

Regional cerebellar volumes are related to early musical training and finger tapping performance



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ABSTRACT

The cerebellum has been associated with timing on the millisecond scale and with musical rhythm and beat processing. Early musical training (before age 7) is associated with enhanced rhythm synchronization performance and differences in cortical motor areas and the corpus callosum. In the present study, we examined the relationships between regional cerebellar volumes, early musical training, and timing performance. We tested adult musicians and non-musicians on a standard finger tapping task, and extracted cerebellar gray and white matter volumes using a novel multi-atlas automatic segmentation pipeline. We found that early-trained musicians had reduced volume in bilateral cerebellar white matter and right lobules IV, V and VI, compared to late-trained musicians. Strikingly, better timing performance, greater musical experience and an earlier age of start of musical training were associated with smaller cerebellar volumes. Better timing performance was specifically associated with smaller volumes of right lobule VI. Collectively, these findings support the sensitivity of the cerebellum to the age of initiation of musical training and suggest that lobule VI plays a role in timing. The smaller cerebellar volumes associated with musical training and timing performance may be a reflection of more efficiently implemented low-level timing and sensorimotor processes.

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Introduction

Musical performance relies on accurate timing and nuanced rhythm production as vital parts of its power to communicate. The neural correlates of these processes are thought to at least partially involve the cerebellum (E et al., 2012; Zatorre et al., 2007; Ivry et al., 1988, 2002; Koch et al., 2007) a brain structure that has also been associated with plasticity related to musical training, observable when comparing the cerebellar volumes of musicians with those of non-musicians (e.g. Hutchinson et al., 2003). Musical-training related plasticity in other brain areas has been shown to be moderated by the age of initiation of musical training, with evidence pointing to a sensitive period before the age of seven years (Penhune, 2011). However, to the best of our knowledge, it is not known whether cerebellar lobular volumes or the timing processes

associated with the cerebellum are affected by training during this sensitive period. In the present study, we used a novel magnetic resonance imaging (MRI) segmentation algorithm (Chakravarty et al., 2013; Park et al., 2014) to calculate regional volumes within the cerebellum and then examined the associations between the volumes of specific cerebellar regions, musical training experience and timing data from a finger-tapping task in musicians and non-musicians. The goal of the study was to better understand the relationships between age of start of training, cerebellar volume and timing variability. In addition, we hoped to more precisely link timing variability with volumes of specific cerebellar regions.

Previous work in our laboratory suggests that there is a sensitive period for musical training, such that acquisition of musical skill before age seven is associated with long-lasting behavioral and structural brain differences. The differences between early- and late-trained adult musicians include superior performance in sensorimotor synchronization tasks (Bailey and Penhune, 2010; Watanabe et al., 2007), greater connectivity in the region of the corpus callosum that links sensorimotor cortices of the two hemispheres (Steele et al., 2013), and greater gray matter density in the premotor cortex (Bailey et al., 2013). Both behavioral and brain differences are significant even after controlling for total years of musical experience. Overall, these results suggest that sensorimotor integration and timing may be sensitive to early training (Penhune, 2011).

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It may be the case that cerebellar structure and function are also affected by an early age of start, given the evidence linking the cerebellum to musical training. The cerebellum has traditionally been associated with timing and motor processes (Manto et al., 2012), but is now increasingly seen as playing a role in higher level cognitive processes as well (Schmahmann, 1998; Stoodley, 2012), many of which are likely recruited for musical performance, suggesting that the study of musicians can help further our understanding of the functions of the cerebellum.

Musicians have been found to have larger cerebellar volumes than non-musicians and volume was correlated with lifelong intensity of practice (Hutchinson et al., 2003). In a study of mostly right-handed participants, musicians were found to have greater volume of right cerebellar white matter and right superior and middle cerebellar peduncles (Abdul-Kareem et al., 2011). Functionally, the cerebellum is likely involved in the perception and production of musical rhythm. A recent meta-analysis (E et al., 2012) identified two PET and five fMRI studies that used rhythm perception and production tasks. The musical rhythm tasks involved right lobules IV and V and bilateral lobules VI and VIIIA/B. Lobule V has also been associated with hand movement while lobules VIIIA/B have been linked to motor tasks (Stoodley & Schmahmann, 2009).

Substantial evidence also points to the cerebellum's involvement in timing on the millisecond scale (Manto et al., 2012). Event-based timing, a form of sub-second timing modeled as a central clock process operating independently of the motor response that is being timed (Wing and Kristofferson, 1973) likely underlies the time-based components of musical performance (Baer et al., 2013). It is typically evaluated using the finger-tapping task (Repp and Su, 2013; Repp, 2005), in which participants first tap in synchrony with an auditory metronome (paced phase); when the metronome stops, they are asked to continue tapping at the same rate (unpaced phase). Timing ability is measured by analyzing the time series of inter-response intervals (IRIs) of the unpaced phase, such that an IRI is defined by the time interval between adjacent taps. The tapping paradigm employed in the present study was also used in a recent study from our group that showed that musicians are substantially less variable in the timing of their unpaced responses compared to non-musicians (Baer et al., 2013). This is consistent with other studies that have demonstrated that musicians are less variable (Franěk et al., 1991; Repp, 2010; Repp and Doggett, 2007), and show less drift away from the prescribed tapping rate compared to non-musicians (Collier and Ogden, 2004).

There is some debate about the precise localization of timing-related processes within the cerebellum. Some studies point to the lateral cerebellar hemispheres (Ivry et al., 1988; Koch et al., 2007), while others indicate the vermis (Bernard and Seidler, 2013; Théoret et al., 2001), and still others suggest the involvement of lobule VI (E et al., 2012; Thaut et al., 2009). Thus, while overall evidence points to a role for the cerebellum in sub-second timing, it is less clear which specific regions of the cerebellum are involved. The analysis of regional cerebellar volumes and their relation to finger tapping performance can help to clarify cerebellar involvement in timing.

To the best of our knowledge, volumetric differences between musicians and non-musicians have not been investigated at the level of individual lobules of the cerebellum, nor has the age of initiation of musical training been considered when investigating cerebellar volumes. In the present study, we analyzed finger tapping data and structural cerebellar imaging data from musicians and non-musicians. We examined the relationships of the volumes of cerebellar lobules with the age of start of musical training, years of training, and timing variability exhibited in the tapping task. We expected to find associations between musical training and the volumes of right lobules IV and V and bilateral lobules VI and VIII, in support of functional imaging studies that have implicated these regions in musical tasks. We also predicted that the volume of lobule VI would be negatively associated with timing variability. Finally, we predicted that earlier age of start of musical training and greater

number of years of musical training would be associated with smaller timer variability.

