Interoception and the musical brain: Evidence from cross-sectional and longitudinal behavioural and resting-state fMRI study

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Abstract

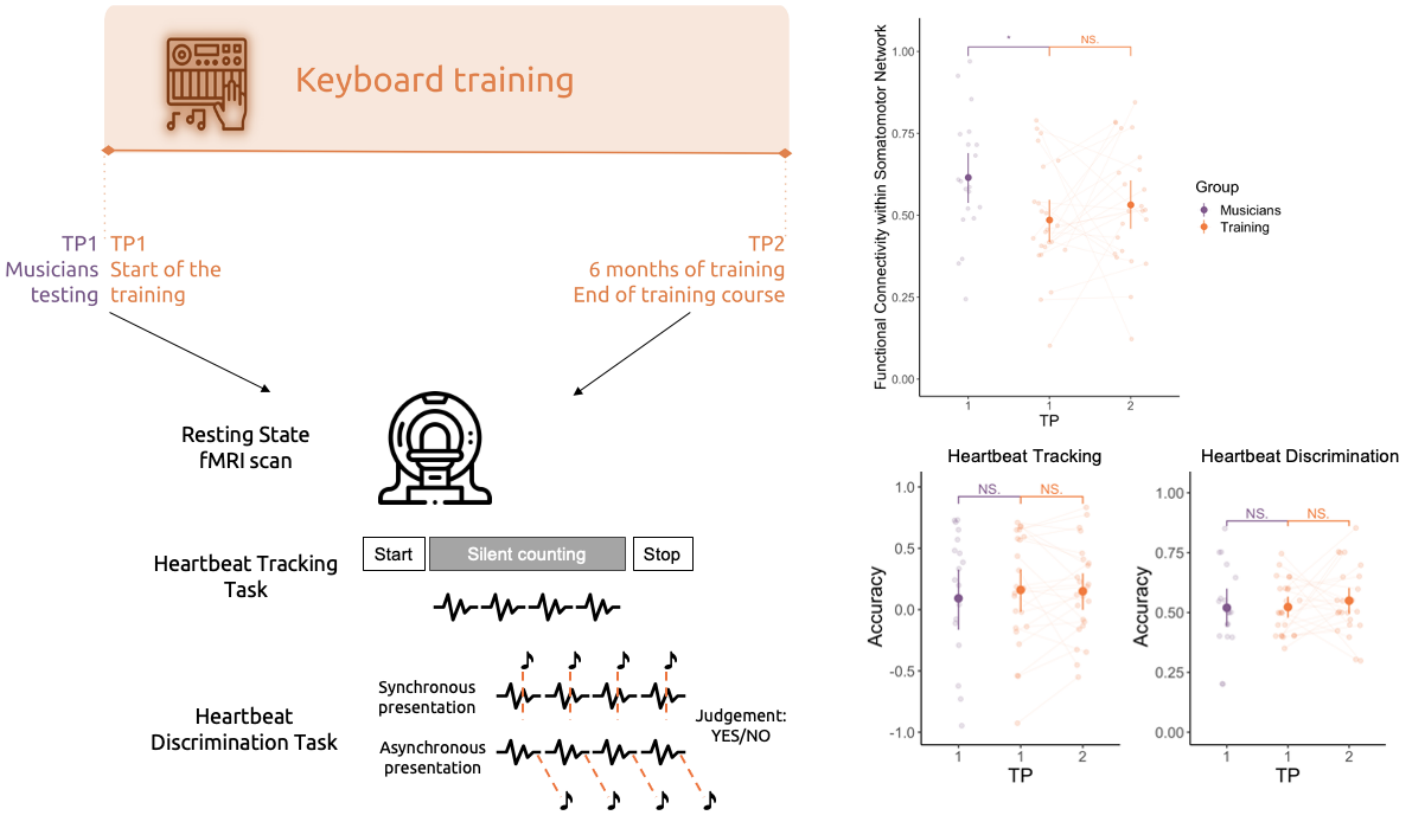
Musical training has been linked to enhanced interoceptive abilities and increased resting-state (RS) functional connectivity (FC) within the interoceptive brain network. We aimed to replicate and extend these findings with a unique cross-sectional and longitudinal study design. Professional musicians and matched individuals with no prior musical experience (training group) were recruited. Participants underwent RS fMRI scans and completed heartbeat counting and discrimination tasks outside of the scanner (time point 1). The training group additionally had RS scans and interoception tests repeated after a 6-month-long keyboard course training (time point 2).

We found no evidence for increased interoceptive abilities in professional musicians relative to non-musicians, nor did we observe any improvements in interoception over the course of musical training. RS FC analysis revealed increased FC within the sensorimotor network in professional musicians compared to the training group at the first time point with no change in FC over time in the Training group.

These findings challenge the view that musical training may improve interoceptive abilities. Yet, the results suggest that musical training is related to increased communication within the sensorimotor RS network, which consists of some hubs important for interoceptive processing (namely pre- and postcentral gyri and supplementary motor area).

Keywords: music; professional musicians; insular cortex; interoception; resting state; functional connectivity; learning

Graphical Abstract



1. Introduction

Gaining expertise in playing a musical instrument involves extensive sensorimotor training: an ability to simultaneously integrate information coming from different sensory modalities (Karpati et al. 2016; Altenmüller 2008). This is reflected by strengthened connections between motor, auditory, somatosensory, and multimodal integration areas in the brain of musicians compared to non-musicians (for review, see (Olszewska et al. 2021)). Yet, recent evidence suggests that the superior integration of sensory information in musicians may go beyond exteroceptive senses (that is senses which provide information from the outside world) and also extend to interoceptive information (that is information coming from inside the body providing cues about the physiological condition of the body (Khalsa et al. 2018)]. Indeed, compared to untrained controls, professional musicians (singers and string players) showed an enhanced ability to sense internal bodily sensations, such as heartbeats (Schirmer-Mokwa et al. 2015). In another study, trained musicians performed better in the heartbeat perception tasks and showed higher self-reported interoceptive sensibility (Hina, Aspell, and Cardini 2020). They also presented a larger electrophysiological index of interoceptive processing - the heartbeat evoked potential amplitude.

At the neural level, multimodal integration has been associated with the activity of the right anterior insula, considered a central hub for interoceptive processing and awareness of bodily feelings (Critchley et al. 2004; Craig 2009; Critchley and Harrison 2013). Additionally, the insular cortex is implicated in diverse musical processes, such as recognizing tempo and melody processing (Platel et al. 1997; Thaut 2003; Thaut, Trimarchi, and Parsons 2014), acquiring associations between sounds and actions while learning music (Mutschler et al. 2007), and experiencing emotional reactions to music (Blood et al. 1999; Koelsch 2014). Importantly, the insula is a part of the brain salience network, which also includes the anterior temporoparietal junction and dorsal anterior cingulate cortex, and is responsible for detecting significant internal and external stimuli and directing behaviour while adjusting predictions about the inner and outer surroundings (Taylor, Seminowicz, and Davis 2009; Seeley et al. 2007). Neuroimaging studies have found that functional connectivity (FC) within the salience network is significantly increased in musicians compared to non-musicians, and that the strength of resting state (RS) FC within this network is positively related to the duration of musical training (Luo et al. 2014), suggesting that musical training may increase communication within the salience network.

The insular cortex can be divided into three subregions based on their patterns of whole-brain functional connectivity during resting-state fMRI: the posterior (PI), ventral anterior (vAI), and dorsal anterior (dAI) subdivisions (Uddin et al. 2014; Deen, Pitskel, and Pelphrey 2011). While, the posterior and mid-insula are functionally connected to areas involved in sensorimotor processes, the dorsal anterior subdivision is connected with areas involved in higher-level cognitive control and the ventral anterior subdivision is linked to regions involved in affective processes. Previous research found that professional musicians have greater connectivity of all insula subdivisions compared to non-musicians with brain networks involved in salience detection (i.e., anterior and medial cingulate cortex), executive control (i.e., dorsolateral prefrontal cortex and the temporoparietal junction), and higher-order cognitive functioning and affective processing (i.e., orbitofrontal cortex and temporal pole) (Zamorano et al. 2017).

Additionally, the years of musical training in musicians were positively correlated with connectivity between the three insular subdivisions and sensorimotor, auditory regions, and the middle occipital cortex (Zamorano et al. 2017), suggesting that increased insular FC may be related to extensive musical training. Yet, to our knowledge, no study so far has looked directly at the *causal* role of musical training in insular subregions FC and interoceptive processing. Therefore, in the present study, we uniquely combined a cross-sectional and longitudinal design to replicate and extend previous findings on music-related interoceptive processing and resting-state FC. Specifically, we recruited a group of professional musicians and a sex, age and education-matched group without musical background, who underwent 6-month-long keyboard training. Based on past research, we hypothesised that (1) professional musicians would show better interoceptive performance compared to non-musicians which would be coupled with (2) enhanced resting-state FC between regions related to interoceptive processing (i.e., different parts of the salience network and sensorimotor regions). Moreover, we suspected that better interoceptive performance in musicians would be particularly enhanced in the task that requires discrimination between exteroceptive (auditory) and interoceptive signals (heartbeats). We also hypothesised that (3) non-musicians would show an improvement in interoceptive performance following musical training (4) which would also be coupled with increased resting FC between interoceptive regions.

