. Some of the participants underwent auditory brain stem response (ABR) recordings, diffusion tensor imaging (DTI) and fMRI scanning, the details of which are reported elsewhere (Wong et al., 2011; Chandrasekaran, Kraus, and Wong, 2012; Deng et al., 2016). The participants were native speakers of American English and had no previous experience with Mandarin Chinese or any other tone language. Because music training has been shown to relate to variations in brain function and structure (Herholz and Zatorre, 2012; Kraus and

Chandrasekaran, 2010), we assessed the extent of musical training by self-report. None of the participants were musicians, and none of them had significant musical expertise (less than 6 years of continuous musical experience or learned music prior to 7 years of age). All participants passed a hearing screening test (<25 dB HL hearing thresholds at 500 Hz, 1000 Hz, 2000 Hz and 4000 Hz) and provided informed consent in accordance with the Institutional Review Board (IRB) of Northwestern University. Because working memory capacity, phonological awareness and IQ have impact on language learning (e.g., Gorman, 2012; Fishman, 2011; Pascale & Gathercole, 2007), we used the Woodcock-Johnson Test of Cognitive Abilities (Woodcock et al., 2001) subsets of Sound Blending (SB; a measurement of phonological awareness), Auditory Working Memory (AWM) test and the Test of Nonverbal Intelligence (Brown et al., 1997) to collect the cognitive data. Table 1 summarizes the basic demographic information for both groups of participants.

Procedure Overview

All learners participated in a pre-training behavioral test, pre-training MRI scan, training, post-training MRI scan, and post-training behavioral test (Figure 1A). In the pre-training phase, participants completed cognitive measures (e.g., IQ, SB, and AWM) and the Tone Identification Test. In the pre-training MRI scanning phase, participants performed the tone identification task in the scanner. In the training phase, they underwent a nine-session sound-to-word training program. In the post-training MRI scanning phase, they performed the tone identification task again in the scanner. Finally, they completed the Tone Identification Test and the Generalization Test in the post-training behavioral test phase.

Tone Identification Test (Outside Scanner)

A Tone Identification Test (Tone ID, Wong and Perrachione 2007) was administered before training to all participants in order to ascertain individual differences in non-lexical pitch perception ability. In this test, four native speakers (2 males and 2 females) of Mandarin Chinese each produced five Mandarin vowels /a/, /i/, /o/, /e/, and /ü/ with Mandarin tone 1 (level tone). Pitch patterns of these vowels were resynthesized with tone 1 (level), tone 2 (rising), and tone 4 (falling) imposed by using the Pitch Synchronous Overlap-Add (PSOLA) method provided by the Praat software (<http://www.praat.org>). The tone 3 (dipping) was not used because its pitch pattern was complex and hard to label by nonnative speakers. The participants heard one stimulus and were visually presented two of three pictures (i.e., → = level, ↗ = rising, and ↘ = falling). Participants were asked to press a button corresponding to the pitch pattern of the stimulus they heard. The Tone ID score (proportion of correct responses) is considered a behavioral index of ability of the participant's nonlexical pitch pattern identification ability because the participants were required to attend to the pitch patterns rather than the entire word. For further details of the stimuli and procedures of this test, see Chandrasekaran et al. (2012). The Tone Identification Test was also conducted after training.

Speech Training

The sound-to-word training paradigm used in this study was identical to that described in previous studies (Wong et al., 2011; Chandrasekaran, Kraus, and Wong, 2012; Deng et al., 2016). Following the pre-training MRI scan, the participants underwent a nine-day training

program in which they learned to associate monosyllabic pseudo-words with pictures. The participants had to learn differences in pitch patterns within each syllable in order to learn the associations between the sounds and pictures.

The stimuli consisted of six English monosyllabic pseudo-words (“pesh”, “dree”, “nuck”, “vece”, “fute”, and “ner”). Using the PSOLA method, each pseudo-word was superimposed with four pitch patterns that resembled the Mandarin tones of tone 1 (level), 2 (rising), 3 (dipping) and 4 (falling). Thus, 24 words were constructed, and each word was paired with a picture that represented its meaning. In total, 192 stimuli were constructed by a multi-talker approach (8 talkers). The stimuli from four talkers (2 males and 2 females; talkers A, B, C and D) composed the training set, and the stimuli from another four talkers (2 males and 2 females; talkers E, F, G and H) composed the Generalization set. The stimuli/talkers used in the sound-to-word training procedure were not used in the Tone Identification Test described before. For the multi-talker training group, all participants were trained with the same training set generated by the four talkers. For the single-talker training group, each participant was assigned one training set generated by one of the four talkers (each talker was randomly assigned to four participants).

