VERBAL MEMORY RETRIEVAL ENGAGES VISUAL CORTEX IN MUSICIANS

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Abstract—As one major line of research on brain plasticity, many imaging studies have been conducted to identify the functional and structural reorganization associated with musical expertise. Based on previous behavioral research, the present study used functional magnetic resonance imaging to identify the neural correlates of superior verbal memory performance in musicians. Participants with and without musical training performed a verbal memory task to first encode a list of words auditorily delivered and then silently recall as many words as possible. They performed in separate blocks a control task involving pure tone pitch judgment. Post-scan recognition test showed better memory performance in musicians than non-musicians. During memory retrieval, the musicians showed significantly greater activations in bilateral though left-lateralized visual cortex relative to the pitch judgment baseline. In comparison, no such visual cortical activations were found in the non-musicians. No group differences were observed during the encoding stage. The results echo a previous report of visual cortical activation during verbal memory retrieval in the absence of any visual sensory stimulation in the blind population, who are also known to possess superior verbal memory. It is suggested that the visual cortex can be recruited to serve as extra memory resources and contributes to the superior verbal memory in special situations. While in the blind population, such cross-modal functional reorganization may be induced by sensory deprivation; in the musicians it may be induced by the long-term and demanding nature of musical training to use as much available neural resources as possible. © 2010 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: brain plasticity, functional reorganization, musical training, visual cortex, fMRI.

In neural plasticity studies, there are three major lines of research involving different special populations, including the brain injury patients, the congenitally blind people, and the musically trained people (Johnston, 2009). The musician model of brain plasticity allows more controllable investigation of the structural and functional reorganization as training proceeds in physiologically normal people (Munte et al., 2002). Many studies have identified structural brain differences between musicians and non-musicians in leftward planum temporale (Schlaug et al., 1995a), corpus callosum (Schlaug et al., 1995b), motor cortex (Elbert et al., 1995), cerebella (Hutchinson et al., 2003), and visual-spatial brain regions (Gaser and Schlaug, 2003a,b), possibly related to their superior musical skills. Strong correlations with measures of musical abilities have been identified not only with grey matter volume in the anterior part of Heschl gyrus, but also with the amplitude of the early N30-P50 magnetic components (Schneider et al., 2002, 2005).

Musical training also enhances a range of non-musical cognitive functions, such as verbal memory, visuo-spatial abilities (Chan et al., 1998; Brochard et al., 2004; Hassler et al., 1985; Sluming et al., 2007; but see Schellenberg, 2001 for critiques of such claims for lack of compelling evidence), and pitch processing in language (Schön et al., 2004; Margues et al., 2007; Moreno et al., 2009). Among the first few studies, we previously reported improved verbal memory performance in female college students receiving at least 6 years' training of western musical instruments before the age of 12, compared to matched controls without musical training (Chan et al., 1998). We also showed that such improvement was specific to verbal memory but not present for visual memory (Ho et al., 2003). These results have been corroborated in many other studies (Brandler and Rammsayer, 2003; Helmbold et al., 2005; Hogan and Huesman, 2008; Jakobson et al., 2003; Kilgour et al., 2000; Ohnishi et al., 2001). However, there has been no imaging study conducted to identify the neural correlates of musician's superior verbal memory.

Interestingly, enhanced verbal memory has also been found in another line of brain plasticity research involving the congenitally blind people (Hull and Mason, 1995; Pozar, 1982; Roder et al., 2001; Tillman and Bashaw, 1968). Although the blind people are known to have better auditory processing abilities and enlarged auditory cortex (Elbert et al., 2002; Lessard et al., 1998; Stevens and Weaver, 2009), relative to the normal population, their superior verbal memory was found to be related to activation in the visual cortex but not in the auditory cortex, and the results were interpreted as showing that visual cortex served as extra memory resources in the blind people due to functional reorganization (Amedi et al., 2003).

 $0306\text{-}4522/10\ \$$ - see front matter @ 2010 IBRO. Published by Elsevier Ltd. All rights reserved. doi:10.1016/j.neuroscience.2010.03.027

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Abbreviations: BOLD, blood oxygen level dependent; IFG, inferior frontal gyrus; LOC, lateral occipital complex; PT, planum temporale; ROI, region of interest; SD, standard deviation.

This raises an intriguing possibility that the visual cortical areas may also underlie the superior verbal memory in musicians, as is the case for the blind people. Besides improved verbal memory, the two populations also share other characteristics, such as better auditory processing abilities and enlarged auditory cortex (Chin, 2003; Elbert et al., 2002; Schlaug et al., 1995a; Stevens and Weaver, 2009), suggesting commonalities in their brain reorganization.