2. Methods

2.1. Participants

Using G Power (Faul et al. 2009) and based on results from previous studies on interoception in musicians (Schirmer-Mokwa et al. 2015), with an expected power of 0.8 and an effect size of 1.04, we estimated that a minimum sample size of 16 participants per group would be appropriate to replicate the previous result of the difference between musicians and non-musicians regarding interoceptive accuracy. We recruited 44 healthy volunteers (all female university students) to participate in the study. Participants were right-handed, had normal or corrected-to-normal vision and unimpaired hearing, BMI within normal range, presented no history of psychiatric and neurological illness and showed no MRI contradictions (i.e., claustrophobia, having any metal implants, teeth braces or bridges, or cardiac pacemakers). 20 of them (age range 19-26 years, M = 21.9, SD = 2.1) completed formal secondary music education on a keyboard instrument (piano, harpsichord, pipe organ, accordion) and had a total of 11-20 years of experience with keyboard instruments (M=15.2, SD=1.88) (herefrom referred to as Musicians). The remaining 24 volunteers (age range 18-23, M=21.3, SD=1.4) were recruited to the longitudinal arm of the study to undergo a 26-week piano training course (herefrom referred to as the Training group). The participants in the Training group were musically naïve, except for compulsory music classes in the general curriculum.

All participants provided written informed consent and were reimbursed for their time. The Research Ethics Committee at the Institute of Psychology of the Jagiellonian University, Kraków, Poland approved the study and the experiment has been carried out in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2. Experimental design

Musicians attended a single session during which they underwent a 10-min resting state (RS) scan and a structural scan. As this study was a part of a larger project, between the RS scan and structural scan, participants completed several music-related tasks, which will be described elsewhere. During the RS scan participants were asked to rest with their eyes open focusing on a fixation cross in the centre of the screen with the instruction to try to relax, not to think of anything in particular, and not to fall asleep. Following the scan, participants underwent interoception testing as described below (Figure 1). Participants in the Training group underwent two such sessions, before and after the 6-month keyboard playing course. Briefly, the keyboard training involved biweekly sessions with an experienced piano teacher. Participants were additionally required to practice individually for around 4 hours per week (30 mins a day). By the end of the course, participants were able to play from memory (at least) 8 piano pieces of various complexity, as well as mastered technique basics, such as staccato/legato, technical motor exercises, and some gross and fine motor skill exercises. The training was run using a note-free technique, so participants were not able to read musical score. Progress on the course was assessed by the teacher as well as by one of the authors of the study (AO) during video calls on weeks when there were no sessions with the teacher.

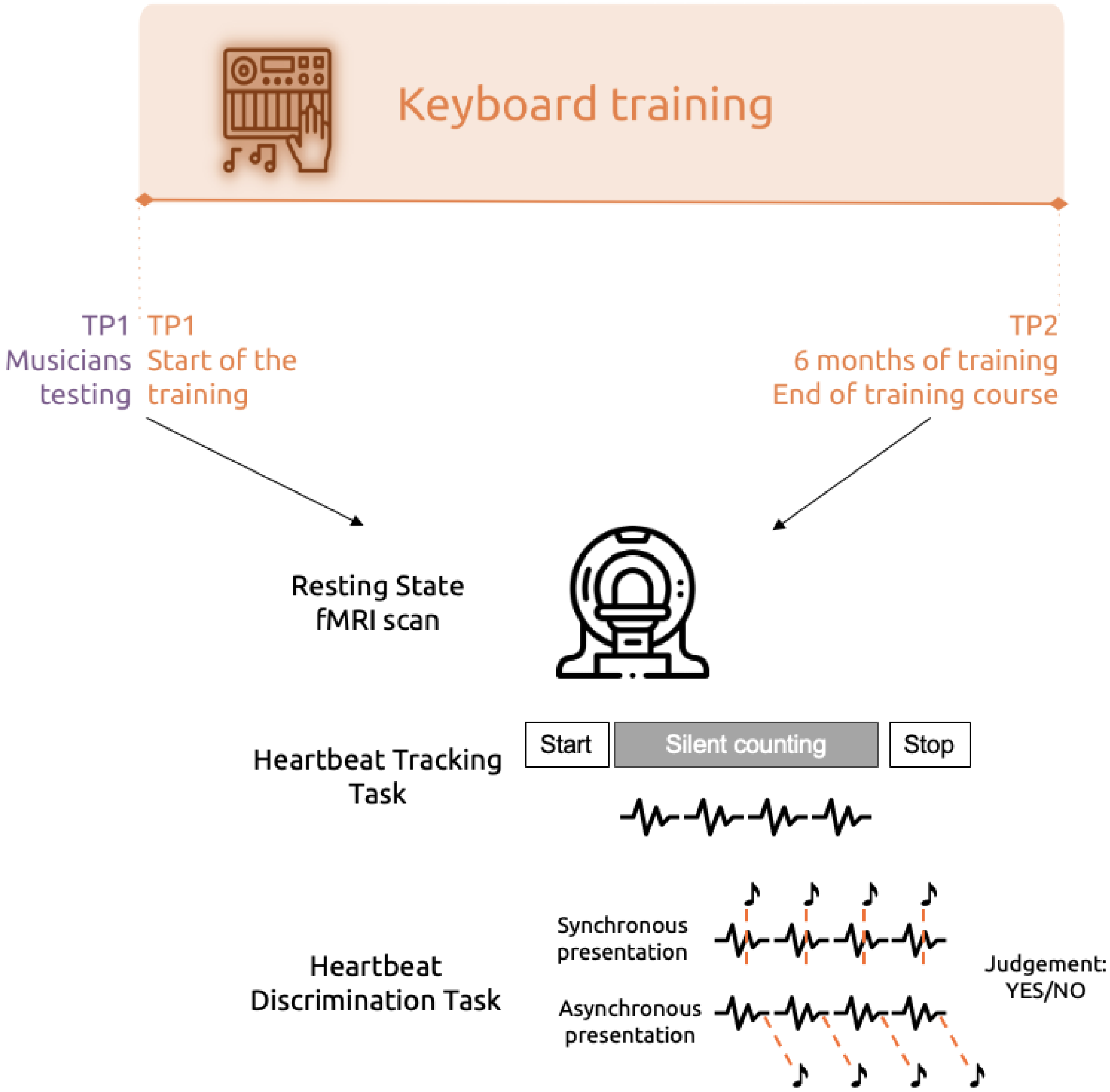


Figure 1. Experimental design overview.

2.3. Interoception testing

Participants completed several behavioural and self-report measures of interoceptive performance to comprehensively assess distinct dimensions of interoceptive abilities: accuracy, sensibility and insight (Garfinkel et al. 2015; Khalsa et al. 2018; Suksasilp and Garfinkel 2022).

Interoceptive sensibility, that is subjectively perceived awareness of one's bodily sensations, was measured using the awareness subscale of the Body Perception Questionnaire (BPQ)-Short Form (Cabrera et al. 2018). BPQ consists of 26 questions on awareness of bodily feelings, such as respiratory sensations or stomach and gut pains in daily life. The awareness of these sensations is rated on a five-point scale (from 0—Never to 4—Always). The sum of item responses serves as an index of interoceptive sensibility.

Interoceptive accuracy, that is the objective ability to perceive one's internal bodily sensations, was assessed using both the heartbeat (HB) tracking and discrimination tasks. These tasks have distinct psychophysiological properties; hence, their combination enhances inferential power (A. Schulz et al. 2021) and both were used previously in context of interoception and music (Schirmer-Mokwa et al. 2015; Hina, Aspell, and Cardini 2020).

In the **HB tracking task** (Garfinkel et al. 2015; Schandry 1981), participants were instructed to count silently, without manually checking, heartbeats they feel in the body during variable time periods. These ratings were compared against the actual number of HBs, as recorded objectively and noninvasively by a clinical-grade pulse oximeter (Nonin Inc.) fitted with a soft (i.e., not spring-loaded) cuff, placed over the participant's index or middle finger of their non-dominant hand. There were six trials with variable time windows of 25, 30, 35, 40, 45, and 50 s, presented in a randomized order. The accuracy score equalled 1/6 ∑ [1 − (|nbeats real − nbeats reported|)/((nbeats real + nbeats reported)/2)] (Hart et al. 2013).
Notably, performance in the HB tracking task can potentially be affected by various factors, including knowledge of one's heart rate or counting seconds instead of heartbeats; thus, its validity has recently been criticized (e.g., (Ring and Brener 2018; Desmedt et al. 2020) but see (A. Schulz et al. 2021; Ainley et al. 2020) for further discussion). To account for these potential confounds, we provided clear instructions, explicitly stating that participants should not guess or try to estimate their heart rate in any way, only report heartbeats that they actually feel, and assured participants that reporting no beats at all was acceptable as well. Providing such explicit instructions has proved to reduce the influence of confounding variables on HB tracking performance (Desmedt et al. 2020).

