The “Silent” Imprint of Musical Training

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Abstract: Playing a musical instrument at a professional level is a complex multimodal task requiring information integration between different brain regions supporting auditory, somatosensory, motor, and cognitive functions. These kinds of task-specific activations are known to have a profound influence on both the functional and structural architecture of the human brain. However, until now, it is widely unknown whether this specific imprint of musical practice can still be detected during rest when no musical instrument is used. Therefore, we applied high-density electroencephalography and evaluated whole-brain functional connectivity as well as small-world topologies (i.e., node degree) during resting state in a sample of 15 professional musicians and 15 nonmusicians. As expected, musicians demonstrate increased intra- and interhemispheric functional connectivity between those brain regions that are typically involved in music perception and production, such as the auditory, the sensorimotor, and prefrontal cortex as well as Broca's area. In addition, mean connectivity within this specific network was positively related to musical skill and the total number of training hours. Thus, we conclude that musical training distinctively shapes intrinsic functional network characteristics in such a manner that its signature can still be detected during a task-free condition. *Hum Brain Mapp* 37:536–546, 2016. © 2015 Wiley Periodicals, Inc.

Key words: resting state; functional connectivity; musicianship; musical expertise; instantaneous coherence

INTRODUCTION

One of the most distinctive signatures of musical training are functional [Elmer et al., 2012; Ohnishi et al., 2001; Tervaniemi et al., 2005] and structural [Bermudez et al., 2009; Elmer et al., 2013; Gaser and Schlaug, 2003; Hyde et al., 2009; Schlaug et al., 1995a] changes in brain regions involved in auditory processing, coordinating fast motor movements [Muentz et al., 2002], and supporting cognitive control [Moreno et al., 2011; Schulze et al., 2011; Sluming et al., 2007; Zuk et al., 2014] as well as sensory-to-motor coupling mechanisms [Ellis et al., 2012; Pantev et al., 2009; Zatorre et al., 2007]. Functional and structural alterations of the Heschl's gyrus (HG) [Schneider et al., 2002, 2005; Seither-Preisler et al., 2014] and the planum temporale

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(PT) [Elmer et al., 2013; Ohnishi et al., 2001] have repeatedly been shown to correlate fairly well with the ability of musicians to identify spectrotemporal acoustic variations [Elmer et al., 2012, 2013; Seither-Preisler et al., 2014]. Furthermore, the degree of malleability of the sensorimotor cortex is associated with finger tapping speed [Jäncke et al., 1998] and manual dexterity [Krings et al., 2000; Schlaug et al., 2009]. Additionally, in particular violinists were reported to show functional (Elbert et al., 1995) as well as structural adaptations (Bangert and Schlaug, 2006) in the left hand motor area. Even the ventro- and dorsolateral prefrontal cortex (PFC), both regions involved (among other functions) in sight-reading [Sergent et al., 1992] and contributing in excerpting cognitive control functions [MacDonald et al., 2000; Zuk et al., 2014], are affected by musical training.

During music production, acoustic cues have to be integrated into a multimodal processing stream via feedforward and feedback loops. These loops are principally mediated by intra- and interhemispheric fiber tracts conveying excitatory and inhibitory signals [Lotze et al., 2003]. In this context, the arcuate fasciculus constitutes the most eligible candidate enabling impulse transmission between the auditory-related cortex (ARC) and frontal brain regions [Catani et al., 2005; Catani and Mesulam, 2008]. In addition, transcallosal fibers crossing the isthmus of the corpus callosum are fundamentally involved in the synchronization of brain activity between bilateral ARCs. Meanwhile, there is even evidence showing that musical training has an influence on the functional–structural [Elmer et al., 2014; Engel et al., 2014; Halwani et al., 2011; Kühnis et al., 2014; Steele et al., 2013] skeleton of both pathways.

In the last decades, the investigation of resting state networks has gained increasing attention. Today, it is widely accepted that neuronal activity during rest reflects functional meaningful activity rather than noise *per se* [Damoiseaux et al., 2006; Deco and Corbetta, 2011; Otten et al., 2006; Sadaghiani and Kleinschmidt, 2013; Scheeringa et al., 2012; Weissman-Fogel et al., 2010]. In fact, functional connectivity during rest has been shown to be shaped by repetitive training in different domains [Langer et al., 2013; Urner et al., 2013; Vahdat et al., 2011], to mirror prior task-related neuronal activity [Deco and Corbetta, 2011], as well as to be predictive of behavioral performance [Noh et al., 2014; Otten et al., 2006]. In addition, resting state functional connectivity seems to constitute, at least partially, a physiological marker of the underlying structural skeleton [Deco and Corbetta, 2011; Greicius et al., 2009; Jung et al., 2013; Taubert et al., 2011].