There was no more than one training session per day and no more than a 2-day gap between the training sessions. Each training session, which included the training phase and the Word Identification Test, lasted approximately 30 min. The 96 stimuli (6 syllables $\times$ 4 tones $\times$ 4 talkers) were divided into six groups of four words of the same syllable. Thus, the words in each group were minimally contrasted in pitch patterns. At the end of each group, the participants were tested on the four words that they had just learned. The participants heard one of the four words and then selected the corresponding picture out of the four picture options. Feedback (correct/incorrect) was used to allow the participants to recognize and correct their mistakes. After six groups were finished, a final Word Identification Test was conducted. In this test, the 24 trained words were randomly presented to the participants, and they were asked to identify each word by selecting the corresponding picture from 24 possible choices without feedback. The participants were given as much time as needed to identify the words.

After the post-training MRI scan, a Generalization Test was administered according to the same procedure used in the Word Identification Test. All items in the Generalization set were words spoken by four new talkers (talkers E, F, G and H). Thus, we were able to examine whether our participants recognized the words that they had learned in a new context (i.e., words spoken by new talkers). The Generalization Test score (correct proportion) was used as the final learning outcome. Both the multi-talker and the single-talker training groups performed the same Generalization test.

The Tone Identification Task (Inside Scanner)

For the tone identification task, auditory stimuli were from the Tone Identification Test described before. The participants heard one syllable (vowels with superimposed linear rising, level, or falling pitch patterns synthesized from four talkers) and were visually presented three different pictures (i.e., $\rightarrow$ = level, $\nearrow$ = rising, and $\searrow$ = falling) representing the pitch pattern of the auditory stimulus. The participants decided whether the pitch was

level, rising, or falling on each trial (40 trials in total). Silent trials (40 trials in total) in which no stimuli were presented were interspersed randomly with task trials. The participants were instructed to indicate their choice on an MRI-compatible button box. BOLD responses were collected using a sparse sampling design (Belin, Zatorre, Lafaille, Ahad, and Pike, 2000; Chandrasekaran et al., 2011; Hall, Haggard, Akeroyd, Palmer, Summerfield, Elliott, Gurney, and Bowtell, 1999; Wong et al., 2007). The participants were imaged in the first 2 seconds of a TR, followed by 12 seconds (6 stimuli) of stimulus presentation when no scanning occurred (Figure 1B).

MRI Scanning

For all participants, anatomical and functional images were acquired using a Siemens 3T Trio MRI scanner (Erlangen, Germany). Axial anatomical images were acquired using a T1-weighted high-resolution 3D magnetization-prepared rapid gradient-echo (MPRAGE) sequence (repetition time (TR) = 2300 ms, echo time (TE) = 3.36 ms, flip angle = 9°, matrix size = 256 × 256, slice thickness = 1 mm, and field of view (FOV) = 22 cm).

Functional images were acquired axially using a susceptibility T2*-weighted echo planar imaging (EPI) pulse sequence (TE = 21 ms, TR = 14000 ms, flip angle = 90°, in-plane resolution = 3.4375 mm × 3.4375 mm, 36 slices with a slice thickness = 3 mm, and FOV = 220 mm).

Task-fMRI Data Analysis

The fMRI data were analyzed using AFNI (Cox, 1996; <https://afni.nimh.nih.gov/afni/>), similar to previous studies (Chandrasekaran et al., 2011; Wong et al., 2007). The functional images were subjected to motion correction, spatial smoothing (FWHM 6 mm), signal scaling and linear detrending. For the current sparse sampling design, image acquisition occurred during the first 2 seconds of the TR (14 seconds). The images reflect either a stimulus event or a null event (when no stimulus was presented). This procedure removed the need to convolve the task-related extrinsic waveforms with a hemodynamic response function (HRF) before the statistical analysis. The waveforms of the modeled events were treated as regressors in a multiple linear regression of the voxel-based time series. The beta coefficient values, signifying the fit of the regressors to the functional scanning series voxel-by-voxel, were obtained for each participant. The beta coefficient map for each participant was used for further analysis. Anatomical and functional images from each participant were normalized to a standard stereotaxic template (ICBM_152).