To additionally control for time estimation ability confounding performance in the heartbeat tracking task, we also employed a **Time Estimation Task** (TET), designed to match the HB tracking task. Participants were asked to estimate how much time elapsed during intervals of 24, 31, 34, 41, 44, and 51 s, presented in a randomised order. No feedback related to their performance was provided. The formula used to calculate the TET accuracy score was the following: 1/6 ∑ (1−(|actual elapsed time−estimated elapsed time|]/actual elapsed time)).

In the **HB discrimination task** (Garfinkel et al. 2015; Whitehead et al. 1977), participants judged whether a series of 10 tones (presented at 440 Hz and lasting 100 ms) were in sync or out of sync with their heartbeat. On synchronous trials, the 10 notes occurred at the rising edge of the finger pulse pressure wave; on asynchronous trials, they followed 300 ms later. Half the tones were thus presented "on the heartbeat" and half were delayed (Wiens and Palmer 2001). The order of these synchronous and delayed trials was randomized for each participant. As in both conditions, the tones were presented at the same rate, participants could not use the tempo of tones or other knowledge about their heart rate to guide responses. Since the discrimination task delivered external feedback that could be used to infer heart rate, this task was always performed after the HB tracking task. As per signal detection theory, each trial was categorised as either a Hit, Miss, False Alarm or Correct Rejection depending on the trial type and participants' responses. To quantify the performance, we calculated an accuracy score [Accuracy = (NHits + NCorrect rejections)/Ntrials]. For completeness, we also calculated d' as a signal detection theory index of individual sensitivity to heartbeats [d' = z(False Alarms) − z(Hits), where a value of d′ = 3 is close to perfect performance while a value of d′ = 0 is chance ("guessing") performance]. D' is a subject bias-free measure of performance (the overall propensity to say "yes").

At the end of each trial, in both the tracking and discrimination tasks, participants immediately rated how confident they were in their answers on a scale of 0-100, where 0 denoted a guess and 100 denoted complete confidence. The mean confidence ratings reflected the HB perception sensibility (Garfinkel et al. 2015). Additionally, to control for the effect of heart rate knowledge, participants were also asked to estimate their average resting state heart rate at the very end of the study.

We also computed **interoceptive insight** scores (the metacognitive awareness of one's performance), which reflect the extent to which confidence predicts task accuracy (Garfinkel et al. 2015; Khalsa et al. 2018). The insight score for the HB tracking task was assessed by calculating the within-participant Pearson correlation, *r*, between confidence and accuracy scores. Due to binary (yes/no) responses on the HB discrimination task, interoceptive insight was calculated using the meta-d' index, which quantifies metacognitive sensitivity (i.e., the efficacy with which confidence ratings discriminate between correct and incorrect judgments) in a signal detection theory framework (Maniscalco and Lau 2012, 2014). Meta-d' was selected as a measure of interoceptive insight as it produces un-confounded metacognition estimates (Fleming and Lau 2014; Barrett, Dienes, and Seth 2013; Fleming 2017). The meta-d' was calculated in Matlab using the script available under the link: http://www.columbia.edu/~bsm2105/type2sdt/trials2counts.m.

2.4. Behavioural data analysis

To confirm whether musicians present higher interoceptive abilities than non-musicians, we first compared indexes of performance on interoceptive measures and TET between Musicians and the Training group at TP1 with a series of independent samples t-tests. Next, to see whether interoceptive abilities increased over the course of the training, we analysed the same indexes in the Training group across time with paired-sample *t*-tests. Additionally (post hoc), we also conducted equivalent Bayesian statistics (BF_{10}), extending insights to guide interpretation of significance (*p* values) according to how likely the alternative hypothesis is versus the null. We interpret Bayesian Factors (BF_{10}) according to heuristics of <0.10 indicating strong evidence for H0, 0.10–0.33 moderate evidence for H0, 0.33–1 anecdotal evidence for H0, 1–3 anecdotal evidence for H1, 3–10 moderate evidence for H1, and >10 strong evidence for H1 (Lee and Wagenmakers 2013). Statistical analyses (both frequentist and Bayesian) were conducted in JASP version 0.16.2 (JASP Team, 2022) and the visualisations were made in RStudio version 2022.02.3 (R Studio Team 2022).

2.5. MRI Data Acquisition

Neuroimaging data were acquired on a 3-Tesla Siemens Magnetom Trio scanner with a 32-receive channel head coil. Functional data (424 volumes) were first acquired using echo-planar imaging pulse sequence with multi-band acceleration factor 3, repetition time [TR]=1550 ms, echo time [TE] = 30.4 ms, flip angle [FA] = 56°, isotropic voxel size of 2.5 × 2.5 × 2.5 mm). Anatomical T1-weighted scans were acquired at the end of the scanning session using a magnetization-prepared rapid gradient-echo sequence (MPRAGE) with a voxel size of 1 × 1 × 1 mm isotropic (field of view = 256 × 176 × 256 mm [A-P; R-L; F-H]) in sagittal orientation.

2.6. fMRI Data Analysis

At the subject level, fMRI data were preprocessed using a standard fMRIPrep pipeline [fMRIPrep 20.2.3 (Esteban, Markiewicz, Goncalves, et al. 2021; Esteban et al. 2019) RRID:SCR_016216, which is based on Nipype 1.6.1 (Gorgolewski et al. 2011; Esteban, Markiewicz, Burns, et al. 2021); RRID:SCR_002502] excluding slice-time correction because of multiband acquisition and introducing ICA-AROMA (Pruim et al. 2015) for additional motion artefacts removal, particularly important for RS analysis. For participants in the Training group, the additional longitudinal function was implemented to account for multiple data acquisitions from the same subject. Details of the preprocessing steps can be found on the OSF. The data exclusion criterion due to excessive motion was if 10 or more volumes exceeded the framewise displacement threshold of a single voxel dimension (2.5 mm).

The MNI normalized, smoothed and ICA-AROMA denoised outputs from fMRIPrep were then further analysed in CONN Toolbox version 20b (www.nitrc.org/projects/conn, RRID: SCR_009550; (Whitfield-Gabrieli and Nieto-Castanon 2012)) for SPM12 (Wellcome Trust Centre for Neuroimaging, University College, London, UK, http://www.fil.ion.ucl.ac.uk/spm/software/spm12) running on MATLAB 2020b (Mathworks, http://www.mathworks.com). A band pass filter (0.008 - 0.09 Hz) was applied to the functional data, preceded by linear detrending and nuisance regression of subject-specific measures. The aCompCor method for artefact correction was implemented which performs linear regression of undesired confounders, such as signal from white matter and cerebrospinal fluids, to recover the neuronal BOLD signal of interest (Behzadi et al. 2007).

Functional connectivity estimates

For the functional connectivity (FC) analysis was performed in two ways:

(1) to replicate and extend previous findings on changes in insular-based FC in musicianship (Zamorano et al. 2017), we employed the seed-to-voxel FC approach, and

(2) to explore global changes in FC in the brain, we used atlas-based approach by following the methods described previously (Teeuw et al. 2019).

Insular-based FC

Bilateral posterior (PI), ventral anterior (vAI), and dorsal anterior (dAI) insula masks were used based on the functional segregations of the insular cortex (Deen, Pitskel, and Pelphrey 2011). The resulting six masks were used as regions of interest (ROI) in a voxelwise seed-to-voxel analysis to determine the connectivity patterns of each seed in the Musicians and the Training group. All correlation coefficient maps were transformed using Fisher's r-to-Z transformation prior to any statistical analysis.

First, to validate the main insula ROI connectivity patterns against those published previously (Deen, Pitskel, and Pelphrey 2011; Zamorano et al. 2017), we entered individual z-transformed connectivity maps from all participants (from both groups, N = 44, at TP1) for each ROI into one-sample *t*-tests. Secondly, we subjected the maps to independent-samples analysis to compare insular connectivity maps between Musicians and the Training group at TP1 (one-tailed test due to the apriori hypothesis based on previous results). To correct for multiple comparisons, a cluster-level extent threshold of $p < .05$ (p-FDR corrected) combined with a voxel threshold of $p < .001$ p-uncorrected as per Gaussian Random Factor theory (Worsley et al. 1996) was applied. Lastly, to evaluate insular FC changes following keyboard training, we subjected the Training group maps from TP1 and TP2 to paired-sample t-test analysis.

Atlas-based FC

FC matrices were obtained for the resting-state networks atlas provided by the CONN toolbox (Whitfield-Gabrieli and Nieto-Castanon, 2012; https://web.conn-toolbox.org/). The atlas is based on the independent component analysis (ICA) of resting-state scans of 497 unrelated adults from the Human Connectome Project. It provides maps of eight canonical resting-state networks: the Default Mode (DMN; 4 components), Sensorimotor (SMN; 3), Visual (VN; 4), Salience (SN; 7), Dorsal Attention (DAN; 4), Frontoparietal (FPN; 4), Language (LN; 4), and Cerebellar (CN; 2) Networks see supplementary information for details on the CONN atlas (Supplementary Materials 1). Further decomposition of each network into sub-regions that include homologous contra-lateral regions allows for studying patterns of FC within RS networks.