Materials and methods

Participants

Fifty-eight participants were included in this study (thirty-eight musicians and twenty controls selected to have less than three years of musical training or experience). All had high-resolution T1 MRI scans as part of a larger study (Bailey et al., 2013; Steele et al., 2013). Thirty-one participants (twenty musicians) returned for behavioral testing on the finger-tapping task. Demographic and musical experience data for both sets of participants are presented in Table 1. All were right-handed, neurologically healthy, and gave informed written consent to participate. They were also administered the Musical Experience Questionnaire (Bailey and Penhune, 2010), from which we extracted the age at which they first began to play an instrument, and the total years of musical experience, including practice and formal training. The Concordia University Human Research Ethics Committee and the McGill University/Montreal Neurological Hospital and Institute Research Ethics Board approved the experimental protocol.

Image acquisition and processing

Structural MRI scans were acquired using a Siemens Trio 3 T MRI scanner with a 32-channel head coil (TR = 2300 ms, TE = 2.98 ms, voxel size = $1 \times 1 \times 1 \text{ mm}^3$). All MRI processing was done on the General Purpose Cluster at the SciNet supercomputer center. Total brain volume was estimated from the gray and white matter of the cerebrum and the cerebellum, calculated using parts of the CIVET pipeline (Ad-Dab'bagh et al., 2006). The cerebellum was segmented in native space using the method of multiple automatically generated templates of different brains (MAGeT Brain; Chakravarty et al., 2013; Park et al., 2014). The MAGeT algorithm is a multi-atlas label fusion technique that is ideal when confronted with the challenge of using a limited number of atlases as input for the segmentation of a dataset. The algorithm first matches a subset of the input images to a set of expertly labeled atlases. The newly labeled images are now referred to as "templates". The atlases, supplemented by this subset of segmented input, form the template library, where each template now has as many possible candidate labels as there are atlases. For example, in the present study, we used five atlases and randomly chose 20 input images for the template library (evenly split between male and female and between musician and non-musician, with the musicians evenly split between early- and late-trained). This generated a template library of 100 different segmentations. MAGeT then matches each input image to each of the templates, to generate all possible candidate segmentations for each input image. In a final step, the label of each voxel in an input image is determined by voxel voting, such that the most frequently occurring label among all the candidate segmentations becomes the final label. In the present study, five high-resolution atlases, produced from healthy participants not part of our study were manually segmented based on the atlas of Schmahmann et al. (1999), as described in Park et al. (2014). The Schmahmann nomenclature was used to refer to sub-regions of the cerebellum, wherever possible. The deep cerebellar nuclei were included in the volumes of left and right white matter that were estimated from the MAGeT segmentations as it is difficult to identify these nuclei in our T1-weighted MRI data.

The generation of the high-resolution cerebellar atlases (Fig. 1a) used for MAGeT and the validation of the MAGeT algorithm on the cerebellum are described elsewhere (Park et al., 2014). The segmentations used in the present study (Fig. 1b) were checked manually by an expert rater (co-author MTMP). We focused our analysis on those lobules for which we hypothesized associations with musical experience and

Table 1
Demographic and musical training data.

	N	Mean age (years)	Age of start of training (years)	Years of training
MRI data				
Musicians	38 (15 female)	25.3 (5.3)	8.6 (3.4)	16.3 (4.3)
ET	18 (10 female)	22.6 (4.1)	5.8 (1.1)	16.2 (4.1)
LT	20 (5 female)	27.8 (5.2)	11.2 (2.7)	16.4 (4.7)
Non-musicians	20 (10 female)	26.0 (4.4)	10.6 ⁺ (4.2)	1.0 ⁺ (0.5)
Tapping & MRI data				
Musicians	20 (6 female)	26.3 (6.3)	9.0 (3.5)	16.9 (4.4)
Non-musicians	11 (7 female)	25.6 (4.1)	11.6 ⁺⁺ (5.1)	1.2 ⁺⁺ (0.4)

Note. ET: early-trained musicians. LT: late-trained musicians. Parenthesized values are standard deviations, unless otherwise noted. ⁺Four participants had no musical training, ⁺⁺Three participants had no musical training.

timing (right lobules IV and V, bilateral lobules VI and VIII), as well as on bilateral white matter.

Behavioral stimuli, task conditions and procedure

The experimental set-up for the finger-tapping task was identical to that used in a previous study (Baer et al., 2013), including the use of motion capture equipment to record finger movement. Participants used their right index finger to tap on a tabletop in synchrony with an auditory metronome (1 kHz 20 ms tone) for 35 cycles (paced phase). The metronome then stopped and they were asked to continue tapping at the same rate for approximately 35 additional cycles (unpaced phase) until a final tone sounded to indicate the end of the trial. Participants performed a block of six such trials for each of three different rates (250, 500 and 750 ms inter-stimulus intervals), with a 30 s rest between trials. The order of tapping rates was counterbalanced across participants.

Behavioral apparatus

Finger movement was recorded with the Visualeyex VZ3000 3D motion tracking system, manufactured by Phoenix Technologies. An infrared light emitting diode (LED) was attached with Velcro tape to the nail of the right index finger. Infrared-sensitive cameras tracked the position of the marker in three-dimensional space at a sampling rate of 200 Hz and to a spatial resolution of 0.015 mm. A National Instruments 6221 Data Acquisition board was used to synchronize the Visualeyex system with the computer-generated metronome tone, which was heard through a pair of Sony MDR-7506 headphones. Each participant was

seated at a table of height 70.0 cm, on a chair with independently adjustable seat and armrests.

Behavioral data analysis

Adjusting the local coordinate reference frame of the 3D motion capture data so that the xy-plane coincided with the tabletop, we analyzed the z-coordinate of motion, corresponding to finger height, to automatically detect the onset of each tap, using custom software written in Matlab. As described in detail elsewhere (Baer et al., 2013), our algorithm first identified local maxima on the acceleration curve of finger motion and then adjusted the corresponding points on the position curve so that they coincided with nearby local minima. This was a more reliable method of detecting tap onset points than examining the position curve directly for local minima. We then focused on data from the unpaced phase, when internal timing processes, rather than synchronization with external stimuli, were likely to predominate. The inter-response intervals (IRIs) of the tapping cycles of the unpaced phase, defined as the duration in time between adjacent taps, were calculated. We excluded the first two cycles of the unpaced phase from all analyses (Zelaznik and Rosenbaum, 2010).

