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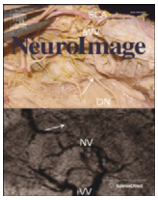

Neuroplasticity of semantic representations for musical instruments in professional musicians

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ABSTRACT

Professional musicians constitute a model par excellence for understanding experience-dependent plasticity in the human brain, particularly in the auditory domain. Their intensive sensorimotor experience with musical instruments has been shown to entail plastic brain alterations in cortical perceptual and motor maps. It remains an important question whether this neuroplasticity might extend beyond basic perceptual and motor functions and even shape higher-level conceptualizations by which we conceive our physical and social world. Here we show using functional magnetic resonance imaging (fMRI) that conceptual processing of visually presented musical instruments activates auditory association cortex encompassing right posterior superior temporal gyrus, as well as adjacent areas in the superior temporal sulcus and the upper part of middle temporal gyrus (pSTG/MTG) only in musicians, but not in musical laypersons. These areas in and adjacent to auditory association cortex were not only recruited by conceptual processing of musical instruments during visual object recognition, but also by auditory perception of real sounds. Hence, the unique intensive experience of musicians with musical instruments establishes a link between auditory perceptual and conceptual brain systems. Experience-driven neuroplasticity in musicians is thus not confined to alterations of perceptual and motor maps, but even leads to the establishment of higher-level semantic representations for musical instruments in and adjacent to auditory association cortex. These findings highlight the eminent importance of sensory and motor experience for acquiring rich concepts.

Introduction

Concepts in long-term memory are the central building blocks of human cognition, which form the fundament for object recognition, language and thought (Humphreys et al., 1988; Levelt et al., 1999). Traditionally, concepts have been conceived as abstract mental entities distinct from perceptual and motor systems (Anderson, 1983; Mahon and Caramazza, 2009; Tyler and Moss, 2001). Recent modality-specific approaches assume an embodiment of concepts (Gallese and Lakoff, 2005; Kiefer et al., 2008), meaning that they are essentially grounded in the sensory and motor brain systems depending on the specific learning experience (Barsalou et al., 2003; Kiefer et al., 2007; Kiefer and Spitzer, 2001; Martin and Chao, 2001; Pulvermüller, 2005). The notion of multiple modality-specific semantic systems has received empirical support from an increasing number of neuropsychological and brain imaging studies convincingly demonstrating that conceptual processing activates sensory and motor areas depending on the relevance of conceptual features (Hoenig et al., 2008; Kiefer, 2005; Martin et al., 1996; Warrington and McCarthy, 1987). Within this research field, it remains an important question whether activity in sensory areas during conceptual processing depends on prior sensory and motor experience with a given class of objects. A related crucial question is whether intensive sensory and motor experiences will yield enriched conceptual contents.

It is well documented that training perceptual and motor skills induces changes in the structural and functional organization of sensory and motor areas in laboratory settings (Bao et al., 2004; Buonomano and Merzenich, 1998; Polley et al., 2006; Zhou and Merzenich, 2007). For example, training participants to visually identify biological motion increased activity in a motion-sensitive area of the posterior superior temporal sulcus which was correlated with the degree of perceptual learning (Grossman et al., 2004).

In contrast to these well established effects of training perceptual and motor skills, evidence for neuroplasticity in the conceptual domain is scarce. This may be due to the still prevailing view of abstract conceptual representations (Anderson, 1983; Mahon and Caramazza, 2009; Tyler and Moss, 2001): only modality-specific approaches to conceptual memory, but not amodal theories predict the establishment of conceptual memory traces in sensory and motor

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brain areas as a function of expertise or training. Amodal theories in contrast sometimes even propose innate conceptual circuits (Mahon et al., 2009). They would locate the effects of training in higher-level heteromodal association cortex (Nieuwenhuys et al., 2008), for instance in anterior temporal areas close to the temporal pole (Rogers et al., 2004).

A few training studies that investigated concept acquisition for novel objects are suggestive of experience-dependent formation of conceptual representations in the sensory and motor brain systems. In the first study (James and Gauthier, 2003), participants learned associations between novel objects ("greebles") and verbal labels of object features referring to a given modality (auditory and object motion). In a sequential matching task at test, the authors found stronger activity to objects associated with auditory words ("buzzes") in the superior temporal gyrus, which responded to sounds in general. Activity in the superior posterior temporal sulcus, which was sensitive to motion processing, was greater for objects associated with motion words ("hops"). In the second study (Weisberg et al., 2007) the learning of tool-like functions for novel objects was assessed. During training, participants had the opportunity to interact with the objects. In a sequential matching task with photographs of the objects, activity in brain regions (left middle temporal gyrus, left intraparietal sulcus and premotor area) previously implicated in the processing of manipulable objects such as tools (Kellenbach et al., 2003; Noppeney et al., 2006) was increased after training in comparison to a pre-training baseline. In the third study (Kiefer et al., 2007), plasticity of conceptual representations was investigated by training human participants with novel objects ("nobjects") under different training conditions. During training, participants were asked to either make an action pantomime towards the detail feature of the novel object or to point to it. In a categorization task at test, the neural correlates of the acquired conceptual representations were assessed by measuring electrical brain activity. Only in the pantomime group, in which a meaningful action was performed towards the object during training, early activation in frontal motor regions and later activation in occipito-parietal visual-motor regions were found. In the pointing training group, in which the action during training was not meaningfully related to the object, these effects were absent. The results of the Kiefer et al. (2007) study suggest that activity in visuomotor areas during conceptual processing depends on the specific learning experience.

Although training studies with novel objects provide valuable information about experience-dependent formation of conceptual representations, it is unclear whether these findings generalize to concepts of real objects: Training of novel objects is accomplished within a few days and involves only a few learning episodes as well as limited sensory experiences while real-world conceptual representations are shaped by numerous, multimodal experiences with objects, accumulated over several years. Object representations acquired during short-term training of novel objects in laboratory situations and real-world conceptual representations might be different to some extent. In particular, short-term training of novel objects may lead to the establishment of specific episodic representations that are distinct from highly overlearned more abstract categorial conceptual representations of real objects (Schacter and Tulving, 1994; Tulving, 1972). It is thus essential to test the notion of experience-dependent conceptual plasticity in modality-specific cortex with real-world concepts that are formed across years.

Given the notorious difficulty to control for the complex heterogeneity of sensory and motor experiences among individuals, it is advisable to tackle such questions in experts with homogeneous intensive experiences that clearly and specifically distinguish this group of individuals from laypersons with regard to perceptual and action-related experience.

