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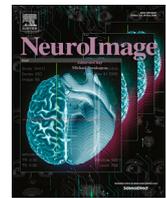
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Reading music and words: The anatomical connectivity of musicians' visual cortex



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ABSTRACT

Musical score reading and word reading have much in common, from their historical origins to their cognitive foundations and neural correlates. In the ventral occipitotemporal cortex (VOT), the specialization of the so-called Visual Word Form Area for word reading has been linked to its privileged structural connectivity to distant language regions. Here we investigated how anatomical connectivity relates to the segregation of regions specialized for musical notation or words in the VOT. In a cohort of professional musicians and non-musicians, we used probabilistic tractography combined with task-related functional MRI to identify the connections of individually defined word- and music-selective left VOT regions. Despite their close proximity, these regions differed significantly in their structural connectivity, irrespective of musical expertise. The music-selective region was significantly more connected to posterior lateral temporal regions than the word-selective region, which, conversely, was significantly more connected to anterior ventral temporal cortex. Furthermore, musical expertise had a double impact on the connectivity of the music region. First, music tracts were significantly larger in musicians than in non-musicians, associated with marginally higher connectivity to perisylvian music-related areas. Second, the spatial similarity between music and word tracts was significantly increased in musicians, consistently with the increased overlap of language and music functional activations in musicians, as compared to non-musicians. These results support the view that, for music as for words, very specific anatomical connections influence the specialization of distinct VOT areas, and that reciprocally those connections are selectively enhanced by the expertise for word or music reading.

1. Introduction

The most ancient attested musical notation is almost as old as written language itself (Kilmer and Civil, 1986). Once reading was invented, humans readily realized that not only speech but also music could be stored and transmitted in a durable visual form, rather than in a fleeting acoustic form. Accordingly, parallels should be expected between brain systems for word and for music reading (Mongelli et al., 2017; Wong and Gauthier, 2012). In the present work, we studied the anatomical pathways through which information is conveyed from the visual cortex, where written symbols are identified, to distant regions where language

and music are represented. We assessed this crucial stage of reading both in professional musicians and in non-musicians, in order to identify the anatomical substrate of expert music reading.

Learning to read essentially consists in establishing novel links between the visual system, which identifies letters or groups of letters, and the language system, which accesses word sounds and meaning. In the visual system, the invariant recognition of letter strings is achieved in a reproducible part of the left ventral occipitotemporal cortex (VOT), the so-called visual word form area (VWFA) (Cohen et al., 2000). This region is thought to be selected for reading because it has desirable visual properties, such as preference for foveal stimuli (Hasson et al., 2002) or

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Topography of peak activations to words and music

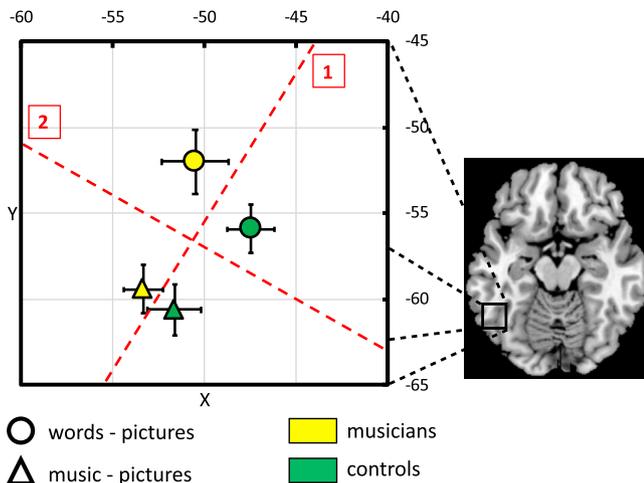


Fig. 1. Topography of activations to words and music. Mean MNI X and Y coordinates of individual peaks of activation for music (triangles) and words (circles), in controls (green) and musicians (yellow). Individual peaks were identified by comparison to pictures of faces, houses and tools. Activations for music were posterior and lateral to activations for words, and did not differ between groups. Error bars represent standard error of the mean. The first two axes of the principal component analyses are shown in red. Figure adapted from Mongelli et al. (2017) but adjusted to the current sample.

sensitivity to line junctions (Szwed et al., 2011), but also because it shows preferential anatomical and functional connectivity with remote language areas (Bouhali et al., 2014; Stevens et al., 2017), even before reading acquisition (Li et al., 2019; Saygin et al., 2016). Reciprocally, reading acquisition reinforces the anatomical connections between the VWFA and perisylvian language areas. Thus, in adults, white-matter fractional anisotropy (FA) increases in proportion to the level of literacy in the posterior segment of the left arcuate fasciculus (Thiebaut de Schotten et al., 2012). Similarly in children, active reading instruction in struggling readers results in increased FA in the left arcuate and inferior longitudinal fasciculi (Huber et al., 2018).

Word reading should not be the only case in which expertise in using visual symbols is both determined by, and has an impact on the connectivity between the visual system and distant areas. Thus, in the vicinity of the VWFA, areas have been identified that are in charge of processing numbers and digits (Amalric and Dehaene, 2016; Shum et al., 2013; Yeo et al., 2017), or musical notations (Mongelli et al., 2017; Stewart et al., 2003; Wong and Gauthier, 2010). It is currently unknown whether expertise in number or music reading has such bidirectional causal links with the anatomical connectivity between the visual cortex and distant regions involved in numerical or musical processing.

Here, we study the anatomical projections from VOT cortex towards distant regions involved in music and language processing. In previous study, Mongelli et al. (2017) investigated music and word reading with fMRI, in professional musicians and in a group of matched non-musicians. They observed that the VOT regions that subtend music and word processing are overlapping but distinct: activation to musical scores peaked posterior and lateral to word-related activations, irrespective of musical expertise (see Fig. 1 and Table 1 for a replication on the current sample). Moreover, in musicians relative to controls, music-related activations were more extended, while word-reading peaks were more anterior and lateral, possibly reflecting competition between the two domains for cortical space (Dehaene et al., 2010).

In the same subjects as Mongelli et al. (2017), we delineate the white matter tracts stemming from VOT activations to words and to music, compare those tracts, and assess the impact of musical expertise on their topography, volume, and fractional anisotropy.