It may be argued that associating brain plasticity changes in musicians with that in the blind individuals based on some behavioral similarities is too speculative. because neuroplasticity results from developmental changes due to long-term training in the former but deafferentiation in the latter. However, there has been evidence showing cross-modal neural plasticity in healthy sighted participants, similar to that in blind participants. Schmithorst and Holland (2003) reported visual cortical activations for musicians during harmony processing, and Saito et al. (2006) reported similar visual activations in mah-jong experts during tactile discrimination. These two studies lend support to the hypothesis that visual cortex may undergo functional reorganization not only because of sensory visual deprivation, but also because of long-term training.

The present functional MRI study tested this hypothesis with an adaptation of the Chan et al. (1998) paradigm. College students with and without musical training were asked to encode a list of words presented auditorily, and then to retrieve them. Brain scanning was performed during both encoding and retrieval to identify potential group differences.

A pitch judgment task was included as baseline to control for confounding factors, such as general attentiveness and motor responses. To assess visual cortical activations during the word retrieval condition, ideally, the baseline condition should not involve visual cortical activations. The often-used resting baseline does not meet this requirement as such visual activations have been reported during resting, possibly due to visual imagery (Kosslyn, 2005). For pitch judgment tasks, no such activations were found in either musicians or non-musicians (Hyde et al., 2008; Gaab et al., 2003; Platel et al., 1997; Zatorre et al., 1998). Clearly, pitch judgment does not engage similar acoustic and phonologic processes as do word encoding and retrieval. It is therefore not a good control if one were to examine the auditory cortex. However, specific to the visual cortex, the pitch judgment task should match the two memory tasks as none would engage any visual processing in absence of cross-modal plasticity changes.

Another region of interest, in addition to the visual cortex, was the left planum temporale (PT) in the auditory cortex, as Chan et al. (1998) predicted functional activity in left PT to distinguish between musicians and non-musicians, based on its structural differences across the two groups.

EXPERIMENTAL PROCEDURES

Participants

Twenty healthy right-handed female college undergraduates participated in the study. Half of them were in the experimental group without any systematic musical training and the other half were in the control group with musical training, referred to as non-musicians and musicians respectively for simplicity. All musicians were pianist who had started piano training before age seven for a continued period of more than 8 years, and passed the National (China) Amateur Piano Test Band 6. None had received systematic trainings for any other musical instruments.

Note the musician participants were not professional musicians and there were no particular reasons to believe they were gifted in music. Firstly, in China, most children study music not because they are gifted but because their parents want them to do so. Secondly, the National (China) Amateur Piano Test (Band 1–10 from low to high) is for amateur pianists on basic musical skills. Band 6 is the upper boundary of the preliminary level which nearly all piano players can pass with reasonable practice. This point is important in that gifted children may have started with better verbal aptitude before any musical training, making giftedness a confounding factor between our musicians and non-musicians.

The two participant groups were matched in age (controls: age range 20–23 years, mean±SD=21.6±1.3 years; musicians: age range 20–23 years, mean±SD=21.3±1.1 years) and academic performance as measured by Grade Point Average (GPA, all participants were between 3 and 3.5) for all the courses they had taken in college. All participants had normal hearing, normal or corrected-to-normal vision. None reported any history of head injury or neurological or psychiatric disorders. Written informed consent was obtained from each participant prior to experiment according to a protocol approved by the IRB of the Institute of Psychology, Chinese Academy of Sciences.

Stimuli and procedure

The study adopted a block design where participants performed in separate blocks, one for each of the three tasks, including word encoding, word retrieval, and the pitch judgment control. To discourage visual imagery that may be more likely to occur with eyes closed, participants were instructed to fixate a central cross on a computer screen throughout all experimental blocks. However, due to technical limitation, eye movements were not recorded, which is a potential confound for the comparison of visual cortical activities

In the 40-s encoding blocks, 20 words were presented auditorily, each for 1000 ms with 1000 ms inter-stimulus-interval (ISI). The words were two-syllable concrete Chinese nouns, sampled from a wide variety of semantic categories, such as natural land-scapes, fruits, animals, and tools. Participants were instructed to remember as many words as possible. To encourage deep encoding, they had to judge whether the words referred to natural or artificial objects and responded with left or right button press.

In the 30-s retrieval blocks, participants were instructed to silently recall as many words as possible. They need to press a button every time they recalled a word. In the 20-s pitch judgment blocks, 10 pairs of pure tones were presented. The first tone was present for 1000 ms followed by the second tone for another 1000 ms. The two tones could be either a low-high pair (500 vs. 2000 Hz) or a high-low pair (2000 vs. 500 Hz) and participants were to press a left button in the first case and a right button in the second

A nonferrous response box was held in the participant's right hand to record their responses. There were two buttons in the response box and participants used their right index and middle fingers to press left and right buttons respectively during encoding

and pitch judgment. During retrieval, they only used their right index finger to press the left button each time they recalled a word, as it was impossible to ask participants to output retrieved words inside the MRI scanner without introducing motion artifacts. This task assignment was meant to provide a crude measure of recall performance.

