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Musical Training Predicts Cerebello-Hippocampal Coupling During Music Listening

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AQ: 1

Cerebello-hippocampal interactions occur during accurate spatiotemporal prediction of movements. In the context of music listening, differences in cerebello-hippocampal functional connectivity may result from differences in predictive listening accuracy. Using functional MRI, we studied differences in this network between 18 musicians and 18 nonmusicians while they listened to music. Musicians possess a predictive listening advantage over nonmusicians, facilitated by strengthened coupling between produced and heard sounds through lifelong musical experience. Thus, we hypothesized that musicians would exhibit greater functional connectivity than nonmusicians as a marker of accurate online predictions during music listening. To this end, we estimated the functional connectivity between cerebellum and hippocampus as modulated by a perceptual measure of the predictability of the music. Results revealed increased predictability-driven functional connectivity in this network in musicians compared with nonmusicians, which was positively correlated with the length of musical training. Findings may be explained by musicians' improved predictive listening accuracy. Our findings advance the understanding of cerebellar integrative function.

Keywords: fMRI, professional musicians, perception, plasticity, training

AQ: 2

Supplemental materials: http://dx.doi.org/10.1037/pmu0000215.supp

Cerebellar function beyond the sensorimotor realm is becoming more widely accepted (Koziol et al., 2014; O'Reilly, Beckmann, Tomassini, Ramnani, & Johansen-Berg, 2010; Salmi, Rinne, Koistinen, Salonen, & Alho, 2009; Salmi et al., 2010; Watson, Koutsikou, Apps, & Jones, 2015), evidencing an anterior sensorimotor versus posterior cognitive-emotional dichotomy in the cerebellum (Imamizu, Kuroda, Miyauchi, Yoshioka, & Kawato, 2003; Koziol et al., 2014; Stoodley, 2012). Evidence gathered in the last 20 years supports cerebellar contributions to learning skills (Bellebaum & Daum, 2011), working memory and other language

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functions (Bellebaum & Daum, 2011; Leggio, Chiricozzi, Clausi, Tedesco, & Molinari, 2011; Leiner, 2010; Schmahmann & Sherman, 1998; Steinlin, 2008; Tavano & Borgatti, 2010), spatial and episodic memory (Leggio et al., 2011; Rochefort et al., 2011; Schmahmann & Sherman, 1998), emotion control (Colibazzi et al., 2010; Tavano & Borgatti, 2010), event prediction (Forster & Brown, 2011), empathy and predicting others' actions (Gazzola & Keysers, 2009; Ramnani & Miall, 2004; Schulte-Rüther, Markowitsch, Fink, & Piefke, 2007; Singer et al., 2004), imitation (Jackson, Meltzoff, & Decety, 2006), planning and decision-making (Hogan et al., 2011; Ito, 2008; Tavano & Borgatti, 2010), and cognitive developmental disorders including autism (Shukla, Keehn, Lincoln, & Müller, 2010; Steinlin, 2008). Notably, new research has reported important functional interactions between the posterior cerebellum and the hippocampus (Iglói et al., 2014; Krook-Magnuson, Szabo, Armstrong, Oijala, & Soltesz, 2014; Onuki, Van Someren, De Zeeuw, & Van der Werf, 2015; Rochefort et al., 2011; Wikgren, Nokia, & Penttonen, 2010), for which several potential structural and functional connectivity pathways exist, evidenced by both animal and human studies. Animal studies have demonstrated direct connections between the hippocampus and the fastigial nucleus (Arrigo et al., 2014; Heath, Dempesy, Fontana, & Myers, 1978; Heath & Harper, 1974; Liu, Zhang, Yuan, Wang, & Li, 2012; Oganesian, Melik-Musian, Fanardzhian, & Grigorian, 1980; Snider & Maiti, 1976; Wikgren et al., 2010; Yu, Gao, Wang, & Chen, 1989). These findings support the existence of a direct anatomical substrate through which posterior cerebellum and hippocampus may influence one another. Thus, although no known path has been defined between the cerebellum and hippocampus, there is evidence for a bidirectional communication between these structures.

Moreover, a recent systematic review by Yu and Krook-Magnuson (Yu & Krook-Magnuson, 2015) on the novel area of cerebello-hippocampal (CER-HIPP) interactions emphasized the crucial role of CER-HIPP functional connectivity for spatial (Burguiere et al., 2005; Iglói et al., 2014; Petrosini, Leggio, & Molinari, 1998; Rochefort et al., 2011; Rochefort, Lefort, & Rondi-Reig, 2013) and temporal processing (Clark, Manns, & Squire, 2002; Eichenbaum, 2014; Kirsch et al., 2003; Koekkoek et al., 2003; Logan & Grafton, 1995; Paleja, Girard, Herdman, & Christensen, 2014; Thompson & Steinmetz, 2009; C. Weiss & Disterhoft, 2011; Wikgren et al., 2010).

Using functional MRI (fMRI), Onuki et al. (2015) observed coactivation between the left hippocampus and the cerebellum (bilateral lobule VI, right crus I, left lobule VIIIb) during accurate spatiotemporal prediction of finger movements. More specifically, participants were prompted to press with one finger assigned buttons at a precise moment following visual cues (flashing moving markers). Thus, both temporal and spatial information were required for successfully predicting the precise moment and location of the finger press. Because CER-HIPP coupling was absent in conditions lacking the spatiotemporal integration component required to make accurate predictions (i.e., conditions requiring reactive instead of predicted finger movements, and an imagery version thereof), this coupling was thus interpreted to be an indicator of participants' accurate predictions based on integrating both spatial and temporal information.