Table 1

Mean location of individual peaks for music and word functional activations, for musicians (first row) and non-musicians (second row) (\pm standard error of the mean). These peaks were obtained respectively by the contrast of one-bar piano musical scores, and word pairs, to the mean of faces, tools, and houses.

	Mean coordinates of music peaks	Mean coordinates of word peaks
Musicians	-53 -59 -9 \pm (1 1.4 1.3)	-50 -52 -12 \pm (1.8 1.8 1.7)
Non-musicians	-52 -60 -9 \pm (1.5 1.5 1.3)	-47 -56 -13 \pm (1.3 1.4 1)

We formulated two predictions. First, we assumed that the VOT region subtending music reading is selected, among other causes, by virtue of its preexisting connections with distant areas involved in music processing. We therefore predicted that this region should show a connectivity pattern distinct from that of the neighboring word selective region. Moreover, if this pattern is causally involved in cortical specialization for music, it should be present even in the absence of musical expertise.

Second, we predicted that musical literacy should modulate the topography or structure of music projections, since expertise in a given domain typically modifies the properties of related fascicles (Scherf et al., 2014; Thiebaut de Schotten et al., 2012). However, demonstrating such an impact is a priori challenging, as projections involved in music and in word reading should not differ much in either their origin or their targets. Indeed, the word- and music-related peaks used as tracking seeds are adjacent (Mongelli et al., 2017) and the brain areas subtending language and music are known to be overlapping (Koelsch, 2009; Peretz et al., 2015).

2. Methods

2.1. Participants

Twenty-one adult musicians and 23 control non-musicians were analyzed in the initial functional study by Mongelli et al. (2017). The experiments received ethical approval by the institutional review board of the INSERM (protocol C13-41). All participants gave written informed consent and received monetary compensation for their participation in the study. As two musicians did not have time to complete the diffusion acquisition, the final sample included in the current study consisted in 19 musicians and 23 controls. Both groups were matched in gender (musicians: 9 females/10 males; controls: 11F/12M; $\chi^2(1) = 0, p = 1$) and age (musicians: 31.5 ± 8.7 years of age; controls: 29.9 ± 10.4 years; Wilcoxon rank sum test $W = 272, p = .18$). All participants were right-handed according to the Edinburgh inventory (Oldfield, 1971). Musicians were either professional musicians or masters' students at one of the most prestigious music schools in France (CNSM, *Conservatoire National Supérieur de Musique et de Danse de Paris*). They varied in their type of musical practice, but they started learning to read both words and music around the same age (words: 4.8 ± 1.3 years; music: 5.8 ± 3 years; Wilcoxon signed rank test: $V = 115.5, p = .19$). Musicians and controls also learned to read words at the same age (controls: 5.2 ± 0.9 years; Wilcoxon rank sum test $W = 160.5, p = .55$).

2.2. Functional paradigm

In order to localize category-specific regions in the ventral occipito-temporal cortex, participants performed a repetition detection task in the MRI, while they were presented with five categories of black and white stimuli: faces, tools, houses, pairs of words, and piano music scores (1 bar). Stimuli were blocked by category. Each block comprised 8 trials of 1s (600 ms of presentation and 400 ms of blank screen) and was followed by a period of rest (7.8s). There were 6 blocks for each category. Repetitions occurred for 20% of trials (50% of blocks had 1 repetition, 33% had 2 and 17% had 3). Full details on the stimuli and experimental settings can be found in Mongelli et al. (2017).

2.3. fMRI acquisition and analysis

We used a 3-Tesla MRI (Siemens Trio) with a 32-channel head coil, and a multiband echo-planar imaging sequence sensitive to brain oxygen-level-dependent (BOLD) contrast (54 contiguous axial slices, 2.5 mm isotropic voxels, in-plane matrix = 80×80 ; TR = 1160 ms; angle = 62° , TE = 25 ms). 420 vol were acquired. The first four volumes were discarded to reach equilibrium. Five additional BOLD volumes with reverse phase encoding direction were also acquired. T1-weighted MPRAGE images were acquired with 1 mm isotropic resolution (TR = 2300 ms, TE = 2.18 ms, flip angle = 9° , matrix = $176 \times 256 \times 256$).

Functional images were realigned, treated with the FSL “topup” toolbox in order to correct EPI distortions due to B0 field inhomogeneity, normalized to the standard MNI brain space and spatially smoothed with an isotropic Gaussian filter (3 mm FWHM). A two-level analysis was then implemented in SPM8 software (<http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>).

For each participant, data were high-pass filtered and modelled by regressors obtained by convolution of the five experimental conditions plus the button presses with the canonical SPM hemodynamic response function. Individual contrast images for the five types of stimuli minus rest were obtained at the first level and used to derive individual activation maps and peaks (see the next paragraph). To further take into account between-subject differences in functional anatomy, these individual contrast maps were smoothed with an additional isotropic Gaussian filter (2 mm FWHM) and entered into a second-level whole-brain ANOVA with subjects as random factor, stimulus category as within-subject factor, and musical status as between-subject factor. This two-step smoothing approach was chosen as a compromise between more localized activation peaks at the individual level, as described below, (while still applying smoothing to increase signal-to-noise ratio) and inter-individual overlap of activations at the second level of analysis.

2.4. Extraction of functional peaks for music and words

We used the same individual peaks as identified in [Mongelli et al. \(2017\)](#). Specifically, individual peaks of activation to words and music were extracted within a region of interest (ROI) centered around an unbiased group-level activation peak common to both types of stimuli. This peak was identified by contrasting words plus music minus the other three categories, pooling controls and musicians (MNI -54 -55 -15, $Z > 8$). We then defined a left occipito-temporal ROI, by taking an anatomical mask including the inferior occipital, inferior temporal, and fusiform gyri ([Tzourio-Mazoyer et al., 2002](#)), and restricting this mask from 15 mm anterior to 15 mm posterior to the unbiased activation peak (i.e., MNI $y = -40$ to $y = -70$). In each subject, we searched this ROI for the voxel most strongly activated (i.e., with the highest t value) by music minus all other stimuli (except words), and by words minus all other stimuli (except music).