Each participant completed a single run consisting of six repetitions of a fixed sequence. The sequence started with an encoding block, followed by a retrieval block, and then by a pitch judgment block. Each block was preceded by a 2-s instruction screen reminding of the task for that block. Each of the six encoding blocks contained the same word list with pseudo-randomized order. Following the scanning, verbal memory performance was assessed for each participant by presenting 20 new words randomly mixed with the 20 test words for recognition. The new words were also concrete nouns comparable to the test words in semantic contents. Participants responded by pressing either a left or a right button to indicate "old" or "new" responses and their response times were also recorded.

All stimuli were programmed with the E-Prime software (Psychology Software Tools, Inc., Pittsburgh, PA, USA) and delivered via an audio–visual stimulus presentation system designed for MRI environment. There was a practice session outside the scanner to familiarize participants with the task. Volume was adjusted for each participant individually for clear and comfortable hearing inside the scanner.

Image acquisition

Scanning was conducted on a 1.5 T Siemens SONATA scanner using a three-axis local gradient coil optimized for whole-brain echo-planar imaging. A fast FLASH (fast low-angle shot imaging) (TR=30 ms, TE=1.17 ms, FOV=32.5 cm, matrix=192×256, slice thickness=1.3 mm, gap=0.26 mm, 128 sagittal slices) sequence was used to acquire a high-resolution 3D anatomical whole brain image for spatial normalization. For functional images, 20 axial images parallel to the anterior commissure/posterior commissure (AC/PC) plane and covering the whole brain were acquired for each TR with a T2* gradient echo EPI (echo planner imaging) pulse sequence sensitive to blood oxygenation level dependent contrast (TR=2 s, TE=60 ms, FOV=22 cm, matrix=64×64, flip angle=90 degrees, slide thickness=5 mm, gap=1.5 mm). The whole run produced 288 image volumes and lasted 576 s.

Image analysis

Image analysis was performed using AFNI software package (Cox, 1996, http://afni.nimh.nih.gov/afni). Preprocessing consisted of slice acquisition correction, head motion correction, and spatial smoothing (Gaussian kernel, full-width-at-half-magnitude=6 mm). To further eliminate motion-related and physiological artifacts, and other noise, an fMRI data enhancing technique we previously developed based on ranking and averaging independent component analysis by reproducibility (RAICAR) was applied on the dataset (Dong et al., 2009; McKeown et al., 2005; Yang et al., 2008). Briefly, with this technique, the data for each participant were decomposed using independent component analysis for 30 times, and the components with low reproducibility index (<100) were eliminated. Three persons with experience in fMRI data analysis, blind to participants grouping, then independently eliminated components representing artifacts or noise, based on their activation maps and shape of their mixing time courses. Only components classified by two or more persons as artifact or noise were eventually eliminated. The final remaining components were reconstructed backward to produce a putatively de-noised dataset used in further analysis.

For individual analysis, voxel-wise brain responses were estimated with general linear models for the encoding and retrieval

conditions, relative to the pitch judgment condition. The resulting functional images, along with the anatomical images, were then transformed into standard stereotaxic space (Talairach and Tournoux, 1988), re-sampled to $3\times3\times3$ mm³ voxel size with linear interpolation. At the group level, random-effect analyses using *t*-tests were conducted to generate activation maps for each group during encoding and retrieval, and for cross-group comparisons. Two anatomical region of interest (ROIs) (one in the left and one in the right hemisphere) including Brodmann's area (BA) 17 and 18 using the TT_N27 template in AFNI (Eickhoff et al., 2005) were pre-defined for focused examination of visual cortical activities. For all voxels in the ROI, the percentage signal changes were extracted, pooled, and compared across the two participant groups.

Effect size was computed for all activated regions using the G*Power software (Erdfelder et al., 1996; available at www.psycho. uni-duesseldorf.de/aap/projects/gpower/). For each region, mean percentage signal changes for individual participants were first computed pooling over all voxels in the region. The group means and standard deviations of these individual values were then entered into the G*Power software to obtain the effect size measures. Two sets of means and standard deviations (SDs) were used for effects in between-group comparisons, one for musicians, and one for non-musicians. Only one set of mean and SD was used for within-group comparisons that, in the present study, were all one-sample *t*-tests (e.g., encoding vs. pitch judgment for musicians).

For regions of interest that were not significantly activated, *post-hoc* power analysis was performed to assess the reliability of the negative results. For a given region, its effect size was first computed as described above and then entered into the same G*Power software at a conventionally-adopted power level of 0.80. The outcome was the expected sample size that would have been needed to reject the null hypothesis.