Based on this state of knowledge, the present work aimed at examining the influence of music training on functional network characteristics during rest by using a graph-theoretical approach, without defining any *a priori* seed regions. In particular, we reasoned that the imprint of intense music training should even be manifested during task-free periods, in terms of increased functional con-

nectivity in networks typically involved in musical performance. By measuring a homogeneous group of string players, we specifically expect to find altered connectivity measures between the right sensorimotor cortex, the prefrontal, and the ARCs.

MATERIALS AND METHODS

Subjects

Fifteen professional string players (all graduates from music conservatory; five males; mean age = 24.2 years, standard deviation (SD) = 3.21; mean cumulative number of training hours = 10,831, SD = 5,797.99) and fifteen control subjects (all students from local universities without musical training; seven males, mean age = 26.07 years, SD = 4.98), participated in the study. All participants were consistently right handed as revealed by the Annett Handedness Inventory [Annett, 1970]. None of the subjects reported taking any medication or drugs, nor suffered from any past or present neurological or psychiatric disease. Subjects gave written informed consent and were paid for participation. This study was approved by the local ethics committee according to the Helsinki declaration.

Cognitive Capability and Musical Aptitude

To exclude between-group differences in intelligence, all subjects performed three subtests of the German “Wechsler Adult Intelligence Scale—3rd edition (WAIS-III)” [Wechsler, 1997], namely the subtest necessary to calculate the *Working Memory Index* (Number Sequencing and Repetition), the *Perceptual and Organization Index* (Mosaic Test), and the *Processing Speed Index* (Digit-Symbol Coding) [Waldmann, 2008]. Musical aptitude was quantified with the “Advanced Measures of Music Audition” (AMMA) test [Gordon, 1989]. In this test, subjects have to decide if two short piano sequences are equal or rhythmically/tonally different. Group differences in biographical data (IQ, age, and musical aptitude) were evaluated in IBM SPSS statistics 21 (<http://www-01.ibm.com/software/ch/de/analytics/spss/>) by using *t*-tests for independent samples (two-tailed). To test for a relationship between training hours and musical aptitude, a partial correlation analysis (corrected for age) was performed within the musicians group (one-tailed *t*-test).

Experimental Procedure, EEG Recording, and Data Processing

High-density electroencephalography (EEG) (256 channels) was recorded for 7 min (eyes open) with a sampling rate of 1,000 Hz by using the Geodesic Netamp system (Electrical Geodesics, Eugene, Oregon). During EEG recording, data were band pass filtered between 0.1 and

100 Hz, electrode Cz was used as recording reference, and impedances were kept below 30 k Ω . Data were preprocessed offline with the BrainVision Analyzer software (BrainVision Analyzer 2.2; <http://www.brainproducts.com/downloads.php>). Thereby, artifact-affected electrodes (in the outermost circumference, chin and neck) were removed, resulting in a 204-electrode array [Langer et al., 2013]. An independent component analysis was applied to correct remaining eye movement artifacts [Jung et al., 2000]. Data were band-pass filtered between 3 and 15 Hz to remove remaining muscle artifacts. After preprocessing, data were recomputed against an average reference, segmented into single sweeps of 2 s, and subjected to network analyses. The presentation of the resting state modality (i.e., fixation cross to minimize muscle artifacts in the EEG) was controlled by the Presentation software (Neurobehavioral Systems, USA, <http://www.neurobs.com>).