Several measures of temporal variability in the unpaced phase were calculated. The average coefficient of variation (standard deviation divided by the mean) of the IRI across all trials of a condition is a general measure of tapping variability, normalized by interval duration. We next separated out long-term drift away from the prescribed rate by estimating drift as a linear trend in the time series of responses of the unpaced phase. We calculated the slope of this trend line as an estimate of drift and also calculated the variance of the linearly detrended IRI time series. Next, we broke down this remaining variance

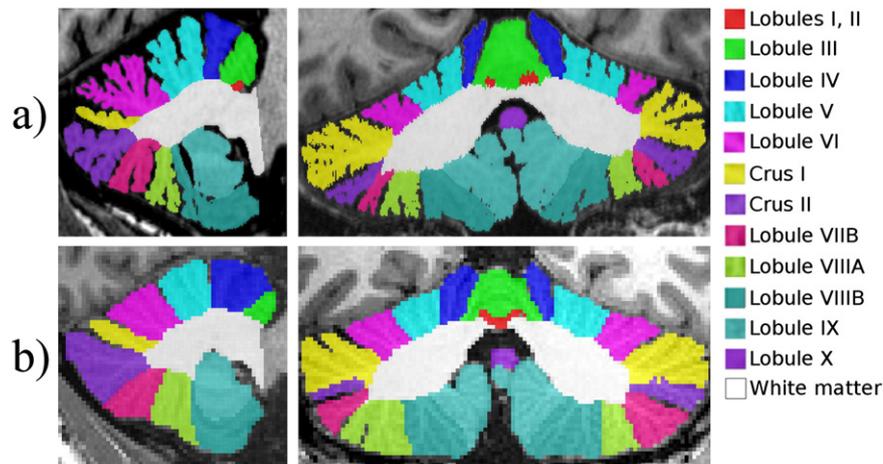


Fig. 1. Midline cerebellar sagittal and coronal slices. (a) Manually segmented high-resolution cerebellar atlases acquired from super-sampling 3 T images from 5 healthy participants who were not part of this study. 0.3 mm isotropic voxels. (b) MAGEt-labeled cerebellum of a musician, 1 mm isotropic voxels.

into timer and motor sources, using the Wing and Kristofferson (1973) model.

Group differences were analyzed using repeated-measures ANOVAs. The Greenhouse–Geisser correction was applied where necessary, based on the results of Mauchly's test of sphericity. The results of multiple pairwise comparisons for the ANOVAs are reported using Bonferroni-adjusted p -values. Given the exploratory nature of this study, the balance between the likelihood of committing Type I and Type II errors was taken into account in not correcting for multiple comparisons in the correlational analyses. Effect sizes are reported using the bias-corrected Hedges' g , to guard against overestimation due to small samples (Fritz et al., 2012).

Results

Differences in cerebellar volume between musicians and non-musicians

These analyses compared the total brain volume, total cerebellar volume, and regional cerebellar volumes of musicians and non-musicians. The two groups did not differ significantly in age, $t(56) = .511$, $p = .61$. The non-musicians' duration of musical experience ranged from 0 to 2 years ($M = 1.0$) and none were currently playing an instrument. Musicians' musical experience ranged from 9.5 to 25 years ($M = 16.3$) and all were currently playing (Table 1). Musicians practiced an average of 13.9 h per week.

The cerebellar lobule segmentation that MAGeT produces uses images that are not normalized by transformation to standardized space. To control for known sex differences in cerebellar volume, we planned to normalize our measures with respect to total brain volume (Hutchinson et al., 2003). To confirm the appropriateness of this control, we compared total brain volume in a 2 (sex) \times 2 (musician/non-musician) ANOVA. There was a main effect of sex ($F(1, 54) = 23.105$, $p < .001$), with females having smaller total brain volume, but no effect of musical training and no interaction (Fig. 2). We also evaluated the effect of sex on absolute cerebellar volume with a 2 (sex) \times 2 (musician/non-musician) ANOVA and found a significant effect, $F(1, 54) = 21.081$, $p < .001$, such that females had smaller cerebellar volumes, but no effect of musical experience and no interaction. Based on these results, all subsequent analyses used cerebellar volumes normalized with respect to total brain volume.

Comparing musicians and non-musicians on total cerebellar volume, which averaged 10.92% of total brain volume ($SD = 0.90$), there were no significant differences, $F(1,56) = .011$, $p > .05$. Further, no significant

differences were found when we compared the two groups on volumes of bilateral lobules IV, V, VI and VIIIA/B and bilateral white matter.

Relationship of cerebellar volumes to age of start of training and years of musical experience

Based on previous work identifying a sensitive period for initiation of musical training (Bailey and Penhune, 2010; Steele et al., 2013; Watanabe et al., 2007), we split the musicians into two groups: early-trained musicians (ET; $N = 18$) who started at or before the age of 7 years and late-trained (LT; $N = 20$) who started after the age of 7 years. Their demographic and musical experience data are also presented in Table 1. These groups did not differ in their total years of musical experience, $t(36) = -0.146$, $p > .05$.

Comparisons between ET and LT groups showed that ET musicians had significantly smaller normalized volumes of lobules IV, V and VI in the right hemisphere, smaller white matter volume in both hemispheres, and smaller total cerebellar volume, compared to LT musicians. ET musicians also had significantly smaller white matter volume in both hemispheres compared to non-musicians. There were no significant differences between LT and non-musicians. These findings are summarized in Table 2. The unbiased Hedges' g effect size values indicate that early musical training had a large effect on regional cerebellar volumes. Because ET musicians significantly differed from LT musicians in age ($M = 22.6$ and 27.8 respectively; $t(36) = -3.417$, $p < .01$) we examined possible correlations between age and either total or regional cerebellar volumes. No significant correlations were found, indicating that any differences in cerebellar volumes between the ET and LT groups were not due to a difference in current age.

We next examined correlations between the normalized volumes of the same cerebellar regions and the age at which musicians began playing and their total years of musical experience. We found significant positive correlations between the age of start of musical training and the volumes of left, $r(36) = .489$, $p < .01$, and right, $r(36) = .456$, $p < .01$, white matter and left lobule VIIIA, $r(36) = .346$, $p < .05$. This indicates that later start of training was associated with larger volume in these regions (Table 3 and Fig. 3). We also found significant negative correlations between years of musical experience and right lobule VI, $r(36) = -.335$, $p < .05$, and left lobule VIIIA, $r(36) = -.365$, $p < .05$. These data indicate that greater experience was associated with smaller volumes. The correlations with both age of start and years of musical experience remained significant even after controlling for one against the other, indicating that each variable accounted for distinct portions of the variance of these regional volumes.