Following previous research (Teeuw et al. 2019), FC measures were obtained using Pearson correlation between spatially averaged denoised time series between two components. All FC correlations were transformed using Fisher's r-to-Z transformation prior to any statistical analysis. Mean FC for subsets of connections (i.e., mean FC between the RS networks and within components of a given RS network) was calculated as the average of the r-to-Z-transformed correlations across the subset of connections. The statistical analysis was analogous to the one for insular subregions and was conducted using CONN's *conn_withinbetweenROItest* function.

Additionally, to prove the robustness of our results, we have replicated the atlas-based FC analysis using a different parcellation (from the Harvard-Oxford atlas). The results are reported in Supplementary Materials 2.

3. Results

3.1. Exclusions and missing data

None of the participants was excluded due to excessive motion or failure to progress on the keyboard training; therefore, all 44 volunteers were included in the final analysis. Due to technical issues, two participants from the Training group had missing data from the HB discrimination task at TP1.

3.2. Behavioural results

Descriptive statistics for performance in the tasks for each group and time point is provided in Table 1. Firstly, to confirm the validity of interoceptive tasks, we run a correlation analysis between all behavioural measures for both groups together (Musicians and Training group at TP1, Table 2). The analysis confirmed that indexes of interoceptive accuracy were significantly, and positively correlated with each other. Similarly, confidence in the HB tracking and discrimination tasks were also significantly correlated. Yet, measures of interoceptive insight were not. For the HB discrimination task, confidence was correlated with accuracy, indicating that subjective assessment tracked well performance in this task. Importantly, interoceptive accuracy was not correlated with performance in the TET, suggesting that participants were following the instructions and counting HBs and not seconds. Overall, these analyses confirm the validity of the employed measures.

	Measure	N	Musicians Mean	SD	N	Training group: TP1 Mean	SD	N	Training group: TP2 Mean	SD
Accuracy	TET	20	0.80	0.13	24	0.76	0.16	24	0.78	0.15
	HBT	20	0.09	0.56	24	0.16	0.45	24	0.20	0.42
	HBD - Accuracy	18	0.52	0.18	24	0.52	0.11	24	0.55	0.14
	HBD - d'	18	0.10	0.90	24	0.06	0.61	24	0.24	0.72
Confidence	TET	20	71.18	12.93	24	76.45	13.17	24	75.86	15.94
	HBT	20	62.53	26.77	24	62.01	18.72	24	61.39	23.31
	HBD	18	59.57	12.40	24	59.56	16.86	24	59.98	22.86
Insight	TET	20	0.08	0.48	24	0.09	0.49	24	0.22	0.48
	HBT	19	0.46	0.40	23	0.29	0.55	22	0.30	0.55
	HBD	18	-0.31	1.12	24	0.37	1.32	24	0.13	1.16
Interoceptive sensibility	BPQ	20	68.75	15.02	24	68.58	13.91	24	71.54	13.23
	HR	20	76.97	10.87	24	75.01	9.23	24	74.17	9.62
	estHR	20	61.85	18.77	24	50.67	21.79	24	61.50	15.36

Table 1. Descriptive statistics. Performance in the tasks for each group and time point (TP). TET - time estimation task, HBT - heartbeat tracking task, HBD - heartbeat discrimination task, BPQ - Body Perception Questionnaire, HR - measured heart rate, estHR - participants' estimated heart rate.

	Variable		Accuracy				Confidence			Insight				
			TE	HBT	HBD - Accuracy	HBD - d'	TE	HBT	HBD	TE	HBT	HBD	BPQ	HR
Accuracy	**TE**	r	—											
		p-value	—											
	HBT	r	-0.136	—										
		p-value	0.378	—										
	HBD - Accuracy	r	0.076	0.384 *	—									
		p-value	0.633	0.012	—									
	HBD - d'	r	0.052	0.398 **	0.989 ***	—								
		p-value	0.743	0.009	< .001	—								
Confidence	**TE**	r	0.221	-0.043	0.035	0.006	—							
		p-value	0.150	0.783	0.828	0.970	—							
	HBT	r	0.005	-0.210	0.003	-0.048	0.083	—						
		p-value	0.977	0.171	0.983	0.764	0.592	—						
	HBD	r	0.269	0.012	0.350 *	0.326 *	0.336 *	0.571 ***	—					
		p-value	0.085	0.941	0.023	0.035	0.030	< .001	—					
Insight	**TE**	r	0.049	-0.157	-0.132	-0.133	0.177	-0.113	-0.153	—				
		p-value	0.753	0.309	0.406	0.402	0.252	0.465	0.333	—				
	HBT	r	-0.101	0.252	0.186	0.228	0.017	-0.254	-0.115	0.132	—			
		p-value	0.525	0.107	0.250	0.157	0.913	0.105	0.481	0.405	—			
	HBD	r	-0.266	0.103	0.187	0.175	0.165	0.035	-0.123	-0.012	0.111	—		
		p-value	0.088	0.518	0.236	0.269	0.298	0.826	0.439	0.940	0.496	—		
	BPQ	r	0.010	0.375 *	0.132	0.135	0.069	0.022	0.077	0.074	0.097	-0.051	—	
		p-value	0.949	0.012	0.404	0.393	0.656	0.886	0.627	0.634	0.543	0.748	—	
	HR	r	-0.164	-0.359 *	-0.360 *	-0.335 *	-0.090	0.209	-0.074	0.133	-0.213	-0.185	-0.038	—
		p-value	0.289	0.017	0.019	0.030	0.562	0.174	0.643	0.391	0.175	0.242	0.805	—
	estHR	r	0.159	-0.002	0.154	0.186	-0.085	-0.128	-0.224	-0.032	0.012	-0.088	0.258	0.109
		p-value	0.302	0.988	0.330	0.238	0.583	0.408	0.154	0.839	0.940	0.578	0.091	0.480

* p < .05, ** p < .01, *** p < .001

Table 2. Pearson's correlation coefficients between all behavioural measures for both groups together (Musicians and Training group at TP1). TET - time estimation task, HBT - heartbeat tracking task, HBD - heartbeat discrimination task, BPQ - Body Perception Questionnaire, HR - measured heart rate, estHR - participants' estimated heart rate. * $p < .05$, ** $p < .01$, *** $p < .001$

The analysis comparing Musicians and the Training Group at TP1 revealed no significant differences between the groups in any aspect of the interoceptive measures assessed (see Figure 2 and Table 3 for details). Moreover, there were also no significant group differences in performance in the TET, suggesting that both groups showed highly comparable time estimation ability as well as interoceptive performance. Similarly, we did not find any evidence for expected improvement in interoceptive or time estimation abilities following the keyboard training (see Figure 2 and Table 4 for details). These conclusions are largely supported by Bayesian statistics, which suggest moderate to anecdotal evidence for the null hypothesis for all comparisons of interoceptive measures, with the exception of the difference in the insight score for the HBD task, which suggests anecdotal evidence for H1 (see Tables 3 and 4 for details).

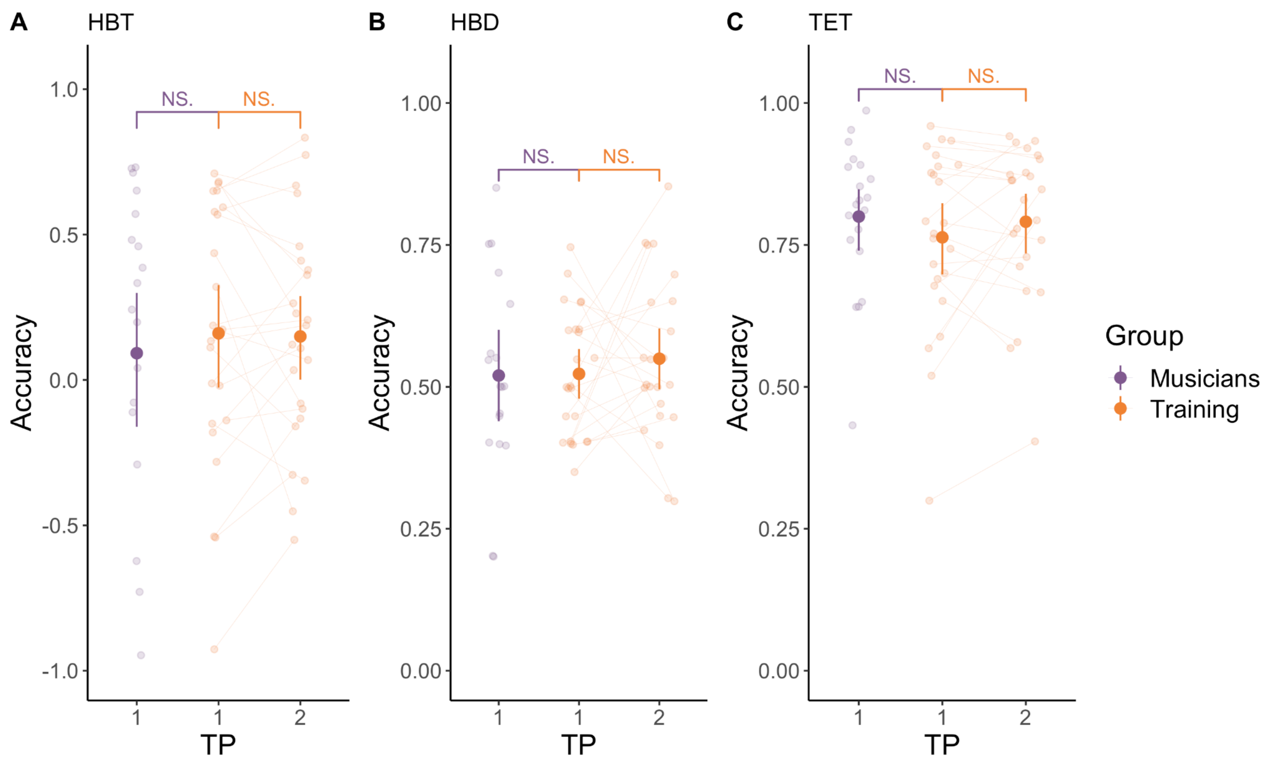


Figure 2. Comparison of performance on the heartbeat tracking (HBT), discrimination (HBD) and time estimation (TET) tasks between groups and time points (TP).