RESULTS

Behavioral performance

The average numbers of button presses across the six retrieval blocks for the two participant groups are shown in Table 1. The overall numbers were comparable across participant groups (musicians: 12.5 ± 2.9 , non-musicians: 12.8 ± 3.4 , df=18, P>0.5). These numbers may not accurately reflect the number of different words recalled as some participants indicated recalling the same item more than once within a single retrieval block and pressing the button each time the item was recalled.

Response accuracies in the pitch judgment task were very high and reached ceiling for both groups (musicians: $100.0\pm0.0\%$, non-musicians: $99.5\pm1.6\%$, df=18, P>0.1), suggesting adequate task engagement in all participants.

The musician group showed better verbal memory performance in the post-scanning recognition test than the

Table 1. Mean number of button presses in each retrieval block for the musician and non-musician groups

1	2	3	4	5	6
9.0	10.3	13.1	12.8	14.9	14.7
1.6	1.7	2.6	2.4	1.4	2.0
8.8	10.9	12.1	13.9	15.6	15.6
2.6	1.5	2.6	2.1	2.2	3.0
	1.6	1.6 1.7 8.8 10.9	9.0 10.3 13.1 1.6 1.7 2.6 8.8 10.9 12.1	9.0 10.3 13.1 12.8 1.6 1.7 2.6 2.4 8.8 10.9 12.1 13.9	9.0 10.3 13.1 12.8 14.9 1.6 1.7 2.6 2.4 1.4 8.8 10.9 12.1 13.9 15.6

Table 2. Summary of activated regions in encoding and retrieval tasks for the musician and non-musician groups

Condition	Anatomic structures	Volume (ml)	Talairach coordinates			t-statistic	Effect size
			X	У	Z	<i>df</i> =16	
Musician encoding	Left medial frontal gyrus	7452	-37	15	29	5.07	1.23
	Left inferior frontal gyrus	3969	-34	10	27	4.50	1.09
	Left lingual gyrus	3645	-20	-87	-6	4.45	1.19
	Left hippocampus	2916	-34	-19	-13	4.28	1.30
	Right insula	2673	32	17	8	5.18	1.19
	Right lingual gyrus	2592	13	-83	-1	3.81	0.88
	Left superior frontal gyrus	2214	-28	41	14	3.53	0.89
Non-musician encoding	Left medial frontal gyrus	5832	-35	8	31	4.76	1.61
	Left inferior frontal gyrus	5184	-51	24	20	4.09	1.36
	Right insula	2295	29	18	12	3.42	1.26
	Left parahippocampal gyrus	1458	-35	-32	-13	3.36	1.12
	Left hippocampus	1215	-33	-14	-16	3.29	1.08
Musician retrieval	Left middle occipital gyrus	8694	-27	-82	-7	5.94	0.81
	Left middle frontal gyrus	7209	-31	44	22	4.25	1.63
	Left cerebellum	5859	-1	-58	-34	4.94	0.94
	Right lingual gyrus	4968	13	-88	2	4.37	1.41
	Right hippocampus	3861	29	-43	5	4.20	0.74
	Left inferior frontal gyrus	3591	-44	11	29	5.60	1.98
	Left medial frontal gyrus	3051	-4	7	46	5.82	1.06
	Left insula	3024	-34	12	8	4.81	1.17
	Right insula	2916	35	11	5	5.49	2.06
	Right cingulate gyrus	2673	3	13	39	5.23	1.21
	Left parahippocampal gyrus	1269	-28	-43	-10	5.03	1.05
Non-musician retrieval	Left inferior frontal gyrus	9639	-33	9	29	5.67	1.64
	Left cingulate gyrus	7560	-4	11	40	5.30	1.35
	Left cerebellum	6291	-3	-51	-24	4.40	1.02
	Right cingulate gyrus	5562	5	18	33	4.24	1.08
	Right insula	3213	32	15	7	4.21	2.14
	Left insula	2889	-30	19	7	4.20	1.73
	Right middle frontal gyrus	1809	38	37	29	3.60	1.52
	Left precuneus	1782	-19	-73	38	4.40	0.97

Note: All activations were thresholded at P<0.05 and multiple comparisons corrected using Monte Carlo simulations. Talarirach coordinates and t-statistics were for the peak voxel in a given region of activation. See Methods for the computation of effect sizes.

control group by showing a slightly but significantly higher recognition accuracy (mean \pm SD: 99.8 \pm 0.8% vs. 98.3 \pm 2.1%, two-sample *t*-test, *df*=18, *P*<0.05). There was only one participant in the musician group who made only one mistake in recognition. For non-musicians, there were five persons who made a total of seven mistakes.