The mean positions of these peaks are reported in [Table 1](#) and [Fig. 1](#). The differences in peak location observed by [Mongelli et al. \(2017\)](#) were replicated in this slightly smaller sub-sample (19 musicians/23 controls, instead of 21 musicians/23 controls). Namely, using a rotation of the MNI coordinate axes using principal component analysis (since MNI coordinate axes are not independent due to the 3D slant of temporal cortex), we observed that (1) along the first axis accounting for 60% of variance (see [Fig. 1](#)), there was a significant difference in peak location between word and music peaks ($F(1,40) = 20.0$; $p = 10^{-4}$) by which word peaks were more antero-mesial than music peaks, while no significant group effect or group \times peak interaction were observed ($p > 0.24$); (2) along the second axis accounting for 27% of variance, activation peaks were significantly more anterolateral for musicians than for controls ($F(1,40) = 5.5$, $p = .024$). This effect of expertise along the second axis was strong for words ($F(1,40) = 6.5$, $p = .015$), and non-significant for music ($p = 0.31$), although the interaction was not significant ($p = .35$). There were no other significant differences or

interactions.

2.5. DWI acquisition and preprocessing

High-angular-resolution DWI data was acquired in 60 uniformly distributed directions with a b-value of 1500 s/mm^2 . Six volumes with no diffusion gradient ($b = 0 \text{ s/mm}^2$) were acquired along the session. We acquired 70 near-axial slices at an isotropic resolution of $2 \times 2 \times 2 \text{ mm}^3$ (in-plane matrix 110×110) with a posterior-anterior phase of acquisition and whole-head coverage. In order to reduce artifacts, the acquisition was peripherally-gated to the cardiac cycle ([Jones et al., 2002](#)) with an echo time of TE = 85 ms. and a TR equivalent to 24 R-R intervals. Diffusion data were pre-processed using ExploreDTI ([Leemans et al., 2009](#)). After correction for eddy current distortions and subject motion, the diffusion tensor model was estimated using a nonlinear least-squares method in order to estimate fractional anisotropy (FA) maps. Realigned diffusion volumes were then processed in FSL for probabilistic tractography. Local diffusion directions were estimated with a q-ball model estimating constant solid angle orientation diffusion functions (CSA ODFs), using the qboot command ([Aganj et al., 2010](#)).

2.6. Tractography

Individual functional peaks for music- and word-specific activations were transformed back from MNI space into native space, and then transformed into one voxel in diffusion space using a rigid-body transformation. Each peak voxel in diffusion space was then dilated into a one-voxel radius sphere (6 mm diameter) that served as a seed for probabilistic tractography. This procedure was used to ensure that all seeds had the same size, so that there would be no bias in the tractography for the comparison between groups and peak types. Despite the close proximity of music and word peaks, individual music and word seeds only overlapped in 3 participants (1 control and 2 musicians, with 2 out of 7 voxels overlapping in each participant) with no statistical difference between group (permutation test $p = 0.45$).

Probabilistic tractography was run in FSL using the *probtrackx2* command, propagating streamlines from each seed in one direction within the brain mask, and using distance correction (to counteract the drop in connectivity distribution with distance from the seed). Connectivity distribution maps were then normalized to the MNI152 template brain (at 2 mm resolution) using diffeomorphic transformations with the Advanced Normalization Tools (<http://www.picsl.upenn.edu/ANTS/>), and smoothed with a 4 mm-FWHM Gaussian kernel. Statistical differences in connectivity were finally analyzed using permutation testing with the *randomise* function, with 5,000 permutations and threshold-free cluster enhancement (TFCE, [Smith and Nichols, 2009](#)). Age and sex were entered as covariates in all models, as age has an adverse effect on connectivity (e.g. [Rojkova et al., 2016](#)), and gender effects have been reported notably in the arcuate fasciculus ([Catani et al., 2007](#)) and in the cortical structure of the VWFA ([Altarelli et al., 2013](#); [Simon et al., 2013](#)). In addition, when comparing the connectivity of music and reading tracts, individual distance between the two peaks was added as a covariate, as seeds closer together have more similar tracts. Figures only report results within the left hemisphere, as no significant difference in connectivity was observed between peaks or groups in the right hemisphere.

2.7. Tract properties and similarities

The volume and fractional anisotropy (FA) of white matter tracts may be correlated to cognitive skills and expertise ([Iaria et al., 2008](#); [Luders et al., 2012](#); [Oechslin et al., 2010](#); [Thiebaut de Schotten et al., 2012](#); [Zatorre et al., 2012](#)). Hence, in order to investigate the impact of expertise on those variables, we computed for each participant and each tract (i) the mean FA value across all voxels in the tract, and (ii) the total number of voxels in the tract (computed in MNI space to ensure

