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Increased functional connectivity in the ventral and dorsal streams during retrieval of novel words in professional musicians

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Abstract

Current models of speech and language processing postulate the involvement of two parallel processing streams (the dual stream model): a ventral stream involved in mapping sensory and phonological representations onto lexical and conceptual representations and a dorsal stream contributing to sound-to-motor mapping, articulation, and to how verbal information is encoded and manipulated in memory. Based on previous evidence showing that music training has an influence on language processing, cognitive functions, and word learning, we examined EEG-based intracranial functional connectivity in the ventral and dorsal streams while musicians and nonmusicians learned the meaning of novel words through picture–word associations. In accordance with the dual stream model, word learning was generally associated with increased beta functional connectivity in the ventral stream compared to the dorsal stream. In addition, in the linguistically most demanding "semantic task," musicians outperformed nonmusicians, and this behavioral advantage was accompanied by increased left-hemispheric theta connectivity in both streams. Moreover, theta coherence in the left dorsal pathway was positively correlated with the number of years of music training. These results provide evidence for a complex interplay within a network of brain regions involved in semantic processing and verbal memory functions, and suggest that intensive music training can modify its functional architecture leading to advantages in novel word learning.

KEYWORDS
dorsal and ventral streams, functional connectivity, music training, plasticity, word learning

1 | INTRODUCTION

Biologically grounded models of speech and language processing (Bornkessel-Schlesewsky & Schlesewsky, 2013; Friederici, 2009, 2012; Hagoort, 2014; Hickok & Poeppel, 2007; Rauschecker & Scott, 2009)

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postulate that a bilaterally organized ventral stream, projecting from the posterior superior temporal gyrus (i.e., pSTG) and the inferior parietal lobule (i.e., IPL) toward the temporal pole, contributes to mapping phonological representations onto lexical-semantic representations. The left pSTG has been proposed to support phoneme recognition based on low-level acoustic features, with a higher selectivity for

consonant-vowel (CV) syllables compared to other natural sounds (Jäncke, Wüstenberg, Scheich, & Heinze, 2002; Leaver & Rauschecker, 2010). In addition, the middle-posterior part of the middle temporal gyrus [i.e., MTG, Brodmann area (BA) 21] has been identified as an important region for word recognition (Binder et al., 1997; Friederici, 2012; Hickok & Poeppel, 2004; Saur et al., 2008), whereas the anterior temporal lobe accommodates lexical-semantic processing at the sentence-level and grammatical or compositional aspects of speech processing (DeWitt & Rauschecker, 2012; Friederici, 2012; Hickok & Poeppel, 2007).

The second main pathway involved in language processing is strongly lateralized to the left hemisphere and mediates impulse propagation between the pSTG and the IPL and Broca's area (Hickok & Poeppel, 2007; Rilling et al., 2008). This dorsal stream facilitates articulatory processes as well as the coupling of the speech signal with articulatory representations. Such sensorimotor integration mechanisms in the left hemisphere have previously been shown to support complex verbal memory functions (Rauschecker, 1998; Rodríguez-Fornells, Cunillera, Mestres-Missé, & de Diego-Balaguer, 2009; Schulze, Vargha-Khadem, & Mishkin, 2012), for example, when it comes to imagine syllables (Tian, Zarate, & Poeppel, 2016) or to perform rhyming tasks (Pillay, Stengel, Humphries, Book, & Binder, 2014).

The IPL [comprising the angular and supramarginal gyri (AG/SMG)] constitutes a posterior point of intersection of the two processing streams. This brain region has previously been shown to house a variety of supramodal conceptual functions that are important for language, including pre-lexical-, lexical-, and verbal mnemonic functions, phonological categorization (Joanisse, Zevin, & McCandliss, 2007; Turkeltaub & Coslett, 2010), semantic processing (Ferreira, Göbel, Hymers, & Ellis, 2015; Obleser & Kotz, 2010; Price, 2010), short-term memory (Buchsbaum et al., 2011; Gaab, Gaser, Zaehle, Jancke, & Schlaug, 2003) and working memory (Buchsbaum et al., 2011). By contrast, Broca's area represents the anterior point of convergence of the two processing streams and has been proposed to accommodate both domain-general and language-selective functions (Fedorenko, Duncan, & Kanwisher, 2012). Regarding language processing, this territory has been associated with the planning and execution of articulation (Eickhoff, Heim, Zilles, & Amunts, 2009), linguistic- and phonological processes (Friederici, 2012; Rilling et al., 2008), short-term memory (Hickok et al., 2014), working-memory (Clos, Amunts, Laird, Fox, & Eickhoff, 2013; Fedorenko et al., 2012; Hagoort, 2014) and episodic- and semantic memory (Johnson, Saykin, Flashman, McAllister, & Sparling, 2001).

Nowadays, it is generally acknowledged that professional musicians can serve as a reliable model for better understanding how experiential factors interact with perceptual and higher cognitive functions (Münte, Altenmüller, & Jäncke, 2002). This field of research brought to light training-related functional (Zuk, Benjamin, Kenyon, & Gaab, 2014) and structural (Bermudez, Lerch, Evans, & Zatorre, 2009) changes in several brain regions situated along the two processing streams: in the pSTG (Bermudez et al., 2009; Elmer, Meyer, & Jancke, 2012) in the IPL (Schulze, Zysset, Mueller, Friederici, & Koelsch, 2011), in the somatosensory and motor cortices (Bangert & Schlaug, 2006; Hyde et al., 2009), in the ventral (Sluming, Brooks, Howard, Downes, & Roberts,

2007) and dorsal part of the frontal lobe (Bermudez et al., 2009), and in different subregions of the temporal lobe (Gaser & Schlaug, 2003; Oechslin, Meyer, & Jäncke, 2010). In this context, it is noteworthy to mention that such plastic changes are not restricted to local brain regions but are rather part of complex neural networks. In fact, previous work showed that musicians are characterized by increased functional and structural connectivity between the left pSTG/IPL and Broca's area (Halwani, Loui, Rüber, & Schlaug, 2011; Klein, Liem, Hänggi, Elmer, & Jäncke, 2016; Oechslin, Imfeld, Loenneker, Meyer, & Jäncke, 2010), between the bilateral auditory-related cortices (Elmer, Hänggi, & Jäncke, 2016; Kühnis, Elmer, & Jäncke, 2014), between the auditory-related cortex and the somatosensory cortex (Klein et al., 2016), and within temporal brain regions (Jäncke, Langer, & Hänggi, 2012).

Previous studies have highlighted several brain regions that are responsive to both speech and music stimuli, including the primary and associative auditory cortex (Farbood, Heeger, Marcus, Hasson, & Lerner, 2015; Rogalsky, Rong, Saberi, & Hickok, 2011), the inferior parietal lobe and the ventral part of the prefrontal cortex (Farbood et al., 2015) as well as brain regions situated in the middle-anterior part of the temporal lobe (Farbood et al., 2015; Koelsch, 2011). Interestingly, several brain regions previously shown to be altered as a function of music training are distributed along the ventral and dorsal processing streams (Bermudez et al., 2009). Moreover, the influence of music training on the structural organization of the brain has also been shown to be accompanied by behavioral advantages in several domains of speech processing (see Besson, Chobert, & Marie, 2011 for review), including voice-onset time (VOT; Chobert, Francois, Velay, & Besson, 2014; Elmer et al., 2012), duration (Kühnis, Elmer, Meyer, & Jäncke, 2013; Tervaniemi et al., 2009), pitch (Marie, Delogu, Lampis, Belardinelli, & Besson, 2011), timbre (Bidelman, Weiss, Moreno, & Alain, 2014), and linguistic and emotional prosody (Lima & Castro, 2011; Marques, Moreno, Castro, & Besson, 2007). Notably, recent results also revealed that both short- and long-term music training have a positive influence on diverse cognitive functions, including auditory- (Strait, Slater, O'Connell, & Kraus, 2015) and visual attention (Wang, Ossher, & Reuter-Lorenz, 2015), short-term-, working- and verbal memory (George & Coch, 2011; Schulze & Koelsch, 2012), and on general executive functions (Zuk et al., 2014). Based on such a multifaceted influence of music training on speech processing and cognition, Dittinger and collaborators recently examined the influence of music training on novel word learning in adults (Dittinger et al., 2016) and in 8–12-year-old children (Dittinger, Chobert, Ziegler, & Besson, 2017). Thereby, the authors focused on the development of the N400 component and on the N400 effect (unexpected minus expected words) as an index of novel word learning (frontal N400 or FN400 in a learning phase) and retrieval from episodic and semantic memory (in matching and semantic tasks). As a main result, the authors revealed a behavioral advantage of musicians and musically-trained children during the cognitively most demanding "semantic task" that was associated with larger N400 effects over centro-posterior scalp sites. These findings are particularly interesting in that they lead to suggest a relationship between music training and semantic facilitation during word learning.