Connectivity Analyses in the Intracranial Space

Functional connectivity is a measure displaying statistical correlations of neural activity between different brain regions [Friston, 2011]. Thereby, following a graph-theoretical approach, a node represents a brain region, while an edge displays the connection between the nodes, here measured as instantaneous coherence (see below). In the context of this study, functional connectivity was evaluated for the artifact-free segmented EEG data (2 s segments, 210 segments per subjects) with the sLORETA toolbox (<http://www.uzh.ch/keyinst/loreta.htm>; see Pascual-Marqui [2002]). Intracranial instantaneous coherence [De Vico Fallani et al., 2010; Jäncke and Langer, 2011; Langer et al., 2012, 2013; Pascual-Marqui, 2007] was calculated between the centroid voxels of 84 regions of interest (ROIs) related to the Brodmann areas in sLORETA (BAs; 42 in each hemisphere) [Brodmann, 1909] for the frequency bands of interest: theta (6.5–8 Hz), alpha1 (8.5–10 Hz), and alpha2 (10.5–12 Hz) [Kubicki et al., 1979; Langer et al., 2012, 2013]. We specifically focused on “low-frequency” oscillations because they are relatively uncontaminated by artifacts [Goncharova et al., 2003] and have previously been shown to contribute to the propagation and integration of information across long-range brain circuits [Ward, 2003]. In particular, this connectivity measure is calculated by dividing the square of the cross-spectrum of a particular frequency f from two regions x and y by the power spectra of these two region:

$$SC_{xy}(f) = \frac{|S_{xy}(f)|^2}{S_{xx}(f)S_{yy}(f)}$$

Thus, the resulting matrix of every single subject contains the mean functional connectivity values of the 7 min resting state period (average of 210 segments of 2 s each per subject) between all predefined 84 BAs for all single-frequency bands.

TABLE I. Specification of the brain regions underlying the centroid voxel of the BAs obtained from the NBS analysis

BA	MNI coordinates (x, y, z)	Brain structure
BA41	(45, -30, 10)	A1
BA41	(55, -20, 5)	A1
BA42	(-60, -25, 10)	PT
BA42	(-60, -10, 15)	A1
BA42	(65, -25, 10)	PT
BA3	(35, -25, 50)	PM/SS
BA25	(-10, 20, -15)	vmPFC
BA44	(-50, 10, 15)	Broca's area

Planum temporale, PT; primary auditory cortex, A1; primary motor cortex, PM; primary somatosensory cortex, SS; ventromedial prefrontal cortex, vmPFC.

The Juelich Histological and the Harvard–Oxford cortical atlases (<http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/Atlases>; implemented in FSL: <http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FSL>) were used for a more detailed specification of brain regions underlying the coordinates of the centroid voxel of the BAs. Coordinates are depicted in Table I for the BAs between which the two groups showed a difference in functional connectivity as revealed by the NBS analysis (see below).

Network-Based Statistics

For evaluating between-group differences in functional connectivity during the 7 min resting state period, the individual 84×84 connectivity matrices (with the instantaneous coherences between the predefined 84 ROIs) of the single subjects entered the Matlab-based toolbox Network-based Statistic (NBS) [Zalesky et al., 2010], separately for the frequency bands theta, alpha1, and alpha2. In contrast to traditional statistical network evaluations, where for each connection a hypothesis test is performed and the p -values are corrected for multiple comparisons, NBS tests networks as a whole, thereby accounting for dependencies between the connection values of each individual. In the first step, a t -test is calculated for each connection. Thereby edges exceeding an initial sensitivity threshold ($t = 3.6$ for the theta and $t = 4.0$ for the alpha frequency band) form a so-called supra-threshold network, constituting a subnetwork (or many disjoint subnetworks) of the network to be tested. The size of the biggest network, called the biggest component serves as a test statistic. A simulation of the unknown distribution of the test statistic is performed by randomly permuting (5000 randomizations) the residuals after fitting a linear model for each connection. Permutation of the residuals is done between the subjects. For each connection, the same permutation is applied. Thereby, the within-subject dependencies of the connection values are preserved. The sizes of the biggest components constitute the simulated distribution. The null hypothesis for a selected alpha error is then tested by comparing the size of the biggest component of the full network

Figure 1.

Network-based statistics between musicians and musical laymen. Increased functional connectivity (depicted in red) in musicians in (A) the theta and (B) the alpha frequency band between BAs depicted with enlarged size ($p < 0.05$, FVE corrected). (C) The node degree measures of the nodes for the alpha frequency band between which the musicians showed an increased func-

tional connectivity (NBS analysis). In the right auditory cortex (BA 41 and 42; visualized in red), the musicians show an increased node degree value compared to the nonmusicians ($p < 0.05$, FDR corrected). Intra- and interhemispheric connectivities are shown in the sagittal, horizontal, and coronal views. A = anterior, L = left hemisphere, R = right hemisphere.

to be tested, with the simulated distribution of the sizes of the biggest components of the simulated random networks. This procedure mimics a familywise error rate correction of the traditional procedure, where for each edge a separate hypothesis test is performed. The BrainNet Viewer (<http://www.nitrc.org/projects/bnv/>; Xia et al. [2013]) was used for visualization of the results (Fig. 1A, B).