Individuals with special skills and unique learning biographies are particularly suited for the investigation of the associated plastic brain changes (Hänggi et al., 2009; Nielsen and Cohen, 2008). Using this expertise approach to conceptual neuroplasticity, two earlier studies suggested that sports expertise modulates neural processing of action language (Beilock et al., 2008; Lyons et al., 2010): hockey players as well as hockey fans showed more activity in dorsal premotor cortex than novices when they passively listened to sentences describing ice-hockey actions. These findings indicate that brain areas subserving sport skills contribute to language comprehension in an experience-dependent fashion. However, the passive listening task with action-related sentences used in these experiments strongly encourages participants to imagine the corresponding action, particularly in experts. It is therefore open, whether experience-dependent activation in premotor areas reflects processing of the conceptual content of the sentence or post-conceptual strategic imagery. Furthermore, if experience-dependent neuroplasticity of conceptual representations is a general computational principle, it should not be confined to actions, but generalize to sensory experiences as well.

Due to the unique intensive auditory learning history of professional musicians, a musician's brain is an ideal model to address experience-dependent conceptual neuroplasticity particularly in the auditory domain. Professional musicians, for instance, exhibit structural and functional brain specializations of both perceptual and motor maps due to their intensive sensory experience and motor training during acquisition and maintenance of their special skill (Altenmüller, 2001; Elbert et al., 1995; Münte et al., 2002; Pantev et al., 1998). However, it still remains unknown whether prior musical experience merely induces neuroplastic changes in basic perceptual and motor maps or even shapes higher-level cognition at the conceptual level.

Musicians intensively interact with musical instruments and experience their acoustic (e.g. pitch, timbre), visual (e.g. wooden, brass), action-related (e.g. pick, beat) and somatosensory (e.g. pressure on hands, lips) properties. In particular, detailed sound information is available for a broad variety of musical instruments in orchestra musicians. As memory traces of modality-specific object features are thought to be formed by perception and motor actions according to modality-specific theories (Barsalou et al., 2003; Kiefer et al., 2007; Martin and Chao, 2001; Pulvermüller, 2005), acoustic and motor representations should become an integral part of the concept for this object class in musicians. Such a conceptualization of musical instruments is presumably less present in musically naïve persons due to a lack of direct acoustic and motor experience. Conceptual knowledge about musical instruments in musically naïve persons might be less rich in the sense that it predominantly rests on visual conceptual features and verbal associations.

The ability of music to convey meaningful, especially emotional information has hardly ever been a matter of doubt, suggesting a close relationship between music and language in the human brain. That music can in fact activate representations of meaningful concepts (Daltrozzo and Schön, 2009; Koelsch et al., 2004), with emotion being a primary pathway to the establishment of meaning in music (Steinbeis and Koelsch, 2008), has only recently been demonstrated experimentally using functional magnetic resonance imaging (fMRI) and event-related potentials (ERPs). Based on these findings, close interconnections have been proposed between stores for lexical-semantic knowledge and a musical lexicon hosting knowledge about melodic contours, timbre, etc. in right superior temporal areas that belong to the auditory association cortex (Koelsch, 2005; Koelsch and Siebel, 2005). While it is well established that music is capable of activating semantic (and especially emotional) meaning, it remains unknown whether musical experience itself might contribute to the formation and enrichment of conceptual knowledge about musical instruments, e.g. by establishing conceptual acoustic representations for this object class in auditory association cortex. Previous findings and theoretical considerations (Kiefer et al., 2008; Simmons and Barsalou, 2003) suggest that conceptual acoustic information is processed in higher-level auditory cortex encompassing posterior superior temporal gyrus, as well as in adjacent areas in superior temporal sulcus and middle temporal gyrus (BA 21, 22), but not in lower-level auditory cortex (Heschl's gyrus) in contrast to sound perception (Woolsey, 1982). In an attempt to integrate cytoarchitectural and clinical findings in humans with experimental evidence from non-human primate research it has been claimed that the posterior superior temporal gyrus (BA 22) receives input directly from the lower-level auditory areas (BA 41, 42) and therefore forms the proximal auditory association cortex (Nieuwenhuys et al., 2008). In human participants, neighboring areas in MTG were found to be sensitive to higher-level acoustic stimuli such as complex sounds or voices and were frequently activated in addition to STG suggesting a similar function (Kiefer et al., 2008; Lewis et al., 2004; Maeder et al., 2001; Specht and Reul, 2003; Zatorre et al., 1996). The observation that conceptual sound processing only involves auditory association cortex and adjacent areas, but not primary auditory cortex may reflect the absence of the vivid sound experience typically present in sound perception and sound imagery (Kiefer et al., 2008).

Here we take advantage of the intensive experience of musicians with their instruments to locate neuroplastic changes in conceptual representations of musical instruments using fMRI during two different experimental tasks. In the conceptual task, professional orchestra musicians and musical laypersons performed semantic matching decisions on simultaneously presented picture–word pairs. Picture–word matching requires access to conceptual representations (Jolicoeur et al., 1984) and is a well-established task for the investigation of the functional (Jolicoeur et al., 1984; Tanaka et al., 1999; Tanaka and Taylor, 1991) and anatomical basis of conceptual representations (Fuggetta et al., 2009; Hurley et al., 2009; Marshall et al., 1990; Mathalon et al., 2002). Picture–word matching is a conceptual task that does not require intentional retrieval of object sounds. It therefore allows to test whether acoustic conceptual features are activated during conceptual processing even when these features are not task-relevant. This strongly suggests an automatic access to such features (De Houwer et al., 2009; Moors and De Houwer, 2006; Posner and Snyder, 1975). The picture–word matching task has also the advantage over more complex sentence paradigms to discourage participants from using sound imagery strategies because it simply asks participants to focus on the conceptual congruency between object and name. Picture–word stimuli either referred to musical instruments (e.g., tuba; Fig. 1), or control objects, for which acoustic features are of low relevance (e.g., crown). The semantic relationship between object and word on each trial was systematically varied: In half of the trials the word was the name of the object (matching condition), while in the other half the name did not match the object but belonged to the same object class (either musical instruments or control objects). In the perceptual task, participants listened to real sounds (e.g., saxophone; see the Supplementary Material for a complete list). This task served as