Finger tapping performance

To assess the accuracy with which both groups could synchronize to the target metronome rates, we calculated the mean IRI of the paced and unpaced phases. The musician and non-musician groups both had mean IRI values that were close to the intervals defined by the metronome (Table 4). Musicians were significantly more accurate than non-musicians in the paced phase of the two slowest rates ($p < .05$ at 500 and 750 ms). In the unpaced phase, non-musicians had significantly shorter IRIs than musicians at the two slowest rates ($p \leq .001$ at 500 ms and at 750 ms) but overall both groups of participants were able to carry out the tapping task.

Focusing on the unpaced phase in order to examine internal timing processes, we first examined the coefficient of variation of the IRI. A 2 (musical training) \times 3 (rate) repeated measures ANOVA indicated a main effect of musical training, $F(1, 29) = 11.123$, $p < .01$, such that musicians had a smaller coefficient of variation across all rates (Fig. 4). Further, the unbiased Hedges' g effect size value ($g = 1.22$) indicated a large practical significance of musical training. Next, we focused on the linearly detrended variability of the IRI. Again, a significant main effect of musical training was found, $F(1, 29) = 6.670$, $p < .05$, indicating

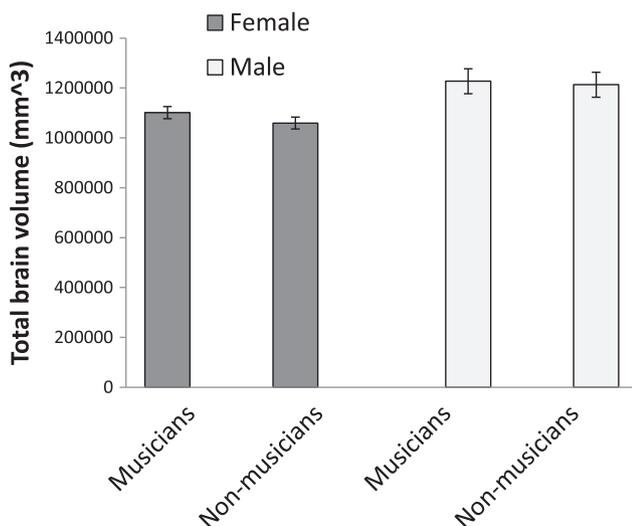


Fig. 2. Total brain volume, showing a significant main effect of gender. Standard error bars are shown.

Table 2
ANOVA results for cerebellar regions predicted to differ in musicians.

Region	<i>F</i> (2,55)	<i>p</i>	Significant pairwise comparisons (<i>p</i> -values in parentheses)	Bias-corrected Hedges's <i>g</i> effect size (95% CI in square brackets)
Total cerebellum	4.300	.018	ET < LT (.015)	0.87 [0.21, 1.54]
Right lobule IV	4.128	.021	ET < LT (.018)	0.95 [0.28, 1.63]
Right lobule V	3.286	.045	ET < LT (.039)	0.76 [0.10, 1.42]
Right lobule VI	3.413 ^a	.04 ^a	ET < LT (.041)	0.80 [0.12, 1.47]
Right lobule VIIIA	0.246	.783	None	/
Right lobule VIIIB	1.448	.244	None	/
Right white matter	6.053	.004	ET < LT (.005); ET < NM (.036)	1.01 [0.33, 1.69] 0.89 [0.22, 1.56]
Left lobule VI	2.247	.115	None	/
Left lobule VIIIA	2.565	.086	None	/
Left lobule VIIIB	1.227	.301	None	/
Left white matter	6.909	.002	ET < LT (.002); ET < NM (.020)	1.07 [0.39, 1.75] 0.98 [0.31, 1.65]

Note. All volumes were normalized with respect to total brain volume. Between-subjects factor was group, with three levels: ET, LT, non-musician (NM).

^a Significant after removing a single outlier from the ET group (*Z* score = 2.7 with respect to the mean of the ET group), *F*(2, 54) = 3.413, *p* = .04.

that musicians were less variable and that musical training had a large effect ($g = 0.94$). As expected (Wing, 2002), there was also a significant main effect of tapping rate, such that variability increased with interval duration, $F(2, 58) = 45.339$, $p < .001$. An interaction between musical training and rate did not reach significance, $F(2, 58) = 3.136$, $p = .082$, but pairwise comparisons revealed that musicians had significantly smaller IRI variability at the 500 ms ($p < .01$) and 750 ms ($p < .05$) rates, compared to non-musicians. Further, musical training had large effects on IRI variability at these two rates ($g = 1.03$ at 500 ms and 0.79 at 750 ms).

To assess long-term drift away from the target tapping rate, we examined the absolute value of the slope of the linear trend that was removed from the IRI time series of the unpaced phase. We found a significant main effect of musical training, $F(1, 29) = 6.514$, $p < .05$, with musicians exhibiting significantly less drift than non-musicians (Fig. 5), and a large effect of musical training ($g = 0.93$). There was also a significant main effect of rate, $F(2, 58) = 14.105$, $p < .001$, such that drift increased with interval duration. No significant interaction between rate and musical training was found, $F(2, 58) = 1.254$, $p = .293$.

To test whether musicians' less variable tapping performance was due to reduced timer variability or to reduced motor variability or a combination of the two, we used the Wing and Kristofferson (1973) model to estimate the portion of the total unpaced IRI variability

attributable to central timer and to motor functions. Consistent with the prediction of the model, we found a main effect of rate, $F(2, 58) = 52.255$, $p < .001$, such that timer variability increased with interval duration (Fig. 6A), but we did not find any significant effect of musical training or interaction between the two independent variables. Nevertheless, post hoc pairwise comparisons showed that musicians were less variable at the 250 and 500 ms rates compared to non-musicians ($p < .05$), with large effect sizes for musical training ($g = 0.75$ and 0.98 at 250 and 500 ms rates, respectively).

In contrast, for the motor component of variability, we found main effects of musical training, $F(1, 29) = 11.905$, $p < .01$, and rate, $F(2, 58) = 18.084$, $p < .001$, such that motor variability was smaller in musicians and larger as interval duration increased. Further, the effect size of musical training on motor variability ($g = 1.26$) suggested high practical significance for musical training on this aspect of performance. We also found an interaction between musical training and rate, $F(2, 58) = 10.005$, $p < .01$, such that musicians had significantly less motor variability at the 500 ms ($p < .05$) and 750 ms ($p < .01$) rates. Within the group of musicians, motor variability did not differ significantly between rates, consistent with the prediction of the Wing and Kristofferson model. However, motor variability of the non-musicians increased significantly as interval duration increased (Fig. 6b).