Imaging results

The imaging data from two participants were discarded due to excessive head movements, one for each group. For the encoding condition, as shown in Table 2, musicians and non-musicians showed similar activations in left inferior and medial frontal gyrus, left hippocampus, and right insula, relative to the pitch judgment control. Crossgroup comparison, that is, (musician encoding—musician pitch judgment control) vs. (non-musician encoding—non-musician pitch judgment control), revealed no significant brain activations during encoding.

For the retrieval condition, musicians showed significant activations in left middle, inferior, and medial frontal gyrus, right hippocampus, bilateral insula, right cingulate gyrus, left parahippocampal gyrus, left cerebellum, and bilateral early visual cortex, relative to pitch judgment. The

left visual cortical activation extended to the ventral lateral occipital complex (ventral LOC). Non-musicians showed activations in left inferior frontal gyrus, right middle frontal gyrus, bilateral insula, bilateral cingulated gyrus, left cerebellum, and left precuneus, but not any visual cortical regions. Cross-group comparison (musician retrieval-musician pitch judgment control) vs. (non-musician retrieval non-musician pitch judgment control) revealed significantly greater activations for musicians than non-musicians in left medial frontal gyrus, right inferior frontal gyrus, left amygdala, right hippocampus, and bilateral lingual gyrus and left middle occipital gyrus (including bilateral early visual cortex, left fusiform gyrus, and left ventral LOC; see Table 3, Fig. 1). As shown in Table 3, the effect sizes for these activations were all reasonably large. Within the visual areas, the activation pattern was left-lateralized, with 188 voxels activated in the left side and 32 voxels in the right side.

More focused analysis using the anatomically-defined ROI (Brodmann areas 17 and 18) confirmed the results from whole brain analysis for both the encoding and the retrieval conditions (see Fig. 2). Specifically, for the encoding condition, neither the left nor the right ROI showed

Table 3. Summary of brain regions showing greater activity for musicians than non-musicians during retrieval task

Anatomical structures	Volume (<i>ml</i>)	Talairach coordinates			t-statistic	Effect size
		x	У	z	df=16	
Left lingual gyrus and middle occipital gyrus	5076	-30	-83	-8	6.17	1.18
Right inferior frontal gyrus	4239	53	19	8	5.37	1.53
Right hippocampus	3078	30	-10	-18	4.39	1.82
Left amygdala	1215	-25	-7	-10	3.94	1.33
Left medial frontal gyrus	918	-7	59	14	3.12	1.23
Right lingual gyrus	864	16	-83	3	4.78	0.90

Note: All activations were thresholded at P<0.05 and multiple comparisons corrected using Monte Carlo simulations. Talarirach coordinates and t-statistics were for the peak voxel in a given region of activation. See Methods for the computation of effect sizes.

significant differences across the musician and the non-musician groups (df=16, P>0.20). The *post-hoc* power analysis indicated that, for these negative results to achieve significance, the expected sample size would be very large (140 for the left ROI and 86 for the right ROI). For the retrieval condition, both ROIs showed significantly different activations across the two groups and the effect size was 0.98 for the left ROI and 1.03 for the right.

For either encoding or retrieval, voxel-wise comparisons did not reveal activation differences across the two groups of participants in any auditory cortical regions, including PT. The *post-hoc* power analysis showed that for the musician vs. non-musician comparison during encoding, the effects in the left and right PT were so weak as to require 702 and 144 participants respectively to reach significance. For the same comparison

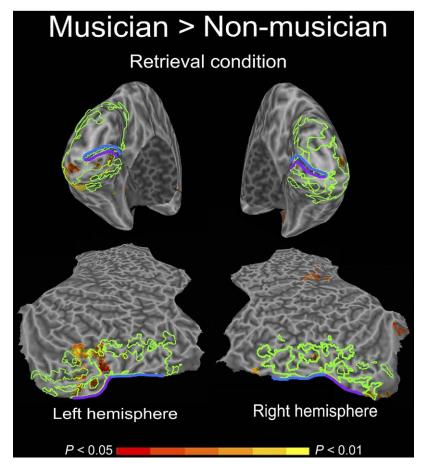


Fig. 1. The cortical surfaces (top: inflated, bottom: flattened) showing brain regions with significantly greater activation for musicians than non-musicians during the retrieval task. The green lines show the border of the early visual cortex ROI (Brodmann 17 and 18). The purple and blue lines mark the edges where the cortical surface was cut apart for flattening to indicate how the inflated surfaces correspond to the flattened surfaces. The color bar shows voxel-wise *P*-value, corrected for multiple comparisons. For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.