In the present study, we wanted to determine whether coupling between the cerebellum and left hippocampus could be present during a perceptual condition that involves a predictive temporal component. Music listening provides an excellent context that relies heavily on predictive mechanisms without actual movement (Gebauer, Kringelbach, & Vuust, 2015; Huron, 2006; Maidhof, Vavatzanidis, Prinz, Rieger, & Koelsch, 2010; Meyer, 1956; Narmour, 1990; Rohrmeier & Koelsch, 2012; Schenker, 1935; Schoenberg, 1978; Vuust, Ostergaard, Pallesen, Bailey, & Roepstorff, 2009). As experts in the musical domain, musicians possess optimized predictive models of musical structure, allowing them to more accurately anticipate upcoming musical events (Ericsson & Towne, 2010; Drake & Palmer, 2000; Hansen, Vuust, & Pearce, 2016; Lehmann & Gruber, 2006). In addition, the superior abilities in timing and error correction observed in musicians have been attributed to the cerebellum (Chen, Penhune, & Zatorre, 2008), a structure that, along with other motor-related areas, undergoes reorganization ostensibly by the impact of musical motor learning (Baer et al., 2015; Gaser & Schlaug, 2003; Hutchinson, Lee, Gaab, & Schlaug, 2003; Koeneke, Lutz, Wüstenberg, & Jäncke, 2004; Ungerleider, Doyon, & Karni, 2002).

Because CER-HIPP coupling is suggested to be a marker of predictive accuracy (Onuki et al., 2015), differences in predictive listening accuracy may manifest as differences in CER-HIPP functional connectivity. Thus, a stronger CER-HIPP coupling in musicians compared with nonmusicians could be an indicator of improved predictive listening accuracy.

In the present study, we used an fMRI paradigm that enables the use of naturalistic stimulation (continuous music) to study cognitive functions without the need for controlled tasks. We recorded fMRI brain responses from 18 musicians and 18 nonmusicians while they attentively listened to music of different genres. We were interested in CER-HIPP functional connectivity during moments of high predictability in the music (i.e., when participants are purportedly engaged in making accurate predictions). The use of a perceptual segmentation task to obtain a measure of predictability in the current study was justified and motivated by background literature on information-theoretic descriptions of musical events as relating to their perceived predictability (cf. Juhász, 2004; Pearce, Müllensiefen, & Wiggins, 2010). AQ: 3

The unpredictability (unexpectedness) of upcoming events is higher at event boundaries than elsewhere (Egermann, Pearce, Wiggins, & McAdams, 2013; Hafer & Weiss, 1974; Harris, 1954; Juhász, 2004; Narmour, 1990; Pearce, Ruiz, Kapasi, Wiggins, & Bhattacharya, 2010; Pearce & Wiggins, 2012; Shannon, 1951). In other words, segment boundaries are located at the peaks of highest information content of a signal (Abdallah & Plumbley, 2009; Pearce & Wiggins, 2006). Maximum-information-based segmentation methods have been similarly applied in text segmentation (Charniak, 2000; Low, Ng, & Guo, 2005; McCallum, Freitag, & Pereira, 2000; Ratnaparkhi, 1999; Reynar & Ratnaparkhi, 1997), applying the information theory criterion as a marker of sentence boundaries. These boundaries mark the highest points of uncertainty in the signal because, after a segment boundary, the next upcoming events are the hardest to predict (less likely to be anticipated accurately).

This conforms with event segmentation theory (Zacks, Speer, Swallow, Braver, & Reynolds, 2007), according to which an event boundary is distinguished when perceptual or conceptual features of the activity change, making the anticipation of upcoming information more difficult. At such points, a transient increase in prediction error occurs, which gives rise to the subjective experience that a new event has begun (Zacks et al., 2007). Thus, measures of information content in the music can be obtained using segmentation tasks.

In the present study, a real-time perceptual segmentation test was used to obtain segments in the music with high predictability (low information content). A different participant sample was used to avoid the effect of becoming familiar with the exposure. Participants had to identify segment boundaries defined as instants of significant change in the music. This allowed us to measure the CER-HIPP connectivity during the segments of the music in which prediction is possible because information content is low. Segment boundaries represent consequently an indirect but robust measure of predictability in the music based on information theory used recurrently in the literature.

The test was pooled separately for musicians and nonmusicians. Thus, the resulting boundaries identified in the music reflect the within-group consensual points of highest unpredictability in the music.

Using this segmentation approach, we are able to reliably obtain segments of the music in which information content is low, and thus accurate predictive listening is likely to happen. This variable was used to conduct psychophysiological interaction (PPI; Friston et al., 1997) analyses to estimate how the CER-HIPP functional connectivity depended on the predictability of the music. We hypothesized musicians to show increased predictability-driven functional connectivity in the CER-HIPP network compared with nonmusicians, as a marker of musicians' improved prediction accuracy during listening.

Materials and Method

We proceeded as follows: First we obtained fMRI responses from participants during music listening. Following this, a perceptual test was conducted in a different participant pool (see *Participants*) to estimate the points of highest predictability in the music. Next, PPI analyses were performed between two hippocampal seeds and the cerebellum using the predictability variable. This was followed by *t* tests between groups to find whether CER-HIPP coupling was driven by musical predictability differently in musicians and nonmusicians. Lastly, we investigated the relationship between musical training and predictability-driven functional connectivity in musicians.