In this EEG study, we re-evaluated the data of the professional musicians and non-musicians of the Dittinger et al. (2016) study by focusing on intracranial functional connectivity in the theta, alpha, and beta frequency bands to examine the dynamic interplay between key regions of the ventral- (i.e., between the IPL and middle part of the middle temporal lobe) and dorsal streams (i.e., between the IPL and Broca's region). Although the functional role of these different frequency bands is not yet well understood, low frequency oscillations in the theta range have been proposed to support neural communication between distinct brain regions over long-range circuits (Polanía, Nitsche, Korman, Batsikadze, & Paulus, 2012; Ward, 2003), information integration (Ward, 2003), and mnemonic processes (Albouy, Weiss, Baillet, & Zatorre, 2017). Theta oscillations may also contribute to "packing" the multitime speech (Giraud & Poeppel, 2012) and possibly music signal (Doelling & Poeppel, 2015) into units of the appropriate temporal granularity and to the processing of syntactic and semantic violations (Bastiaansen, Magyari, & Hagoort, 2010; Carrus, Koelsch, & Bhattacharya, 2011). Otherwise, beta oscillations have been shown to be involved in a wide range of cognitive functions such as working memory (Siegel, Warden, & Miller, 2009) or decision making (Wong, Fabiszak, Novikov, Daw, & Pesaran, 2016), and to language processing (Carrus et al., 2011). They also seem to play an important role in music processing and are increased with music training (Doelling & Poeppel, 2015). Finally, alpha oscillations may support short-term and working memory functions (Obleser, Wöstmann, Hellbernd, Wilsch, & Maess, 2012) and anticipation and expectation processes (Weisz, Hartmann, Müller, Lorenz, & Obleser, 2011).

According to the results of Dittinger et al. (2016), and based on the literature reviewed above, we expected increased connectivity in musicians in the bilateral ventral stream which contributes to access lexical-semantic information. Furthermore, we predicted that neural oscillations in the left dorsal stream, which has been shown to be functionally (Klein et al., 2016) and structurally (Halwani et al., 2011) influenced by music training, will be more strongly synchronized for facilitating the preactivation of the phonological word forms, sensory-to-motor coupling mechanisms (Cunillera et al., 2009; López-Barroso et al., 2013), and possibly the manipulation of information in working memory (Albouy et al., 2017).

2 | MATERIALS AND METHODS

2.1 | Participants

According to previous work (Elmer et al., 2012; Klein et al., 2016), we applied strict criteria and only evaluated the data of musicians who started music training before the age of 10 years. Consequently, one subject was excluded from the analyses (i.e., age of commencement = 15 years). The professional musicians (MUS, totally 14, 8 women; 3 pianists, 2 accordionists, 4 violinists, 1 cellist, 1 guitarist, 1 hornist, 1 tubist, and 1 flautist; mean number of practice years = 17.4, range = 11–24, SD = 4.1) and nonmusicians (NM, totally 15, 8 women) who participated in the present study did not differ in age (MUS: mean age = 25.0 years, age range = 19–30, SD = 4.0; NM:

mean age = 25.7 years, age range = 19–33, SD = 4.8; $F_{(1,27)}$ = .20, p = .66) and were comparable in education ($F_{(1,27)}$ = 0.48, p = .50) and in socio-economic background (criteria of the National Institute of Statistics and Economic Studies; MUS = 4.4; NM = 4.9; $F_{(1,27)}$ = 1.05, p = .31). All participants were native French speakers and none of them was bilingual but all had some knowledge of English as a second language. Most importantly, none of the participants had previous experience with the Thai language. None of the subjects reported past or current audiological or neurological deficits. The study was conducted in accordance with the declaration of Helsinki, and all participants gave their informed consent before enrolling in the experiment.

2.2 | Cognitive capability and musical aptitudes

Standardized psychometric tests were used to assess between-group differences in short-term and working memory [forward and reverse Digit Span, WISC-IV (Wechsler, 2003)], visual attention [NEPSY (Korkman, Kirk, & Kemp, 1998)], and fluid intelligence [progressive matrices, PM47 (Raven, Corporation, & Lewis, 1962)]. Musical aptitudes were quantified by means of two subtests [adapted from the MBEA battery (Peretz, Vuvan, Lagrois, & Armony, 2015)] consisting of listening to short pairs of piano sequences and deciding whether the sequences were rhythmically or tonally same or different.

2.3 | Stimulus material

2.3.1 | Auditory stimuli

Auditory stimuli consisted of nine natural monosyllabic Thai words, namely /ba1/, /pa1/, /pʰa1/, /ba:1/, /pa:1/, /pʰa:1/, /ba:0/, /pa:0/, /pʰa:0/. The words varied in vowel duration, with short- (/ba1/, /pa1/ and /pʰa1/; 261 ms on average) and long vowels (/ba:1/, /pa:1/, /pʰa:1/, /ba:0/, /pa:0/ and /pʰa:0/; 531 ms on average). They also varied in fundamental frequency, with low tone- (/ba1/, /pa1/, /pʰa1/, /ba:1/, /pa:1/ and /pʰa:1/; F0 = 175 Hz on average) and mid tone vowels (/ba:0/, /pa:0/ and /pʰa:0/; F0 = 218 Hz on average). Furthermore, words contained voicing contrasts (/ba1/, /ba:1/ and /ba:0/, VOT = −144 ms vs./pa1/, /pa:1/ and /pa:0/, VOT = 3 ms) as well as aspirated contrasts (/pa1/, /pa:1/ and /pa:0/, VOT = 3 ms vs./pʰa1/, /pʰa:1/ and /pʰa:0/, VOT = 77 ms). The stimuli were registered by a female Thai-French bilingual speaker, digitally recorded, and normalized to a mean level of 70 dB by using the Praat software (http://www.fon.hum.uva.nl/praat/).

2.3.2 | Visual stimuli

Nine pictures representing familiar objects (i.e., bear, flower, key, chair, bell, eye, strawberry, train, and glass) were selected from the set of 260 pictures built by Snodgrass and Vanderwart (1980). These pictures are black-and-white line drawings standardized on name agreement, image agreement, familiarity, and visual complexity. For the "semantic task" (i.e., see the experimental procedure), new pictures that the participants had not seen before in the experiment and that were semantically related or unrelated to the original pictures (and, consequently, to the novel words meaning) were chosen from the internet by two of the authors (ED and
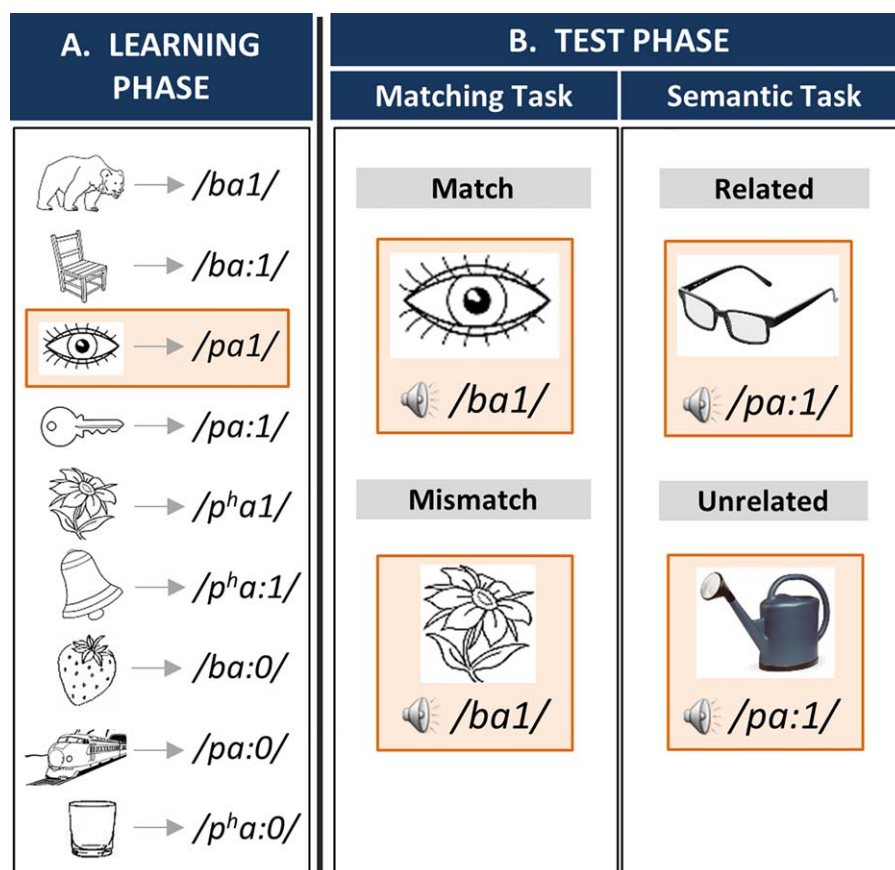
FIGURE 1 Schematic representation of the experimental design [Color figure can be viewed at wileyonlinelibrary.com]

MB). Sixty students from our university (age range = 19–25 years) were asked to rate the semantic relatedness between new and old pictures on a scale from 1 (= unrelated) to 7 (= related). Half of the presented pairs were semantically related and the other half were semantically unrelated. Overall, this was confirmed by the students' ratings. All pictures were presented with an angular size of 24.9°.