Whole Brain General Linear Model (GLM)

BOLD activation of each participant was entered into a 2 (training: pre-training, post-training) × 2 (group: multi-talker, single-talker) ANOVA (using the AFNI function 3dANOVA3). A corrected threshold of $p < 0.05$ was determined based on a Monte Carlo simulation (using the AFNI function 3dClustSim, with the per-voxel p value set to 0.05 and the per-cluster alpha value set to 0.05) of significant voxels within a “sound vs baseline” contrast mask that responded to sound relative to baseline at uncorrected $p < 0.05$ (negative values were excluded to avoid artifacts generated from brain deactivation during the listening task; Chandrasekaran et al., 2011).

The BOLD activation in regions showing a significant training $\times$ group interaction was further explored by extracting the mean beta coefficient value for the experimental conditions from the significant clusters. Statistical analysis was conducted using IBM SPSS Statistics Version 22.

ROI Analysis

Large individual differences in training induced neuroplasticity have been identified by previous studies (e.g., Wong et al., 2007; Yang et al., 2015). We took advantage of these individual differences and conducted further ROI analyses that did not rely on the between-group comparisons. Coordinates for the pLSTG ROI were chosen based on a previous study that showed greater activation in this region following sound-to-word training in successful compared to less successful learners (Wong et al, 2007; Wong et al, 2011). The speaker's voice was first identified in the anterior part of the right superior temporal area (Belin and Zatorre, 2003). The aRSTG ROI was selected based on a previous study that showed increased activation for the multi-talker listening condition relative to the single-talker listening condition in the anterior part of the RSTG (Chandrasekaran et al., 2011). As detailed in Touroutoglou, Bickart, Barrett, and Dickerson (2014), we created conjunction ROIs based on these prior ROIs. We first created spherical ROI (radius, 6 mm) for each region based on the relevant coordinates (Table 2). Because there were sound and silence (baseline) trials in the sparse sampling design, the “sound vs baseline” contrast (sound presentation condition minus silent condition) produced both task-related activation and deactivation. The task-related deactivation was located in the default mode network regions, such as the cingulate cortex, medial frontal cortex and medial temporal lobe (see supplementary materials). Although the deactivation of DMN may reflect the demands of attention and working memory in a specific task (Maver & Amaurer, 2010), the current study focused on sound processing- related activation rather than DMN deactivation. Thus, we then applied the sound vs baseline contrast (sound presentation condition minus silent condition) to each ROI to exclude the voxels that were irrelevant for sound presentation (Chandrasekaran et al., 2011). The data were extracted from a conjunction of the spherical ROI and the sound vs baseline contrast, such that only those voxels within the conjunction that responded to sound relative to baseline at $p < 0.05$ were included (negative values were excluded). The conjunction ROIs (the number of voxels for each ROI is shown in Table 2) were used for further analysis.

To measure the magnitude of task-evoked brain activation, mean beta values from the conjunction ROIs were obtained. We then correlated the mean beta values with the Generalization scores to reveal the contribution of brain activation to speech learning. We also focused on the contributions of FC between pLSTG and aRSTG to speech learning. Thus, we calculated the pLSTG-aRST FC strength for each group and correlated that strength with Generalization scores.

Results

Behavioral Results

Accuracy data from the tone identification tasks outside of the scanner were analyzed in a 2 (training: pre-training vs post-training) $\times$ 2 (group: multi-talker vs single-talker) repeated measures ANOVA. We found a significant main effect of training ($F_{(1,30)} = 25.6$, $p < 0.001$), revealing greater identification accuracy post training ($M = 0.86$, $SD = 0.14$) than pre-training ($M = 0.80$, $SD = 0.14$) (Figure 2A). No main effect of group was found ($F_{(1,30)} = 0.06$, $p = 0.81$), and no significant interaction between training and group was found ($F_{(1,30)} = 3.13$, $p = 0.087$).