		t	df	p	Mean Difference	SE Difference	Cohen's d	95% CI for Cohen's d Lower	95% CI for Cohen's d Upper	Bayesian Independent Samples T-Test BF_{10}	error %
Accuracy	**TE**	-0.82	42	0.416	-0.04	0.05	-0.25	-0.84	0.35	0.39	0.006
	HBT	0.45	42	0.655	0.07	0.15	0.14	-0.46	0.73	0.32	0.006
	HBD - Accuracy	0.07	40	0.948	0.00	0.05	0.02	-0.59	0.63	0.31	0.005
	HBD - d'	-0.19	40	0.854	-0.04	0.23	-0.06	-0.67	0.55	0.31	0.005

	TE	1.33	42	0.190	5.26	3.95	0.40	-0.20	1.00	0.61	0.006
Confidence	**HBT**	-0.08	42	0.939	-0.53	6.88	0.00	-0.62	0.57	0.30	0.006
	HBD	0.00	40	0.998	-0.01	4.72	0.00	-0.61	0.61	0.31	0.005
	TE	0.00	42	0.956	0.01	0.15	0.02	-0.58	0.61	0.30	0.006
Insight	**HBT**	-1.17	40	0.249	-0.18	0.15	-0.36	-0.97	0.25	0.52	0.006
	HBD	1.77	40	0.085	0.68	0.39	0.55	-0.08	1.17	1.04	0.006
Interoceptive sensibility	**BPQ**	-0.04	42	0.970	-0.17	4.37	-0.01	-0.61	0.58	0.30	0.006
	HR	-0.65	42	0.521	-1.96	3.03	-0.20	-0.79	0.40	0.35	0.006
	estHR	-1.80	42	0.078	-11.18	6.20	-0.55	-1.15	0.06	1.08	0.007

Table 3. Independent samples t-test results (frequentist and Bayesian) comparing Musicians and the Training group at TP1. BF_{10} from 0.10 to 0.33 indicates moderate evidence for H0, BF_{10} from 0.33 to 1 indicates anecdotal evidence for H0, and BF_{10} from 1 to 3 indicates anecdotal evidence for H1 (Lee and Wagenmakers 2013). TET - time estimation task, HBT - heartbeat tracking task, HBD - heartbeat discrimination task, BPQ - Body Perception Questionnaire, HR - measured heart rate, estHR - participants' estimated heart rate.

	Measure	**t**	**df**	**p**	**Cohen's d**	**BF_{10}**	**error %**
	TE	-0.57	23	0.575	-0.12	0.25	0.025
	HBT	-0.43	23	0.672	-0.09	0.23	0.024
	HBD - Accuracy	-0.64	23	0.528	-0.13	0.26	0.025
Accuracy	**HBD - d'**	-0.88	23	0.389	-0.18	0.30	0.025
	TE	0.15	23	0.884	0.03	0.22	0.024
	HBT	0.15	23	0.881	0.03	0.22	0.024
Confidence	**HBD**	-0.11	23	0.917	-0.02	0.22	0.024
	TE	-0.99	23	0.331	-0.20	0.33	0.026
	HBT	-0.46	20	0.654	-0.10	0.25	0.020
Insight	**HBD**	0.60	23	0.555	0.12	0.25	0.025
Interoceptive sensibility	**BPQ**	-1.83	23	0.080	-0.37	0.90	0.024

HR	0.52	23	0.612	0.11	0.24	0.025
estHR	-2.04	23	0.053	-0.42	1.24	0.023

Table 4. Paired samples t-test results (frequentist and Bayesian) comparing the Training Group performance in the tasks before and after the 6-month keyboard training. BF_{10} from 0.10 to 0.33 indicates moderate evidence for H0, BF_{10} from 0.33 to 1 indicates anecdotal evidence for H0, and BF_{10} from 1 to 3 indicates anecdotal evidence for H1 (Lee and Wagenmakers 2013). TET - time estimation task, HBT - heartbeat tracking task, HBD - heartbeat discrimination task, BPQ - Body Perception Questionnaire, HR - measured heart rate, estHR - participants' estimated heart rate.

3.3. fMRI results

Insula-based FC

Results from seed-to-voxel whole-brain connectivity analyses across all participants (at TP1) replicated previously reported bilateral connectivity patterns of left and right PI, dAI, and vAI (Deen, Pitskel, and Pelphrey 2011; Zamorano et al. 2017) (see Fig. 3 and Table 5). Specifically, the PI showed FC with bilateral sensorimotor regions, including the precentral gyrus and premotor areas, the postcentral gyrus, temporal and parietal cortices, and the cerebellum. Furthermore, the PI was connected with the entire insula, frontal and parietal operculum, and the cingulate gyrus. The connectivity pattern of the dAI was centred on the bilateral entire insula, frontal pole, operculum cortex, inferior frontal and orbitofrontal cortex, pre- and postcentral gyri, superior temporal gyrus and parietal cortices (encompassing the supramarginal and Heschl's gyrus), and the precuneus. Finally, the connectivity pattern of the vAI showed bilateral connectivity with the insular cortices, the adjacent frontal operculum, the frontal pole, the orbitofrontal cortices, the anterior and middle cingulate cortex, premotor cortex, parietal cortices, auditory temporal regions, and the hippocampus.

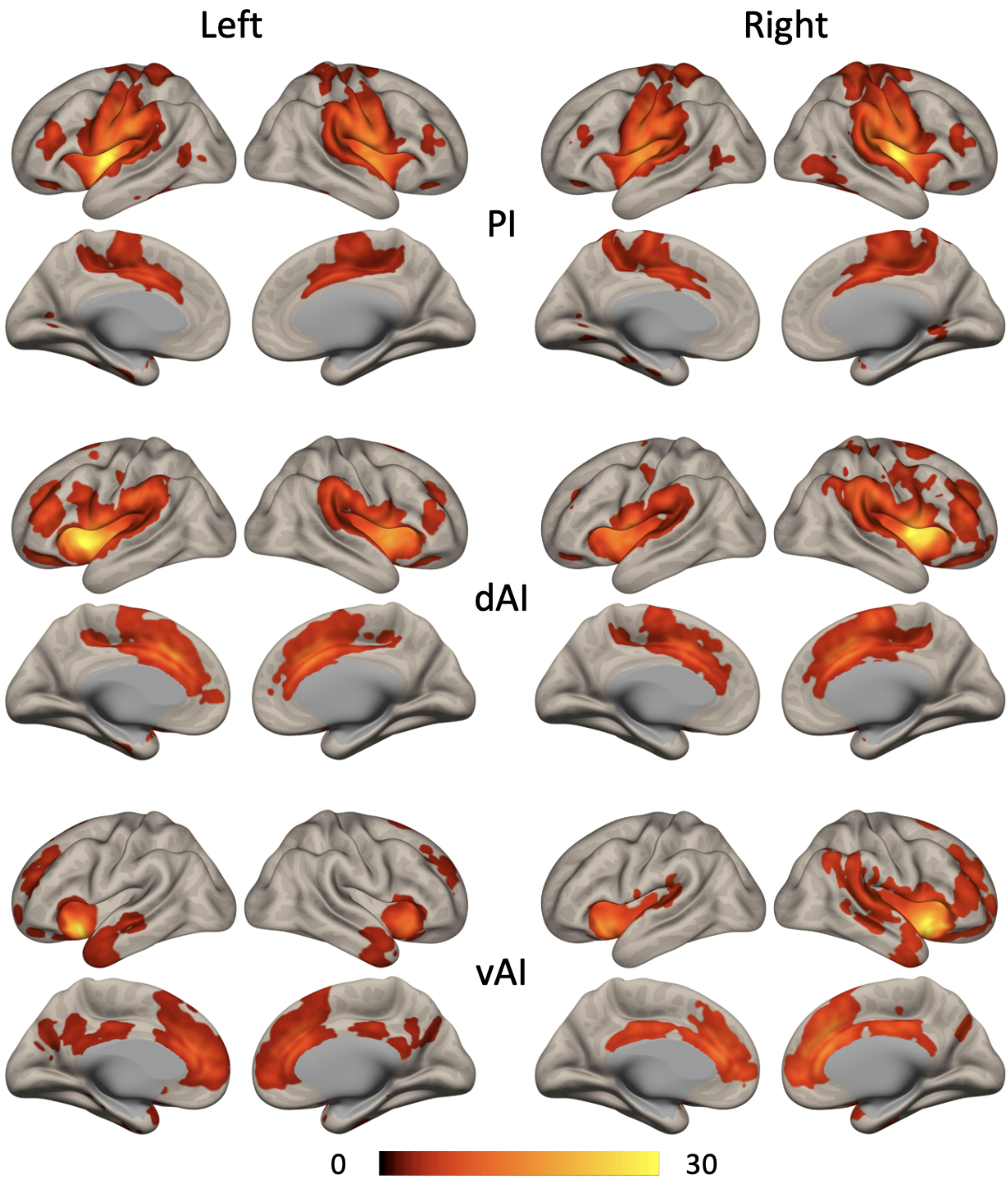


Figure 3. Insular subregions FC patterns for all participants pooled together (at TP1). Colourbar represents the *t*-statistics range.