2.4 | Experimental procedure

Encoding and retrieval of newly learned words was assessed by means of three consecutive tasks consisting of an "associative learning phase," a "matching task," and a "semantic task" (Figure 1). During the "associative learning phase," participants had to learn the meaning of auditory words through picture-word associations. Each of the nine picture-word pairs was presented 20 times, resulting in 180 trials that were pseudorandomly presented within two blocks of 3 min each. Each picture was presented on the screen for 2000 ms (total trial duration), and one out of the nine words was binaurally presented with a stimulus onset asynchrony (SOA) of 750 ms. Picture–word associations were different across participants to avoid spurious effects due to specific associations and serial order effects. Note that the picture–word associations were arbitrary in that the learned meaning did not correspond to the real meaning of the Thai words. In the "associative learning phase," no behavioral response was required from the participants. During the "matching task", pictures were presented on the screen followed by a word (SOA = 750 ms, total trial duration = 3750 ms) that matched or mismatched the associations previously learned, and participants were asked to press one out of two response keys, accordingly. Response hand was counter-balanced across participants. A row of "x" was presented 2750 ms after picture onset, and participants were asked to blink during this time period (1000 ms) to minimize artefacts during word presentation and maximize power for independent component analysis (i.e., ICA-based artefacts correction). Each word was pseudorandomly presented 20 times, half in match- and half in mismatch conditions. A total of 180 trials were presented in two blocks of 5.6 min each. Finally, in the "semantic task," we tested for semantic integration and retrieval of the newly learned words by presenting new pictures that the participants had not seen before and that were semantically related or unrelated to the meaning of the words previously learned. In each trial, a new picture was followed by a word (SOA = 1500 ms, total trial duration = 4500 ms), and participants were asked to press one out of two response keys depending upon whether the word was semantically related or unrelated to the new picture. Response hand was counterbalanced across participants, and a familiarization task including four trials was administrated before starting the task. A row of "x" was presented 3500 ms after picture onset, and participants were instructed to blink during this period (1000 ms). Each word was presented 12 times but none of the new pictures was repeated so that on each trial the word was associated with different related (i.e., 50%) or unrelated (i.e., 50%) pictures. A total of 108 trials were presented pseudorandomly within two blocks of 4 min each. In all three tasks, auditory stimuli were presented through HiFi headphones

(HD590, Sennheiser Electronic GmBH, Wedemark, Germany) at 70dB sound pressure level and stimulus presentation, and the collection of behavioral responses, were controlled by the "Presentation" software (NeuroBehavioral Systems, Version 11.0).

2.5 | EEG data acquisition

EEG was continuously recorded with a sampling rate of 512 Hz and a band-pass filter of 0–102.4 Hz by using a Biosemi amplifier system (Amsterdam, BioSemi Active 2). Thirty-two active Ag/Cl electrodes (Biosemi Pintype) were located at standard positions according to the international 10/20 System. EEG recordings were referenced on-line to a common electrode (CMS) included in the headcap (next to Cz). Two additional electrodes were placed on the left and right mastoids. The electrooculogram (EOG) was recorded from flat-type active electrodes placed 1 cm to the left and right of the external canthi, and from an electrode beneath the right eye. Electrode impedance was kept below 5 kΩ. EEG preprocessing was done by using the Brain Vision Analyzer software (Version 1.05.0005 & Version 2.1.0; Brain Products, GmbH). Thereby, all data were rereferenced off-line to the averaged left and right mastoids, filtered with a bandpass filter of 1–30 Hz (slope of 24 dB/oct), and independent component analysis (ICA) and inverse ICA were used to identify and remove components associated with vertical and horizontal ocular movements. Finally, DC detrends and artifacts above a gradient criterion of 10 μV/ms or a max–min criterion of 100 μV were automatically removed. For each participant, EEG responses to the pictures were segmented into single sweeps of 950 ms, including a pre-stimulus baseline of 200 ms. After baseline correction, the pre-stimulus period was removed, and the single sweeps were subjected to functional connectivity analyses by using the sLORETA toolbox (http://www.uzh.ch/keyinst/loreta.htm). In the present work, we explicitly abstained from evaluating functional connectivity during the period of acoustic stimulation (i.e., the words) because such a procedure would reflect the alignment of neural oscillations due to the often-reported increased auditory acuity of professional musicians rather than capture word learning per se.

2.6 | Functional connectivity analyses

Functional connectivity (sLORETA software package; http://www.uzh.ch/keyinst/loreta.htm) was evaluated using lagged coherence values as a measure of variability between two oscillatory time series in specific frequency bands (Lehmann, Faber, Gianotti, Kochi, & Pascual-Marqui, 2006; Thatcher, 2012). Lagged coherence reflects the coherence between two EEG time series independent from volume conduction since the instantaneous zero-lag contribution has been excluded mathematically (Nolte et al., 2004; Stam & van Straaten, 2012). Such a correction is desired when using estimated intracranial signals (EEG tomography), because zero-lag connectivity in a given frequency band is often due to nonphysiological effects or intrinsic physical artifacts (e.g., volume conduction and low spatial resolution) that usually affect connectivity indices. Thus, this measure of functional connectivity is thought to contain only physiological information.

In the current implementation of sLORETA (Pascual-Marqui et al., 2011), EEG data are rereferenced to an average reference, and computations are made within a realistic head model (Fuchs, Kastner, Wagner, Hawes, & Ebersole, 2002) relying on the Montreal Neurological Institute (MNI) 152 template (Mazziotta et al., 2001). The 3D solution space is restricted to cortical gray matter, as determined by the probabilistic Talairach atlas (Lancaster et al., 2000). The intracranial volume is partitioned in 6,239 voxels at 5 mm spatial resolution. sLORETA images represent the electric activity at each voxel in the neuroanatomic MNI space as the exact magnitude of the estimated current density. Anatomical labels and BAs are reported using MNI space, with correction to Talairach space (Brett, Johnsrude, & Owen, 2002).

Based on the specific hypotheses described in the introduction, we selected three regions of interest (ROI) in each hemisphere. These three ROIs (Figure 2a–c) consisted of BA 39/40 (ROI 1, AG/SMG), BA 44/45 (ROI 2, Broca's area), and BA 21 (ROI 3, middle part of the middle temporal gyrus, MTG). For functional connectivity analyses in the ventral and dorsal streams, a method using a single voxel at the centroid of the ROIs was chosen. Details on sLORETA connectivity algorithms can be found in previous reports by Pascual-Marqui et al. (2011). For each group and for each task, functional connectivity during the first 750 ms after picture presentation was computed in the theta (4–7 Hz), alpha (8–12 Hz), and beta frequency range (13–20 Hz).

2.7 | Statistical analyses

All statistical analyses were performed by using IBM SPSS statistics (version 22). Psychometric data were evaluated by means of univariate ANOVAs, and musical aptitudes were assessed by a 2 × 2 ANOVA (i.e., two groups and two subtests). Error rates (ERRs) and reaction times (RTs) were evaluated for both the "matching task" and the "semantic task" by means of separate univariate ANOVAs [corrected for multiple comparisons by using the Bonferroni procedure, Bonferroni-corrected p value for 2 tests (i.e., 2 tasks) = 0.03]. Functional connectivity was assessed in all three tasks (i.e., "associative learning phase," "matching task," and "semantic task") by means of separate 2 × 2 × 2 ANOVAs (i.e., two groups, two streams, and two hemispheres) for each frequency band [corrected for multiple comparisons, Bonferroni-corrected p value for 9 tests (i.e., 3 tasks × 3 frequency bands) = 0.005]. Finally, correlation analyses between the error rate in the semantic task and the cumulative number of training years (normally distributed, see Figure 5a), as well as left-hemispheric theta connectivity, were computed according to Spearman's rho (one-tailed) separately for the ventral and dorsal streams.