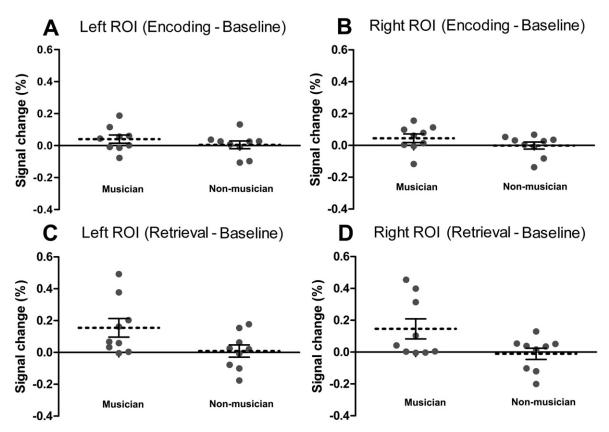


Fig. 2. Mean percentage BOLD signal changes for the two participant groups during the encoding and retrieval tasks, relative to the pitch judgment baseline in the anatomically defined visual cortical ROIs. (A, B) for left and right ROIs during encoding; (C, D) for left and right ROIs during retrieval. The dots indicate mean values of signal change for individual participants (nine for the musician group, and nine for the non-musician group). The horizontal dashed lines indicate the group average of the individual signal changes. The error bars show standard errors.

during retrieval, the corresponding numbers were 294 and 92.

DISCUSSION

As a follow-up of our previous behavioral research, this study presents the first piece of brain imaging evidence regarding the neural correlates of the extensively-documented superior verbal memory in musicians, relative to non-musicians.

Even though the memory task involved only auditory stimuli but no visual sensory stimulation, musicians but not non-musicians showed visual cortex activation during retrieval. Such visual activations cannot be attributed to some general processing differences between the two participant groups, as the group comparison did not reveal any auditory cortex activation for either retrieval or encoding. These results suggest that the visual cortex may facilitate the retrieval process in musicians and contribute to their superior verbal memory. The present study failed to support a prediction from Chan et al. (1998) that the left PT should distinguish between musicians and non-musicians, because no group difference in brain activation was found in either left or right PT. And a reasonable increase in sample size is unlikely to produce any qualitative changes to these negative results. As shown by the power analysis, the required sample sizes for positive findings in these two

regions were far more than that are typically used in similar studies. This suggests that PT, although critical for auditory and musical processing in general, may not be important for superior verbal memory in musicians.

Related to this issue, also with a non-musical task, Sluming et al. (2007) reported PT activations for both musicians and non-musicians but no difference between the two groups (the authors did not comment on this negative result). Note that given our interest in the visual cortex, we would only report cortical regions showing greater activity for the memory task than the pitch judgment baseline. There were deactivations in PT (i.e., stronger activity in pitch judgment than memory encoding), which had been considered less relevant and ignored in results reporting. That only deactivations but no activations were found may be due to the specific tasks we used. For the verbal memory task, there was only one item presented in each trial during encoding and no stimulus presented at all during retrieval. In contrast, the pitch judgment task always involved a pair of stimulus in each trial and required a comparison between the two.

Other than the visual cortex, the musician group also showed more activation in frontal cortices, hippocampus, and amygdala during retrieval, relative to the non-musician group. Frontal cortices and hippocampus are heavily involved in many memory processes (e.g., Ranganath et al.,

2005; Karlsgodt et al., 2005; Kramer et al., 2005), including verbal memory (e.g., Sederberg et al., 2007). Amygdala serves to enhance functions of the medial temporal lobe memory system (Dolcos et al., 2004) and influences memory consolidation (McGaugh, 2004). There are studies (e.g., Greenberg et al., 2005) showing activations in amygdala, hippocampus, and inferior frontal gyrus during episodic retrieval, with pronounced functional connectivity among each other.

Echoing a previous report in the blind participants who like musicians possess superior verbal memory and show visual cortical activities during verbal memory retrieval, the present results support our hypothesis that the same neural substrates may underlie enhanced verbal memory abilities in both the blind and the musically-trained populations. This establishes a novel connection between two lines of brain plasticity research involving participant groups with distinctive characteristics, which may help constrain theoretical models and identify general features of neural plasticity. Note that the visual cortical activations identified in the Amedi et al. study were mostly in early visual cortex, while we found activations both in early visual cortex and left ventral LOC. Further, while the Amedi et al. (2003) study examined the retrieval but not the encoding stage, we scanned both stages and were able to show the former but not the latter stage to be critical to the superior memory in musicians.

Amedi et al. (2003) interpreted their results as reflecting reorganizational changes to the visual cortex, driven by sensory deprivation in the visual modality in the blind people, making it a region of extra memory resources. Different from their study, the present study shows that sensory deprivation is not a necessary condition for such reorganization. This is particularly informative given that most studies demonstrating cross-modal plasticity involves afferent input deprivation in one way or another (for a review, see Johnston, 2009).