Participants

fMRI experiment. A total of 36 healthy participants with no history of neurological or psychological disorders participated in the fMRI experiment. The participants were screened for inclusion criteria before admission to the experiment (no ferromagnetic material in their body, no tattoo or recent permanent coloring, no pregnancy or breastfeeding, no chronic pharmacological medication, and no claustrophobia), and upon admission to the experiment, they signed an informed written consent. The participant pool was selected to be equally divided between professional musicians (n = 18; age = 28.2 ± 7.8; female = 9) and nonmusicians (n = 18; age = 29.2 ± 10.7; female = 10; left-handers = 1). The criteria for musicianship were having more than 5 years of music training, having finished a music degree in a music academy, reporting themselves as musicians, and working professionally as a performer. As for the type of musicians, there were classical (n = 12), jazz (n = 4), and pop (n = 2) musicians. The instruments played were strings (violin = 4; cello = 2; double bass = 1), piano (n = 8), winds (trombone = 1; bassoon = 1), and mixed (n = 1). The musicians' group was homogeneous in terms of the duration of their musical training, onset age of instrument practice, and amount of years of active instrument playing. These details were obtained and crosschecked via questionnaires and the Helsinki Inventory for Music and Affect Behavior (Gold, Frank, Bogert, & Brattico, 2013). There were no significant differences between the musician and nonmusician groups with respect to cognitive performance, socioeconomic status, or personality and mood questionnaire (see Table S1 in the online supplemental materials for a detailed list of background variables tested).

The experiment was undertaken with the understanding and written consent of all participants. The study protocol proceeded upon acceptance by the ethics committee of the Coordinating Board of the Helsinki and Uusimaa Hospital District. This study was part of a larger project ("Tunteet"), including several experimental sessions, fMRI paradigms, and questionnaires, whose findings will be reported in separate papers. AQ: 4

Perceptual experiment. A separate participant pool (N = 36) took part in the perceptual experiment (18 nonmusicians [7 female] and 18 musicians [10 female]). The rationale for using a different participant pool allows to minimize familiarity effects with the music, which could affect the listening task during the fMRI scanning (or vice versa, the perceptual task), leading to participants reacting differently to cadential closure, repetition, and other features that could contribute to expectation violations. However, to minimize differences, groups were matched in terms of their demographic variables. The mean age of the participants was 27.45 years (SD = 4.54). They were all students or graduates from different faculties of the University of Jyväskylä and of the JAMK University of Applied Sciences. Participants were rewarded with a movie ticket as a token for their participation. Musicians had an average of 14.39 years (SD = 7.49) of musical training. The musical style played by 12 of the musicians was classical music, whereas the other six musicians played nonclassical musical styles. The main instruments played by participants were piano (five), guitar (four), flute (two), bass guitar (one), clarinet (one), saxophone (one), cello (one), violin (one), viola (one), and voice (one). AQ: 5
All the nonmusicians reported having had no musical training, whereas all of the selected musicians considered themselves either as semiprofessional (12) or professional (six participants) musicians at the time of the data collection. None of the participants reported experience in dance, ballet, or sound engineering. Six participants were very familiar with at least one stimulus, but nobody reported having performed any of the examples. As a general rule, we referred to a participant as musician when he or she had reported more than 8 years of musical training and had also self-considered himself or herself as semiprofessional musician or professional musician. We discarded, for example, participants who, in a multiple-choice questionnaire, reported to be amateur musicians. In contrast, we considered participants to be nonmusicians if they considered themselves as nonmusicians and if they did not report any musical training.

Stimuli

Three musical pieces were used in the experiment: (a) *Stream of Consciousness* by Dream Theater, (b) *Adios Nonino* by Astor Piazzolla, and (c) *Rite of Spring* (comprising the first three episodes from Part 1: Introduction, Augurs of Spring, and Ritual of Abduction) by Igor Stravinsky. These are a progressive rock/metal piece, an Argentinian New Tango, and an iconic 20th century classical work, respectively, thus covering distinct musical genres and styles. All three selected pieces are instrumental and have a duration of about 8 min (the recording details and Spotify links to the musical stimuli can be found in the Supplementary Document 1).

fMRI Experimental Procedure

Participants' brain responses were acquired while they listened to each of the musical stimuli in a counterbalanced order. For each participant, the stimuli loudness was adjusted to a comfortable but audible level inside the scanner room (around 75 dB). In the scanner, the participants' only task was to attentively listen to the music delivered via high-quality magnetic resonance-compatible insert earphones while keeping their eyes open.