When we split the group of musicians into ET ($n = 7$) and LT ($n = 13$) subgroups, no significant differences were found for any of the timing measures. We examined the correlations of both the age at which musical training began and the total number of years of musical experience, with the timing of finger tapping. A marginally significant correlation between years of experience and Wing–Kristofferson timer variability at 500 ms ($r = -.435$, $p = .055$) was found. Additionally, the correlation between years of experience and the absolute value of the slope of the linear trend at 750 ms was marginally significant ($r = -.413$, $p = .07$). No significant correlations with motor variability were found. Thus, there was some evidence indicating that greater years of training may be associated with smaller timer variability and less drift.

Relationship between cerebellar volumes, timing and musical experience

Using the subset of participants with both behavioral and MRI data, we examined the relationships between cerebellar volumes, timing measures and musical experience. This subset of participants did not differ from the larger sample in age ($t(87) = .417$, $p = .678$), total brain volume ($t(87) = .639$, $p = .524$) or normalized total cerebellar volume ($t(87) = -.459$, $p = .648$). Furthermore, the musicians from these two groups did not differ in their years of musical experience ($t(56) = .760$, $p = .450$).

To limit the number of separate analyses, we only examined the correlations for regions previously found to be associated with musical experience for the larger group (bilateral white matter, right VI and

Table 3
Bivariate Pearson coefficients of normalized regional cerebellar volumes with musical experience (*p*-values in parentheses) for the 38 musicians pooled together. Partial correlations for age of start, after controlling for years of experience, and years of experience, after controlling for age of start, are also shown for the significant bivariate correlations.

Region	Age of start		Years of experience	
	Bivariate	Partial	Bivariate	Partial
Total cerebellum	.273 (.097)	/	-.296 (.071)	/
Right lobule IV	.275 (.095)	/	-.015 (.927)	/
Right lobule V	.222 (.180)	/	-.239 (.149)	/
Right lobule VI	.260 (.115)	/	-.335* (.040)	-.350* (.034)
Right lobule VIIIA	.270 (.101)	/	-.061 (.715)	/
Right lobule VIIIB	.230 (.164)	/	.099 (.552)	/
Right white matter	.456** (.004) ⁺	.474** (.003)	-.251 (.128)	/
Left lobule VI	.314 (.055)	/	-.295 (.072)	/
Left lobule VIIIA	.346* (.033)	.376* (.022)	-.365* (.024)	-.393* (.016)
Left lobule VIIIB	.131 (.432)	/	.141 (.399)	/
Left white matter	.489** (.002) ⁺⁺	.505** (.001)	-.231 (.163)	/

* Significant at $p < .05$.

** Significant at $p < .01$.

⁺ Marginally significant after removal of a single outlier, $r = .295$, $p = .077$.

⁺⁺ Significant after removal of the same single outlier, $r = .337$, $p = .041$.

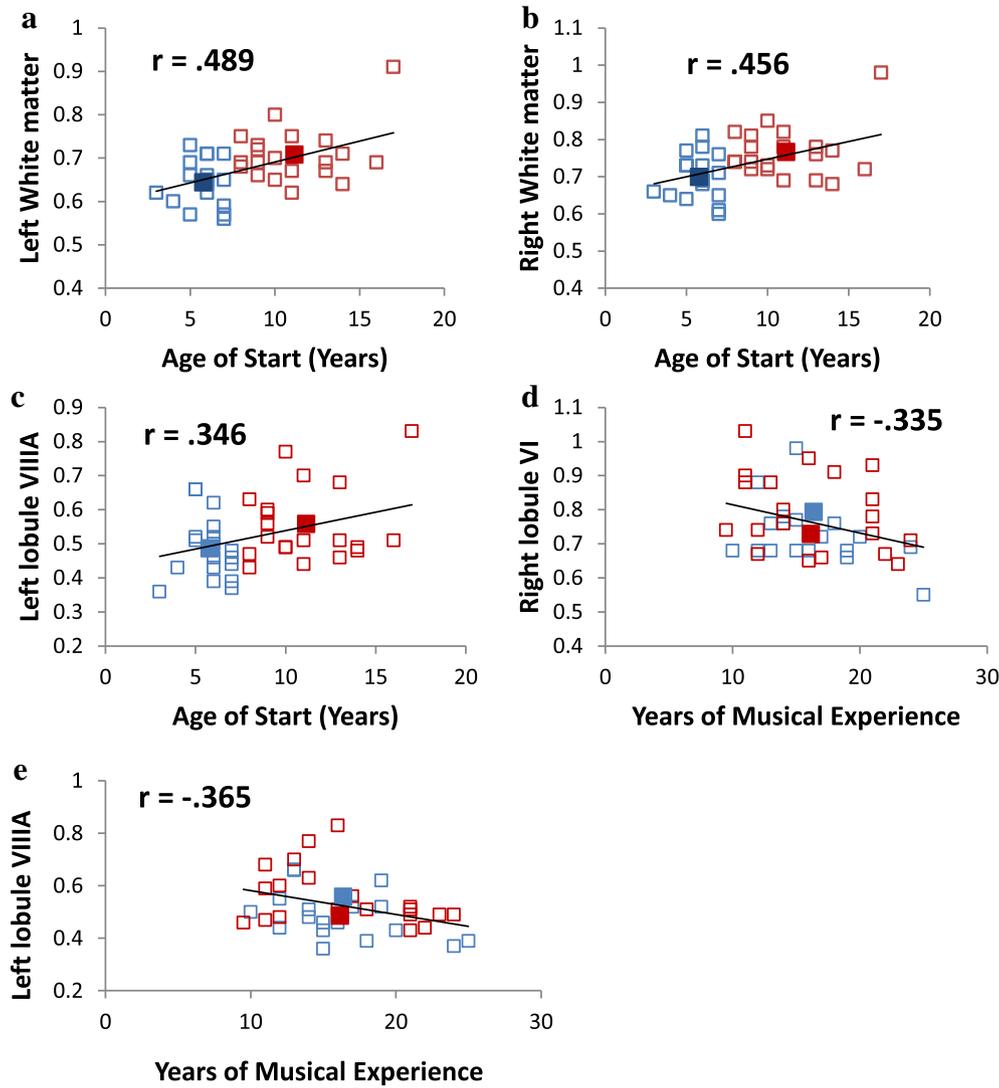


Fig. 3. Scatter plots for 38 musicians showing correlations between the age of start of musical experience and normalized volumes of (a) left cerebellar white matter, (b) right cerebellar white matter, and (c) left lobule VIIIA, and between the years of musical experience and normalized volumes of (d) right lobule VI and (E) left lobule VIIIA. ET musicians are shown in blue, LT musicians in red. Filled squares represent subgroup means.

left VIIIA). Significant correlations were found between the coefficient of variation of the unpaced IRI and right lobule VI (Table 5; Fig. 7). Interestingly, breaking down this variability into timer and motor components using the Wing and Kristofferson (1973) model, we found that timer variability correlated significantly with right lobule VI ($r = .409$ at 250 ms, $.400$ at 500 ms, $.381$ at 750 ms; Table 5; Fig. 7) while motor variability did not. This indicates that lower timer variability is related to smaller volumes of right lobule VI.