Cross-modal functional reorganization is assumed to rely on pre-existing but latent anatomical connections between different modalities, and presumably in the present situation, between visual cortex and the classical memory areas (Distler et al., 1993; Rempel-Clower and Barbas, 2000; Rockland and Van Hoesen, 1994) as suggested by Amedi et al. (2003). Some of these connections projecting to the visual cortex are known to be much more extensive in the early childhood but wiped out progressively with age (Dehay et al., 1984). The early starting in musical training may be a critical factor allowing effective use of these connections when they are relatively more available (Elbert et al., 1995). The nature of musical training, long-term, demanding, and requiring multisensory interactions, may be other factors in triggering the need to use as much available neural resources as possible. The same factor of extra task demand may also be at work in the case of sensory deprivation where one modality, supported by other modalities in the normal populations, has to work all by its own in the blind people.

We extracted the mean blood oxygen level dependent (BOLD) signal changes in the two visual cortical ROIs for

each time point to produce signal time courses for each of the six blocks. We then averaged the time courses for the first three blocks (first half of the run) and the second three blocks (second half of the run) separately. As shown in Fig. 3A, B, for musicians, in both the left and the right visual cortex ROIs, the time courses show increasing magnitude, reaching a peak around 12 s and then gradually leveling off. This particular temporal pattern of signal change seems to mirror retrieval characteristics where retrieval effort within each block was more active in the earlier period with more frequent and successful retrieval of studied items, relative to the later period. Interestingly, as shown in Fig. 3C, D, in both ROIs, the signal peaks were reached more rapidly in the second half of the run, compared to the first half (left ROI: 11.3 ± 6.8 s vs. 17.8 ± 7.2 s. df=8, P=0.001; right ROI: 10.8 \pm 7.1 s vs. 15.0 \pm 8.6 s, df=8, P<0.05). For non-musicians, there are no similar temporal patterns of signal change (Fig. 3A, B), nor any differences in time-to-peak between the two halves of the run (Fig. 3E, F).

When the same procedure was conducted in all cortical regions activated for both groups during retrieval, including right anterior cingulate (ACC), left inferior frontal gyrus (IFG, BA45), and bilateral insula, none of these regions showed any changes in time-to-peak from the first to the second half of the run in either group (see Fig. 4 for an sample illustration using IFG). Therefore, the time-topeak shortening was specific to musicians and only in the visual cortex. In the imaging literature, similar changes of peak time have been interpreted to indicate that the areas demonstrating such changes are progressively more engaged in the ongoing performance of the task (Duff et al., 2007; Rombouts et al., 2005), which reflects the relevance and usefulness of these areas to the task. We therefore take these results as additional evidence supporting the functional role of visual cortex in the present memory task.

Based on previous research (Chan et al., 1998; Ho et al., 2003), we hypothesize that musical training improves verbal memory. However, across-group difference in memory performance in the present study, as measured with recognition accuracy was small and not very convincing. This may be because the experimental tasks used here were relatively easy. For example, participants repetitively memorized the same set of words across six blocks. Our results therefore imply that even when musicians and non-musicians show similar levels of performance in relatively easy memory tasks, they may still engage different neural mechanisms. Clearly more evidence is needed to fully establish the association between musical training and improved verbal memory and to identify the specific aspects of musical training, for example, musical score reading, that account for the superior verbal memory in musicians. One interesting new direction would be to compare musicians and non-musicians with standard memory tests.

Amedi et al. (2005) showed that the auditory cortex can be suppressed due to visual processing. This raises the possibility that when our participants were doing the pitch judgment task, they may have also suppressed the visual