fMRI Scanning and Preprocessing

Scanning was performed using a 3T MAGNETOM Skyra whole-body scanner (Siemens Health Care, Erlangen, Germany) and a standard 20-channel head neck coil, at the Advanced Magnetic Imaging Centre (Aalto University, Espoo, Finland). Concurrent electroencephalogram was also acquired with BrainVision amplifier (BrainProducts, Germany), and the data will be reported elsewhere, not being of interest to the current study goal of fMRI AQ:6-7 signal reliability. Using a single-shot gradient echo planar imaging sequence, 33 oblique slices (field of view = 192 × 192 mm; 64 × 64 matrix; slice thickness = 4 mm, interslice skip = 0 mm; echo time = 32 ms; flip angle = 75°) were acquired every 2 s, providing whole-brain coverage. T1-weighted structural images (176 slices; field of view = 256 × 256 mm; matrix = 256 × 256; slice thickness = 1 mm; interslice skip = 0 mm; pulse sequence = Magnetization-Prepared Rapid Gradient-Echo [MPRAGE]) were AQ: 8 also collected for individual coregistration. The fMRI scans were preprocessed on a MATLAB platform using SPM8 (Statistical Parametric Mapping), VBM5 for SPM (Voxel Based Morphometry; Ashburner and Friston, 2000); Wellcome Department of Imaging Neuroscience, London, United Kingdom), and customized scripts developed by the present authors. For each participant, low-resolution images were realigned on six dimensions using rigid body transformations (translation and rotation corrections did not exceed 2 mm and 2°, respectively), segmented into gray matter, white matter, and cerebrospinal fluid, and registered to the corresponding segmented high-resolution T1-weighted structural images. These were in turn normalized to the Montreal Neurological Institute (Evans, Kamber, Collins, & MacDonald, 1994) segmented standard a priori tissue templates using a 12-parameter affine transformation. Functional images were then blurred to best accommodate anatomical and functional variations across participants and to enhance the signal-to-noise by means of spatial smoothing using an 8 mm full-width-at-half-maximum Gaussian filter. Movement-related variance components in the fMRI time series resulting from residual motion artifacts, assessed by the six parameters of the rigid body transformation in the realignment stage, were regressed out from each voxel time series. Following this, spline interpolation was used to detrend the fMRI data, followed by temporal filtering (Gaussian smoothing with kernel width = 4 s). We tested for differences in the amount of head movement between the groups by means of an independent samples *t* test using participants' *SD*s of each of the six movement components, which resulted for any of the movement components in no significant differences at $\alpha = 0.05$. AQ: 9

Brain responses to the three stimuli were concatenated, making a total of ~24 min worth of data. The rationale behind this was to combine stimuli representing a wide range of musical genres and styles, to cancel out effects that the specific kinds of music may have on the phenomenon under investigation. The final time series had 702 samples after the first four samples of each of the three runs were removed to avoid artifacts due to magnetization effects. AQ: 10

Hippocampal Seeds

Guided by Onuki et al. (2015)'s findings, we used the left hippocampus as the seed for PPI analyses. Furthermore, due to the functional heterogeneity of the hippocampus, we divided the left hippocampus into anterior and posterior. The anterior hippocampus has been reported to be implicated in novelty processing and movement, as well as in stress, and emotion and affect, whereas the posterior hippocampus seems to relate to familiarity and space-related processing, and performs primarily cognitive functions (Colombo, Fernandez, Nakamura, & Gross, 1998; Fanselow & Dong, 2010; Strange, Fletcher, Henson, Friston, & Dolan, 1999). AQ: 11

We used an anatomical criterion for selecting two hippocampal seeds corresponding to anterior and posterior aspects of the left hippocampus. The uncus is a distinctive and recognizable landmark for parcellation of the hippocampus, which enables to distinguish the anterior (uncus) and posterior (body and tail) aspects of the hippocampus. Thus, the boundary between anterior and posterior hippocampal aspects was determined by the presence of the uncus in coronal slices.

Following this, we created seeds by averaging the voxels time courses that fell into each of the anterior and posterior subareas of the left hippocampus. Using the automated anatomical labeling (Tzourio-Mazoyer et al., 2002) mask, this happened at Y = 55.

Perceptual Variable Representing Predictability

We aimed to test whether CER-HIPP functional connectivity was modulated by the degree of predictability of the music more in musicians than in nonmusicians. PPI analyses served this purpose because they answer the question whether the strength of the functional connectivity depends on a third factor, in this case, a perceptual variable selected for representing the degree of predictability of the music. This variable was obtained in a real-time perceptual experiment, which took place with a computer in a sound-attenuated room. Participants were instructed in written form to mark instants of significant change as they listened to the music by pressing the space bar of the computer keyboard ("Your task is to mark instants of significant musical change by pressing the space bar of the computer keyboard. Whenever you find an instant of significant change, please press the spacebar key to mark it as you listen to the music. You will not have a chance to listen to the whole example before you start marking. Instead, during your first and only listen of each example, you will give us your 'first impression'."). After completing a trial, they listened and marked different musical stimuli, which were presented in a randomized order. Participants were instructed to give their "first impression" because they would not have a chance to listen to the whole example before they started marking. The interface included a play bar that offered basic visual-spatial cues regarding the beginning, current time position, and end of the examples.

Each stimulus was presented to participants as four musical extracts:

- Piazzolla: 0–02:00, 01:57–03.57, 03:54–05:54, 05:51–08:07.968.
- Dream Theater: 0–02:00, 01:57–03.57, 03:54–05:54, 05:51–07:50.979
- Stravinsky: 00:05–02:05, 02:02–04:02, 03:59–05:59, 05:56–07:52.243

We concatenated the segmentation data to obtain a set of indicated boundaries for the complete stimulus. The kernel density estimation (KDE; Silverman, 1986) of these data was computed separately for musicians and nonmusicians to estimate its probability density curve. The chosen Gaussian kernel width was of 1.66 s, which was found to yield the optimal correlation between the KDE of musicians and nonmusicians. Between-groups consistency was high, $r = .9$, $p < .001$. However, nonmusicians seemed to indicate more segments in the music. The sampling interval used to compute the KDE was 10 Hz. The KDE time series for each group was convolved with the canonical double-gamma hemodynamic response function to match the hemodynamic response delay typical of blood-oxygen-level dependent brain responses, and was downsampled to 0.5 Hz to
AQ: 12 match the sampling rate of the fMRI scanner.