Table 4
Mean inter-response intervals of the paced and unpaced phases.

	Interval duration					
	250 ms		500 ms		750 ms	
	Paced	Unpaced	Paced	Unpaced	Paced	Unpaced
Musicians	249.69 (0.76)	254.01 (6.40)	499.91 (0.71)	509.41 (11.64)	749.86 (.84)	765.31 (22.89)
Non-musicians	246.46 (8.58)	252.78 (8.49)	498.44 (2.76)	492.42 (11.31)	747.45 (5.02)	725.28 (35.40)
<i>p</i> -Values	.101	.651	.030	<.001	.043	.001

Note. All values in milliseconds. Standard deviations in parentheses.

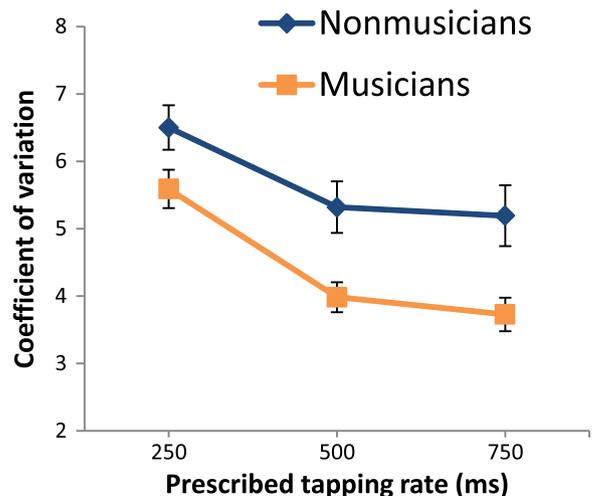


Fig. 4. Coefficient of variation of the unpaced phase plotted against the prescribed tapping rate. Standard error bars are shown.

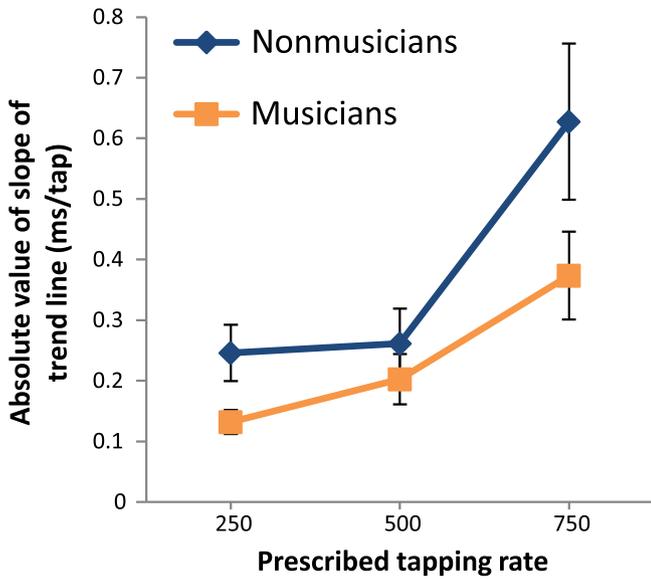


Fig. 5. Linear drift in the unpaced phase, represented by the absolute value of the slope of the linear trend line of the IRI time series. Bars represent standard error.

Discussion

The goal of the present study was to illuminate the relationships between musical experience, timing, and regional cerebellar volumes. We used a novel automatic segmentation pipeline to measure cerebellar regional volumes in structural MR images and combined this with measures of musical experience and finger tapping variability in musicians and non-musicians. We found that ET musicians had smaller total and regional cerebellar volumes compared to LT musicians but found no differences between LT musicians and non-musicians. Consistent with this, earlier age of start was related to smaller volumes of bilateral white matter and left lobule VIIIA. Further, greater duration of musical experience was associated with smaller volumes of right lobule VI and left lobule VIIIA. In terms of tapping performance, we found that musicians showed less long-term drift than non-musicians and were less variable, due to both reduced timer variability and reduced motor variability. We also found evidence that, in both musicians and non-musicians, better timing performance was related to smaller volume of right lobule VI. Taken together, these results show that earlier age of start, greater musical experience and better timing performance are all associated with smaller volumes of cerebellar white and gray matter in regions associated with perceptual and motor timing.

The finding of smaller cerebellar volumes in ET musicians contrasts with previous results showing increased white matter in the corpus callosum and greater gray matter in the premotor cortex of ET musicians in parallel studies in a partially overlapping sample (Bailey et al., 2013; Steele et al., 2013). However, it is consistent with studies reporting reduced structural and functional contributions to performance in expert musician and dancer populations (Granert et al., 2011; James et al., 2013; Jäncke et al., 2000; Krings et al., 2000; Nigmatullina et al., 2013). This differential impact of early training and experience on brain structure in specific cerebellar lobules may be accounted for by the role of these lobules in sensorimotor tasks and the effects of expertise in automating such tasks, lessening the need to process sensory feedback, as suggested by James et al. (2013) in explaining their findings of musicians' greater versus lesser gray matter density in cognitive versus sensorimotor areas.