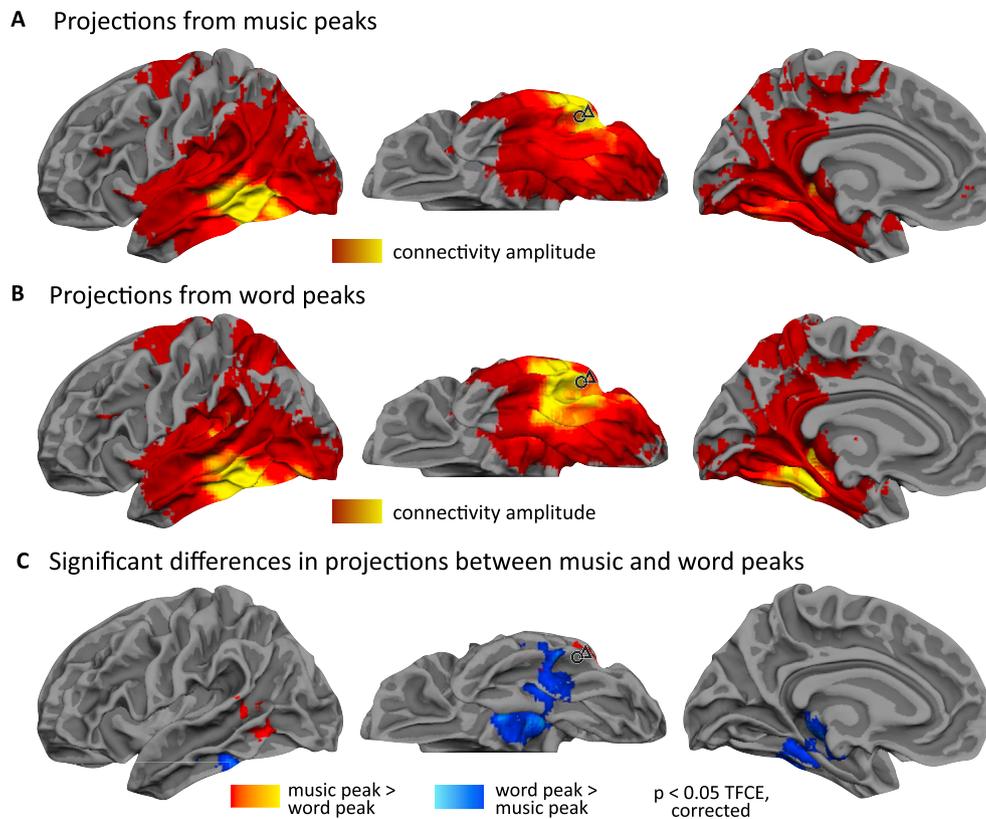


Fig. 2. Average projections obtained by probabilistic tractography from individual music peaks (A) and word peaks (B), and their statistically significant differences (C), displayed on the white-matter surface of the left hemisphere, pooling musicians and control participants. Triangles and circles (central panel) indicate the average location of music and word peaks, respectively.

comparability of these numbers between participants). The effects of group, peak (word vs. music), and of their interaction on FA and volumes were assessed by stepwise mixed linear models, with subjects as a random factor and gender, age and distance between peaks as confound variables. These models were implemented in R software using the ‘lme4’ package (Bates et al., 2012). The effect of interaction of group x peak was obtained by likelihood ratio tests of the full model against the model without the interaction term. Main effects of group and peak were each assessed by comparing models with both main effects against models removing only the effect in question.

Moreover, to assess the spatial similarity between music and word activations, we computed the cross-correlation between the functional contrast maps of words and of music, compared to the mean of faces, tools and houses, within a probabilistic atlas of grey matter mask (atlas provided in FSL thresholded at 50% likelihood). Only positive contrast values were retained, so as to compare the similarity between activations more specific to words and music. We also assessed the spatial similarity between the projections of music and word tracts. To do so, the cross-correlation between the endpoints of both tracts in each subject was computed within the same grey matter mask. Cross-correlation values both of functional networks and tracts were Fisher-transformed, and then compared between groups. Because the z-transformed tract cross-correlation values were largely skewed, permutation-based multiple linear regressions were applied using the ‘lmPerm’ package in R (Wheeler, 2010), with distance, age and gender as covariates.

3. Results

3.1. Connectivity of music and word peaks

Probabilistic connectivity maps were obtained by tractography from individual functional peaks for reading musical notation and printed

word pairs (hereafter music and word tracts). Pooling musicians and controls together, the anatomical connections of word and music seeds were very similar on inspection. They spanned almost all the temporal lobe, as well as a large extent of insular, parietal and motor cortices (Fig. 2A and B). Still, the connectivity patterns of word and music peaks differed significantly (Fig. 2C) based on a permutation test controlling for the distance between the peaks. Word peaks had preferential connections towards more anterior aspects of the ventral temporal lobe spanning from the inferior temporal gyrus (ITG) to the hippocampus. Music peaks showed stronger dorsal connections to the posterior inferior temporal sulcus (pITS), superior temporal sulcus (pSTS), and superior temporal gyrus (pSTG).

We then investigated the impact of musical expertise on the topography of projections from word and music seeds, and on properties of the corresponding fiber tracts.

3.2. Effects of musical expertise on the topography of projections from word and music peaks

We expected that in musicians, music peaks should show increased connections with distant regions involved in music processing. However, such increase may be difficult to identify, depending on the extent to which target music regions are distinct from language areas. Indeed, the more both are overlapping, the more likely it is that subtle rerouting of the connections from the music peak would escape detection.

In each group, the comparison of word minus music connectivity maps showed stronger connections from word as compared to music peaks, in the ventral temporal area previously identified in the pooled analysis (Fig. 3 A and B). The difference was located in the left hippocampus in controls (around MNI -22 -28 -10), while it seemed more posterior and lateral in musicians (OTS, around MNI -46 -42 -24), just anterior to the word peaks. There was no region more connected to music