3 | RESULTS

3.1 | Cognitive ability and musical aptitudes

Musicians and nonmusicians did not significantly differ in terms of fluid intelligence ($F_{(1, 27)} = .93$, $p = .34$), verbal working memory (i.e., reverse digit span; $F_{(1, 27)} = 2.25$, $p = .15$), or visual attention ($F_{(1, 27)} = 3.89$, $p = .06$). However, musicians scored better on the short-term memory
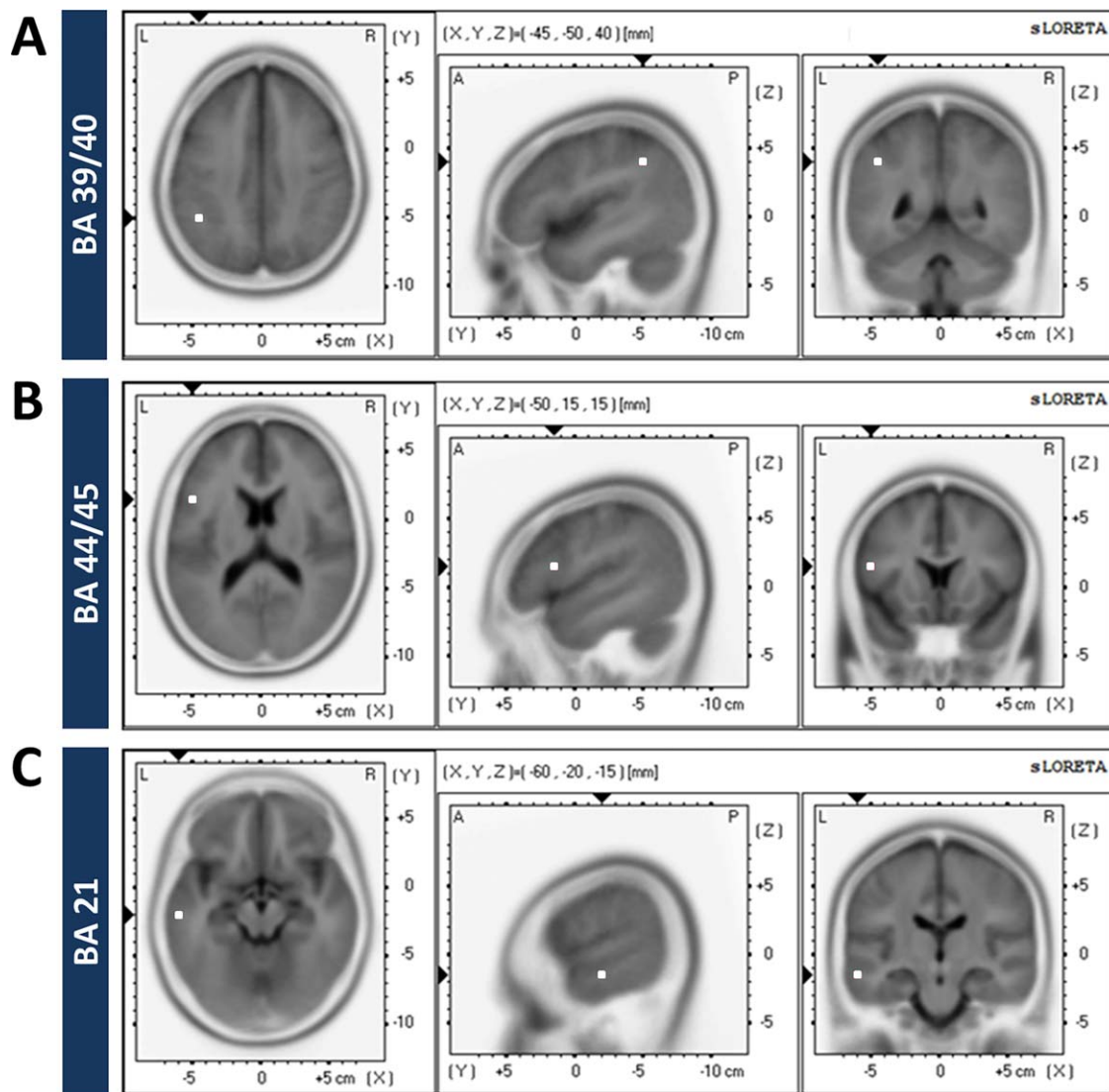
FIGURE 2 Left-hemispheric ROIs positions within the three-dimensional MNI space. (a) Centroid voxel corresponding to BAs 39/40; (b) centroid voxel corresponding to BAs 44/45; (c) centroid voxel corresponding to BA 21 [Color figure can be viewed at wileyonlinelibrary.com]

test (i.e., forward digit span test; $F_{(1, 27)} = 4.84$, $p = .04$), and outperformed nonmusicians on both tonal and rhythmical subtests of musical aptitudes (main effect of Group: $F_{(1,27)} = 14.01$, $p < .001$).

3.2 | Behavioral data

The evaluation of ERRs and RTs during the "matching task" did not reveal significant group differences (ERRs: $F_{(1,27)} = .28$, $p = .60$, and RTs: $F_{(1,27)} = .15$, $p = .70$; see Figure 3a). By contrast, in the "semantic task" musicians made significantly fewer errors than nonmusicians ($F_{(1,27)} = 5.02$, $p = .03$, Bonferroni-corrected; see Figure 3b), whereas the two groups did not differ in RTs ($F_{(1,27)} = .44$, $p = .51$, see Figure 3b).

3.3 | Functional connectivity

Functional connectivity did not differ between the two groups in the "associative learning phase." By contrast, in both the "matching task" and in the "semantic task," results revealed a main effect of stream in

the beta frequency range that originated from increased connectivity in the bilateral ventral stream compared to the dorsal stream ("matching task": $F_{(1,27)} = 19.97$, $p < .001$ and "semantic task": $F_{(1,27)} = 14.26$, $p < .001$, Bonferroni-corrected; see Figure 4a). Moreover, in the "semantic task" we also found a significant group × hemisphere interaction effect in the theta frequency range ($F_{(1,27)} = 9.37$, $p = .005$, Bonferroni-corrected). Post-hoc univariate ANOVAs for each hemisphere yielded a significant group difference in the left ($F_{(1,27)} = 5.66$, $p = .02$) but not in the right ($F_{(1,27)} = .21$, $p = .65$) hemisphere that originated from increased theta connectivity in musicians compared to nonmusicians (Figure 4b). Finally, to further explore hemispherical contributions within the two groups, we tested the asymmetry index [i.e., asymmetry index = (connectivity left − connectivity right)/(connectivity left + connectivity right) × 0.5] against zero (i.e., no asymmetry). Results showed symmetrical hemispheric theta connectivity within the musicians group (one-sample t test against zero, $t_{(13)} = .31$, $p = .76$, two-tailed), whereas nonmusicians were characterized by a right-sided asymmetry (one-sample t test against zero, $t_{(14)} = -4.53$, $p < .001$, two-tailed).
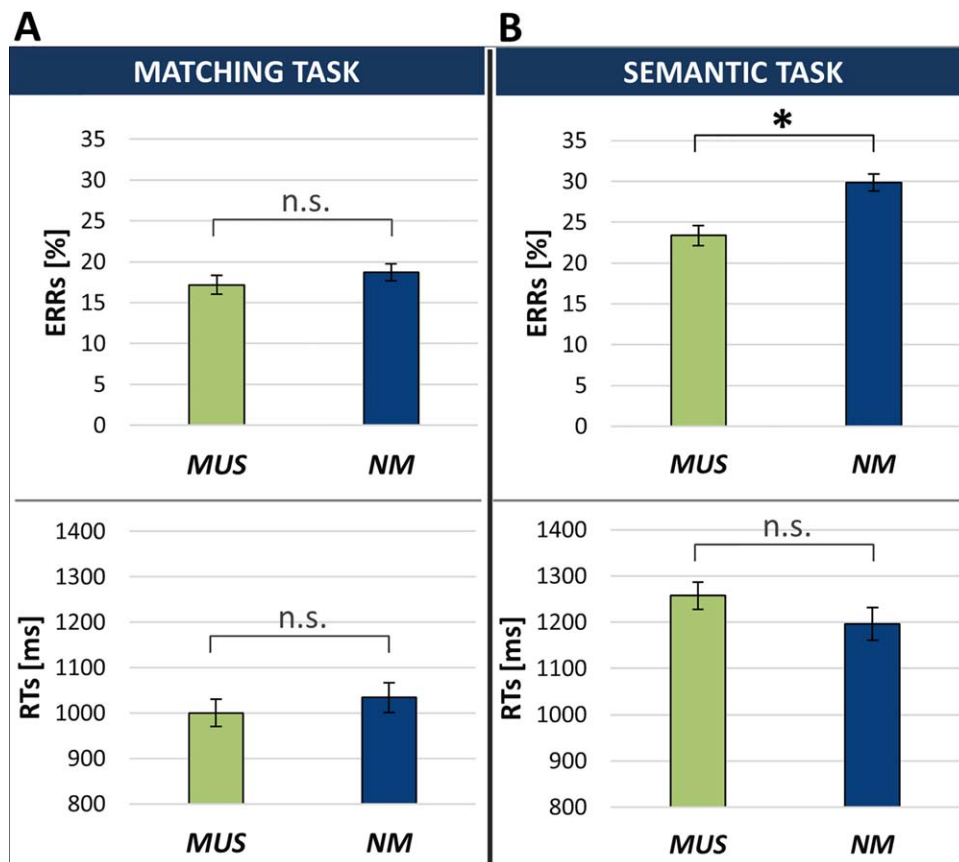
FIGURE 3 Behavioral results (ERRs: upper part and RTs: lower part) are shown separately for musicians (MUS) and nonmusicians (NM). (a) Matching task; (b) Semantic task. The bars depict SE of mean. *$p < .05$, n.s. = not significant [Color figure can be viewed at wileyonlinelibrary.com]