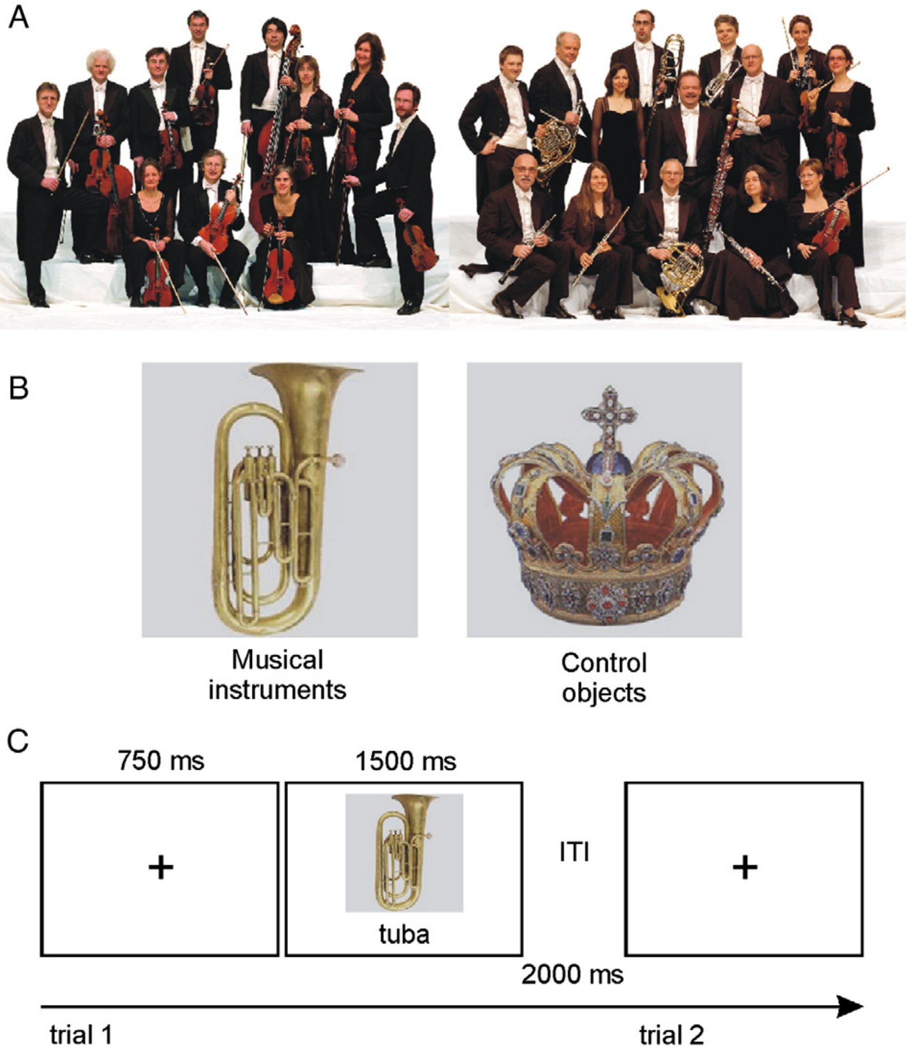

Fig. 1. Subjects, material, and study protocol. A, Participants from the Ulm philharmonic orchestra (photos by courtesy of Carola Hölting). B, Example pictures from the stimulus material. C, Experimental procedure of the conceptual picture–word matching task. Shown is a matching example, picture and word tuba. ITI: inter-trial interval.

functional localizer to identify brain areas involved in sound perception. We expect that only in musicians conceptual processing of visually presented musical instruments during picture–word matching suffices to activate higher-level auditory areas that also support sound perception. This would demonstrate that intense sensory experience with musical instruments establishes conceptual representations of acoustic features for this object class in auditory association cortex.

Materials and methods

General

Twenty professional musicians (14 males; mean age = 37 years; mean education time = 19 years) from the Ulm philharmonic orchestra and 20 musical laypersons (13 males; mean age = 36 years; mean education time = 18 years) participated in the two experiments (i.e., the conceptual and the perceptual task) of the present study. Control subjects were community volunteers who were recruited mainly via newspaper advertisement. All subjects were right-handed (Oldfield, 1971) native German-speaking volunteers with normal or corrected-to normal visual acuity. The musicians in our study usually started playing a musical instrument on average at the age of six. At the time of the study the musicians had 27 years of intense musical experience on average. Seventy-five percent (50%) of the musicians played two (three) or more instruments. Nine of the 20 control participants had never played a musical instrument. Eleven received routine flute lesions in elementary school or tried to play an instrument later in life, but none of the control participant continued playing a musical instrument after an initial training of 0.5–2 years. On average, control participants did not play a musical instrument for about 20 years. Exclusion criteria for all participants demanded the absence of any history of psychiatric or neurological disorders as well as intake of medication that might influence brain metabolism or vigilance. They participated after giving written informed consent; the procedures of the study have been approved by the local Ethical Committee. Control subjects and musicians were paid 25 € as compensation for participation. Experimental control and data acquisition were performed by the ERTS software package (Berisoft, Frankfurt, Germany). In the fMRI experiments visual stimuli were delivered through MR-compatible video goggles (Resonance Technology, Los Angeles, U.S.A.), and acoustic stimuli through MR-compatible pneumatic headphones (Siemens, Erlangen, Germany).

Stimuli and procedure for the conceptual acoustic task (experiment 1)

The stimulus material comprised two sets of 46 picture–word pairs: musical instruments (MI), and control objects (CO) with little relevance of acoustic features. Half of the picture–word pairs (23 per set) were congruent, i.e., the object name matched the object picture, while the other half was incongruent (23 per set), i.e., the object name did not match the object picture, but the named object always belonged to the same object class as the pictured object (i.e., musical instruments or control objects). This conceptual task does not require intentional retrieval of object sounds. Subjects indicated their decisions about the semantic match between word and picture by pressing one of two response keys. Word-picture sets for instruments and control objects differed only with respect to the relevance of acoustic features, but were matched for confounding visual, conceptual and linguistic variables (Fig. 2). A total of 92 picture–word pairs were presented visually for 1500 ms, preceded by a fixation cross and a blank screen of 750 and 300 ms duration, respectively. The two material sets were formed according to the results of a preceding norming study (Fig. 2): Subjects who participated in the norming study did not participate in the main experiments and were musical laypersons. Subjects of the first group ($n = 16$) had to rate a sample of 78 object names (28 MI, 50 CO) for relevance of acoustic, visual, and motor features on a scale from 1 to 6 (indicating low to high relevance of a given feature type). They were asked how strongly they would associate acoustic, visual, and motor features with the named object. Subjects of the second independent group ($n = 16$) had to rate a remaining sample of 65 object pictures (28 MI, 37 CO) for familiarity, visual complexity as well as emotional valence (pleasant vs. unpleasant) in the same way. The final sets (23 MI, 23 CO) differed significantly only with regard to the relevance of acoustic features (rating index MI = 5.4 vs. CO = 1.6; $p < 0.00001$), but were comparable for visual (MI = 4.0 vs. CO = 4.1; $p = 0.32$) and motor features (MI = 4.4 vs. CO = 4.1; $p = 0.09$). Stimulus sets were also matched for visual complexity (MI = 4.2 vs. CO = 4.0; $p = 0.29$), familiarity (MI = 2.7 vs. CO = 3.1; $p = 0.11$), emotional valence (MI = 2.5 vs. CO = 2.3; $p = 0.32$), word length (MI = 8.0 vs. CO = 8.2; $p = 0.78$) and word frequency (MI = 25.9 vs. CO = 24.6; $p = 0.95$) according to the CELEX lexical data base.