Cluster peak coordinates (MNI)			**Cluster size**	**p-FDR**	**Region**	**Side**
x	**y**	**z**				
Left dAI						
-40	12	-2	13098	0.000	Insular Cortex	Left
46	14	0	8306	0.000	Frontal operculum	Right
-6	24	30	6006	0.000	Cingulate gyrus	Left

36	36	34	325	0.000	Frontal Pole	Right
8	-8	-2	204	0.000	Thalamus	Right
-38	-16	42	82	0.012	Precentral gyrus	Left
-30	-12	-34	76	0.015	Parahippocampal gyrus	Left
6	-42	-46	54	0.047	Brain-Stem	Right
Left PI						
-40	-8	4	12050	0.000	Insular Cortex	Left
40	-4	2	10453	0.000	Insular Cortex	Right
-2	10	36	5585	0.000	Cingulate gyrus	Left
-48	-48	-20	330	0.000	Inferior Temporal Gyrus	Left
46	38	12	227	0.000	Frontal Pole	Right
-26	38	-12	210	0.000	Frontal Pole	Left
-52	-64	10	186	0.000	Lateral Occipital Cortex	Left
12	-72	-48	169	0.000	Cerebellum	Right
-16	-74	-54	166	0.000	Cerebellum	Left
-16	-66	-20	164	0.000	Cerebellum	Left
16	-62	-20	148	0.000	Cerebellum	Right
-28	-12	-30	115	0.001	Parahippocampal gyrus	Left
24	36	-10	75	0.007	Frontal Pole	Right
6	-44	-46	46	0.037	Brain-Stem	Right
-14	-66	10	44	0.037	Intracalcarine Cortex	Left
50	-42	-22	44	0.037	Inferior Temporal Gyrus	Right
Left vAI						
-4	44	12	6942	0.000	Paracingulate gyrus	Left
-34	16	-12	4474	0.000	Insular Cortex	Left
34	20	-8	2167	0.000	Insular Cortex	Right
2	-24	34	1518	0.000	Cingulate gyrus	Right
-24	38	38	741	0.000	Frontal Pole	Left
48	-4	-36	704	0.000	Inferior Temporal Gyrus	Right
12	-68	34	196	0.000	Precuneus Cortex	Right
-26	-38	-6	114	0.001	Parahippocampal gyrus	Left
6	-6	-2	98	0.003	Thalamus	Right
26	-28	-12	84	0.006	Hippocampus	Right

0	-22	-16	57	0.025	Brain-Stem	
-2	-28	0	55	0.026	Thalamus	Left
Right dAI						
38	4	6	14967	0.000	Insular Cortex	Right
-32	12	8	6587	0.000	Insular Cortex	Left
4	20	36	6136	0.000	Cingulate gyrus	Right
12	-16	-4	452	0.000	Thalamus	Right
-20	-78	-54	191	0.000	Cerebellum	Left
-38	-16	42	183	0.000	Precentral gyrus	Left
-14	-14	8	120	0.001	Thalamus	Left
24	-34	64	109	0.002	Postcentral Gyrus	Right
-26	42	-10	108	0.002	Frontal Pole	Left
-12	-36	52	104	0.002	Postcentral Gyrus	Left
6	-44	-46	59	0.019	Brain-Stem	Right
-28	36	28	52	0.026	Middle Frontal Gyrus	Left
Right PI						
40	-8	4	20803	0.000	Insular Cortex	Right
-40	-8	4	9390	0.000	Insular Cortex	Left
50	-44	-18	941	0.000	Inferior Temporal Gyrus	Right
14	-22	0	568	0.000	Thalamus	Right
-16	-24	2	397	0.000	Thalamus	Left
-10	-72	-46	224	0.000	Cerebellum	Left
-46	-42	-18	199	0.000	Inferior Temporal Gyrus	Left
-16	-66	-18	167	0.000	Cerebellum	Left
26	36	-14	137	0.000	Frontal Pole	Right
16	-76	-52	126	0.001	Cerebellum	Right
-52	-64	8	122	0.001	Middle Temporal Gyrus	Left
-44	34	14	121	0.001	Inferior Frontal Gyrus	Left
-28	36	-10	108	0.001	Frontal Orbital Cortex	Left
20	-52	0	102	0.001	Lingual Gyrus	Right
16	-64	-18	90	0.002	Cerebellum	Right
-28	-14	-30	46	0.032	Parahippocampal gyrus	Left
-30	-30	-24	43	0.037	Temporal Fusiform Cortex	Left

Right vAI						
38	14	-10	10978	0.000	Insular Cortex	Right
0	38	22	6768	0.000	Paracingulate gyrus	
-36	16	-10	3269	0.000	Insular Cortex	Left
12	-68	36	181	0.000	Precuneus Cortex	Right
24	62	2	132	0.001	Frontal Pole	Right

Table 5. Insular subregions FC clusters peaks and statistics.

The comparison of insular FC patterns between Musicians and the Training group at TP1, revealed some differences in FC of the right PI and dAI (Figure 4). The right PI in Musicians showed increased FC with the left inferior temporal gyrus (Peak: -54, -60, -16, $t(42) = 4.40$, $p < .001$, cluster size = 78 voxels). The right dAI showed increased FC with the right frontal pole (Peak: 34, 40, 38, $t(42) = 4.78$ $p < .001$, cluster size = 85 voxels). There were no significant differences in insular FC in the Training group across time.

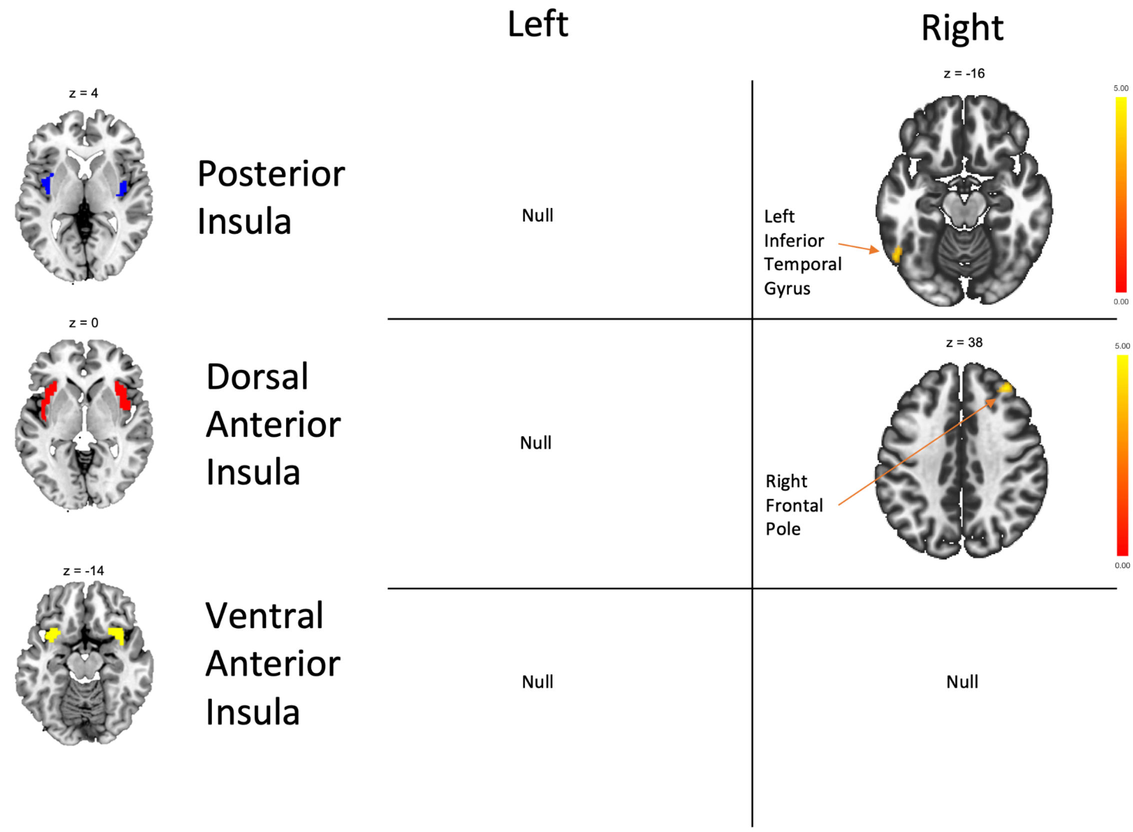


Figure 4. Group differences (Musicians > Training group at TP1, one-tailed *t*-test) in insular subdivisions FC pattern. On the left side, the location of insular subregions (bilateral) is presented. Colourbar represents the *t*-statistics range.