3.4 | Relationship between functional connectivity and music training

To verify that the increased left-hemispheric theta connectivity we revealed in musicians was related to training, we performed additional correlative analyses. In particular, within the musicians group we correlated the number of training years with left-sided theta connectivity in the "semantic task," separately for the ventral and the dorsal streams (i.e., according to Spearman's rho for non-Gaussian distributed data, one-tailed, Figure 5a). Results revealed a significant positive relationship
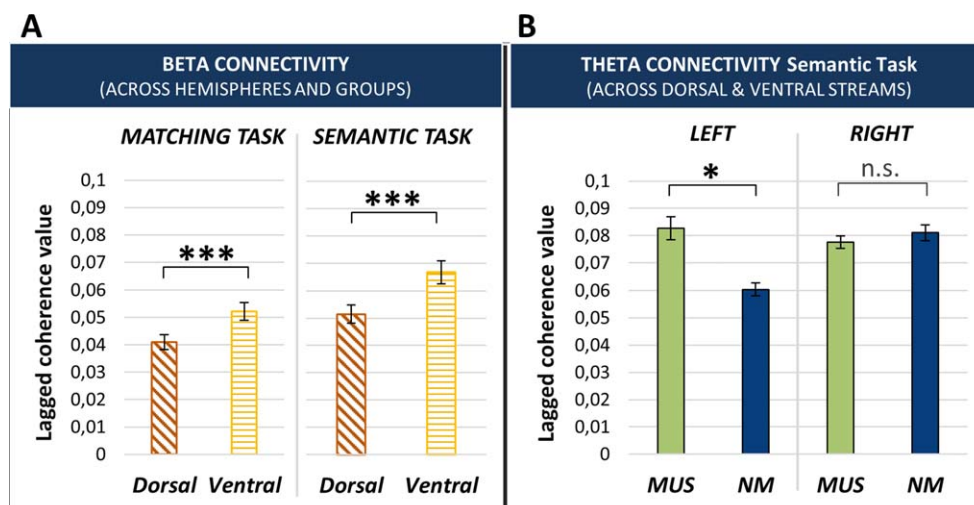
FIGURE 4 Mean functional connectivity. (a) Beta connectivity averaged across hemispheres and groups is shown separately for the tasks ("matching task" and "semantic task") and processing streams (dorsal; ventral). (b) Theta connectivity during the "semantic task" averaged across processing streams is shown separately for the hemispheres ("left" and "right"), and groups (MUS; NM). Mean values with SE bars. *$p < .05$; ***$p < .001$; n.s. = not significant [Color figure can be viewed at wileyonlinelibrary.com]
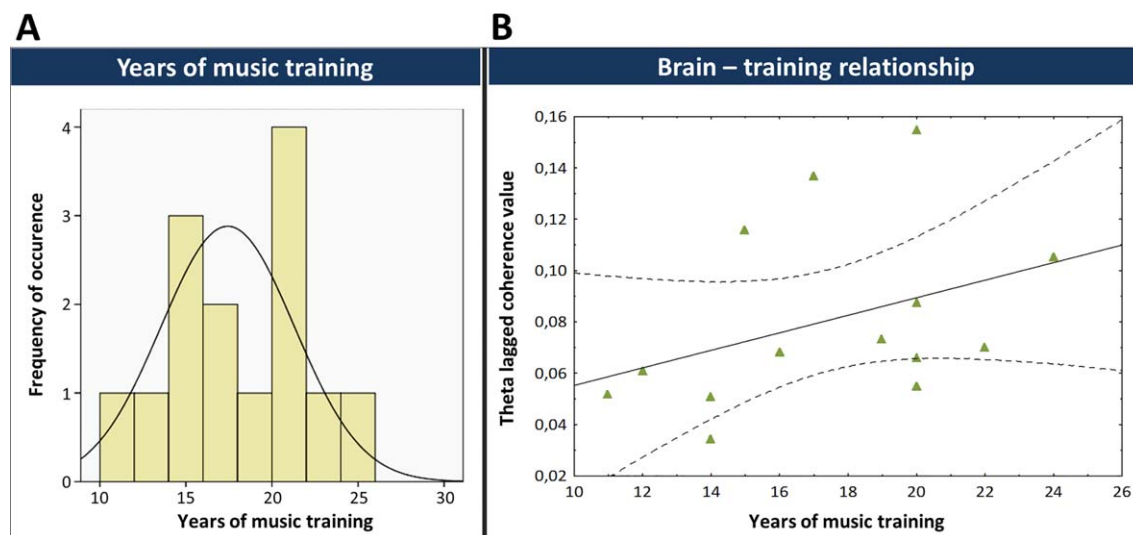
FIGURE 5 (a) Bimodal distribution of the variable "cumulative number of training years" with a superimposed Gaussian function. (b) Significant positive correlation between the left-hemispheric theta connectivity in the dorsal stream during the "semantic task" and the cumulative number of training years (one-tailed) [Color figure can be viewed at wileyonlinelibrary.com]

for the dorsal stream ($r_{(14)} = .52$, $p = .03$, Figure 5b) but not for the ventral stream ($r_{(14)} = .08$, $p = .39$). By contrast, no significant correlations were obtained between error rates in the semantic task and number of training years ($r_{(14)} = .24$, $p = .21$, one-tailed) or left-sided theta connectivity (dorsal stream: $r_{(28)} = -.12$, $p = .27$; ventral stream: $r_{(28)} = -.12$, $p = .28$, one-tailed).

4 | DISCUSSION

In this study, we compared novel word learning in musicians and nonmusicians by using three concatenated tasks that are dependent upon a variety of perceptual and cognitive functions typically involved in both music and language processing (Dittinger et al., 2016). Based on previous evidence pointing to an optimization of perceptual discrimination (Chobert et al., 2014; Marie et al., 2011), short-term and working memory (George & Coch, 2011; Schulze & Koelsch, 2012), executive functions (Zuk et al., 2014), and audio–visual integration (Bidelman, 2016; Paraskevopoulos, Kraneburg, Herholz, Bamidis, & Pantev, 2015) in musicians, we predicted that the musicians' advantage in word learning would translate into increased EEG-based functional connectivity along the ventral- and dorsal processing streams. Results consistently revealed increased beta coherence in the ventral compared to the dorsal stream during both the "matching-" and "semantic tasks." Moreover, musicians outperformed nonmusicians during the cognitively most demanding "semantic task" and exhibited increased theta coherence over the left hemisphere compared to nonmusicians. Finally, left-dorsal functional connectivity in the theta frequency range was positively correlated with the number of years of music training, leading to suggest training-related adaptations. In turn, we will discuss these findings in more details by integrating the results in neuro-linguistic and musical frameworks.

4.1 | Neural dynamics underlying word learning and semantic generalization

As expected and in line with current models of speech and language processing (Bornkessel-Schlesewsky & Schlesewsky, 2013; Friederici, 2012; Hagoort, 2014; Hickok & Poeppel, 2007; Rauschecker & Scott, 2009), results generally revealed increased beta functional connectivity in the ventral stream compared to the dorsal stream during both the "matching- "and "semantic tasks." This connectivity pattern is taken to reflect the neural dynamics underlying novel word learning and, specifically the mapping of phonological information with lexical-semantic representations. Several arguments support this interpretation. First, increased activity in the IPL was observed during the learning of new phonological associations (i.e., using pseudowords; Breitenstein et al., 2005) and during the retrieval of previously learned novel words (Cornelissen et al., 2004; Hultén, Laaksonen, Vihla, Laine, & Salmelin, 2010). In addition, activity in the IPL has been shown to be modulated by the semantic richness of words (Ferreira et al., 2015), leading to suggest that this region also contributes to the retrieval of semantic information (Obleser & Kotz, 2010; Price, 2010). Second, the middle-posterior part of the MTG is involved in mediating lexical-semantic access at the word level (Friederici, 2012; Hickok & Poeppel, 2007), and the retrieval of semantic information in word learning tasks (Mestres-Missé, Càmara, Rodriguez-Fornells, Rotte, & Münte, 2008). For example, activity in the MTG is increased when participants retrieve meaningful word-forms compared to word-forms without meaning (Takashima, Bakker, van Hell, Janzen, & McQueen, 2014). Third, increased beta coherence during word encoding has previously been shown to be predictive of successful retrieval (Weiss & Rappelsberger, 2000). In addition, it has been proposed that beta oscillations contribute to the maintenance of a cognitive state (Engel & Fries, 2010), as for example, in the context of repetition priming paradigms (Ghuman, Bar, Dobbins, & Schnyer, 2008). Taken together, these results emphasize a crucial role of beta

oscillations in mediating learning and retrieval of newly learned words from semantic memory.

4.2 | Novel word learning and musical expertise

In line with our main hypothesis, musicians outperformed nonmusicians in the most difficult "semantic task," in which pictures that had not been presented before in the experiment were paired with the newly learned words to test for semantic generalization. This finding is not surprising since difficult tasks are typically more sensitive for detecting expertise-related influences than simple ones (Schön, Magne, & Besson, 2004). The positive influence of music training on semantic processing extends previous findings showing a facilitation of speech perception and syntactic processing in musicians compared to nonmusicians (Besson et al., 2011; Gordon, Fehd, & McCandliss, 2015; Jentschke & Koelsch, 2009). While the specific origin of the behavioral advantage we revealed in musicians is still unclear, Dittinger et al. (2016) proposed two complementary interpretations, namely "cascading effects" and "multidimensional facilitation effects." According to "cascading effects," the behavioral advantage of musicians may be driven by enhanced auditory perception that facilitates the building-up of new phonological representations and lexical-semantic access (bottom–up effects). Otherwise, the multidimensional nature of music training may also improve several cognitive functions such as picture–word integration, short- and long-term memory that are necessary for word learning (top–down effects).

4.3 | Musicians exhibit increased theta coherence in the left hemisphere

In the "semantic task," results revealed increased theta coherence in musicians compared to nonmusicians in the left but not in the right hemisphere, irrespective of processing stream. However, this finding does not necessarily mean that the left hemisphere was more strongly involved than the right one, and especially it does not preclude a right-hemispheric contribution to language learning (Price, 2010; Vigneau et al., 2011). In fact, the additional statistical analyses performed on asymmetry index data clearly showed symmetrical theta connectivity in musicians and a right-sided asymmetry in nonmusicians. The symmetrical recruitment of the two processing streams in musicians is, at least in part, compatible with results showing that individuals with a more symmetrical distribution of the arcuate fasciculus performed better at remembering previously learned words compared to those characterized by a strong left-hemispheric asymmetry (Catani et al., 2007). Moreover, the right-sided theta asymmetry found in nonmusicians is in line with the results of Takashima et al. (2014) showing higher right-than left-hemispheric connectivity between the STG and the MTG for successfully recognized words associated with complex and colored pictures. Even though the different laterality effects we observed as a function of music training are relevant for better comprehending experiential influences, the underlying mechanisms still need to be worked out.