Graph-Theoretical Small-Worldness and Regional Node Degree Analysis

Small-world network topologies imply a high segregation and integration, thereby indicating the presence of

highly specialized and interconnected functional modules [Rubinov and Sporns, 2010]. Thus, small-world networks are characterized by a high cluster coefficient (C_{real}) and a short path length (L_{real}) compared to a random network ($C_{\text{rand}}, L_{\text{rand}}$) [Bullmore and Sporns, 2009]. Mathematically, small worldness is defined by the small-world indices γ ($C_{\text{real}}/C_{\text{rand}}$), λ ($L_{\text{real}}/L_{\text{rand}}$), and σ (λ/γ) [Humphries et al., 2006; Sporns et al., 2007]. C and L were calculated with the Matlab-based Brain Connectivity Toolbox (<http://www.brain-connectivity-toolbox.net>; Rubinov and Sporns, 2010) for the real and a random network (100 randomizations) based on the averaged-weighted connectivity matrix across all subjects. These indices were calculated separately for

matrices thresholded from $r = 0.65$ – 0.95 in increments of 0.05 to test which thresholded connectivity matrix represents best small world organization ($\sigma \gg 1$). The highest σ was obtained for the matrix thresholded with $r = 0.95$. This threshold was then applied to the connectivity matrices of every single subject for further analyses (node degree).

Subsequently, to evaluate efficiency in information transmission between the BAs involved in the functional network of the between-group NBS analysis (Table I), the node degree was calculated with the Brain Connectivity Toolbox for the individual thresholded ($r = 0.95$) matrices. Thereby, the number of connections of a particular node in a network to other nodes was calculated. To test for group differences in the node degree measures, Mann–Whitney U tests (according to a deviation from a normal distribution) were computed in SPSS for the node degree values (false discovery rate (FDR) corrected) [Benjamini and Hochberg, 1995; Yekutieli and Benjamini, 1999].

Brain–Behavior Relationships

Partial correlation analyses (corrected for age; one-tailed hypothesis testing; FDR corrected) were calculated in the musicians between the total AMMA score and total training hours during life to show an association between training and musical skill. In addition, we calculated correlations separately between the total AMMA score and training hours and the connectivity values per edge of the obtained network in the NBS analysis. Furthermore, the mean connectivity value of the network and the node degree values of the respective nodes (Table II) were correlated with the AMMA score and the cumulative training hours during life.

RESULTS

Autobiographical and Behavioral Data

The two groups did not differ in terms of age ($t_{(28)} = 1.22$, $p = 0.23$; two-tailed) and cognitive capability ($t_{(28)} = -1.68$, $p = 0.1$; two-tailed). However, as expected, musicians outperformed the controls in the AMMA test (total score: $t_{(28)} = -5.87$, $p < 0.001$; tonal score: $t_{(28)} = -5.29$, $p < 0.001$; rhythm score: $t_{(28)} = -5.23$, $p < 0.001$; two-tailed). Partial correlation analysis (corrected for age) within the musicians revealed a positive relationship between the cumulative training hours during life and musical skill. This implies that the more hours musicians have trained, the higher was the total AMMA score ($r = 0.754$, $p = 0.001$; one-tailed t -test; see Fig. 2A).

Network-Based Statistics

Musicians showed significantly increased functional connectivity in the theta (Fig. 1A) and alpha1 (Fig. 1B) fre-

quency range (theta: $p = 0.049$; alpha1: $p = 0.01$, FWE corrected) compared to the control group. In particular, results revealed increased interhemispheric connectivity between the bilateral PT (theta, alpha1), left PT and right sensorimotor cortex (theta, alpha1), right PT and left ventromedial prefrontal cortex (vmPFC; theta, alpha1). Increased intrahemispheric connectivity was also found within left (theta, alpha1) and right (alpha1) PT and A1, between left PT and left Broca pars opercularis (theta), between right A1 and right sensorimotor cortex (alpha1). A detailed summary of these results is shown in Table II. Comparison between the two groups did not reveal any increased functional connections in the nonmusicians compared to the expert group across all examined frequency bands.