Effect of musical expertise on music and word tracts

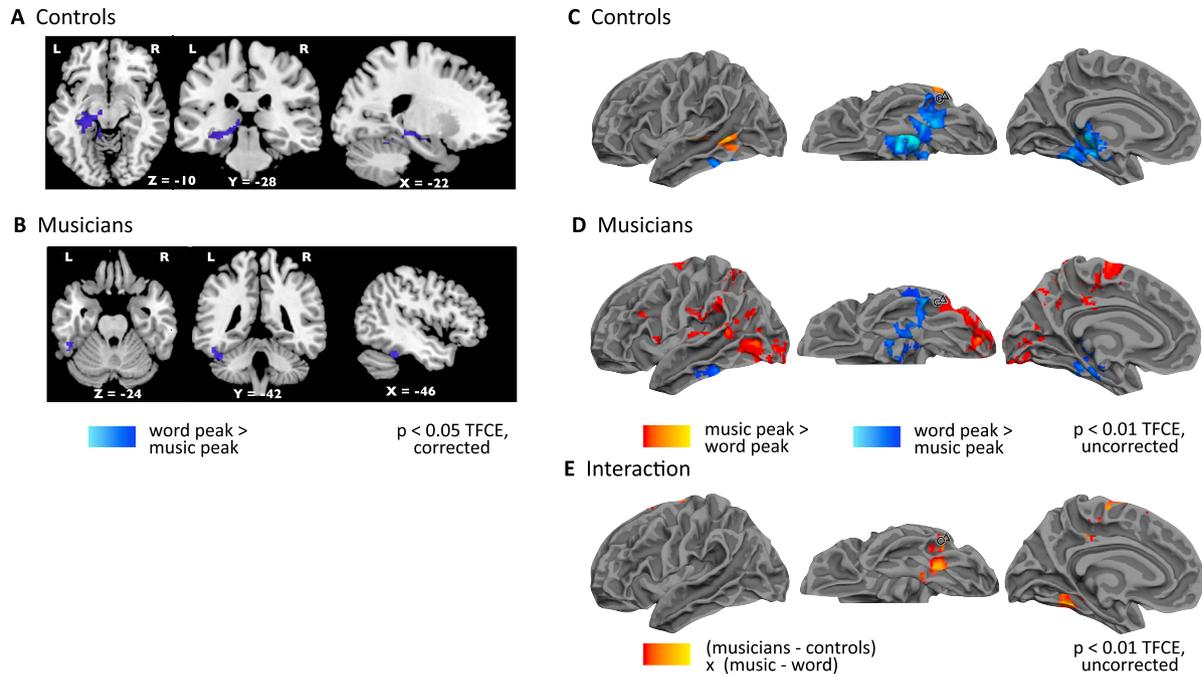


Fig. 3. Effects of musical expertise on the connectivity of word and music peaks. (A–B) Comparison of music and word tracts in controls (A) and in musicians (B), at a voxelwise threshold of $p < 0.05$ TFCE FWE corrected, showing an advantage for words over music (blue). (C–D) The same contrasts displayed on the white matter surface, at a voxelwise threshold of $p < 0.01$ TFCE uncorrected. Regions in orange show an advantage for connectivity to music peaks over word peaks. (E) Interaction of group \times peak, at $p < 0.01$ TFCE uncorrected. Triangles and circles (central panel in C–E) show the average location of individual music and word peaks, respectively.

than to word peaks in either the control or in the musician group, likely due to a decrease in power when splitting the data into two groups, and to the close proximity of music and word seeds in VOT. There was no significant group \times peak interaction.

Analyses with uncorrected threshold. This first analysis thus showed no significant correlate of musical expertise. When lowering the statistical threshold to $p < 0.01$ uncorrected for exploratory purposes, both musicians and controls showed a higher connectivity for music than for word peaks in the posterior lateral temporal lobe, as in the pooled analysis. At this uncorrected threshold, it is interesting to observe that musicians showed stronger connectivity to music than to word peaks far beyond the ventral temporal lobe, including ventral and lateral occipital cortex, posterior superior temporal cortex (notably Heschl’s gyrus), the inferior parietal lobule and intraparietal sulcus, the insula, the inferior and middle frontal gyri and the premotor cortex (Fig. 3 C and D). An interaction of group \times peak was found in the ventral pathway (ITG, OTS, fusiform and lingual gyri, between $y = -60$ and $y = -40$), as well as in the premotor cortex (Fig. 3E). Note that this interaction is not an artefact

due to the difference between groups in the location of word seeds. Indeed, in an analysis restricted to music peaks, whose location does not differ between groups, we observed that this same ventral area tended to be more connected in musicians than in controls (see Supplementary Fig. 1A).

In summary, the projections from word and music peaks showed trends of sensitivity to musical expertise. We then addressed the same issue using other indices of anatomical connectivity.

3.3. Effects of musical expertise on the structure of word and music tracts

We assessed our prediction of an impact of musical expertise on music tracts using overall tract FA and volumes, which respectively reflect the micro- and macrostructure of tracts. Tract FA showed a main effect of group (likelihood ratio test on hierarchical linear mixed models: $\chi^2(1) = 10.49$, $p = 0.0012$; Fig. 4A), with higher FA in musicians, but no group \times peak interaction and no main effect of peak ($p > 0.83$). Tract volumes showed an interaction of peak by group ($\chi^2(1) = 4.02$, $p = 0.045$;

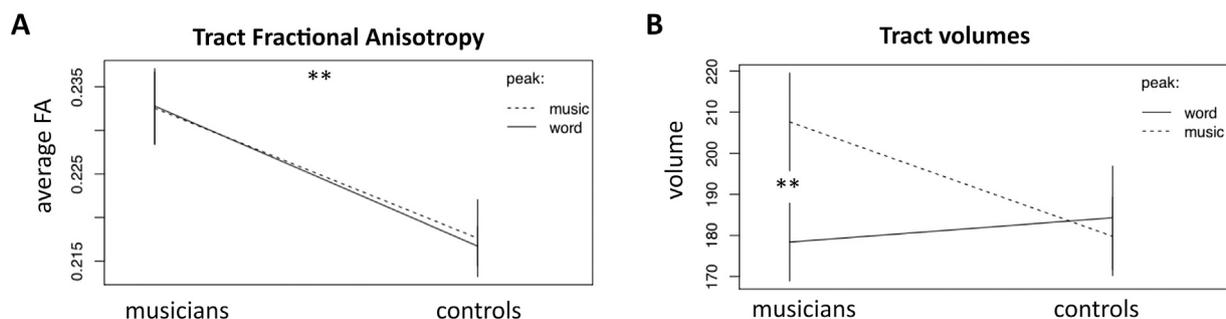
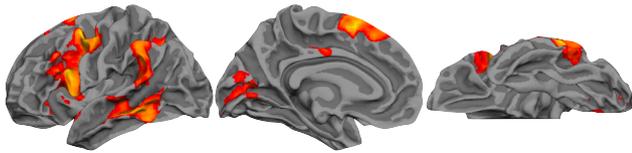


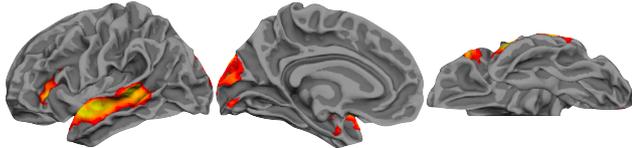
Fig. 4. Average Fractional Anisotropy (A) and total volume (B) of tracts seeded from the music and word peaks, in musicians and controls. (Group means \pm standard errors of the mean are represented. **: $p < 0.01$.)