4.4 | Theta coherence in the left dorsal stream is increased in musicians compared to nonmusicians

In line with previous literature indicating an influence of music training on the functional (Klein et al., 2016) and structural (Halwani et al., 2011; Oechslin et al., 2010) architecture of the left dorsal stream, theta coherence was increased between the left IPL and Broca's area in musicians compared to nonmusicians. In addition, functional connectivity in the left dorsal stream was correlated with the number of years of music training, thereby pointing to an influence of music training on the neural dynamics involved in novel word learning. As increased functional connectivity in the left dorsal stream was paralleled by a behavioral advantage in the "semantic task," results are interpreted as indicating a contribution of this connectivity pattern to task-related mnemonic functions. In this context, there are several alternative explanations that may account for the mnemonic advantage of musicians. A first possibility is that increased theta synchronization between the left IPL and Broca's area contributed to build more robust multimodal memory traces by linking novel phonological representations to the respective articulatory codes (López-Barroso et al., 2013). Such sensory-to-motor coupling mechanisms are required for retrieving the phonological codes of new words (i.e., Thai) that are not part of the phonetic repertoire of the mother tongue (i.e., French). A second possibility is that musicians possibly preactivated the target words corresponding to the pictures by using articulatory strategies. A similar mechanisms has previously been described by Tian and collaborators (Tian et al., 2016) who found increased activity in a left frontal-parietal sensorimotor network when participants were instructed to imaging consonant-vowel syllables by using an articulation-based imagery strategy compared to a hearing-based one. Finally, based on recent results, it may be that increased theta oscillations in the left dorsal stream of musicians are related to the manipulation of acoustic information in working memory (Albouy et al., 2017). In fact, working memory is necessarily required for retrieving from memory the old learned pictures semantically related to the new ones while at the same time selecting the corresponding target word. Certainly, all these lines of argumentation are not conclusive, and can only be proofed by applying word learning tasks specifically targeting at increasing computational demands on sensory-to-motor coupling mechanisms, articulatory-based imagery strategies, and working memory load in a parametric manner.

5 | LIMITATIONS

A limitation of this study is that we used a source estimation approach for evaluating functional connectivity between a-priori defined brain regions without taking into account the underlying grey- and white-matter architecture. Consequently, we cannot exclude that the alignment of neural oscillations between the ROIs was indirectly mediated by other brain regions. Therefore, future studies should try to combine functional and structural connectivity with morphometric analyses in order to better comprehend the differential contribution of the dorsal and ventral streams to word learning in individuals with and without

music training. In addition, the results of the present study were interpreted according to sound-to-meaning and sound-to-articulation mapping mechanisms. However, we are aware that other distinctions have been proposed by several authors (Bornkessel-Schlesewsky & Schlesewsky, 2013; see Cloutman, 2013 for review) by taking into account time-variant (i.e., dorsal stream) and time-invariant (i.e., ventral stream) neural computation in the two processing streams. According to this framework, the coupling of speech sounds with articulation and working memory functions may rely on time-dependent processes in the dorsal stream, whereas the building-up of word representations through sound-to-meaning mapping mechanisms may engage the time-independent ventral stream. Finally, increased theta functional connectivity in both the ventral and dorsal processing streams in professional musicians compared to nonmusicians does not necessarily imply that music training was the cause of these findings. For example, while the correlation between left theta connectivity in the dorsal stream and the number of years of music training was significant, no such correlation was found with the level of performance in the semantic task. Therefore, longitudinal experiments with nonmusicians are needed to demonstrate a causal link between music training and increased functional connectivity.

6 | CONCLUSIONS

In line with previous models of speech processing (Friederici, 2012; Hickok & Poeppel, 2004, 2007), we found that the bilateral ventral stream generally contributed to novel word learning, irrespective of musical expertise. In addition, we provided evidence for a relationship between the behavioral advantages of musicians in the "semantic task" and the alignment of theta oscillations in the left-sided ventral- and dorsal streams. This specific connectivity pattern was interpreted as reflecting facilitated access to lexical-semantic information though the engagement of articulation strategies and manipulation of information in working memory. Our results not only constitute a first step toward a better understanding of the influence of music training on dynamic neural networks during word learning, but also complement previous knowledge about the contribution of the ventral and dorsal streams to word learning.

CONFLICT OF INTEREST

The authors declare no competing financial interests.

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REFERENCES

Albouy, P., Weiss, A., Baillet, S., & Zatorre, R. J. (2017). Selective entrainment of theta oscillations in the dorsal stream causally enhances auditory working memory performance. *Neuron*, 94(1), 193–206.e5.

Bangert, M., & Schlaug, G. (2006). Specialization of the specialized in features of external human brain morphology. *The European Journal of Neuroscience*, 24(6), 1832–1834.

Bastiaansen, M., Magyari, L., & Hagoort, P. (2010). Syntactic unification operations are reflected in oscillatory dynamics during on-line sentence comprehension. *Journal of Cognitive Neuroscience*, 22(7), 1333–1347.

Bermudez, P., Lerch, J. P., Evans, A. C., & Zatorre, R. J. (2009). Neuroanatomical correlates of musicianship as revealed by cortical thickness and voxel-based morphometry. *Cerebral Cortex*, 19(7), 1583–1596.

Besson, M., Chobert, J., & Marie, C. (2011). Transfer of training between music and speech: Common processing, attention, and memory. *Frontiers in Psychology*, 2.

Bidelman, G. M. (2016). Musicians have enhanced audiovisual multisensory binding: Experience-dependent effects in the double-flash illusion. *Experimental Brain Research*, 234(10), 3037–3047.

Bidelman, G. M., Weiss, M. W., Moreno, S., & Alain, C. (2014). Coordinated plasticity in brainstem and auditory cortex contributes to enhanced categorical speech perception in musicians. *European Journal of Neuroscience*, 40(4), 2662–2673.

Binder, J. R., Frost, J. A., Hammeke, T. A., Cox, R. W., Rao, S. M., & Prieto, T. (1997). Human brain language areas identified by functional magnetic resonance imaging. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 17(1), 353–362.

Bornkessel-Schlesewsky, I., & Schlesewsky, M. (2013). Reconciling time, space and function: A new dorsal-ventral stream model of sentence comprehension. *Brain and Language*, 125(1), 60–76.

Breitenstein, C., Jansen, A., Deppe, M., Foerster, A.-F., Sommer, J., Wolbers, T., & Knecht, S. (2005). Hippocampus activity differentiates good from poor learners of a novel lexicon. *NeuroImage*, 25(3), 958–968.

Brett, M., Johnsrude, I. S., & Owen, A. M. (2002). The problem of functional localization in the human brain. *Nature Reviews Neuroscience*, 3(3), 243–249.

Buchsbaum, B. R., Baldo, J., Okada, K., Berman, K. F., Dronkers, N., D'esposito, M., & Hickok, G. (2011). Conduction aphasia, sensory-motor integration, and phonological short-term memory - an aggregate analysis of lesion and fMRI data. *Brain and Language*, 119(3), 119–128.

Carrus, E., Koelsch, S., & Bhattacharya, J. (2011). Shadows of music–language interaction on low frequency brain oscillatory patterns. *Brain and Language*, 119(1), 50–57.

Catani, M., Allin, M. P. G., Husain, M., Pugliese, L., Mesulam, M. M., Murray, R. M., & Jones, D. K. (2007). Symmetries in human brain language pathways correlate with verbal recall. *Proceedings of the National Academy of Sciences of the United States of America*, 104(43), 17163–17168.

Chobert, J., Francois, C., Velay, J.-L., & Besson, M. (2014). Twelve months of active musical training in 8- to 10-year-old children enhances the preattentive processing of syllabic duration and voice onset time. *Cerebral Cortex*, 24(4), 956–967.

Clos, M., Amunts, K., Laird, A. R., Fox, P. T., & Eickhoff, S. B. (2013). Tackling the multifunctional nature of Broca's region meta-analytically: Co-activation-based parcellation of area 44. *NeuroImage*, 83, 174–188.

Cloutman, L. L. (2013). Interaction between dorsal and ventral processing streams: Where, when and how? *Brain and Language*, 127(2), 251–263.

Cornelissen, K., Laine, M., Renvall, K., Saarinen, T., Martin, N., & Salmelin, R. (2004). Learning new names for new objects: Cortical effects as measured by magnetoencephalography. *Brain and Language*, 89(3), 617–622.

Cunillera, T., Càmara, E., Toro, J. M., Marco-Pallares, J., Sebastián-Galles, N., Ortiz, H., ... Rodríguez-Fornells, A. (2009). Time course and functional neuroanatomy of speech segmentation in adults. *NeuroImage*, 48(3), 541–553.

DeWitt, I., & Rauschecker, J. P. (2012). Phoneme and word recognition in the auditory ventral stream. *Proceedings of the National Academy of Sciences*, 109, E505–E514.