For the tone identification task inside of the scanner, we analyzed identification accuracy in a 2 (training: pre-training vs post-training) $\times$ 2 (group: multi-talker vs single-talker) repeated measures ANOVA. We found a significant interaction between training and group ($F_{(1,30)} = 21.89$, $p < 0.001$). Post hoc analysis revealed that while there was no significant difference between the multi-talker and the single-talker group before training, the accuracy of the multi-talker group ($M = 0.83$, $SD = 0.14$) was higher than that of the single-talker group ($M = 0.74$, $SD = 0.12$) after training (Figure 2B).

On the Generalization Test, the mean proportion correct was 0.60 ($SD = 0.23$) and 0.62 ($SD = 0.24$) for the multi-talker and single-talker groups, respectively (Figure 3C). An independent sample t-test of Generalization scores revealed no between-group differences ($t_{(30)} = 0.24$, $p = 0.81$). For each training group, we divided the participants into a high Tone ID group and a low Tone ID group according to Tone ID score before training: the highest performing eight participants were grouped into the high Tone ID group and the rest of the participants were grouped into the low Tone ID group. We then conducted a 2 (training group: multi-talker vs single-talker) $\times$ 2 (Tone ID group: high vs low) ANOVA on Generalization scores. We found a significant main effect of Tone ID ($F_{(1, 28)} = 10.57$, $p = 0.003$), showing that Generalization scores in the high Tone ID group were higher than in the low Tone ID group. The interaction effect and the main effect of training were not significant. According to previous studies (Perrachione et al., 2011; Sadakata and McQueen, 2014), learning success may depend on the interaction between pre-training perceptual ability and the training paradigm. We found that for participants with low tone ID scores, single-talker training ($M = 0.54$, $SD = 0.20$) was superior than multi-talker training ($M = 0.44$, $SD = 0.17$), whereas for participants with high tone ID scores, multi-talker training ($M = 0.76$, $SD = 0.19$) was better than single-talker training ($M = 0.69$, $SD = 0.24$). However, the interaction effect was not significant ($F_{(1, 28)} = 1.46$, $p = 0.24$) likely due to the sample size differences between the two studies. We conducted further analysis without choosing an arbitrary cutting point for high vs low Tone ID groupings and did not find a significant interaction effect. Details were reported in supplementary materials. It is worth noting that the present study was designed to examine neural differences induced by different training approaches, rather than finding a training-by-learner interaction.

As shown in Figure 3D, Word ID performance improved with both types of training. Using group, age, gender, IQ, pre-training Tone ID, AWB, and SB as predictors, a multiple linear regression was conducted using the Generalization score as the dependent variable for all

participants. Only pre-training Tone ID ($\beta = 0.47$, $p = 0.012$) predicted Generalization scores. Group, age, gender, IQ, AWM and SB did not predict Generalization scores ($\beta = 0.14$, $p = 0.39$, $\beta = 0.10$, $p = 0.62$, $\beta = -0.17$, $p = 0.41$, $\beta = 0.17$, $p = 0.40$, and $\beta = 0.30$, $p = 0.11$, $\beta = -0.08$, $p = 0.68$, respectively).

Whole-Brain GLM Results

The GLM analysis revealed a significant interaction effect between training (pre-training, post-training) and group (multi-talker, single-talker) in the left postcentral gyrus (Table 3, Figure 3 A). A 2×2 repeated measures ANOVA performed in this cluster revealed a significant interaction effect ($F_{(1,30)} = 12.69$, $p < 0.01$) but no main effects of training ($F_{(1,30)} = 1.75$, $p = 0.19$) or group ($F_{(1,30)} = 2.91$, $p = 0.09$). Post hoc testing revealed no differences between the multi-talker group ($M = 0.12$, $SD = 0.18$) and the single-talker group ($M = 0.13$, $SD = 0.18$) before training, whereas brain activation was stronger for the multi-talker group ($M = 0.19$, $SD = 0.21$) than for the single-talker group ($M = -0.03$, $SD = 0.21$) after training.

A main effect of training (Table 3, Figure 3 B) was observed in several regions. For the post-training > pre-training contrast, several clusters showed stronger activation, including the left middle frontal gyrus, the left superior frontal gyrus and the right superior temporal gyrus. For the pre-training > post-training contrast, a single cluster located in the right thalamus was found. A main effect of group (Table 3, Figure 3 C) was observed in a single large cluster located in the right and left cerebellum.