Word and music reading networks in musicians

Overlap of word and music networks



Word reading > Music reading



Music reading > Word reading

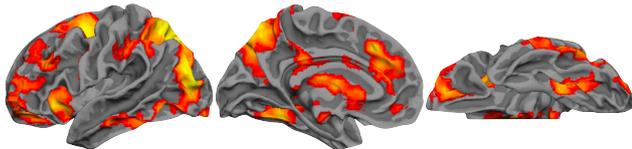


Fig. 5. Word and music reading activations in musicians, from data in Mongelli et al. (2017). *Top:* Overlap of word and music reading networks (conjunction of words – pictures and music – pictures). *Middle:* Regions more activated by words than by music. *Bottom:* Regions more activated by music than by words. ($p < 0.001$ voxelwise, cluster FWE $p < 0.05$).

Fig. 4B), with no main effect of peak or group ($p > 0.2$). This significant interaction was driven by larger music than reading tracts in musicians ($\chi^2(1) = 8.92$, $p = 0.003$), but not in controls ($p = 0.73$).

3.4. Effects of musical expertise on tract similarity

As mentioned before, the similarity of the whole-brain language and music networks may conceal the impact of musical expertise on the tracts seeded from the visual music peak. Indeed, in musicians, there is a major topographical overlap of activations related to language and music (see Peretz et al., 2015 and Koelsch, 2009 for reviews), a result that was replicated here (Fig. 5). This yields the prediction that musical expertise should induce an increased similarity not only between the functional networks, but also between the fiber tracts associated to music and to word reading.

We first assessed the topographical similarity between the functional activations induced by music and words, by computing the spatial cross-correlation of word- and music-specific activation maps. The functional networks for word and music reading were more similar in musicians than in controls ($p = 0.0008$, using a permutation-based multiple linear regression accounting for age, gender and distance between seeds). We then computed the spatial cross-correlation between the cortical projections of word and music white matter tracts at the individual level. Similarly to the functional activations, projections from word and music seeds were more similar in musicians than in controls ($p = 0.04$, using a permutation-based multiple linear regression accounting for the same confound variables). There was no significant within-group correlation between the similarity in functional activations, and the similarity of tract projections. Higher similarity in functional activations was only marginally correlated to larger similarity in tracts' projections in controls ($p = 0.09$), but not in musicians ($p = 0.24$).

4. Discussion

Musicians show subregions of their VOT cortex more specific to word or to music reading. Using diffusion MRI, we investigated the anatomical

connectivity of those two VOT regions in adult non-musicians and in professional musicians, addressing two main questions. First, does connectivity differ between the two VOT regions irrespective of musical expertise, and, second, is musical expertise associated with changes in connectivity?

4.1. Overall topography of projections

Irrespective of expertise, word and music peaks were both found to be connected to the temporal lobe at large, as well as to a large extent of insular, parietal and motor cortices (Fig. 2A and B). Notably, these regions encompassed perisylvian language areas such as the superior temporal gyrus, the supramarginal gyrus and the inferior frontal cortex, which belong both to the word reading network (Cattinelli et al., 2013; Martin et al., 2015; Taylor et al., 2013), and to the network of regions activated during music processing (Koelsch, 2005; Koelsch et al., 2005; Minati et al., 2008; Fig. 5). These projections were relatively similar to those previously reported for the VWFA, and included the endpoints of the major white-matter fascicles which connect this region: the arcuate fasciculus, the vertical occipital fasciculus, the inferior longitudinal fasciculus and the inferior fronto-occipital fasciculus (Bouhali et al., 2014; Yeatman et al., 2013). Moreover, we observed projections towards superior parietal and motor cortex, which were not prominent in previous reports. Such additions, compared to the reports of Yeatman et al. (2013) and Bouhali et al. (2014), may be linked to differences in methodological approaches, including the use of probabilistic vs. deterministic tractography, the application here of an additional correction for the distance bias by weighting connections according to their distance to the seed, or the use of number of streamlines vs. percent overlap of binarized tracts as a measure of connectivity.

4.2. Differences in topography between word and music tracts

Functional specialization is thought to result from “connectivity fingerprints”, that is, from the pattern of long-distance anatomical connectivity (Mars et al., 2018; Passingham et al., 2002), partly accounting for category-specialization in the VOT cortex (Bouhali et al., 2014; Mahon and Caramazza, 2011; Osher et al., 2015; Saygin et al., 2012; Stevens et al., 2017). Hence, our first prediction was that VOT regions specialized in word and music reading should differ in their connectivity pattern. As those connectivity biases should predate perceptual and cognitive experience (Li et al., 2019; Saygin et al., 2016), at least some differences should exist regardless of music practice. Averaging both groups, we indeed observed that connectivity patterns differed significantly between music and word peaks. Music peaks were more connected to the posterior lateral temporal lobe, including the pITS, pSTS and pSTG. Conversely, word peaks were more connected to VOT regions anterior to the VWFA, spanning from the ITG laterally, to the fusiform, parahippocampal and hippocampal gyri medially (Fig. 2C).

In the participants of the present study, the posterior lateral temporal lobe was recruited in musicians during both music and word reading (Fig. 5). Accordingly, this region is known to belong to the usual reading network, with an involvement in processing word phonology and semantics (Graves et al., 2010; Price, 2012; Visser et al., 2012), but it has also been shown to participate in music processing. Thus, intracranial cortical stimulation to the left posterior STG and MTG in musicians cause music reading arrest or hesitations (Roux et al., 2007), and several cases of alexia for music have been reported following lesions to the left temporo-parietal cortex (see Hébert and Cuddy, 2006 for a review). Selective activations for musical notation have also been reported to correlate with an index of perceptual fluency with notes in the pSTS and PMTG (Wong and Gauthier, 2010). Beyond studies of music reading, both lesion (Di Pietro et al., 2004; Stewart et al., 2006) and imaging (Koelsch, 2005) studies support an important role of the posterior part of the lateral temporal cortex in auditory music processing, with notably an involvement of the PMTG in musical semantics (Koelsch, 2005). Such