The peaks of this curve were located where significant changes with highest consensus within groups occur. Predictability can be then derived from an information theory point of view. The degree of entropy or information content in the music would be maximal at the consensual boundaries, as these perceptual boundaries denote a significant change from preceding musical events and are thus not predictable from preceding musical cues. The same criterion has been previously used to detect segment boundaries in folk song melodies (Juhász, 2004), whereby high entropy implies a next interval hard to predict, at which point this may indicate a segment boundary. Thus, accurate predictive listening is likely to happen during segments of music between boundaries.

With the current segmentation approach, our *predictability* regressor describes the moments of highest unpredictability in the music (segment boundaries) with consistency across participants. Furthermore, the segmentation approach renders more reliable points of unpredictability in the music within the groups of interest because it only focuses in the highest consensual points of unpredictability.

PPI Analyses

This perceptual variable made it feasible to conduct PPI analyses to evaluate whether CER-HIPP functional connectivity was mediated by the degree of predictability of the music. PPI analyses are task-dependent functional connectivity analyses, which allow the study of how brain regions interact in a task-dependent manner (Friston et al., 1997). PPI measures how functional connectivity is affected by an external (psychological) variable, that is, how the presence or absence of it modulates the functional connectivity. The statistical model for PPI is the multiple linear regression,

$$x_i = x_k \times g_p \cdot \beta_i + [x_k g_p G] \cdot \beta_G + e_i, \tag{1}$$

where x_k denotes the physiological responses (the fMRI signal at a seed region, here the hippocampal seed), g_p denotes the psychological variable (here the predictability of the music) convolved with a canonical hemodynamic response function, $x_k \times g_p$ represents the psychophysiological interaction term between the hippocampal seed activity and the predictability of the music, x_i denotes the brain responses at each voxel within the cerebellum, β_i denotes the beta parameter estimates corresponding to the PPI term; β_G is a matrix of the beta estimates corresponding to x_k and g_p, as confounding variables, and other potential covariates of no interest (G); and e_i is the error term. Thus, the PPI term represents the explanatory variable in a multiple linear regression, and the inclusion of x_k and g_p as nuisance regressors guarantees any confounding effect induced by their variability alone to be ruled out. Cerebellar areas in which activity is best predicted by the PPI term indicate areas with strongest correlation with the hippocampal seed as a function of the predictability of the music. The resulting beta parameter estimates were Z-transformed using the standard deviation of each of the beta distributions, calculated from the confidence intervals of the respective beta coefficients. AQ: 13

The significance of the z scores had to be estimated due to the intrinsic serial correlation of the fMRI time series derived from the smoothness of the hemodynamic response. To this purpose, we estimated the effective degrees of freedom of the data following a nonparametric permutation-based approach (Pyper & Peterman, 1998) as shown in Eq. 2:

$$\frac{1}{df} \approx \frac{1}{N} + \frac{2}{N}\sum \frac{N-j}{N}\rho_{xx}(j)\rho_{yy}(j), \tag{2}$$

where N is the number of observations, $\rho_{x\xi}(j)$ and $\rho_{yy}(j)$ are the autocorrelations of the interaction term and a random cerebellar voxel time series at lag j, respectively. For each participant and hippocampal seed, the effective degrees of freedom were computed by randomly selecting 10,000 cerebellar voxels. Next, estimates from all trials across participants and seeds were averaged ($M = 306 \pm 5$) and used to compute the significance of the z scores by dividing these by the standard error (Equation 3):

$$z_{corrected} = z_f\sqrt{df - 3} \tag{3}$$

t Tests Between Groups

The Z-transformed PPI beta parameter estimates were compared between groups by means of t tests ($\alpha = 0.01$, one-tailed). The choice of one-tailed t tests responded to the need to test for directional differences between the groups. The resulting spatial maps were further corrected for multiple comparisons using a cluster-wise significance procedure based on permutation tests to derive a null distribution of the cluster sizes (conditional stimulus) at a given significance level, from which a critical conditional stimulus threshold can be selected at a particular family-wise error (FWE) rate. Specifically, group membership was bootstrap resampled with replacement, and t tests were performed at the alpha level given earlier. A critical cluster size of 60 voxels was obtained from a distribution of 10,000 cluster sizes (FWE = 0.05).

Anatomical regions within each cluster were labeled based on the Automated Anatomical Labeling atlas (Tzourio-Mazoyer et al., 2002) implemented in the MarsBaR toolbox v0.43 (Brett, Anton,
AQ: 14 Valabregue, & Poline, 2002), (http://marsbar.sourceforge.net). Clusters were also visually inspected using the probabilistic atlas of the human cerebellum implemented in FSL (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/) to ensure that the automatic assignment was conforming to the neurological knowledge. The x, y, and z coordinates (in Montreal Neurological Institute space) of the maximum voxel Z-value within each anatomical region were retrieved and accordingly labeled.

Correlation Analyses With Years of Musical Training

Additional correlation analyses tested a potential relationship between the duration of the musical training and the predictability-driven functional connectivity in musicians. Only significant voxels resulting from the group comparison were entered in the correlation analysis, that is, those cerebellar areas with greater predictability-driven functional connectivity in musicians compared with nonmusicians. This would further support musical training as a driver for the increased CER-HIPP coupling during music listening.