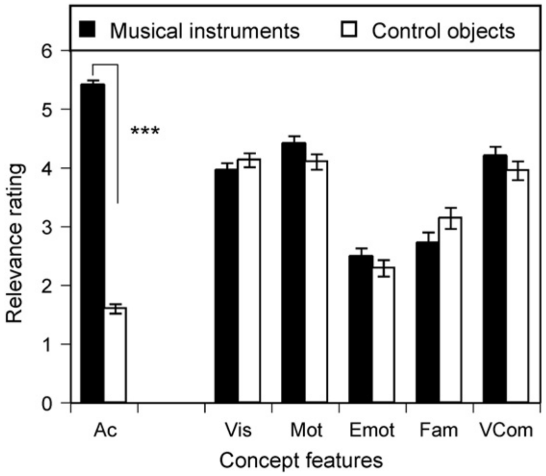

Fig. 2. Norming results of the stimulus material. Shown are the average values of the behavioral ratings for the relevance of acoustic (Ac), visual (Vis), and motor (Mot) features as well as of emotional valence (Emot), familiarity (Fam) and visual complexity (Vcom) of the pictures for musical instruments and control objects. Data were obtained from an independent prior norming study. Musical instruments and control objects differed only with respect to acoustic concept features. $^{***}p < 0.001$; small vertical bars indicate the standard error of means (s.e.m.).

A pilot study with a picture–word matching task ($n = 12$) showed that the two stimulus sets yielded similar reaction times (MI: 962.2 ms vs. CO: 967.7; $p = 0.77$) and error rates (MI: 2.1 vs. CO: 2.4; $p = 0.24$). Hence, picture–word sets exhibited a comparable difficulty in the picture–word matching task. In the fMRI experiment, picture–word pairs were presented in a randomized fashion (event-related design) intermixed with 46 trials in which just a blank screen was shown (null events). For each stimulus, participants had to respond within a time window of 2000 ms before the next trial started. The mean inter-trial interval was 5.9 s varying randomly between 3.2 and 8.6 s. Stimuli were presented within four blocks of 23 trials each plus either 11 or 12 randomly intermixed null events (Dale, 1999). After MR scanning, all subjects were asked to judge the picture–word stimuli of the conceptual task for the relevance of acoustic, visual, and action-related object features, again on a six-point scale from 1 to 6 (indicating low to high relevance).

Stimuli and procedure for the perceptual acoustic task (experiment 2)

A total of twenty sounds from common (natural and artifactual) objects were used as stimuli (for a full list of acoustic stimuli see the Supplementary Material). All acoustic stimuli had a duration of 500 ms (including rise and fall time) and were presented binaurally at about 70 dB nHL via closed headphones. All sounds were presented in blocks with a duration of 24 s each (10 sound stimuli per block with a mean inter-stimulus interval of 850 ms randomly varying between 400 and 1300 ms). Throughout the experiment, a fixation cross was displayed in order to minimize eye movements. Participants' task was to attentively listen to the acoustic stimuli while maintaining fixation. Each acoustic stimulation block was preceded and followed by a resting block in which only the fixation cross was shown. The acoustic stimulation blocks were presented four times in a randomized order. Brain activity in response to sound stimuli was determined by using functional magnetic resonance imaging (see below). For both participant groups, the functional sound localizer was always administered right after the conceptual task in the same scanning session.

fMRI scanning and data analysis

Magnetic resonance imaging was performed on a 3.0 Tesla MR system (Siemens Allegra, Erlangen, Germany). For the functional scans, a T2*-weighted single-shot gradient-echo EPI sequence (TE = 38 ms, TR = 2000 ms, flip angle = 90°, matrix 64 × 64 pixels, field of view (FOV) 210 × 210 mm^2, voxel size 3.3 × 3.3 × 4.9 mm^3) was used. Starting from the bottom of the brain, 30 transversal slices were acquired in interleaved order. Slice orientation was parallel to a line connecting the bases of the frontal lobe and the cerebellum. Image processing and data analyses were performed with SPM5 (Wellcome Department of Imaging Neuroscience) running under Matlab (MathWorks, Inc., Natick, MA). There were five imaging runs for the entire fMRI experiment (four blocks of the conceptual task and one block of the perceptual task), resulting in a total of 961 functional volumes. Run duration was about 7 min. Structural images were acquired with T1-weighted MPRAGE sequence (TR = 2300 ms; TE = 3.9 ms; flip angle = 12°; matrix 256 × 256 pixels, FOV = 256 × 256 mm^2, voxel size 1 × 1 × 1 mm^3). Functional images were corrected for differences in slice-timing and head motion, spatially realigned to the first volume of the first run and smoothed with an isotropic Gaussian kernel of 6 mm FWHM. Before smoothing, the realigned images were spatially normalized to the MNI reference brain (re-sampled voxel size: 2 × 2 × 2 mm^3). A temporal high-pass filter with cutoff frequency 1/128 Hz was applied to the data, and temporal autocorrelation in the fMRI time series was estimated (and corrected for) using a first-order autoregressive model.

Statistical analysis used a hierarchical random-effects model with two levels. At the first level, single-subject fMRI responses were modeled by a design matrix comprised of the stimuli (conceptual task: musical instruments and control objects; perceptual task: blocks of acoustic stimuli) convolved with the canonical hemodynamic response function for both groups (musicians and non-musicians) as well as the six motion parameter estimated from the realignment procedure. To allow for inferences at the population level, a second-level analysis (full factorial model with the factors subject, group, and object type) considered the contrast images of all subjects and treated subjects as an independent random effect per group. In the event-related analysis of the conceptual task, all comparisons were thresholded at a significance level of $p<0.05$ and corrected for multiple comparisons across the entire brain (false discovery rate, FDR). For the analysis of the block design of the perceptual experiment, significance level was set to $p<0.01$ (FDR-corrected for the entire brain). This slightly more conservative threshold was applied because of the comparably higher sensitivity of the blocked fMRI design of the perceptual task over the event-related design of the conceptual task. The spatial extent threshold of clusters was based on the number of expected voxels per cluster in all comparisons.