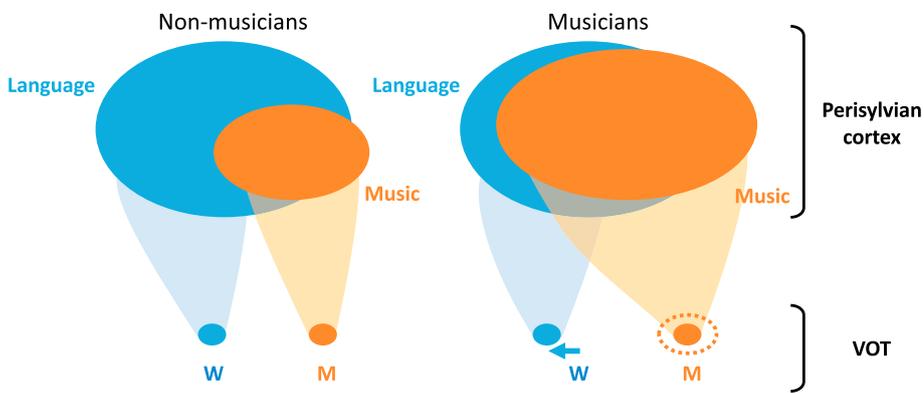


Fig. 6. Schematic depiction of the relationships between the networks for word (blue) and music (orange) reading, in musicians (right) and non-musicians (left). In musical experts, the functional music network is larger and more similar to the language network, while anatomical connections from the VOT music-selective region (M) are larger, and more overlapping with connections from the word-selective region (W). As shown in [Mongelli et al. \(2017\)](#) in musicians, the M region is larger (orange dotted line) and the W region is slightly displaced (blue arrow).

converging evidence indicates that the strong anatomical connectivity of the VOT music peak to the posterior lateral temporal lobe may provide a privileged link between vision and a core component of music processing.

The anterior ventral temporal region with stronger connections to the VOT word peak is involved in lexical and semantic access from written words ([Binder et al., 2009](#); [Binder and Desai, 2011](#); [Price, 2012](#); [Purcell et al., 2014](#); [Wilson et al., 2012](#)), and has been characterized as a multimodal semantic processing hub ([Visser et al., 2012](#)). It is noteworthy that the anterior temporal region we identified extends mesially to the hippocampal gyrus. [Liuzzi et al. \(2019\)](#) reviewed a rich corpus of imaging and neuropsychological evidence, concluding that the mesial temporal lobe, particularly the perirhinal cortex, plays a specific role in reading by binding concrete written words with the visual representation of their referent object. The fact that, contrarily to many words, written music does not refer to concrete objects, may thus explain the stronger connection of the mesial temporal lobe to the word peak than to the music peak.

In summary, supporting our first prediction, the differences in the connectivity of the two VOT regions of interest are congruent with their functional specialization for music and words ([Hannagan et al., 2015](#); [Mahon and Caramazza, 2011](#); [Osher et al., 2015](#)). Another question is whether those differences may *explain* functional specialization in the VOT. Although answering this question is beyond our current scope, we predicted that if the connections of the music and word reading regions were causally involved in their functional specialization, differences should exist even in non-musicians. Generally, we did observe the same pattern of dissociation between the projections of word and music tracts in non-musicians alone as when pooling all participants together ([Fig. 3A and C](#)). Yet, these differences were best observed at a lenient statistical threshold, likely due to halving the sample size, and to the close proximity of word and music peaks.

4.3. Effects of musical expertise

Our second prediction was that intense life-long musical practice would modify the connectivity of VOT regions for reading music. Actually, musical expertise may conceivably also have an impact on the connectivity of the VOT word region, as it has an impact on its precise location ([Mongelli et al., 2017](#)). Therefore, a more accurate formulation of our prediction is that musical expertise should have a different impact on the connectivity of the word and music regions, as revealed by expertise \times region interactions.

4.4. Effects of musical expertise on tract topography

The first set of analyses, based on the topography of projections, yielded results in this direction but somewhat disappointing, as there was no significant interaction of expertise \times region. Still, at an uncorrected threshold, musicians showed a strikingly broader network of regions

more connected to the music than to the word peak ([Fig. 3D](#)). These regions include areas activated both by word and music reading in musicians like the IFG, supramarginal gyrus and pSTG/pSTS ([Fig. 5](#)), but also a number of regions more activated by music than word reading (superior parietal lobule, premotor cortex, and ventral and lateral occipital cortex). As music is a multimodal complex function, musical symbols need to be mapped to auditory, motor, syntactic, harmonic and prosodic representations ([Behmer and Jantzen, 2011](#); [Delogu et al., 2019](#); [Hébert and Cuddy, 2006](#); [Sloboda, 1984](#); [Wolf, 1976](#); [Wong and Gauthier, 2010](#)), which may be facilitated by such broad connections.

In principle, the exact connections supporting musical reading may vary between the types of musical practices and their specific demands (e.g. between singers, pianists and orchestra directors). As the current study included musicians across the board, the non-significant results observed here may thus also be due to the averaging out of these specific demands. Yet, the inclusion of a varied population of musicians is also a strength as it makes the results of the study more generalizable. Furthermore, unlike the motor representations specific to particular instruments, the core of music reading (such as mapping the symbols to auditory, syntactic, harmonic and prosodic representations) is common to all types of musical practice, and all musicians receive a common and intensive training to music reading.

4.5. Effects of musical expertise on tract properties (FA and volume)

A second set of analyses was based not on topography, but on micro- and macro-structural properties of white matter tracts: mean FA and tract volumes ([Saygin et al., 2013](#); [Scherf et al., 2014](#); [Silani et al., 2005](#); [Zatorre et al., 2012](#)). While FA only showed a main difference between musicians and non-musicians, tract volumes showed the predicted expertise \times region interaction.