ROI and Functional Connectivity Results

To evaluate the contribution of brain activation in language learning, we extracted mean beta values from the conjunction ROIs (Table 3) and correlated them with the Generalization scores. As shown in Table 4 and Figure 4, we found that for both the multi-talker group and the single-talker group, brain activation in the pLSTG was positively correlated with Generalization scores only post-training. FC analyses (Figure 5) revealed that for the multi-talker group, the pLSTG-aRSTG FC strength was positively correlated with Generalization scores after training but not before training. For the single-talker group, pLSTG-aRSTG FC strengths were not significantly correlated with Generalization scores. Because a significant interaction effect between training (pre-training, post-training) and group (multi-talker, single-talker) was found in the left postcentral gyrus, we selected the whole cluster as ROI and correlated the mean beta value within the ROI with Generalization scores for each group before and after training. No significant correlations were found ($ps > 0.5$ for all). Taken together, these results indicate that the largest neural difference induced by training approaches lies in both network properties, and regional activation.

Discussion

Numerous behavioral studies have taken advantage of high talker variability to improve effectiveness of speech training (Barcroft and Sommers, 2005; Chandrasekaran et al., 2012; Lively et al., 1993; Wong et al., 2011). However, to our knowledge, the present study is the first to reveal neural plastic induced by multi-talker training. In the present study, we used fMRI to show that post-training brain activation in the pLSTG could account for learning

success after both multi- and single-talker training. More importantly, we identified a multi-talker-specific neuroplastic pattern: activation in the aRSTG and pLSTG-aRSTG FC strength correlated with Generalization scores after multi-talker training but not single-talker training. Thus, aRSTG activation and pLSTG-aRSTG FC may serve to explain how the brain is modified by multi-talker training and why some learners benefit more from this type of training than others.

Similar learning outcome from different training approaches

Our behavioral results demonstrate that native English-speaking subjects were able to learn to associate pitch patterns to word meaning since their performance (Word ID score) improved with training. Participants were randomly assigned to receive multi-talker speech training or single-talker speech training. We matched their basic demographic information, especially ensuring that their pre-training perceptual ability did not differ across groups. Our whole-brain analysis further revealed that there were no group differences in the ROIs, (a group difference was found in the cerebellum), ensuring that our brain-behavior analysis was not biased by the initial brain state. We did not observe a better learning outcome (Generalization score) for multi-talker training than for single-talker training, which replicates earlier findings using the same paradigm (Perrachione et al., 2011). As Perrachione et al. (2011) argued, not all learners benefit from multi-talker training. The behavioral findings in the present study converge with those from Perrachione et al. (2011). The present study further examined the neural mechanisms subserved by multi-talker training.

Brain pathway underlying multi-talker training

Consistent with our prediction, the activation of aRSTG was correlated with learning success after multi-talker training. The role of the aRSTG in the neural representation of a talker's voice was first identified in an active listening task (Belin and Zattore, 2003), and more recently in voice identification tasks (Bonte et al., 2014; Schelinski et al., 2016), a voice discrimination task (Andics, McQueen, Petersson, Gal, Rudas, and Vidnyanszky, 2010), and even in an implicit paradigm that only required participants to attend to loudness change rather than talker change (Chandrasekaran et al., 2011). Given that the aRSTG is sensitive to unattended voice change in speech perception, the neural signal of aRSTG is a particularly effective measure for examining the neural changes responsible for the voice changes that are unrelated to the features to be learned (e.g., pitch pattern changes in our multi-talker training procedure). Furthermore, recent evidence has suggested that the activation of the aRSTG can provide an index for the ability to identify a person's voice. Schelinski et al. (2016) compared the brain activation patterns of adults with and without autism spectrum disorder using a voice identification task. Although they did not find group differences in aRSTG activation, they found that the autism group showed worse task performance than the control group, and a positive correlation between performance and aRSTG activation was observed only in the control group but not in the autism group. Based on these findings, the relationship between aRSTG activation and learning success can be explained as part of the neuroplasticity induced by multi-talker training. One major advantage of multi-talker training is to require learners to establish a high variety of long-term memory representations of phonetic features to be learned through introducing more