Atlas-based FC

Figure 5 presents a within-/between-network connectivity matrix for Musicians and the Training groups at TP1 pooled together. As expected, regions that belong to the same network showed higher FC with each other than with other regions. Yet, we did not find any significant differences between Musicians and the Training group regarding between-network FC (Fig 6). Yet, Musicians showed higher FC within the SMN compared to the Training group at TP1, $t(42) = 2.39$, $p = .011$ (Fig 7). We found no other significant differences between the groups or across time in the Training group (Table 6).

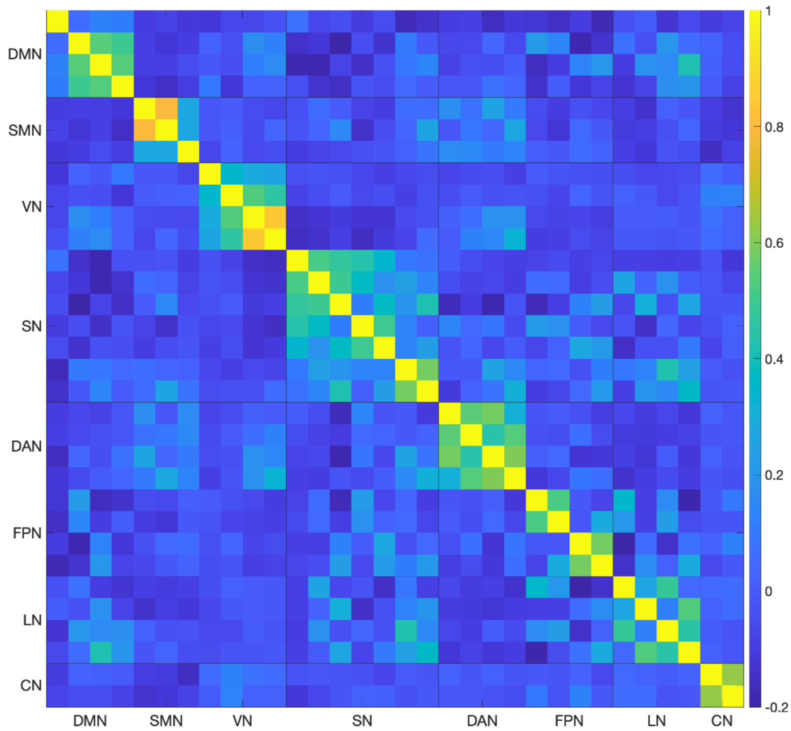


Figure 5. Full connectivity matrix between all pairs of networks components for both groups pulled together (at TP1). Colourbar representents *r*-score. DMN - Default Mode network, SMN - Sensorimotor, VN - Visual, SN - Salience, DAN - Dorsal Attention, FPN - Frontoparietal, LN - Language, and CN - Cerebellar Network.

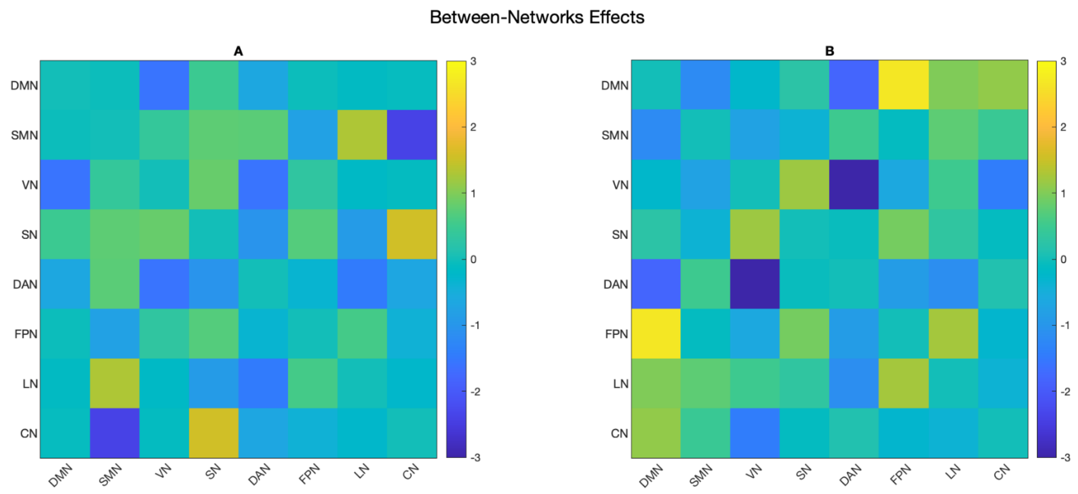


Figure 6. Between-network FC comparison between the groups at TP1 (A) and across time for the Training Group (B). Colour bars represent *t*-statistics. DMN - Default Mode network, SMN - Sensorimotor, VN - Visual, SN - Salience, DAN - Dorsal Attention, FPN - Frontoparietal, LN - Language, and CN - Cerebellar Network.

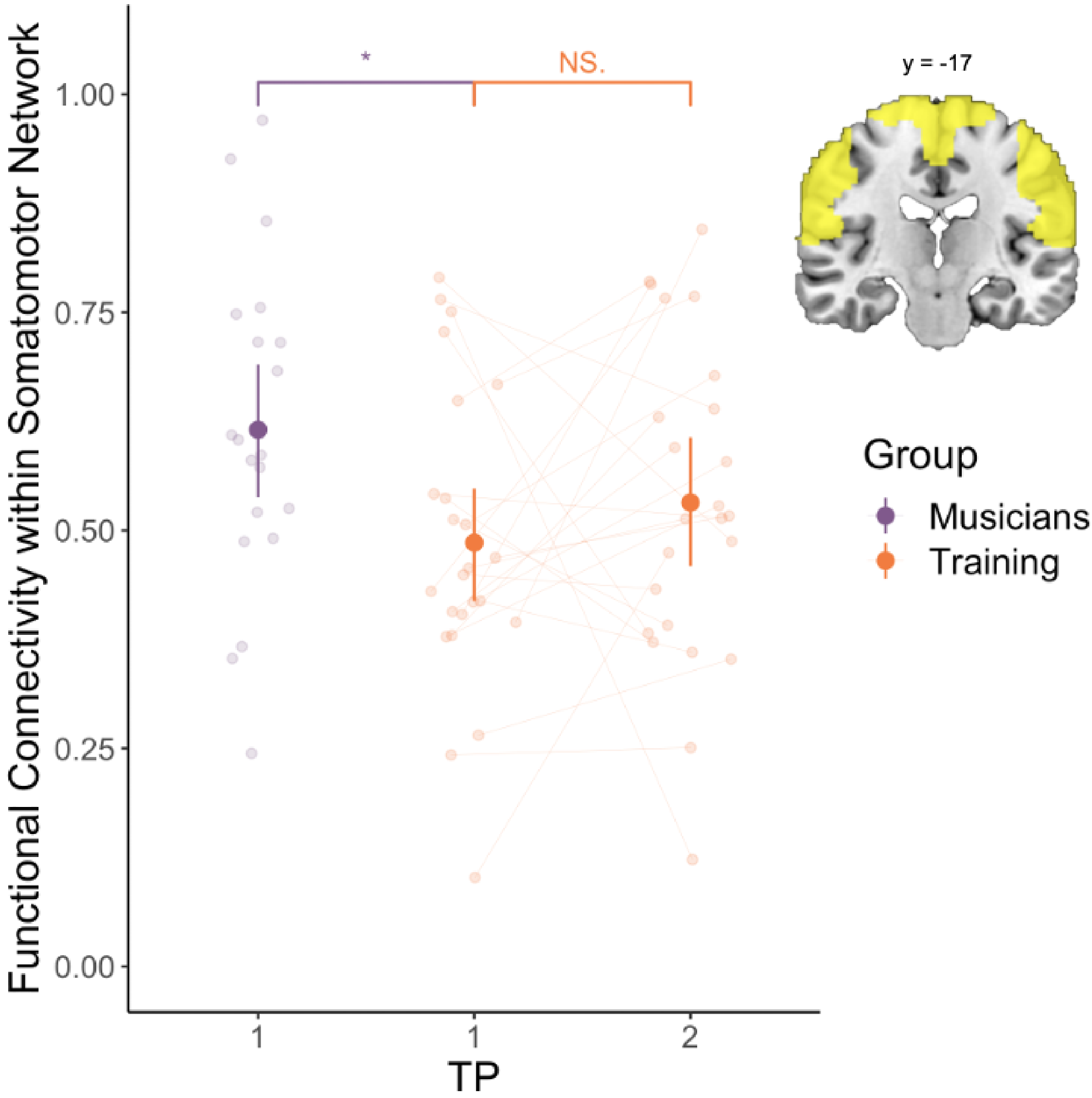


Figure 7. Resting-state functional connectivity within the Somatomotor Network (SMN). Functional connectivity is reflected in Z-scores.