Network-Based Statistics: Brain–Behavior Relationships

By investigating putative interrelationships between the total AMMA score, the cumulative number of training hours during life, and the mean functional connectivity of the network obtained from the NBS analyses within the expert group, we consistently found positive correlations (AMMA: theta (Fig. 2B): $r = 0.583$, $p = 0.03$; alpha1 (Fig. 2C): $r = 0.656$, $p = 0.01$; training hours: theta (Fig. 2D): $r = 0.476$, $p = 0.05$; alpha1 (Fig. 2E): $r = 0.475$, $p = 0.06$; one-tailed hypothesis testing; FDR corrected). Correlation analyses between the single connectivity values for each edge of the networks with the total AMMA score revealed that most relations follow a positive pattern across both frequency bands theta and alpha1. Detailed results are depicted in Table II. Within-group correlation analyses for the nonmusicians did not reveal significant results.

Regional Node Degree Analysis

The node degree measures were compared between the two groups. Thereby, we only selected the nodes (i.e., BAs) of the network showing increased connectivity in musicians compared to nonmusicians (NBS analysis; Table II). Results revealed increased node degree values in musicians in two nodes residing in the right ARC (Fig. 1C; musicians: BA41 (MNI coordinates: 45, -30 , 10; A1): mean = 20.4, SD = 12.96; BA42 (65, -25 , 10; PT): mean = 25.46, SD = 14.42; nonmusicians: BA41 (45, -30 , 10; A1): mean = 8.73, SD = 4.68; BA42 (65, -25 , 10; PT): mean = 13.37, SD = 7.47; Mann–Whitney U test BA41: $p = 0.018$; BA42: $p = 0.045$, FDR corrected). Correlation analyses between the total AMMA score or the total number of training hours during life and the node degree values of BA41 and BA42 did not show significant positive relationships neither in the musicians nor in the control group.

TABLE II. Functional connectivity measures for each pairwise association identified with the network-based statistics tool ($p < 0.05$) for both groups in the theta and the alpha I frequency range

Frequency (Hz)	Network connection (MNI x, y, z)	Mean coherence		Mean coherence musicians $\pm$ SD	t stats	p -value per edge (uncorr)	Correlations with total AMMA score (FDR corr)		Correlations with training hours during life (FDR corr)	
		nonmusicians $\pm$ SD					p -value	r	p -value	r
6.5–8	BA42 (–60, –25, 10) – BA41 (45, –30, 10)	0.18 $\pm$ 0.1		0.43 $\pm$ 0.22	3.84	0.0003	0.06	0.447	0.12	0.347
	BA 42 (–60, –25, 10) – BA 42 (65, –25, 10)	0.21 $\pm$ 0.11		0.47 $\pm$ 0.22	4.01	0.0002	0.03	0.563	0.16	0.289
	BA25 (–10, 20, –15) – BA42 (65, –25, 10)	0.24 $\pm$ 0.12		0.49 $\pm$ 0.23	3.66	0.0005	0.03	0.564	0.05	0.492
	BA42 (–60, –25, 10) – BA42 (–60, –10, 15)	0.26 $\pm$ 0.12		0.53 $\pm$ 0.23	3.85	0.0003	0.03	0.562	0.04	0.512
	BA42 (–60, –25, 10) – BA44 (–50, 10, 15)	0.3 $\pm$ 0.13		0.56 $\pm$ 0.23	3.69	0.0004	0.03	0.602	0.03	0.557
	BA42 (–60, –25, 10) – BA3 (35, –25, 50)	0.18 $\pm$ 0.12		0.43 $\pm$ 0.21	3.8	0.0003	0.03	0.642	0.03	0.572
	BA25 (–10, 20, –15) – BA41 (45, –30, 10)	0.24 $\pm$ 0.16		0.54 $\pm$ 0.19	4.37	<0.0001	0.02	0.613	0.19	0.266
	BA41 (55, –20, 5) – BA41 (45, –30, 10)	0.32 $\pm$ 0.15		0.58 $\pm$ 0.17	4.41	<0.0001	0.16	0.315	0.41	0.070
	BA42 (–60, –25, 10) – BA41 (45, –30, 10)	0.23 $\pm$ 0.17		0.52 $\pm$ 0.2	4.3	<0.0001	0.03	0.570	0.07	0.481
	BA25 (–10, 20, –15) – BA42 (65, –25, 10)	0.29 $\pm$ 0.19		0.57 $\pm$ 0.18	4.06	0.0002	<0.001	0.781	0.07	0.454
8.5–10	BA41 (55, –20, 5) – BA42 (65, –25, 10)	0.38 $\pm$ 0.18		0.66 $\pm$ 0.13	4.68	<0.0001	0.07	0.459	0.19	0.265
	BA42 (–60, –25, 10) – BA42 (65, –25, 10)	0.27 $\pm$ 0.2		0.56 $\pm$ 0.19	4.07	0.0002	0.01	0.742	0.01	0.673
	BA41 (55, –20, 5) – BA3 (35, –25, 50)	0.38 $\pm$ 0.17		0.66 $\pm$ 0.12	4.89	<0.0001	0.06	0.500	0.07	0.461
	BA42 (–60, –25, 10) – BA3 (35, –25, 50)	0.26 $\pm$ 0.18		0.53 $\pm$ 0.18	4.01	0.0002	0.01	0.688	0.01	0.686