variability or inconsistency in the mapping between acoustic patterns and linguistic categories that differ across talkers. More successful learners should adapt more to the voice inconsistency than less successful learners, resulting in a more robust function of the neural substrate (e.g., aRSTG) responsible for the sensitive detection of voice changes (Chandrasekaran et al., 2011) and precise voice encoding (Bonte et al., 2014). It should be noted that the stimuli (vowels with different pitch patterns) used in the tone identification tasks inside of the scanner were different from the items to be learned (pseudo-words with different pitch patterns). Activation of the aRSTG in the tone identification task after training did not directly reflect how well participants had learned the items to be learned. Instead, stronger aRSTG activation might indicate more robust voice processing even in a context in which participants did not need to learn and remember the speech sounds.

We also observed a positive correlation between learning success and FC between the pLSTG and aRSTG in the participants that received multi-talker training. The exact role of the pLSTG in language process is still in debate. One model suggests that the pLSTG is the starting point of the dorsal articulatory pathway (Hickok and Peoppel, 2007). Another model suggests that the pLSTG is involved in integrating different types of information in sentence processing (Friederici, 2011). The pLSTG is also proposed to participate in lexical phonology accessing (Graves et al., 2008). Consistent with this view, previous studies using the sound-to-word paradigm showed that successful learning of lexical pitch patterns was related to the activation of the pLSTG (Wong et al., 2007) and the white matter connectivity in the inferior longitudinal fasciculus branch that goes through the pLSTG (Wong et al., 2011). It is possible that the pathway connecting the aRSTG and pLSTG facilitates accessing lexical phonology in a context with voice variability. This view is supported by evidence showing coactivation of the aRSTG and pLSTG in voice processing tasks using lexical units (Adank, Stewart, Connell, and Wood, 2013; Chandrasekaran et al., 2011; Kreitewolf et al., 2014; Schelinski et al., 2016). Notably, for our participants, the pitch patterns in our fMRI task did not carry any lexical information before training, whereas these pitch patterns became lexically meaningful after training (Wong et al., 2007). Thus, coupling between the activation of the aRSTG and pLSTG might be a result of neural modulation induced by multi-talker training. That is, the aRSTG-pLSTG FC strength might provide an index for how well they learned to process these pitch patterns lexically, thus predicting the learning outcome.

Moreover, the correlation between the aRSTG-pLSTG FC strength and learning success may also reflect the cooperation of linguistic (e.g., lexical phonology) and indexical information (e.g., vocal features) processing in speech learning. Previous behavioral and neuroimaging studies have shown that these two sources of information are coupled to speech perception. For example, b listeners unfamiliar with a language are naive to acoustic variations that signal differences among talkers and differences for meaningful tonal contrasts. Perrachione and Wong (2007) presented both Mandarin and English sentences spoken by several talkers to native English speakers and had them identify the same talkers with another set of sentences. The participants had more difficulty identifying talkers in the Mandarin Chinese sentence context than in the English sentence context, and this effect was due to language proficiency, indicating that talker identification may involve integrated bilateral regions in the auditory area. Consistent with this view, von Kriegstein, Smith,

Patterson, Kiebel, and Griffiths (2010) found that the speech processing regions in the left posterior superior area are sensitive to talker-related vocal tract parameters and the right posterior temporal area is more activated in response to talker-related vocal tract parameter modulation in a speech recognition task than in a voice recognition task. Increased FC between these two areas was identified during speech recognition with different talkers. In the current study, successful learning requires learners to distinguish talker-related acoustic variation and linguistic-related acoustic variation (e.g., pitch patterns) and to build associations between pitch patterns and word meaning. This difficult task may involve cooperation between the voice processing region in the aRSTG and a lexical phonology accessing region in the pLSTG. When perceiving pitch patterns in a multi-talker environment, more strengthened coupling between the aRSTG and pLSTG was observed for more successful learners.