Our first key finding of smaller cerebellar gray and white matter volumes in ET musicians adds to the body of evidence supporting a sensitive period for musical training (Bailey et al., 2013; Penhune, 2011; Schlaug et al., 1995; Steele et al., 2013). The finding that the cerebellum is affected by the same sensitive period cut-off age of seven years is

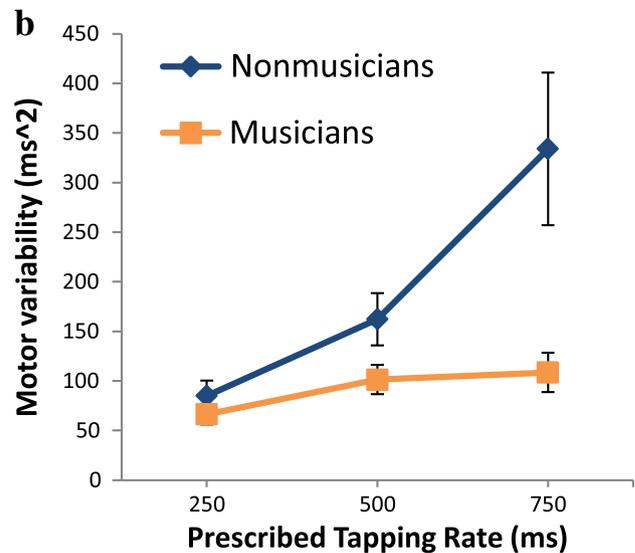
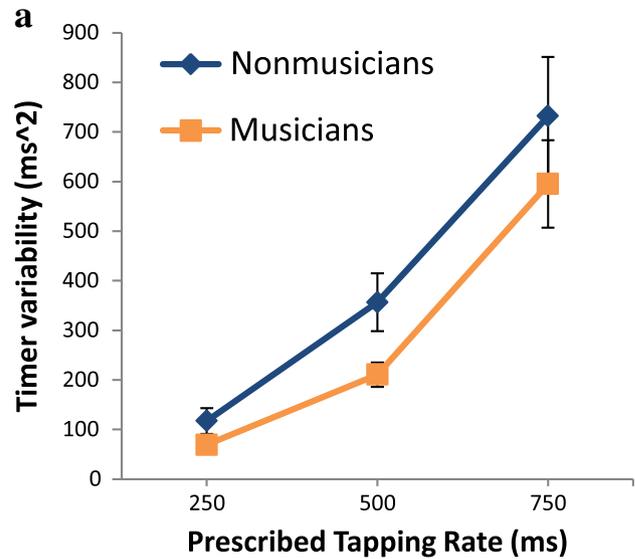


Fig. 6. Timer (a) and motor (b) variability in the unpaced phase, estimated using the Wing-Kristofferson model. Bars represent standard error.

Table 5

Bivariate Pearson correlation coefficients of normalized regional cerebellar volumes with measures of unpaced IRI variability (p -values in parentheses) for 31 participants.

	Right lobule VI	Right white matter	Left lobule VIIIA	Left white matter
Coefficient of variation				
250 ms	.037 (.842)	.075 (.688)	.033 (.860)	.037 (.844)
500 ms	.407* (.023)	.189 (.308)	.119 (.524)	.156 (.401)
750 ms	.394* (.028)	.153 (.412)	.049 (.795)	.129 (.489)
Wing-Kristofferson timer variability				
250 ms	.409* (.022)	.265 (.149)	.294 (.108)	.226 (.222)
500 ms	.400* (.026)	.009 (.964)	.295 (.107)	-.022 (.904)
750 ms	.381* (.034)	.116 (.534)	.057 (.760)	.094 (.617)
Wing-Kristofferson motor variability				
250 ms	-.051 (.786)	-.084 (.652)	-.093 (.620)	-.082 (.660)
500 ms	.312 (.087)	.205 (.268)	-.193 (.297)	.190 (.305)
750 ms	.317 (.082)	.153 (.410)	-.055 (.769)	.144 (.440)

* Significant at $p < .05$.

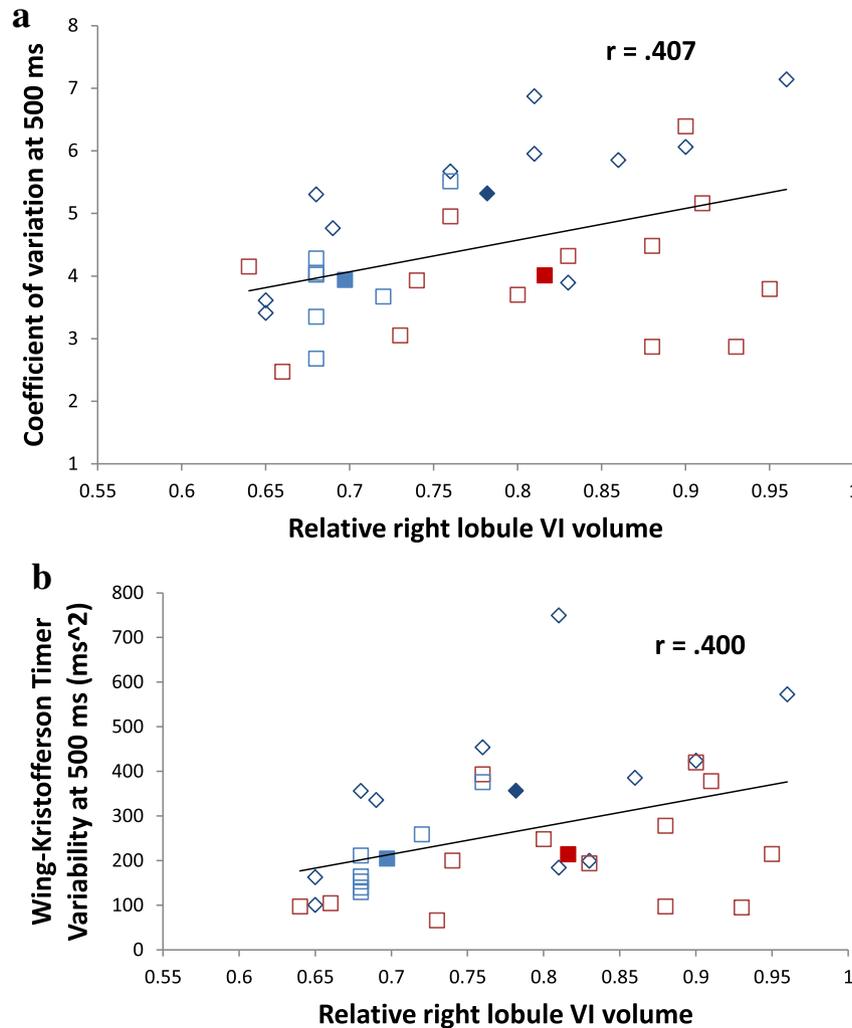


Fig. 7. Scatter plots for 31 participants showing correlations between normalized right lobule VI volume and tapping performance at the prescribed tapping rate of 500 ms based on (a) coefficient of variation of the unpaced IRI and (b) Wing–Kristofferson timer variability. Non-musicians are shown as dark blue diamonds, ET musicians as light blue squares and LT musicians as red squares. Filled diamonds and squares represent subgroup means.

somewhat surprising given what we know of the developmental trajectory of this brain region. Total cerebellar volume peaks relatively late in childhood (11.8–15.5 years), particularly the superior posterior lobe (15.8–18.2 years), which includes lobule VI (Tiemeier et al., 2010). It may be that cerebellar development is at least partially yoked to development in connected brain regions such as M1 and premotor cortex that are also affected by musical training (Bailey et al., 2013) but which have earlier maturational peaks (Gogtay et al., 2004).