To detect brain activity associated with acoustic information pertaining to musical instruments, we first compared the processing of musical instruments with that of control objects separately in both groups. A further analysis specifically tested for an interaction between object class and group to find out brain regions in which musicians show a relatively larger increase to musical instruments than to control objects: $(\text{MI}_{\text{musicians}} \text{ vs. } \text{CO}_{\text{musicians}}) > (\text{MI}_{\text{non-musicians}} \text{ vs. } \text{CO}_{\text{non-musicians}})$. Localization of activation clusters was based on the MNI coordinates of the respective peak voxels. Anatomic labels and corresponding Brodmann areas (BA) were determined using MRIcro (Rorden and Brett, 2000). All functional group activation maps were overlaid on the MNI reference brain.

Results

fMRI experiment 1: conceptual task

Behavioral results

A repeated-measures ANOVA with the within-subject factors object category (musical instruments vs. control objects) and the between subject factor group (musicians vs. non-musicians) revealed a significant main effect for object category ($F(1,38) = 45.40$; $p<0.0001$) which was further qualified by a significant interaction between both factors ($F_{1,38} = 27.74$; $p<0.0001$). Post-hoc contrasts revealed a significant difference between musical instruments and control objects in musicians, but not in non-musicians. A respective two-way ANOVA on error rates yielded no significant main effect. However, there was a significant interaction between object category and group ($F_{1,38} = 5.05$, $p<0.05$). Post-hoc tests showed that the interaction was predominantly driven by a significant difference between musical instruments and control objects in non-musicians. Hence, picture–word matching for musical instruments was faster (M = 843.7 ms, s.e.m. = 29.2 ms in musicians vs. M = 948.3 ms, s.e.m. = 29.2 ms in non-musicians) and more accurate (M = 1.8 %, s.e.m. = 1.4% in musicians vs. M = 5.1%, s.e.m. = 1.4% in non-musicians) than for control objects in musicians compared to non-musicians, reflecting greater expertise with these objects (Fig. 3). Performance for control objects did not differ between participant groups neither with respect to response time (M = 923.2 ms, s.e.m. = 31.9 ms in musicians vs. M = 958.1 ms, s.e.m. = 31.9 ms in non-musicians) nor with respect to error percentages (M = 3.0 %, s.e.m. = 0.8% in musicians vs. M = 5.1%, s.e.m. = 0.8% in non-musicians).

Object ratings

Repeated measures ANOVAs of the object ratings after MR scanning with the within-subject factor object category (musical instruments vs. control objects) and the between factor group (musicians vs. non-musicians) revealed significant interactions between these two factors not only for the relevance of acoustic conceptual features ($F_{1,38} = 15.49$; $p<0.001$), but also for the relevance of visual ($F_{1,38} = 13.91$; $p<0.001$) and action-related conceptual features ($F_{1,38} = 13.37$; $p<0.001$). Hence, musicians

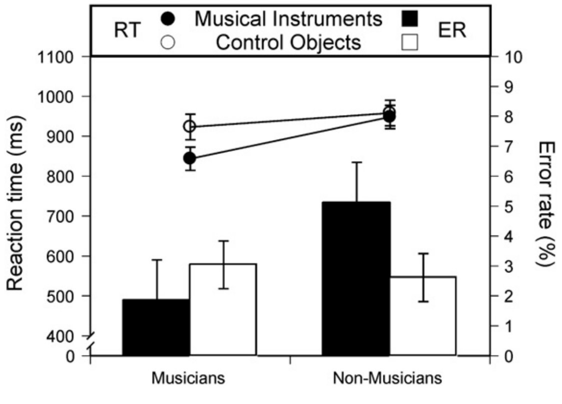

Fig. 3. Behavioral data of the conceptual task. Mean (± s.e.m.) reaction times (RT, upper part, closed and open circles) and error percentages (ER, lower part columns) for musicians and non-musicians as a function of object class.

compared with non-musicians judged acoustic (M: 5.4 in musicians vs. 4.7 in non-musicians), visual (M: 4.6 in musicians vs. 3.9 in non-musicians) and motor features (M: 4.3 in musicians vs. 3.6 in non-musicians) to be substantially more relevant for musical instruments than for control objects (M_{acoustic}: 1.3; M_{visual}: 3.8, M_{action}: 3.6 in musicians) (M_{acoustic}: 1.5; M_{visual}:. 3.9; M_{action}: 4.0 in non-musicians) thereby providing subjective behavioral evidence for a greater conceptual richness (Fig. 4).

Functional imaging results

In the conceptual task, we first compared brain activity between musical instruments and control objects separately for musicians and musical laypersons. The MR signal to musical instruments compared to control objects ($p < 0.05$, corrected for the entire brain volume) was only increased in musicians, but not in musical laypersons. In musicians, musical instruments elicited a higher MR signal within a right-hemisphere cluster including higher-order auditory association cortex encompassing superior temporal gyrus as well as adjacent areas in superior temporal sulcus, and in the upper part of middle temporal gyrus (pSTG/MTG), corresponding to Brodmann areas BA22 and BA21, respectively. Although not genuinely part of auditory association cortex, the posterior part of middle temporal gyrus has been found to be sensitive to acoustic stimuli in a number of previous imaging studies (Fig. 8).

To test whether this conceptual acoustic effect to musical instruments in pSTG/MTG was in fact due to increased activation for musical instruments in musicians, an additional interaction analysis between object (musical instruments>control objects) and group (musicians>non-musicians) was performed. This additional interaction analysis determines brain areas in which musicians compared to non-musicians show a larger increase to musical instruments than to control objects. The interaction analysis again yielded a reliable effect in pSTG/MTG ($p < 0.05$, corrected; Fig. 5), thereby verifying that the activation difference between musical instruments and control objects was significantly larger for musicians than for non-musicians in right pSTG/MTG. Additional interaction effects were obtained outside auditory areas including inferior temporal and parietal areas as well as precuneus, bilateral angular gyrus, and superior frontal gyrus (Fig. 6, Table 1). In order to test whether the two groups also differed with respect to brain activation in response to the control condition in pSTG/MTG, we inclusively masked the between group comparison of the control condition ($\mathrm{CO}_{\mathrm{musicians}} > \mathrm{CO}_{\mathrm{non\text{-}musicians}}$) with a spatial mask from the interaction contrast between group and object class which originally yielded the pSTG/MTG activation. This was done to detect increased group-related control object activation within pSTG/MTG. In order to reduce the risk of obtaining false negative results we chose a rather lenient mask threshold of $p < 0.01$, uncorrected. However, even under such benevolent circumstances there was no significant difference ($p < 0.05$, corrected) between the control conditions of both groups within pSTG/MTG. Hence, activity to control objects did not differ between groups. Finally, separate comparisons of control objects with musical instruments in each group yielded significantly greater activity for control objects ($p < 0.05$, corrected) within pSTG/MTG only in non-musicians, but not in musicians. Thus, the interaction effect between group (musicians>non-musicians) and object (musical instruments>control objects) in auditory association cortex an adjacent areas is due to both an increased activation to musical instruments in musicians and a decreased activation to musical instruments in non-musicians.