Network	Independent t-test TP1		Paired t-test	
	T	*p*	*T*	*p*
Default Mode	-0.16	0.563	-0.29	0.612
Sensorimotor	**2.39**	**0.011**	1.14	0.134
Visual	-0.05	0.519	0.25	0.401
Salience	-0.11	0.545	-0.58	0.716
Dorsal Attention	-0.57	0.715	-1.00	0.836
Frontoparietal	-0.87	0.805	-0.46	0.674
Language	-0.82	0.791	0.03	0.489
Cerebellar	-0.15	0.560	0.54	0.297

Table 6. Within-network functional connectivity differences between the groups at TP1 and across time for the Training group.

4. Discussion

We aimed to replicate and extend past findings of enhanced interoceptive abilities and increased RS FC in musicians with a unique cross-sectional and longitudinal study design. We compared a group of professional musicians and individuals with no musical experience before and after a 6-months-long keyboard training on different facets of interoceptive skills and RS FC.

Overall, our results challenge the view that professional musicians show superior interoceptive abilities, as we found no group differences in any dimension of interoception studied (interoceptive accuracy, sensibility or insight) as assessed with two independent tasks (HB counting and discrimination tasks) and a questionnaire (BPQ). We did not find any group differences also in time estimation accuracy which is in line with previous results (Hina, Aspell, and Cardini 2020). Additionally, we did not observe any significant changes in interoceptive abilities among participants who completed a 6-months long keyboard playing course, indicating that such a (relatively short) musical training does not enhance any measured dimension of interoception.

As we did not replicate previous findings, some important differences in interoceptive assessment and samples studied in the current and past research should be considered when discussing the results. (Hina, Aspell, and Cardini 2020) reported better interoceptive accuracy in musicians on the HB tracking task. Yet, it is not clear whether participants in that study were clearly instructed not to guess or try to estimate their HR during the task, which might have an impact on participants' scores (Desmedt et al. 2020). They also employed HB discrimination task in musicians but the procedures considerably differed from ours. Specifically, (Hina, Aspell, and Cardini 2020) used a procedure where asynchronous trials (N = 8), were either presented at a rate slower than participants' heart rate (N = 4; 80% of the participant's heart rate) or at a faster pace (N = 4; 120% of the participant's heart rate). Therefore, participants could use the stimuli presentation rate, not the synchronicity with HBs itself, as a cue in the task. In contrast, in our task, the stimuli were always presented at participants' current heart rate, the only parameter that differed was the phase at which the stimuli were presented: cardiac systole [at the point where the majority of people feel their HB (Wiens and Palmer 2001)] or diastole. The version of the task used by (Schirmer-Mokwa et al. 2015) more closely resembled ours, so different results cannot be explained by task differences. However, discrepancies may be partly due to differences in the populations studied. They recruited professionally trained classical singers and string players (mean age: 26.2). The control group consisted of age and sex-matched non-musicians (mean age: 27.7 years). Therefore, we also suggest that the selection of the population (in terms of sex distribution, age, and type of musical training received) may play a role in potential differences in interoceptive abilities between the groups studied. Specifically, interoceptive abilities decrease with age (Khalsa, Rudrauf, and Tranel 2009; Murphy et al. 2018) and men tend to show superior cardioceptive accuracy (Prentice and Murphy 2022). The type of musical training could also play a role. In fact, despite similar performance in heartbeat discrimination tasks in singers and string players, accumulated musical practice predicted interoceptive accuracy only in singers (about 49% of variance explained) but not in string players (Schirmer-Mokwa et al. 2015), suggesting that the type of training received may affect interoceptive abilities to a different extent or at a different pace. Noteworthy, while our group of Musicians consisted solely of keyboard instrument players, distinct groups of musicians, such as those who play wind instruments versus those who play keyboard instruments, might exhibit specific enhancements in different interoceptive axes. For instance, wind instrument players may demonstrate heightened respiratory interoception, as opposed to cardiac or gastric interoception. Future research could investigate and compare various interoceptive axes across different groups of musicians.

Regarding FC analysis, we replicated previous reports of FC patterns of different insula subregions (Deen, Pitskel, and Pelphrey 2011; Zamorano et al. 2017). That is, the dAI showed a "cognitive" frontoparietal connectivity pattern, the vAI showed predominant coactivation with regions involved in higher-order cognitive functions and affective processing (e.g., the orbitofrontal cortex), and the PI mainly with sensorimotor areas (see Fig. 3 Table 5). Yet, we were largely unable to reproduce the finding regarding enhanced insular FC in Musicians compared to non-Musicians, whereby professional musicians showed increased FC of all six insular subregions (Zamorano et al. 2017). Compared with the Training group before the start of the keyboard course, Musicians in current study showed only localised increases in FC of the right PI and dAI [with left inferior temporal gyrus, involved in multimodal integration (Mesulam 1998), and right frontal pole engaged in action monitoring (Koechlin 2011), respectively]. These discrepancies may, again, result from the differences in the samples studied. In research by Zamorano et al., whose results we aimed to replicate, the sample size was half the size of ours, participants were older (31.4 +/- 11.2 versus 21 +/- 2.1), hence on average those musicians presented more years of musical training (20 +/- 5.9 vs 15.2 +/- 1.88 yrs of practice). Musicians in the past study also had more varied musical expertise (5 string, 2 keyboard, 4 wood instruments players vs only keyboard players in the present study). Thus, the differences could potentially be attributed to the rather modest sample size in the previous study. Additionally, as previous studies examined older participants, our results may suggest that in young adults (in their early 20s), all of whom were university students, who have lots of daily stimulation and undergo constant learning, such differences in insula-based functional connectivity are not yet visible and may appear later on as the population lifestyle diverge more. Future research could explore this idea further.

Our atlas-based FC analysis comparing FC strength within and between canonical RS brain networks showed no differences in between-network FC and no differences within the Salience network. This goes against some of the previous findings reporting higher FC in musicians between regions of the SN (Wang et al. 2014). Nevertheless, within-network FC analysis between Musician and the Training group revealed significant effects. Specifically, compared to the Training group before the start of the keyboard course (TP1), Musicians showed higher FC within the SMN. Extensive musical training obtained by professional pianists/keyboard players involves developing an interplay between multisensory and motor systems. In fact, task-related structural and functional changes in the brain have been observed both within (Elbert et al., 1995; Lotze et al., 2003; Altenmüller, 2008; Kleber et al., 2010) and between sensorimotor areas (Gaser and Schlaug, 2003; Hirata et al., 2004; Barnes-Burroughs et al., 2005; Baumgartner et al., 2006; Pantev et al., 2009; Herholz and

Zatorre, 2012) in professional musicians; thus, in this sense, our findings are in line with a broad body of literature. Moreover, it is important to remember that somatosensory and motor areas, parts of the SMN, next to the insular cortex, also play a crucial role in the integration of multimodal (intero- and exteroceptive) information about the body (Herman et al. 2021; S. M. Schulz 2016). The increased FC within the SMN in musicians may reflect better integration of various signals about the body: signals about the body's position in space (proprioception), internal cues about the physiological condition of the body (interoception) as well as tactile cues related to playing an instrument. Yet, there were no significant changes in SMN FC across time in the Training group, potentially suggesting that these differences may occur following longer musical training. Importantly, we replicated these results using an independent parcellation (see Supplementary Materials 2 for details), proving the robustness of these findings.

5. Conclusions

Overall, our results challenge the view that professional musicians show superior interoceptive abilities, either interoceptive accuracy, sensibility or insight, or show increased insular RS FC. Yet, our findings suggest that musical expertise is related to strengthened FC within the sensorimotor RS network, which consists of some hubs important for processing body-related information (namely pre- and postcentral gyri and supplementary motor area bilaterally, extending into the opercular cortex). Based on past findings, we also suggest that the selection of the population (in terms of sex distribution, age, and type of musical training received) may play a role in potential differences in interoceptive abilities between the groups studied.

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Data Availability Statement: Behavioural data and analysis code together with the second-level results of the fMRI analyses (functional connectivity matrices and maps) and fmriprep preprocessing details are available via Open Science Framework: https://osf.io/f6a7r/?view_only=7b5748d50b824929acc1deb979ce9318.

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Author Contributions:

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A.O.: Methodology, Investigation, Writing—Reviewing and Editing.

M.G.: Investigation, Writing—Reviewing and Editing.

D.D.: Methodology, Investigation, Project Administration, Writing- Reviewing and Editing.

A.M.: Conceptualisation, Supervision, Project Administration, Funding acquisition, Writing-Reviewing and Editing.

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