Dittinger, E., Barbaroux, M., D'imperio, M., Jäncke, L., Elmer, S., & Besson, M. (2016). Professional music training and novel word learning: From faster semantic encoding to longer-lasting word representations. *Journal of Cognitive Neuroscience*, 28(10), 1584–1602.

Dittinger, E., Chobert, J., Ziegler, J. C., & Besson, M. (2017). Fast brain plasticity during word learning in musically-trained children. *Frontiers in Human Neuroscience*, 11.

Doelling, K. B., & Poeppel, D. (2015). Cortical entrainment to music and its modulation by expertise. *Proceedings of the National Academy of Sciences*, 112(45), E6233–E6242.

Eickhoff, S. B., Heim, S., Zilles, K., & Amunts, K. (2009). A systems perspective on the effective connectivity of overt speech production. *Philosophical Transactions. Series A, Mathematical, Physical, and Engineering Sciences*, 367(1896), 2399–2421.

Elmer, S., Hänggi, J., & Jäncke, L. (2016). Interhemispheric transcallosal connectivity between the left and right planum temporale predicts musicianship, performance in temporal speech processing, and functional specialization. *Brain Structure and Function*, 221(1), 331–344.

Elmer, S., Meyer, M., & Jancke, L. (2012). Neurofunctional and behavioral correlates of phonetic and temporal categorization in musically trained and untrained subjects. *Cerebral Cortex*, 22(3), 650–658.

Engel, A. K., & Fries, P. (2010). Beta-band oscillations–signalling the status quo? *Current Opinion in Neurobiology*, 20(2), 156–165.

Farbood, M. M., Heeger, D. J., Marcus, G., Hasson, U., & Lerner, Y. (2015). The neural processing of hierarchical structure in music and speech at different timescales. *Frontiers in Neuroscience*, 9,

Fedorenko, E., Duncan, J., & Kanwisher, N. (2012). Language-selective and domain-general regions lie side by side within Broca's area. *Current Biology: CB*, 22(21), 2059–2062.

Ferreira, R. A., Göbel, S. M., Hymers, M., & Ellis, A. W. (2015). The neural correlates of semantic richness: Evidence from an fMRI study of word learning. *Brain and Language*, 143, 69–80.

Friederici, A. D. (2009). Pathways to language: Fiber tracts in the human brain. *Trends in Cognitive Sciences*, 13(4), 175–181.

Friederici, A. D. (2012). The cortical language circuit: From auditory perception to sentence comprehension. *Trends in Cognitive Sciences*, 16(5), 262–268.

Fuchs, M., Kastner, J., Wagner, M., Hawes, S., & Ebersole, J. S. (2002). A standardized boundary element method volume conductor model. *Clinical Neurophysiology: Official Journal of the International Federation of Clinical Neurophysiology*, 113(5), 702–712.

Gaab, N., Gaser, C., Zaehle, T., Jancke, L., & Schlaug, G. (2003). Functional anatomy of pitch memory–an fMRI study with sparse temporal sampling. *NeuroImage*, 19(4), 1417–1426.

Gaser, C., & Schlaug, G. (2003). Brain structures differ between musicians and non-musicians. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 23(27), 9240–9245.

George, E. M., & Coch, D. (2011). Music training and working memory: An ERP study. *Neuropsychologia*, 49(5), 1083–1094.

Ghuman, A. S., Bar, M., Dobbins, I. G., & Schnyer, D. M. (2008). The effects of priming on frontal-temporal communication. *Proceedings of the National Academy of Sciences of the United States of America*, 105(24), 8405–8409.

Giraud, A.-L., & Poeppel, D. (2012). Cortical oscillations and speech processing: Emerging computational principles and operations. *Nature Neuroscience*, 15(4), 511–517.

Gordon, R. L., Fehd, H. M., & McCandliss, B. D. (2015). Does music training enhance literacy skills? A meta-analysis. *Frontiers in Psychology*, 6.

Hagoort, P. (2014). Nodes and networks in the neural architecture for language: Broca's region and beyond. *Current Opinion in Neurobiology*, 28, 136–141.

Halwani, G. F., Loui, P., Rüber, T., & Schlaug, G. (2011). Effects of practice and experience on the arcuate fasciculus: Comparing singers, instrumentalists, and non-musicians. *Frontiers in Psychology*, 2, 156.

Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams: A framework for understanding aspects of the functional anatomy of language. *Cognition*, 92(1–2), 67–99.

Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews. Neuroscience*, 8(5), 393–402.

Hickok, G., Rogalsky, C., Chen, R., Herskovits, E. H., Townsley, S., & Hillis, A. E. (2014). Partially overlapping sensorimotor networks underlie speech praxis and verbal short-term memory: Evidence from apraxia of speech following acute stroke. *Frontiers in Human Neuroscience*, 8,

Hultén, A., Laaksonen, H., Vihla, M., Laine, M., & Salmelin, R. (2010). Modulation of brain activity after learning predicts long-term memory for words. *Journal of Neuroscience*, 30(45), 15160–15164.

Hyde, K. L., Lerch, J., Norton, A., Forgeard, M., Winner, E., Evans, A. C., & Schlaug, G. (2009). Musical training shapes structural brain development. *Journal of Neuroscience*, 29(10), 3019–3025.

Jäncke, L., Langer, N., & Hänggi, J. (2012). Diminished whole-brain but enhanced peri-sylvian connectivity in absolute pitch musicians. *Journal of Cognitive Neuroscience*, 24(6), 1447–1461.

Jäncke, L., Wüstenberg, T., Scheich, H., & Heinze, H.-J. (2002). Phonetic perception and the temporal cortex. *NeuroImage*, 15(4), 733–746.

Jentschke, S., & Koelsch, S. (2009). Musical training modulates the development of syntax processing in children. *NeuroImage*, 47(2), 735–744.

Joanisse, M. F., Zevin, J. D., & McCandliss, B. D. (2007). Brain mechanisms implicated in the preattentive categorization of speech sounds revealed using FMRI and a short-interval habituation trial paradigm. *Cerebral Cortex (New York, N.Y.: 1991)*, 17(9), 2084–2093.

Johnson, S. C., Saykin, A. J., Flashman, L. A., McAllister, T. W., & Sparling, M. B. (2001). Brain activation on fMRI and verbal memory ability: Functional neuroanatomic correlates of CVLT performance. *Journal of the International Neuropsychological Society*, 7(1), 55–62.

Klein, C., Liem, F., Hänggi, J., Elmer, S., & Jäncke, L. (2016). The "silent" imprint of musical training. *Human Brain Mapping*, 37(2), 536–546.

Koelsch, S. (2011). Toward a neural basis of music perception – A review and updated model. *Frontiers in Psychology*, 2.

Korkman, M., Kirk, U., & Kemp, S. (1998). *NEPSY: A developmental neuro-psychological assessment*. San Antonio, TX: The Psychological Corporation.

Kühnis, J., Elmer, S., & Jäncke, L. (2014). Auditory evoked responses in musicians during passive vowel listening are modulated by functional connectivity between bilateral auditory-related brain regions. *Journal of Cognitive Neuroscience*, 26(12), 2750–2761.

Kühnis, J., Elmer, S., Meyer, M., & Jäncke, L. (2013). The encoding of vowels and temporal speech cues in the auditory cortex of professional musicians: An EEG study. *Neuropsychologia*, 51(8), 1608–1618.

Lancaster, J. L., Woldorff, M. G., Parsons, L. M., Liotti, M., Freitas, C. S., Rainey, L., ... Fox, P. T. (2000). Automated Talairach atlas labels for functional brain mapping. *Human Brain Mapping*, 10(3), 120–131.

Leaver, A. M., & Rauschecker, J. P. (2010). Cortical representation of natural complex sounds: Effects of acoustic features and auditory object category. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 30(22), 7604–7612.

Lehmann, D., Faber, P. L., Gianotti, L. R. R., Kochi, K., & Pascual-Marqui, R. D. (2006). Coherence and phase locking in the scalp EEG and between LORETA model sources, and microstates as putative mechanisms of brain temporo-spatial functional organization. *Journal of Physiology, Paris*, 99(1), 29–36.

Lima, C. F., & Castro, S. L. (2011). Speaking to the trained ear: Musical expertise enhances the recognition of emotions in speech prosody. *Emotion (Washington, D.C.)*, 11(5), 1021–1031.

López-Barroso, D., Catani, M., Ripollés, P., Dell'acqua, F., Rodríguez-Fornells, A., & de Diego-Balaguer, R. (2013). Word learning is mediated by the left arcuate fasciculus. *Proceedings of the National Academy of Sciences of the United States of America*, 110(32), 13168–13173.

Marie, C., Delogu, F., Lampis, G., Belardinelli, M. O., & Besson, M. (2011). Influence of musical expertise on segmental and tonal processing in Mandarin Chinese. *Journal of Cognitive Neuroscience*, 23(10), 2701–2715.

Marques, C., Moreno, S., Castro, S. L., & Besson, M. (2007). Musicians detect pitch violation in a foreign language better than nonmusicians: Behavioral and electrophysiological evidence. *Journal of Cognitive Neuroscience*, 19(9), 1453–1463.

Mazziotta, J., Toga, A., Evans, A., Fox, P., Lancaster, J., Zilles, K., ... Mazoyer, B. (2001). A probabilistic atlas and reference system for the human brain: International Consortium for Brain Mapping (ICBM). *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 356(1412), 1293–1322.