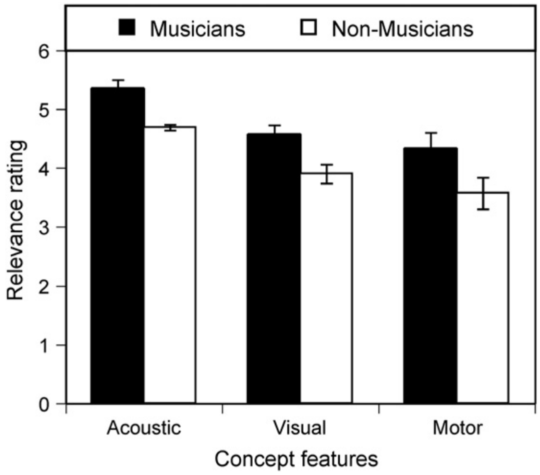

Fig. 4. Sensorimotor conceptual enrichment. Increased relevance ratings of acoustic, visual, and motor features for musical instruments in musicians ($N = 20$) compared to non-musicians ($N = 20$), demonstrating the conceptual enrichment for musical instruments due to the intensive sensorimotor experiences of musicians with these objects. $p < 0.001$ for each of the post-hoc comparisons between musicians and non-musicians; small vertical bars indicate the standard error of means (s.e.m.).

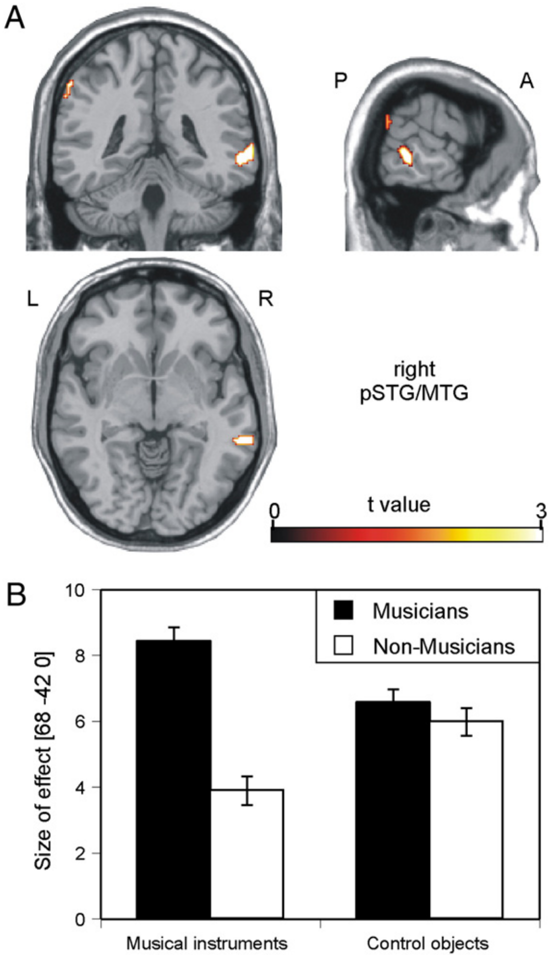

Fig. 5. Functional brain activation pertaining to acoustic conceptual features of musical instruments. A, Brain activation of the conceptual group-by-object contrast: Increased activation to musical instruments compared to control objects for musicians ($N = 20$) compared with non-musicians ($N = 20$) in right pSTG/MTG, $p < 0.05$, corrected. B, Interaction effect within the activation cluster of right pSTG/MTG: the bar chart depicts the effect size for the contribution of musical instruments and control objects to brain activation at the peak voxel of the pSTG/MTG cluster for musicians and non-musicians. The bar chart shows that the interaction effect is due to a differentially larger activation increase for musical instruments compared with control objects in musicians than in non-musicians. P = posterior, A = anterior, L = left, R = right.

fMRI experiment 2: perceptual task

Functional imaging results

In the perceptual task, listening to real sounds ($p < 0.01$, corrected for the entire brain volume) recruited the superior temporal gyrus