Participants' Z-transformed beta coefficients of the respective cerebellar areas were correlated against the years of musical training across musicians. Spearman's rank correlation coefficient (α = 0.05, one-tailed, uncorrected given the small voxel sets) was used because (a) the demographic variable was not normally distributed and (b) its potential relationship with the PPI coefficients may not necessarily need to be a linear one. This nonparametric measure of dependence is in addition less sensitive to outliers.

Results

t Tests Between Groups

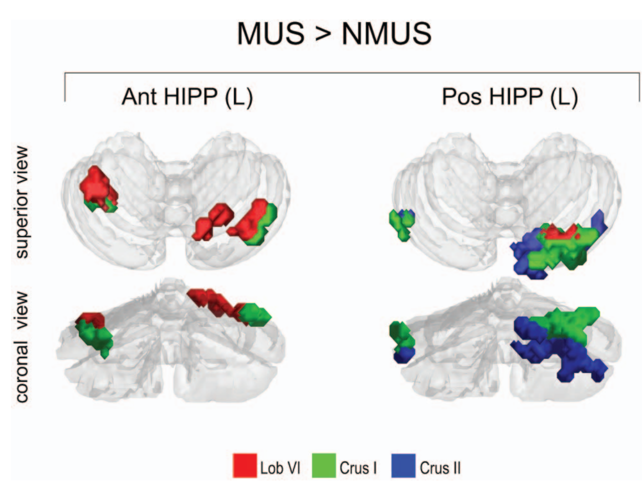
Results from the t tests (α = 0.01, one-tailed; cluster-wise threshold = 60 voxels, FWE = 0.05) comparing the degree of modulation of the CER-HIPP functional connectivity by musical predictability (PPI analyses) yielded significantly greater predictability-driven functional connectivity in musicians for both hippocampal seeds compared with nonmusicians. Significant areas comprised the bilateral lobule VI and crus I (anterior seed), the
AQ: 15 bilateral crus I and II, and right lobule VI (posterior seed). Effect sizes were also computed for all significant voxels. Large effect sizes (Cohen's $d > 0.8$) were extensively found (71% and 100% of significant cerebellar voxels for the left anterior and left posterior hippocampal seeds, respectively), indicating that the difference between musicians' and nonmusicians' CER-HIPP functional connectivity is not only statistically significant but also substantially large. In other words, for both seeds musicians exhibited stronger CER-HIPP coupling than nonmusicians because the degree of musical predictability increased (Figure 1 and Table 1 for list of regions). F1, T1, AQ:16

Correlation Analyses With Years of Musical Training

Correlation tests in musicians (Spearman, α = .05, one-tailed) revealed significant results in the hypothesized direction of effect. AQ: 17
This means that musicians with a longer musical training also exhibited stronger predictability-driven functional connectivity in the CER-HIPP network. Significant areas comprised right lobule VI and right crus I (anterior seed; see Table 2 for list of regions). T2

Discussion

We show here that the degree of predictability of the music had a significantly larger effect on musicians' CER-HIPP coupling compared with that of nonmusicians'. In addition, the length of musical training was positively correlated with the degree of predictability-driven functional connectivity in musicians. In particular, our results revealed that musicians exhibited stronger CER-HIPP coupling than nonmusicians during segments of the music with low information content, where participants are more likely to predict upcoming musical events. The stronger CER-HIPP coupling could hence be a marker of more accurate predictive listening in musicians than in nonmusicians. We speculate action simulation to be a potential-facilitating mechanism enabling accurate predictions. In other words, musicians, during listening, may be AQ: 18
mentally simulating sound-producing actions. This simulation aids in generating predictions about subsequent musical events, a process facilitated via strengthened coupling between produced and heard sounds through lifelong instrument practice.



ONLINE COLOR

Figure 1. Posterior and coronal views of the cerebellum showing regions with increased predictability-driven cerebello-hippocampal functional connectivity in musicians compared with nonmusicians (α = 0.01, one-tailed; cluster-wise threshold = 60 voxels). Clusters were obtained via the 18-connectivity scheme employed in SPM. Regions encroaching less than 5 voxels were discarded. Ant = anterior; Pos = posterior; HIPP = hippocampus; L = left; R = right; MUS = musicians; NMUS = nonmusicians. See the online article for the color version of this figure.

Table 1
Cerebellar Regions With Increased Predictability-Driven Cerebello-Hippocampal Functional Connectivity in Musicians Compared With Nonmusicians (α = .01, One-Tailed; Cluster-Wise Threshold = 60 Voxels) and Vice Versa

	Musicians > Nonmusicians					
	k	max z	p-value	x	y	z
Seed: Ant HIPP (L)						
Cluster #1						
Lobule VI (L)	83	3.54	$p < .0005$	−34	−54	−26
Crus I (L)	70	3.36	$p < .0005$	−36	−56	−26
Cluster #2						
Lobule VI (R)	62	3.50	$p < .0005$	38	−72	−20
Crus I (R)	60	3.44	$p < .0005$	40	−74	−20
Cluster #3						
Lobule VI (R)	62	3.29	$p = .0005$	24	−64	−16
Seed: Pos HIPP (L)						
Cluster #1						
Crus I (R)	306	3.60	$p < .0005$	32	−82	−30
Crus II (R)	297	3.20	$p < .001$	14	−76	−36
Lobule VI (R)	16	2.71	$p < .005$	24	−74	−22
Cluster #2						
Crus I (L)	39	3.39	$p < .0005$	−50	−66	−28
Crus II (L)	21	2.86	$p < .005$	−44	−66	−36

Note. Clusters were obtained via the 18-connectivity scheme employed in SPM. Regions encroaching less than 5 voxels were discarded. k = number of voxels; Ant = anterior; Pos = posterior; HIPP = hippocampus; L = left; R = right; max z = maximal z statistic for the region within the cluster; x, y, and z = respective Montreal Neurological Institute coordinates.