Mestres-Missé, A., Càmara, E., Rodriguez-Fornells, A., Rotte, M., & Münte, T. F. (2008). Functional neuroanatomy of meaning acquisition from context. *Journal of Cognitive Neuroscience*, 20(12), 2153–2166.

Münte, T. F., Altenmüller, E., & Jäncke, L. (2002). The musician's brain as a model of neuroplasticity. *Nature Reviews. Neuroscience*, 3(6), 473–478.

Nolte, G., Bai, O., Wheaton, L., Mari, Z., Vorbach, S., & Hallett, M. (2004). Identifying true brain interaction from EEG data using the imaginary part of coherency. *Clinical Neurophysiology: Official Journal of the International Federation of Clinical Neurophysiology*, 115(10), 2292–2307.

Obleser, J., & Kotz, S. A. (2010). Expectancy constraints in degraded speech modulate the language comprehension network. *Cerebral Cortex (New York, N.Y.: 1991)*, 20(3), 633–640.

Obleser, J., Wöstmann, M., Hellbernd, N., Wilsch, A., & Maess, B. (2012). Adverse listening conditions and memory load drive a common alpha oscillatory network. *Journal of Neuroscience*, 32(36), 12376–12383.

Oechslin, M. S., Imfeld, A., Loenneker, T., Meyer, M., & Jäncke, L. (2010). The plasticity of the superior longitudinal fasciculus as a function of musical expertise: A diffusion tensor imaging study. *Frontiers in Human Neuroscience*, 3.

Oechslin, M. S., Meyer, M., & Jäncke, L. (2010). Absolute pitch—Functional evidence of speech-relevant auditory acuity. *Cerebral Cortex (New York, NY)*, 20(2), 447–455.

Paraskevopoulos, E., Kraneburg, A., Herholz, S. C., Bamidis, P. D., & Pantev, C. (2015). Musical expertise is related to altered functional connectivity during audiovisual integration. *Proceedings of the National Academy of Sciences*, 112(40), 12522–12527.

Pascual-Marqui, R. D., Lehmann, D., Koukkou, M., Kochi, K., Anderer, P., Saletu, B., ... Kinoshita, T. (2011). Assessing interactions in the brain with exact low-resolution electromagnetic tomography. *Philosophical Transactions. Series A, Mathematical, Physical, and Engineering Sciences*, 369(1952), 3768–3784.

Peretz, I., Vuvan, D., Lagrois, M.-E., & Armony, J. L. (2015). Neural overlap in processing music and speech. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1664), 20140090–20140090.

Pillay, S. B., Stengel, B. C., Humphries, C., Book, D. S., & Binder, J. R. (2014). Cerebral localization of impaired phonological retrieval during rhyme judgment. *Annals of Neurology*, 76(5), 738–746.

Polanía, R., Nitsche, M. A., Korman, C., Batsikadze, G., & Paulus, W. (2012). The importance of timing in segregated theta phase-coupling for cognitive performance. *Current Biology: CB*, 22(14), 1314–1318.

Price, C. J. (2010). The anatomy of language: A review of 100 fMRI studies published in 2009. *Annals of the New York Academy of Sciences*, 1191, 62–88.

Rauschecker, J. P. (1998). Cortical processing of complex sounds. *Current Opinion in Neurobiology*, 8(4), 516–521.

Rauschecker, J. P., & Scott, S. K. (2009). Maps and streams in the auditory cortex: Nonhuman primates illuminate human speech processing. *Nature Neuroscience*, 12(6), 718–724.

Raven, J. C., Corporation, P., Lewis, H. K. (1962). *Coloured progressive matrices: Sets A, AB, B*. London, UK: Oxford Psychologist Press.

Rilling, J. K., Glasser, M. F., Preuss, T. M., Ma, X., Zhao, T., Hu, X., & Behrens, T. E. J. (2008). The evolution of the arcuate fasciculus revealed with comparative DTI. *Nature Neuroscience*, 11(4), 426–428.

Rodríguez-Fornells, A., Cunillera, T., Mestres-Missé, A., & de Diego-Balaguer, R. (2009). Neurophysiological mechanisms involved in language learning in adults. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1536), 3711–3735.

Rogalsky, C., Rong, F., Saberi, K., & Hickok, G. (2011). Functional anatomy of language and music perception: Temporal and structural factors investigated using functional magnetic resonance imaging. *The Journal of Neuroscience*, 31(10), 3843–3852.

Saur, D., Kreher, B. W., Schnell, S., Kümmerer, D., Kellmeyer, P., Vry, M.-S., ... Weiller, C. (2008). Ventral and dorsal pathways for language. *Proceedings of the National Academy of Sciences of the United States of America*, 105(46), 18035–18040.

Schön, D., Magne, C., & Besson, M. (2004). The music of speech: Music training facilitates pitch processing in both music and language. *Psychophysiology*, 41(3), 341–349.

Schulze, K., & Koelsch, S. (2012). Working memory for speech and music. *Annals of the New York Academy of Sciences*, 1252, 229–236.

Schulze, K., Vargha-Khadem, F., & Mishkin, M. (2012). Test of a motor theory of long-term auditory memory. *Proceedings of the National*

Academy of Sciences of the United States of America, 109(18), 7121–7125.

Schulze, K., Zysset, S., Mueller, K., Friederici, A. D., & Koelsch, S. (2011). Neuroarchitecture of verbal and tonal working memory in nonmusicians and musicians. *Human Brain Mapping, 32*(5), 771–783.

Siegel, M., Warden, M. R., & Miller, E. K. (2009). Phase-dependent neuronal coding of objects in short-term memory. *Proceedings of the National Academy of Sciences, 106*(50), 21341–21346.

Sluming, V., Brooks, J., Howard, M., Downes, J. J., & Roberts, N. (2007). Broca's area supports enhanced visuospatial cognition in orchestral musicians. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience, 27*(14), 3799–3806.

Snodgrass, J. G., & Vanderwart, M. (1980). A standardized set of 260 pictures: Norms for name agreement, image agreement, familiarity, and visual complexity. *Journal of Experimental Psychology. Human Learning and Memory, 6*(2), 174–215.

Stam, C. J., & van Straaten, E. C. W. (2012). Go with the flow: Use of a directed phase lag index (dPLI) to characterize patterns of phase relations in a large-scale model of brain dynamics. *NeuroImage, 62*(3), 1415–1428.

Strait, D. L., Slater, J., O'connell, S., & Kraus, N. (2015). Music training relates to the development of neural mechanisms of selective auditory attention. *Developmental Cognitive Neuroscience, 12*, 94–104.

Takashima, A., Bakker, I., van Hell, J. G., Janzen, G., & McQueen, J. M. (2014). Richness of information about novel words influences how episodic and semantic memory networks interact during lexicalization. *NeuroImage, 84*, 265–278.

Tervaniemi, M., Kruck, S., De Baene, W., Schröger, E., Alter, K., & Friederici, A. D. (2009). Top-down modulation of auditory processing: Effects of sound context, musical expertise and attentional focus. *European Journal of Neuroscience, 30*(8), 1636–1642.

Thatcher, R. W. (2012). Coherence, phase differences, phase shift, and phase lock in EEG/ERP analyses. *Developmental Neuropsychology, 37*(6), 476–496.

Tian, X., Zarate, J. M., & Poeppel, D. (2016). Mental imagery of speech implicates two mechanisms of perceptual reactivation. *Cortex: A Journal Devoted to the Study of the Nervous System and Behavior, 77*, 1–12.

Turkeltaub, P. E., & Coslett, H. B. (2010). Localization of sublexical speech perception components. *Brain and Language, 114*(1), 1–15.

Vigneau, M., Beaucousin, V., Hervé, P.-Y., Jobard, G., Petit, L., Crivello, F., … Tzourio-Mazoyer, N. (2011). What is right-hemisphere contribution to phonological, lexico-semantic, and sentence processing? Insights from a meta-analysis. *NeuroImage, 54*(1), 577–593.

Wang, X., Ossher, L., & Reuter-Lorenz, P. A. (2015). Examining the relationship between skilled music training and attention. *Consciousness and Cognition, 36*, 169–179.

Ward, L. M. (2003). Synchronous neural oscillations and cognitive processes. *Trends in Cognitive Sciences, 7*(12), 553–559.

Wechsler, D. (2003). *Wechsler Intelligence Scale for children (fourth edition)*. San Antonio, TX: The Psychological Corporation (WISC-IV).

Weiss, S., & Rappelsberger, P. (2000). Long-range EEG synchronization during word encoding correlates with successful memory performance. *Brain Research. Cognitive Brain Research, 9*(3), 299–312.

Weisz, N., Hartmann, T., Müller, N., Lorenz, I., & Obleser, J. (2011). Alpha rhythms in audition: Cognitive and clinical perspectives. *Frontiers in Psychology, 2*, 73.

Wong, Y. T., Fabiszak, M. M., Novikov, Y., Daw, N. D., & Pesaran, B. (2016). Coherent neuronal ensembles are rapidly recruited when making a look-reach decision. *Nature Neuroscience, 19*(2), 327–334.

Zuk, J., Benjamin, C., Kenyon, A., & Gaab, N. (2014). Behavioral and neural correlates of executive functioning in musicians and non-musicians. *PLoS One, 9*(6), e99868.