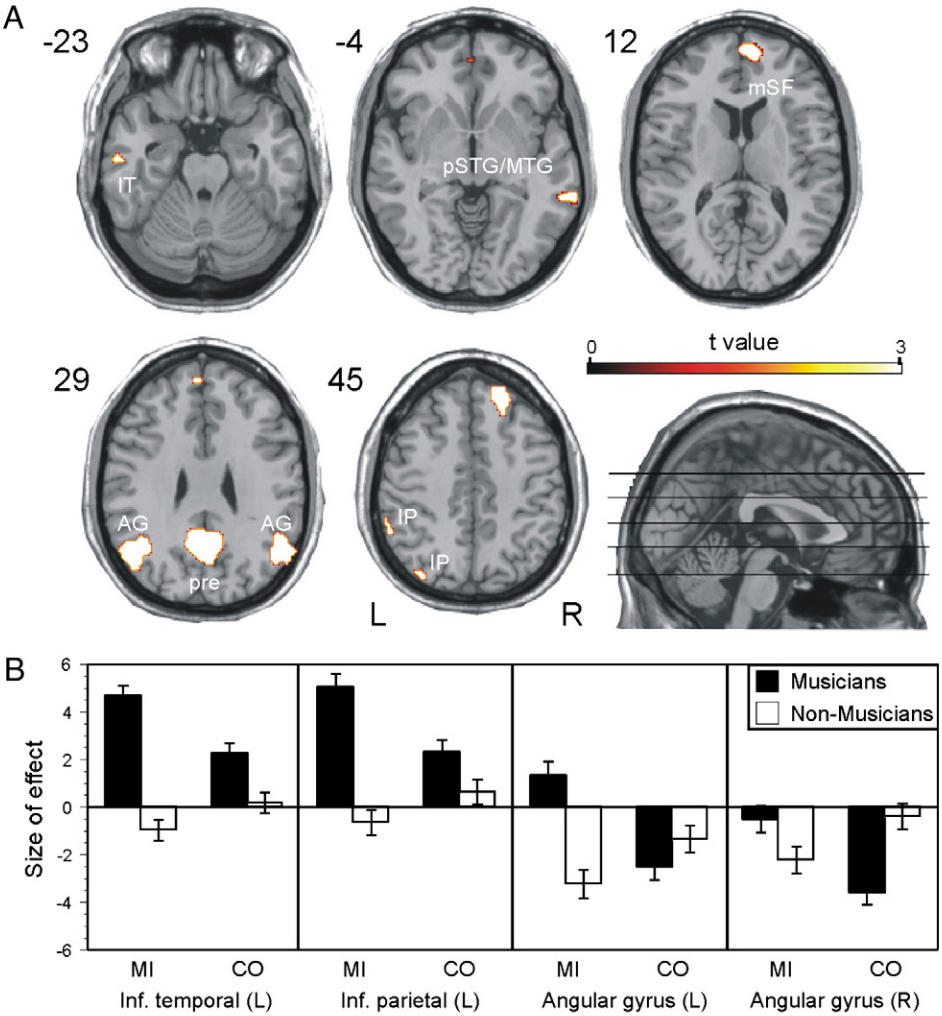

Fig. 6. Functional interaction effects between Group (musicians vs. non-musicians) and Object (musical instruments vs. control objects). A, Multi-slice view of increased functional activation to musical instruments compared to control objects for musicians ($N=20$) compared with non-musicians ($N=20$), $p<0.05$, corrected. iT = inferior temporal gyrus, pSTG/MTG = posterior superior/middle temporal gyrus, mSF = medial superior frontal gyrus, AG = angular gyrus, pre = precuneus, iP = inferior parietal cortex. B, Interaction effects within modality-specific sensory (i.e., visual association cortex in inferior temporal g.) and motor areas (i.e., visuo-motor cortex in inferior parietal lobule) as well as heteromodal association areas (bilateral angular g.). The bar chart depicts the effect size for the contribution of musical instruments and control objects to brain activation at the peak voxel of the respective cluster for musicians and non-musicians.

Table 1
Interaction analysis between group and object class. Maxima of activation clusters showing higher functional activation for musical instruments than for control objects in musicians compared with non-musicians. The statistical threshold was set to $p<0.05$, corrected for the entire brain volume. pSTG/MTG, posterior superior and middle temporal gyrus; FDR, false discovery rate corrected. BA, Brodmann area.

Area	Group × Object Class Interaction						
	BA	Cluster size	x	y	z	t	FDR
Precuneus	23	887	0	−62	24	5.76	0.001
L angular g.	39	573	−44	−60	24	4.95	0.002
R pSTG/MTG	22, 21	90	68	−42	0	4.60	0.005
R medial superior frontal g.	10	195	6	58	10	4.50	0.006
R angular g.	39	553	56	−64	32	4.43	0.007
R superior frontal g.	9	195	14	42	46	4.27	0.009
L medial superior frontal g.	9	127	−6	52	34	4.25	0.009
L inferior temporal g.	20	21	−62	−16	−24	4.05	0.013
L medial superior frontal g	10	29	−14	52	0	3.87	0.019
L inferior parietal g.	7	22	−36	−78	46	3.85	0.019
R inferior temporal g.	20	20	60	−8	−32	3.84	0.020
L inferior parietal g.	40	49	−58	−48	44	3.76	0.023

(STG) including the temporal plane as well as parts of the middle temporal gyrus (MTG) bilaterally in both groups. The temporal plane comprises primary auditory cortex (Fig. 7A) while the neighboring areas in STG encompass auditory association areas (Howard et al., 2000). A comparison between groups (musicians and non-musicians) and sound categories (living and non-living objects) did not yield significant differences. Most importantly, the cluster that responded to real sounds overlapped with the activation cluster of the object-by-group interaction of the conceptual task in right pSTG/MTG (Fig. 7B, Table 2). In order to test for regional overlap between the effects of perceptual sound processing and processing of acoustic conceptual features in pSTG/MTG, we performed a conjunction analysis looking for regions exhibiting common activation in the perceptual contrast (listening to real sounds of objects>rest) and the conceptual object-by-group interaction contrast (musicians MI>CO>non-musicians MI>CO). SPM5 allows to perform such an analysis for rather complex contrasts by use of an inclusive masking procedure. The statistical threshold for the "perceptual" mask was rather conservative ($p<0.01$, FDR voxel-level corrected). This was done to reduce the likelihood of finding overlapping activity just by chance. The statistical threshold for the "conceptual" contrast was $p<0.001$, giving a conjoint significance higher than $p<0.0001$ ($X^2=23.05$, $df=4$), according to Fisher's method of estimating the conjoint significance of tests

(Fischer, 1950; Lazar et al., 2002). Functional brain activity exceeding these thresholds was considered reliable. Commonalities in activation differences pertaining to perceptual and conceptual processing were significantly found within right pSTG/MTG (98 voxels). Notably, the peak coordinates of this conjunction analysis [68–42 0] were identical to those of the pure interaction analysis. Hence, conceptual processing of musical instruments in musicians and sound perception share a common neural substrate in pSTG/MTG of the right hemisphere.