Interestingly, these volumetric differences between ET and LT musicians were not accompanied by performance differences on the tapping task. Performance differences between ET and LT musicians have been observed in visual and auditory rhythm reproduction tasks in other studies in our lab (Bailey et al., 2013; Watanabe et al., 2007). Given the correlations found in the current experiment between years of experience, timer variability and volume of right lobule VI, it may be that more basic timing performance is less affected by early start of training and more strongly related to extent of training.

The second key finding, that measures of musical expertise were associated with smaller cerebellar volumes, is counter to the more typical pattern of musical or other skill being associated with larger volumes of brain regions (e.g. Hutchinson et al., 2003; Maguire et al., 2000), but it is consistent with a recent study of pianists that found reduced variability in piano playing was associated with smaller putamen volume (Granert et al., 2011). Expertise in other fields has also been associated with

reduced cerebellar volumes. Female ballet dancers had smaller bilateral lobules VIII and IX compared to controls, such that the volumes of these lobules were negatively associated with years of dance experience (Nigmatullina et al., 2013). Additionally, it has been suggested that reduced volume is consistent with the reduced activations that have been observed to be associated with skill mastery (Hänggi et al., 2010). For example, professional pianists, compared to controls, have shown reduced activation in motor areas in fMRI studies of tapping (Jäncke et al., 2000; Krings et al., 2000). Along these same lines, in a task of melodic improvisation, musicians and non-musicians performed similarly but showed different patterns of brain activity, such that musicians exhibited deactivation of the temporoparietal junction, a region thought to control bottom-up processing of sensory input (Berkowitz and Ansari, 2010). The authors interpreted this deactivation as a means for musicians to facilitate top-down processing, such as grouping of musical notes into melodies, by filtering out sensory input that is irrelevant to the expert musician.

The unexpected direction of these correlations of measures of experience and expertise with brain volumes could be explained by neural processes that are more efficiently and elegantly implemented during the sensitive period and consequently use less gray and white matter. Gray matter density has been found to increase in relation to musical expertise in areas related to cognitive functions used in musical performance but to decrease in areas related to sensorimotor processes, with

the suggestion that decreases could be related to more efficient motor control processes that may require fewer neurons and less sensory feedback (James et al., 2013). Similar factors may be responsible for the volume decreases observed here. In support of this explanation, we found in a previous study that non-musicians exhibited a negative association between movement jerk and timer variability on a tapping task, while musicians' jerk and timing were decoupled, indicating that musicians were able to achieve superior timing with less sensory feedback (Baer et al., 2013), as jerk is a source of proprioceptive information (Balasubramaniam et al., 2004).

The final key finding was an overall association between the volume of right lobule VI and the variability of the tapping IRI, which is consistent with the evidence from functional imaging and TMS studies that indicates a role for this region in timing (E et al., 2012; Thaut et al., 2009). Furthermore, when we broke down the total IRI variability into timer and motor sources, we found that timer variability correlated with the volume of right lobule VI, but motor variability did not. This suggests that lobule VI is tied more closely to the timing aspects of finger tapping, rather than the motoric aspects of this task and supports the dissociability of timer and motor variability predicted by the Wing and Kristofferson (1973) model. In sum, our key finding of an association of timer variability with right lobule VI volume further contributes to the localization of timing, in a repetitive movement task, by adding to the precision of cerebellar localization to a specific lobule.

Studies relating timing function to the cerebellum have pointed to the involvement of both lateral and vermal regions. Timing has been shown to be disrupted by repetitive transcranial magnetic stimulation (TMS) of, and by lesions to, the lateral cerebellar hemispheres (Ivry et al., 1988; Koch et al., 2007). In contrast, a more recent study that examined the relationship between finger tapping performance and cerebellar volume showed that tapping variability was negatively associated with volume of the vermis (Bernard and Seidler, 2013). Further, at least one TMS study has also implicated the vermis in sub-second timing (Théoret et al., 2001). Lobule VI, which was found to be related to timing variability in the current study includes both vermal and lateral hemispheric regions. Therefore, previous studies that have linked either vermal or lateral regions to timing may not necessarily be inconsistent with each other or with the present findings.

Functional neuroimaging studies have suggested additional roles for some of the lobules we have identified as being associated with timing and musical training. Lobule VI has been associated with sensorimotor control of speech (Mariën et al., 2014) and the activation of lobule VI during verbal working memory tasks may reflect the motoric aspects of subvocalization (Koziol et al., 2013). Lobule VIIIA activation during such tasks may be related to information storage (Stoodley, 2012). It may be that subregions of these lobules have differing functionality or that the lobules as a whole are involved in low-level processes that are common to these varied cognitive and motor tasks. In line with this latter possibility and given the regularity of neuronal organization in the cerebellum, it has been suggested that the cerebellum acts as a general integrator and comparator of sensory input with internal predictions of behavioral outcome to produce more refined and precise behavior than would otherwise be the case (Schmahmann, 1998; Stoodley, 2012).

The results reported in the present study are not sufficient to establish causal connections between musical experience, timing, and cerebellar volumes. It may be that a child with good timing ability will be more motivated to play music compared to a child with less precise timing. It may also be the case that innately good timing and musical training work together to produce expert performance in the adult musician. Investigating timing ability and cerebellar plasticity in a longitudinal context could help to resolve the differential contributions of pre-existing differences and musical training.

We were also limited by the small size of the subsample of musicians for whom we had both MRI and behavioral data, leaving us unable to carry out any mediational analyses. For example, it may be that right

VI volume is mediating the relationship between musical experience and timer variability, evidence which would further strengthen support for the role of right Lobule VI in timing and musical performance and indicate that musical-training-related plasticity in this region results in reduced timing variability. The possibility of a mediational relationship between musical experience, timer variability, and the volume of lobule VI should be investigated in a more focused study with sufficient sample size.

Conclusion

The results of this study yielded important evidence for a sensitive period for initiation of musical experience. Our study also adds to a small but growing body of evidence that links skill mastery with smaller gray and white matter volumes. Finally, a major contribution of this study has been to extend support for a role for cerebellar lobule VI in event-based timing for repetitive auditory–motor synchronization tasks. Overall, our findings contribute to a better understanding of the role of the cerebellum in timing and music and to the nature of neural plasticity in this brain structure.

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