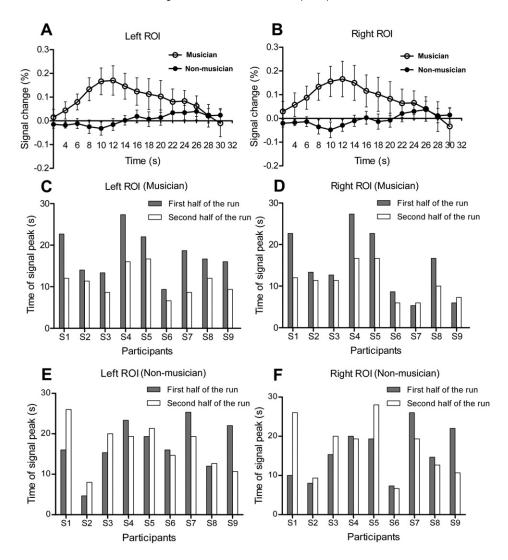


Fig. 3. Time courses for BOLD signal changes within the 30-s retrieval period (averaged across all six retrieval blocks) in left (A) and right (B) ROIs. Musicians (open circles) show increasing signal changes over time, peaking around 12 s and then gradually leveling off, reflecting retrieval characteristics within a retrieval block (see text for more details). Non-musicians (closed circles) are no different from baseline activities. For musicians, two average time courses were also computed, one pooling over block 1–3 (first half of the run) and the other over block 4–6 (second half of the run). The peak times for the two time courses were then identified for each participant and plotted in (C, D) for the two ROIs. Peak times were shortened in the second half of the run (white bars), relative to the first half of the run (gray bars). The corresponding results for non-musicians are provided in (E, F). Note that the error bars reflecting inter-subject variability are smaller for non-musicians. This is not an artifact but can be understood as follows, the musicians engaged the visual cortex during retrieval producing larger individual differences in BOLD signals, that is, different participants may engage their visual cortex to different degrees. Non-musicians, in comparison, did not engage the visual cortex and were therefore not subject to this source of individual variability. In other brain regions similarly activated in both groups, as can be seen for left BA45 in Fig. 4, the error bars would be comparable in size across the two groups.

cortex. Suppose, compared with the controls, musicians somehow suppressed the visual cortex more during pitch judgment, they would show more visual activation in the retrieval>pitch judgment comparison. That is, the crossgroup difference in visual cortical activation found for the retrieval>pitch judgment contrast may have originated from pitch judgment but not memory retrieval. Ideally, testing of this alternative explanation would require a resting baseline, which was not intentionally included in our study. There was only a 16-s resting scan prior to the first experimental block for encoding, which was designed to familiarize the participants with the noisy scanning environment. Though short and non-optimal, it allows a coarse

analysis to see whether musicians and non-musicians differed in visual cortical activations during the baseline pitch judgment task. We compared the percentage signal changes in the pitch judgment task relative to this short resting period without normalization. The results failed to show any evidence of differential visual cortical activation for pitch judgment between musicians and non-musicians (Left ROI: 0.15% vs. 0.21%, df=16, P>0.5; Right ROI: 0.13% vs. 0.31%, df=16, P>0.5).

Following Chan et al. (1998), the present study used concrete words, which may have induced visual imagery in the semantic categorization task. The left-lateralized activation we observed in visual cortex may reflect imagery-

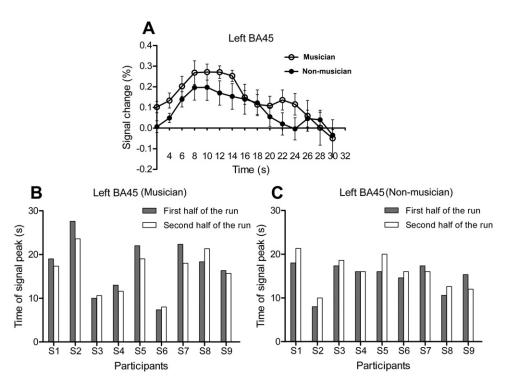


Fig. 4. (A) Time courses for BOLD signal changes within the 30-s retrieval period (averaged across all six retrieval blocks) in left inferior frontal gyrus (BA45) showing an early signal peak during retrieval, as found for the visual ROIs shown in Fig. 3. Peak time computed as for the visual ROIs show no changes from the first half to the second half of the run for either musicians (B) or non-musicians (C).

related activities during retrieval. Many imaging studies have reported such visual cortical activations during visual imagery (e.g., Cui et al., 2007; D'Esposito et al., 1997; Kosslyn et al., 1993, 1995; Sparing et al., 2002). However, there is evidence that musicians and non-musicians showed similar visual imagery abilities (Aleman et al., 2000). Therefore, it is unclear why musicians would engage imagery more than non-musicians for verbal memory per se. One possibility is that musical training may have shaped the visual cortex to be more readily available for help in the verbal memory task to musicians, compared with non-musicians. Further study is needed to reveal specific functions of visual cortex in verbal memory tasks, such as whether visual activation is automatic or under strategic control.

CONCLUSION

In conclusion, the present brain imaging study found enhanced visual cortical activity in musicians in a verbal memory task, compared with non-musicians, suggesting a functional reorganization of the visual cortex underlying the well-documented superior verbal memory performance in musicians. The finding that such reorganization can result from long-term musical experience in the healthy population extends the brain plasticity literature where cortical reorganizations are usually associated with sensory deprivation.

Acknowledgments—We thank Wen Zhou and Yi Jiang for comments on an earlier version of the paper. This work was supported by the National Nature Science Foundation of China (No. 30670674, 30900366), the Youth Foundation of the Institute of Psychology, Chinese Academy of Sciences (No. O9CX012001), and the National Basic Research Program of China (973 Program, 2007CB512300). We declare no conflicts of interest.

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(Accepted 12 March 2010) (Available online 18 March 2010)