Musical experience is crucially linked to prediction (Gebauer et al., 2015; Huron, 2006; Maidhof et al., 2010; Meyer, 1956; Narmour, 1990; Rohrmeier & Koelsch, 2012; Schenker, 1935; Schoenberg, 1978; Vuust et al., 2009), and musicians have been shown to exhibit stronger brain responses to expectation violations in musical contexts than nonmusicians (James, Britz, Vuilleumier, Hauert, & Michel, 2008; Koelsch, Jentschke, Sammler, & Mietchen, 2007; Koelsch, Schmidt, & Kansok, 2002; Oechslin, Van De Ville, Lazeyras, Hauert, & James, 2013; Vuust et al., 2011; Vuust, Brattico, Seppänen, Näätänen, & Tervaniemi, 2012). Previous research has determined that statistical learning produces information-theoretic descriptions of musical notes relative to their perceived expectedness, which additionally correspond to distinctive neural activity (Pearce et al., 2010). Furthermore, reinforcing this information-theoretic view, musicians have been shown to make better use of the predictive cues in low entropy contexts than controls to generate more accurate expectations, evidencing that musical training produces optimized predictive models of musical structure (Hansen & Pearce, 2014; Hansen et al., 2016). In the same line, musicians outperform nonmusicians in making more successful online predictions about the forthcoming musical events given the current musical context (Mackay, 2003).

Our results conform with those by Onuki et al. (2015), who observed CER-HIPP functional connectivity only for accurate predictions. Musicians' stronger functional connectivity between cerebellum and hippocampus during moments of low information content in the music may reflect more accurate predictions being made by musicians compared with those by nonmusicians. This increased predictability-driven functional connectivity was observed in musicians between the cerebellum and both hippocampal seeds. Cerebellar areas comprised the bilateral lobule VI and crus I (anterior seed), the bilateral crus I and, and right lobule VI (posterior seed). These foci represent cognitive-related cerebellar regions in the posterior lobe involved in higher level tasks (spatial processing, executive functions, and emotional processing; Stoodley & Schmahmann, 2009). The anterior hippocampi have been implicated in tasks involving novelty, movement, and emotion, in contrast with its posterior homologue, implicated in familiarity, space-related processing, and cognition (Colombo et al., 1998; Fanselow & Dong, 2010; Strange et al., 1999). Accordingly, in light of what is known about hippocampal functional anteroposterior segregation, the greater implication of the anterior rather than the posterior hippocampi may highlight the novelty aspects of predictive processing during music listening. AQ: 19

Furthermore, our present findings overlap with those by Onuki et al. (2015), who observed prediction-modulated functional connectivity between the left hippocampus and bilateral lobule VI, right crus I, and left lobule VIII. In our study, the observed CER-HIPP coactivation extended also to the left crus I and bilateral crus II. Furthermore, all the cerebellar areas found (lobule VI and crus I–II) are reached by a recently discovered anatomical pathway connecting the hippocampus and cerebellum through the superior cerebellar penducle (Arrigo et al., 2014). In addition, the cerebellar areas recruited are in line with the notion that a cognitive aspect, rather than a motor one, underlies the predictive component of the CER-HIPP coupling under investigation.

The positive correlation observed between years of musical training and predictability-driven CER-HIPP functional connectivity supported the role of musical training in driving the functional connectivity. Thus, cortico-subcortical reorganization seems to be influenced by the demands of musical training. Many studies have supported the assumption that the amount of musical training drives cortical plasticity (Gaser & Schlaug, 2003; James et al., 2014; Musacchia, Sams, Skoe, & Kraus, 2007; Wong, Skoe, Russo, Dees, & Kraus, 2007). For instance, individual variability in predicting upcoming tempo changes during a finger-tapping task was positively correlated with the amount of musical training (Pecenka & Keller, 2009). In our study, the CER-HIPP network showing the relationship between predictability-driven functional connectivity and years of musical training in musicians were lobule VI and crus I for the anterior seed. The involvement of the anterior hippocampus may emphasize aspects of novelty detection

Table 2
Cerebellar Regions Showing Significant Correlation (α = .05, One-Tailed, Uncorrected) Between Increased Predictability-Driven Connectivity (Musicians > Nonmusicians) and Years of Musical Training (Musicians)

Seed: Ant HIPP (L)	k	max z	p-value	x	y	z
Lobule VI (R)	12	2.44	$p < .01$	38	−68	−22
Crus I (R)	6	2.20	$p < .02$	36	−72	−22
Lobule VI (R)	6	1.87	$p < .05$	26	−64	−20

Note. regions encroaching less than 5 voxels were discarded. k = number of voxels; Ant = anterior; Pos = posterior; HIPP = hippocampus; L = left; R = right; max z: maximal z statistic for the region within the cluster; x, y, and z: respective Montreal Neurological Institute coordinates.

pertaining to the phenomenon of predictive processing of the musical structure. Moreover, cerebellar lobule VI is part of a neural mechanism mediating motor resonance (i.e., the activation of the motor system during action observation; Landmann, Landi, Grafton, & Della-Maggiore, 2011). In the context of music listening, this may support the hypothesis of action simulation performed by musicians during listening.