Limitations

There were several limitations in the current study. One major limitation of this study is that the brain-behavior correlations are sensitive to the choice of the size of the ROIs. We observed a trend that the brain-behavior correlation values drop as the sizes of the ROIs increase. These observations suggest that the effects are restricted to the spherical regions centered in the pLSTG and aRSTG coordinates with radii less than 14 mm. Thus, these results should be interpreted with caution when considering the role of individual variations in the BOLD signal in these two regions in language learning. Additionally, individual variations in brain structure may reduce the effectiveness of the ROI-based method. For example, individual differences in the Heschl's gyrus located in the pLSTG are usually large and are reported to be related to language learning abilities (e.g., Wong et al., 2008). The prior ROIs may cover irrelevant regions when using large spheres to define the target region, which shows large individual differences in brain structure. A more focused study using a meta-analysis may help clarify the "objective" location that shows the brain-behavior correlation.

The second limitation of the study may come from the feedback used in our training paradigms. There is evidence that feedback, combined with different training approaches, induces different training effects (e.g., Chandrasekaran et al., 2013) and involves different neural networks (e.g., Yi et al., 2015). We observed a significant correlation between brain activation and the Generalization scores for the single-talker training group but not for the multi-talker training group after training, suggesting that there may be an interesting association between the feedback-related brain network and single-talker training (see supplementary materials). However, we were not able to examine the effect of feedback on training because we did not manipulate the level of feedback (e.g., to provide feedback or not to provide feedback). Future studies on the interaction between the feedback and training approach on the training effect using factorial design may help uncover the nature of the different training approaches.

Finally, we included all of the four Mandarin tone patterns in the word context in the training procedure and tested how the participants learned them in the word context using the Word ID Test and Generalization Test. However, we did not explicitly require the

participants to learn the Mandarin patterns per se, as they may have been confused when identifying these patterns in the vowel context instead of the word context. Because the most difficult pattern for the participants was the dipping tone pattern, we excluded this tone pattern in the Tone identification test to reduce the difficulty of the task. The disadvantage of excluding dipping tone patterns is that the Tone ID task was not able to discriminate the participants who learned the dipping tone pattern from those who did not learn the dipping tone pattern.

Future directions

Personalized training has been proposed to improve the effectiveness of speech training for each learner (Wong, Vuong, and Liu, 2016). Revealing the sources of the variation in training is crucial for optimizing training approaches. There is a growing interest in using brain connectivity data to identify variations in behavior pattern. For example, individual brain connectivity patterns were found to be unique (Finn, Shen, Scheinost, Rosenberg, Huang, Chun, Papademetris, and Constable, 2015) and depend on the specific task state (Geerligs, Rubinov, Cam, and Henson, 2015). A recent study has found that the brain connectivity pattern can be modulated by a motor skill learning process, and the modulation can be an index of learning success (Bassett, Wymbs, Rombach, Porter, Mucha, and Grafton, 2013). These studies suggest that a brain connectivity pattern can reflect both the changes in cognitive state and the unique manner in which an individual responds to the cognitive state. In the context of speech learning, the unique characteristics of a learner were indexed not only by how well he/she learns but also in the way he/she learns. Previous studies demonstrated that the superior efficiency of high variability training compared to that of low variability training may depend on the perceptual abilities of the learner (Perrachione et al., 2011; Sadakata and McQueen, 2014), suggesting that high variability training is not the only way to improve learning. Our data further show the neural substrates of how learners successfully adapted to multi-talker training. A future study should use a larger sample size of participants to investigate why single-talker training can lead to similar learning success (at the group level) and which is most effective for a given individual (at an individual level). Although this study did not reveal the association between pre-training FC and speech learning outcomes, intrinsic FC may be a possible means to reveal individual differences in learning outcome (Chai, Berken, Barbeau, Soles, Callahan, Chen, and Klein, 2016; Deng et al., 2016). Future studies should investigate how pre-training FC predicts multi/single-talker training outcomes and how much variance of the task-related FC reported here can be explained by intrinsic or “trait” FC at rest (Geerligs et al., 2015).

Conclusions

The present study investigated the neural plasticity of multi-talker speech training. We focused on brain activation of a voice processing region (e.g., aRSTG) and a lexical phonology accessing region (e.g., pLSTG) and functional connectivity between them. The current findings suggest that high talker variability in training procedure may enhance neural efficiency in these brain areas and strengthen the cooperation between them. Our findings highlight the brain processing of newly learned speech patterns is influenced by the given training approach.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Highlights

Neural substrates of multi- and single-talker speech training were investigated.