Listed are the averaged coherence values across all subjects separated for the two groups (FWE corrected), the t statistics, and p -values (uncorrected) for the single associations, and the correlation of the coherence values per edge with the total AMMA score and the total number of training hours during life, respectively (FDR corrected).

Figure 2.

Correlations within the musicians between the total AMMA score and (A) the cumulative number of training hours during life, (B) the mean value of functional connectivity in the theta, and (C) the alpha1 frequency band and correlations between the total number of training hours during life and the mean value of functional connectivity for (D) theta and (E) alpha1.

DISCUSSION

The aim of this study was to determine whether the distinctive neurophysiological and anatomical “fingerprint” often observed in musicians could still be detected during task-free conditions. In line with our hypothesis, results showed that brain regions, which are synchronously activated during musical performance build a functional unit that is also detectable during rest. Our findings support this point of view and additionally indicate that the right ARC constitutes a hub (i.e., increased local connectedness) within this network (comparable to Jäncke et al. [2012] with absolute pitch musicians). Notably, we also revealed robust brain–behavior relationships suggesting a training-related intertwining between resting state activity, musicianship, and training. Therefore, we propose that long-

term musical training facilitates the functional interrelationship of distinct brain areas in such a manner that the characteristic electrophysiological signature can still be detected during resting state periods lasting for 7 min.

The resting state network we identified consists of the same brain regions that have repeatedly been shown to be altered as a function of musical expertise (for an overview, consider for example Muentel et al. [2002]). More precisely, at least two previous studies provided evidence for an increased representation of the left-hand area in the somatosensory [Elbert et al., 1995] and motor cortex [Bangert and Schlaug, 2006] of violinists compared to pianists or nonmusicians. In addition, there are also findings pointing to a strong influence of musical training on the functional [Pantev et al., 2001; Schon et al., 2004; Tervaniemi et al., 2006] and structural [Bermudez et al., 2009; Hyde et al.,

2009] architecture of the ARC as well as on functional [Kühnis et al., 2014] and structural [Elmer et al., 2014; Steele et al., 2013] connectivity between bilateral ARCs. Such plastic adaptations might not only favor the processing of a variety of spectrotemporal acoustic cues [Besson et al., 2011; Kühnis et al., 2014] but also promote an inter-hemispheric division of labor [Elmer et al., 2014; Kühnis et al., 2014; Steele et al., 2013]. Thereby, it is assumed that the right ARC is preferably engaged in processing spectral information, whereas the left counterpart is more likely sensitive to fast changing acoustic cues [Griffith and Warren, 2002; Poeppel, 2003; Thierry et al., 2003; Zatorre and Belin, 2001]. This framework is even in line with findings reported by Schneider et al. [2002] who detected a relationship between instrument-dependent pitch perception preference and functional and structural asymmetry of the Heschl’s gyrus. In particular, in string players, this trait is more pronounced in the right hemisphere, whereas musicians playing fast and reactive instruments (i.e., piano) more likely show plasticity effects in the contralateral homologue. Finally, our findings are consistent with an EEG study showing that musical training does not only influence the architecture of auditory and motor cortices *per se* but also the communication between these two brain regions [Ellis et al., 2012; Jäncke, 2012].