Moreover, prior research evidences the consistent involvement of the bilateral lobule VI in timing tasks that include a temporal-spatial perceptual prediction component (Keren-Happuch et al., 2014), which provides strong evidence supporting its role in musicians' predictive listening in the context of music perception. In sum, correlation analyses could further illuminate on the contribution of musical training to the modulation of the CER-HIPP network.

The present findings highlight the question of action simulation as the possible enhancing mechanism supporting the predictive listening ability in musicians. In musical contexts, action simulation is mediated by internal models that trigger auditory and motor images of one's own upcoming actions (Keller, 2008). Such action simulation would allow anticipating the future course of the perceived sounds (Pezzulo, Candidi, Dindo, & Barca, 2013; Sebanz & Knoblich, 2009; Wilson & Knoblich, 2005). Because action simulation depends on the observer's own action experience (Bangert et al., 2006; Baumann, Koeneke, Meyer, Lutz, & Jäncke, 2005; Lahav, Saltzman, & Schlaug, 2007), it is thus particularly strong in professional musicians, given their lifelong experience-based associations between sensory and motor processes (Zatorre, Chen, & Penhune, 2007). In addition, action simulation mechanisms are more readily triggered during music listening in musicians than nonmusicians due to stronger coupled sensorimotor loops (Bangert et al., 2006; Gebel et al., 2013; Haslinger et al., 2005; Kajihara, Verdonschot, Sparks, & Stewart, 2013; Lotze, Scheler, Tan, Braun, & Birbaumer, 2003; Schulz, Ross, & Pantev, 2003; Stewart et al., 2003; Zatorre et al., 2007). Consequently, musicians may be making accurate predictions during music listening to a greater extent than nonmusicians on the basis of action simulation mechanisms.

Action simulation and internal models have been documented to be encoded in the cerebellum in connection with other brain regions, by forming and accessing internal models that facilitate predictions toward the desired goals of cognition in an error-free manner (Ito, 2008). The CER-HIPP loop may be one of the neural mechanisms acting as a facilitator for online spatiotemporal predictions.

AQ: 20 There are several limitations to the current methodology that should be noted. First, the musician samples used in the behavioral and fMRI experiments differ in the average level of musicianship, although no amateur musicians were used for either experiment. Second, although there are advantages to using different types of musicians to capture the general aspects of musicianship rather than the specificities of a target profile of musician, we acknowledge the disadvantage that concerns musicians playing monophonic (e.g., trombone) versus polyphonic (e.g., piano) instruments and their varying levels in prediction accuracy for polyphonic music. Third, participants (both fMRI and perceptual experiment pools) were asked to rate their familiarity with the stimuli on a scale from 1 to 5. Musicians were overall more familiar with two of the three musical pieces used than were nonmusicians (*Adios Nonino* and *Rite of Spring*), whereas there were no differences for *Stream of Consciousness*. However, potential musician–nonmusician differences in familiarity to the musical stimuli would be accordingly reflected in the predictability measure, which is a group-specific measure (see *Perceptual Variable Representing Predictability*). This would in turn account for between-groups differences in familiarity to the stimuli. Furthermore, we argue that it may be challenging to disentangle schematic from veridical expectations (Justus & Bharucha, 2001) on the neural level (i.e., automatic, learned-through-exposure expectations derived from music-syntactic rules [schematic expectations] vs. expectations in a familiar musical piece [veridical expectations]). Evidence shows that musical training increases predictive accuracy during music listening (Hansen & Pearce, 2014; Mackay, 2003). Furthermore, musicians seem to possess schematic knowledge for music styles they are not familiar with for which they exhibit increased predictive accuracy compared with nonmusicians (Hansen et al., 2016). In addition, it has been shown that expectations based on listeners' schematic knowledge of music seem to resist veridical expectancies, evidencing the contribution of expectations despite listeners' familiarity about what will come next (Tillmann & Bigand, 2010). Finally, it should be noted that the approach used does not provide any information regarding the directionality of information flow between cerebellum and hippocampus.

Conclusion

Prior research has suggested CER-HIPP functional connectivity as a marker of accurate spatiotemporal prediction of finger movements. The present study is the first to show CER-HIPP coupling in the absence of explicit movement, while participants listened attentively to music. We further established a relationship between the predictability of the music, participants' musical expertise, and CER-HIPP functional connectivity during music listening. Our findings overlap with those by Onuki et al. (2015) and provide novel evidence for increased CER-HIPP functional integration in musicians as a function of musical predictability compared with nonmusicians, lending further support to the hypothesis of musicians' functional consolidation (plasticity) as a result of their long-term musical training. Furthermore, the present study uses a paradigm that implements a task consisting of only listening attentively to continuous music. This setting provides increased AQ: 21 ecological validity compared with previous approaches in the study of CER-HIPP interaction.

Our current results substantiate and extend previous findings on CER-HIPP coupling while aiding to elucidate the role of this functional network in the context of music listening. In addition, these findings advance the understanding of cerebellar integrative function by extending prior knowledge on cerebellar contributions in the context of prediction and emphasizing the cerebellar role in higher mental functions in healthy physiology. Because the cerebellum is compromised in several behavioral and cognitive developmental and degenerative disorders, as evidenced by neuropsychological, morphological, and functional imaging studies (Bugalho, Correa, & Viana-Baptista, 2006; Peng et al., 2013; Phillips, Hewedi, Eissa, & Moustafa, 2015), the present results are also of clinical significance for disentangling and interpreting the different contributions of specific cerebellar areas in an integrative manner in pathological behavior and cognitive functioning.

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