Activation of the posterior part of the left superior temporal gyrus (pLSTG) was correlated with learning outcome for both training approaches.

Activation of the anterior part of the right superior temporal gyrus (aRSTG) and the functional connectivity between aRSTG and pLSTG were correlated with learning outcome after multi-talker training.

Multi-talker training might enhance neural efficiency of voice processing (aRSTG) and lexical phonology accessing (pLSTG) regions and strengthen the cooperation between them.

Figure 1.

Outline of the experimental design (A) and the fMRI task procedure (B). A: in the pre-training phase, participants completed cognitive measures (e.g., IQ, SB, and AWM) and the Tone Identification Test. In the pre-training and post-training MRI scanning phase, participants performed the same tone identification task in the scanner. In the training phase, different groups received different types to speech training. After training, they completed the Tone Identification Test and the Generalization Test. It is noted that the Generalization score was used as the measure of final learning outcome. B: BOLD responses were collected using a sparse sampling design in which functional images were collected at the first 2 sec following by 12 sec of stimulus presentations (6 vowels) without data collection. The participants decided whether the pitch was level, rising, or falling on each trial.

Figure 2.

Participants' behavioral task performance. A: pitch discrimination performance outside the scanner; B: pitch discrimination performance inside the scanner; C: Generalization (future learning outcome) after training; D: the language training curves over the nine days of training.

Figure 3.

Whole brain activation for experimental conditions. A: Interaction effect between training and group in the left postcentral gyrus. B: Contrast between pre-training and post-training sessions reveals that the right thalamus showed greater activation after training than before training, whereas the left middle frontal gyrus, left superior frontal gyrus and right superior temporal gyrus show greater activation before training than after training. C: Contrast between multi-talker group and single-talker group reveals that clusters in the left and right cerebellum show greater activation for the multi-talker group than for the single-talker group.

Figure 4.

The ROIs (A) and correlations between task activations (β) and learning outcomes with different training approaches (B).

Figure 5. Correlations between task-based functional connectivity (FC) strength and learning outcomes with different training approaches.

Table 1

Basic demographic information for multi-talker and single-talker groups.

	Multi-talker		Single-talker		Group Comparisons	
	n = 16 (9 males)		n = 16 (8 males)		Multi-talker > single-talker	
	Mean	SD	Mean	SD	t	p
Age	26.50	5.09	24.75	3.43	1.14	0.263
IQ	116.25	8.43	111.13	12.65	1.33	0.193
AWM	84.33	10.60	82.75	23.69	0.24	0.814
SB	79.63	16.84	73.00	16.26	1.13	0.267
Tone ID ^a	0.82	0.15	0.78	0.14	0.68	0.499

^aTone ID score before training.

Table 2

Coordinates of regions of interests (ROIs) in task-fMRI data analyses.

ROI	MINI coordinates			Radius (mm)	No. of voxels
	x	Y	z		
pLSTG	-54	-34	10	6	33
aRSTG	63	-13	-2	6	33

Table 3GLM training session $\times$ training approaches ANOVA.

regions	MINI Coordinates(X, Y, Z)	Cluster Size	Peak F/t	Cluster-based Post hoc Tests
Interaction (group $\times$ training)				
Left postcentral gyrus	-43 -37 58	178	14.47	interaction:F (1,30) = 12.69, $p < 0.01$ pre-training : multi-talker > single-talker, $p = 0.91$ post-training: multi-talker > single-talker, $p < 0.01$
Main effect of training: pre-training> post-training				
Left middle frontal gyrus	-49 6 42	285	4.15	
Left superior frontal gyrus	-4 9 58	282	3.69	
Right superior temporal gyrus	66 -23 4	198	3.28	
Post-training>pre-training				
Right thalamus	5 -32 4	128	3.00	
Main effect of group : multi-talker> single-talker				
Right Culmen (right cerebellum)	38 -58 -37	618	-27.5	

Table 4

Correlations between brain activation in ROIs and Generalization.

Correlations between brain activation and Generalization			
		Pre-training	Post-training
pLSTG	Multi-talker	0.43	0.71 **
	Single-talker	0.48	0.63 *
aRSTG	Multi-talker	0.17	0.70 **
	Single-talker	0.19	0.15

*
p < 0.05;**
p < 0.01.