Increased fractional anisotropy in musicians has been reported along many large white-matter tracts throughout the brain, including the corpus callosum ([Bengtsson et al., 2005](#); [Habibi et al., 2018](#); [Schmithorst and Wilke, 2002](#); [Steele et al., 2013](#)), the internal capsule ([Bengtsson et al., 2005](#)), the left and right arcuate fasciculi ([Halwani et al., 2011](#)) and the right and left inferior longitudinal fasciculi ([Schmithorst and Wilke, 2002](#)), although lower FA values have also been reported in the corticospinal tracts and internal capsule ([Imfeld et al., 2009](#); [Schmithorst and Wilke, 2002](#)). Hence, it is not surprising to observe increased FA in both music and word tracts with music expertise.

Musical training is known to improve word reading skills ([Flaugnacco et al., 2015](#); [Gordon et al., 2015](#); [Moreno et al., 2009](#); [Overy, 2003](#)). While this impact could be mediated by several factors such as effects of music practice on phonological awareness ([Gordon et al., 2015](#)), changes in brain structure, like this increase in FA, in domain-general regions or in word-reading tracts specifically could participate in the beneficial impact of music practice onto reading skills.

It is worth noting that beyond the case of word reading, musical training and even music listening (in the context of musical therapy or

not) have been associated with many cognitive benefits in both development and aging (Barrett et al., 2013; Criscuolo et al., 2019; Herholz and Zatorre, 2012; Hyde et al., 2009; Jäncke, 2009; Johansson, 2011; Moreno et al., 2011; Schlaug et al., 2005; Sluming et al., 2007, 2002; but see also Sala and Gobet, 2020, 2017 for meta-analyses with small to null effects of musical training on cognitive development). White-matter plasticity induced by music practice or music listening, possibly supported by increased synchronization during music listening (Alluri et al., 2017; King et al., 2019; Wu et al., 2019), could be a potential mechanism for cognitive transfer to general domains and neuro-protective effects in aging (Elmer and Jäncke, 2018; Kühnis et al., 2014; Strong and Mast, 2019).

The increase in tract volume between music and word tracts was instead specific to musical experts. Importantly, this increase in the volume of music tracts was not confounded by differences in seed locations, since the location of music peaks did not differ between musicians and non-musicians. It was not confounded by differences in the tracts' microstructure either, since the overall difference in FA between musicians and non-musicians affected equally the music and the word tracts. Finally, Mongelli et al. (2017) showed that activation of this region during music reading was larger in musicians than in non-musicians, but this cannot account for the difference in the volume of fiber tracts, as the seeds that we used for tracking all had the same volume.

The increase in the volume of music tracts in musicians is coherent with the broader set of regions preferentially connected to music peaks in musicians than in non-musicians – although the latter finding was only a statistical trend (Fig. 3 C and D). Accordingly, this volume increase results from stronger connectivity to many distant regions overall, rather than from localized changes in tract topography.

4.6. Effects of musical expertise on the similarity between word and music networks

As suggested in the introduction, finding differences between the connections for word and music reading is particularly challenging, not only due to the proximity of the VOT seeds, but also to the similarity between the brain networks subtending language and music processing (Besson et al., 2011; Peretz et al., 2015). Indeed, there is evidence that language and music share brain resources at several levels, ranging from sound processing (Besson et al., 2011) and motor control (Hickok et al., 2003), to the representation of hierarchical structures (Chiang et al., 2018; Kunert et al., 2015), emotions (Ilie and Thompson, 2006; Koelsch, 2005), and memory (Groussard et al., 2010). In a novel analysis of data from Mongelli et al. (2017), we found a highly significant increase in the similarity of functional activations for word and for music reading, in musicians as compared to non-musicians. This increase in similarity with musical expertise likely reflects the richer development of music representations in musicians than in non-musicians, similarly to the mechanisms at play in the case of second language acquisition (Abutalebi and Green, 2007; Berken et al., 2015; Cao et al., 2013; Kim et al., 1997; Perani et al., 1998) or of motor learning and action representations (Beilock et al., 2008; Calvo-Merino et al., 2006, 2004). The same logic predicts that the similarity of connectivity patterns for music and words should also increase with musical expertise, which is precisely what we found.

It is noteworthy that the effects of expertise were quite parallel between functional and anatomical imaging, although the two datasets and methods were fully independent. In musicians, the music-specific activation network was both wider (Mongelli et al., 2017, Fig. 2A) and more similar to the language network than in controls. Likewise, in musicians, the tract seeded from the VOT music region was both larger and more similar to the tract seeded from the VOT word region, than in control subjects (Fig. 6).

5. Conclusion

We found that the VOT region for music reading has preferential

connections with the posterior lateral temporal cortex, while the region for word reading is better connected with anterior temporal regions involved in lexical access (Fig. 2). This pattern prevails in both musicians and controls, indicating that it preexists the acquisition of musical expertise. Those distinct connectivity fingerprints could interact with different innate perceptual biases (Grill-Spector and Weiner, 2014; Srihasam et al., 2014), leading to the “recycling” of those patches of cortex either for music or for word reading (Hannagan et al., 2015). It is beyond the scope of this study to disentangle the relative role of those two constraints, which would be best addressed through longitudinal studies in children learning to read music, similarly to investigations of reading acquisition (Dehaene-Lambertz et al., 2018; Saygin et al., 2016). Moreover, we showed that in musical experts, the white matter tracts connecting the VOT music region are larger than in non-musicians, and also more similar to the tracts connecting the VOT word region. Thus, as in the case of word reading (Thiebaut de Schotten et al., 2012), anatomical connections can both influence specialization for music and, reciprocally, be enhanced by the acquisition of novel musical expertise. This exemplifies the bidirectional links between brain structure and cultural inventions: while cultural inventions flourish under the constraints of innate brain organization, they also in return induce plastic changes in brain anatomy.

CRediT authorship contribution statement

Florence Bouhali: Conceptualization, Methodology, Software, Validation, Formal analysis, Data curation, Writing - original draft, Visualization, Project administration. **Valeria Mongelli:** Software, Investigation, Data curation, Writing - review & editing. **Michel Thiebaut de Schotten:** Conceptualization, Methodology, Writing - review & editing. **Laurent Cohen:** Conceptualization, Methodology, Resources, Writing - review & editing, Visualization, Supervision, Project administration, Funding acquisition.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuroimage.2020.116666>.

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