To date, there is a growing body of literature reporting musical training-related adaptations in musicians within Broca’s area [Sergent et al., 1992] and in particular within the pars opercularis [Maess et al., 2001]. The latter can be considered as being a part of the so-called motor territory [Amunts et al., 1999; Binkofski et al., 2000], which is a point of convergence of the arcuate fasciculus, and has repeatedly been shown to be involved in sensory-to-motor coupling mechanisms [Pantev et al., 2009], sight reading [Sergent et al., 1992; Parsons et al., 2005], and language-selective processing [Fedorenko et al., 2012; Makuuchi and Friederici, 2013]. Furthermore based on the assumption that the concept of functional connectivity implies, at least in part, being a neurophysiological fingerprint of the underlying anatomical architecture [Deco and Corbetta, 2011; Greicius et al., 2009; Jung et al., 2013; Taubert et al., 2011], we propose that the increased functional coupling we revealed between the left PT and Broca’s region might originate from altered structural properties of the arcuate fasciculus found in professional musicians [Engel et al., 2014; Halwani et al., 2011; Wan and Schlaug, 2010].

Currently, it is also widely accepted that music has a strong emotional impact on human beings [Blood et al., 1999; Grewe et al., 2005, 2009; Koelsch et al., 2006; Koelsch, 2014]. Hence, the vast interdependencies we revealed between the vmPFC and ARC, Broca’s region, and the sensorimotor cortex possibly indicate that music perception and production are tightly coupled with emotions [Koelsch et al., 2006] and cognitive [Fedorenko et al., 2012] functions, even during rest. In this context, it cannot be ruled out that the obtained connectivity patterns are a

result of music-related mentation. Although subjects reported after the measurement to not have been focusing on a particular thought during data recording, a complete omission of mental rehearsal of practiced music passages cannot be excluded.

To date, to the best of our knowledge, only two fMRI studies evaluated the influence of musical expertise on functional connectivity during rest [Fauvel et al., 2014; Luo et al., 2012]. In the first study, Luo et al. [2012] selected *a priori* defined seed regions (i.e., left PM, left ARC, left SS, and left visual cortex) for computing connectivity analyses. Results consistently revealed increased connectivity between the *a priori* defined seeds and the contralateral homolog regions. By contrast, Fauvel et al. [2014] selected the seed regions based on between-group differences in gray matter density, and reported increased functional connectivity in musicians between prefrontal, temporal, inferior-parietal, and premotor areas. However, one critical aspect that is worth mentioning is that both studies used fMRI in combination with a seed-based analysis approach. The precarious aspect of this procedure is that it leads to the disadvantage of reductionism, meaning that it only enables to make a statement about the interrelationship between *a priori* defined nodes while completely neglecting residual whole-brain dynamics. A further shortcoming is that data are often contaminated by the detrimental effects of scanner noise, which induces activations within the auditory system. Therefore, fMRI does not provide an optimal environment for measuring pure resting state activity (even more in musicians).

The fact that we found increased connectivity patterns in musical experts in the theta- and lower alpha-frequency ranges might be explained by the evidence that low-frequency oscillatory activity is involved in the propagation of information across long-distanced brain regions [Elmer et al., 2015; Ward, 2003], as it is the case in our findings. Furthermore, theta and alpha oscillatory activity is involved in various brain functions crucial for music processing and production, such as memory [George and Coch, 2011; Schulze and Koelsch, 2012; Ward, 2003], inhibitory functions [Klimesch et al., 2007a; Moreno et al., 2014], or attention [Baumann et al., 2008; Klimesch, 1999; Zuk et al., 2014]. However, regarding the fact that we only found differences in the lower but not in the upper alpha band remains an unsolved issue since there is not at all clarity about the exact functional meaning of the different oscillations.

In summary, based on our results, we propose that the pattern of increased resting state connectivity we found constitutes an idiosyncratic signature of musical training. In fact, here we show that the same brain regions that have repeatedly been shown to be functionally and structurally altered in musicians are indeed hyperconnected on a functional level, even during a task-free condition. Hence, our results constitute an important step toward a holistic and integrative understanding of the “silent”

imprint of musical training on the human brain. Certainly, future studies using multimodal imaging techniques (i.e., simultaneous EEG and MRI measurements) are strictly required in order to achieve a deeper understanding of the functional–structural compliance of neuronal network organization.

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