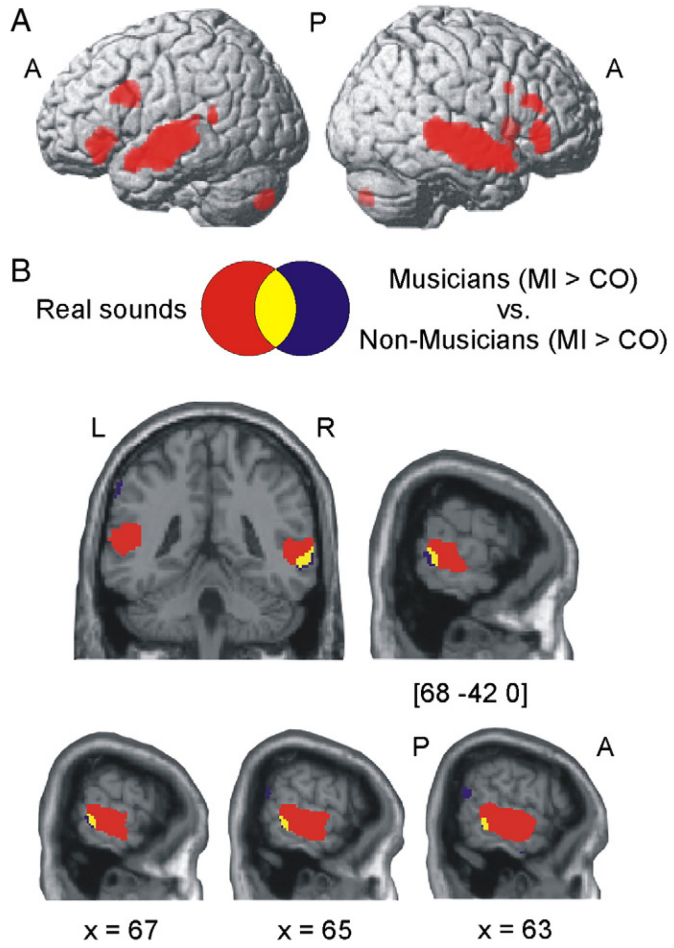

Fig. 7. Perceptual processing of real sounds and overlap between auditory perceptual and conceptual brain activation. A, Perceptual task: Activation during listening to real sounds, $p<0.01$, corrected. B, Functional–anatomical overlap (in yellow): Increased activation to musical instruments compared to control objects in musicians ($N=20$), but not in non-musicians ($N=20$; $p<0.05$, corrected; in red) overlaps with brain activation during listening to real sounds ($p<0.01$, corrected; in blue) in right-hemisphere pSTG/MTG. Color-shaded areas indicate the spatial extent of the two functional contrasts assessing sound perception (real sounds > acoustic noise) and the conceptual group-by-object interaction (group: musicians > non-musicians, object: musical instruments (MI) > control objects (CO)), respectively. Shown are contiguous slices centered on the peak coordinates (68–42 0) obtained from the interaction analysis of the conceptual task. P = posterior, A = anterior, MI = musical instruments, CO = control objects.

Discussion

During conceptual processing of musical instruments only professional musicians activated auditory association cortex encompassing posterior superior temporal gyrus, as well as adjacent areas in superior temporal sulcus and middle temporal gyrus (pSTG/MTG) of the right hemisphere. The unique intensive experience of musicians with musical instruments thus shapes the organization of conceptual knowledge for this object class by establishing acoustic conceptual feature representations for musical instruments in right pSTG/MTG. By contrast, increased right-hemisphere pSTG/MTG activity to musical instruments was absent in non-musicians, while activity to control objects did not differ between groups. The visual conceptual task, which does not afford intentional sound retrieval, sufficed to activate these auditory brain areas in musicians. This shows that conceptual knowledge about musical instruments is substantially enriched in these occupationally specialized individuals and accessed even when only implicitly probed. Furthermore, the results of the perceptual task showed that the activation cluster obtained during auditory perception of real sounds anatomically overlapped with the functional activation cluster of the conceptual task in pSTG/MTG. Hence, neuroplastic changes in musicians in and adjacent to auditory association cortex link conceptual processing of musical instruments with a partial reinstatement of brain activity during sound perception. In sum, experience-dependent neuroplasticity in musicians is not confined to the alteration of perceptual and motor maps (Elbert et al., 1995; Lappe et al., 2008; Pantev et al., 1998; Pantev et al., 2001; Schlaug et al., 1995), but even establishes higher-level acoustic conceptual feature maps for musical instruments represented in and adjacent to auditory association cortex. These plastic changes affect the very building blocks of human cognition by which we conceive our physical and social world.

As non-musicians also possess conceptual knowledge about musical instruments, they performed well in the conceptual task. However, access to conceptual knowledge about musical instruments in musical laypersons does not involve auditory association cortex as in musicians. Within pSTG/MTG, non-musicians did even evidence less brain activity to musical instruments compared to control objects. The reduced activation to musical instruments in pSTG/MTG in non-musicians most likely reflects the missing or impoverished acoustic

Table 2

Perception of real sounds. Maxima of activation clusters showing higher functional activation for real sounds compared to resting fixation in musicians. The statistical threshold was set to $p<0.01$, corrected for the entire brain volume. FDR, false discovery rate corrected. BA, Brodmann area.

Area	Real sounds > resting fixation						
	BA	Cluster size	*x*	*y*	*z*	*t*	FDR
L superior temporal g.	22	1791	−54	−10	−4	8.18	0.0001
R superior/middle temporal g.	22, 21	2448	54	2	−14	6.87	0.0001
L inferior frontal g. (pars opercularis)	48	324	−38	10	24	4.98	0.0001
L inferior frontal g. (pars orbitalis)	47	375	−38	30	−6	4.95	0.0001
R inferior frontal g. (pars triangularis)	45	349	44	32	2	4.94	0.0001
L cerebellum (Crus 2)		120	−14	−80	−42	4.64	0.0001
R putamen	48	170	26	10	−14	4.34	0.001
R inferior frontal g. (pars triangularis)	45	93	46	24	20	4.06	0.002
R inferior frontal g. (pars opercularis)	44	26	38	12	30	4.00	0.003
R cerebellum (Crus 2)		20	16	−82	−40	3.85	0.004
L superior/middle temporal g.	22, 21	43	−62	−44	12	3.82	0.004

experience for this objects class. This suggests that conceptual knowledge on musical instruments in musical laypersons compared with musicians is much less grounded in perception and action and may rather rest on verbal knowledge based upon linguistic word associations (Barsalou et al., 2008; Solomon and Barsalou, 2004). Linguistic associations, which are presumably stored in left hemisphere language areas, contribute comparably to the representation of musical instruments and control object and thus do not elicit differential brain activation.

The interaction analysis between object class (musical instruments>control objects) and participant group (musicians>non-musicians) revealed significantly increased activation for musical instruments in musicians also outside auditory areas including inferior temporal and parietal areas. This suggests that the intensive experience of professional musicians with musical instruments additionally formed modality-specific memory traces for other conceptual features than acoustic ones. Previous neuroimaging and neuropsychological evidence suggest that activation of the inferior parietal cortex reflects the retrieval of action-related knowledge, i.e., knowledge about the specific use of musical instruments (Buxbaum et al., 2006; Canessa et al., 2008; Hwang et al., 2009; Kellenbach et al., 2003; Sirigu et al., 1995; Sirigu et al., 1996; Vingerhoets, 2008), while the inferior temporal activations indicate access to visual object features during the identification of musical instruments (Bell et al., 2009; Pietrini et al., 2004; Sirigu et al., 1995; Vingerhoets, 2008). In light of these findings, our results clearly demonstrate that musicians have acquired experience-dependent conceptual knowledge about musical instruments that is not only enriched with regard to acoustic, but also to visual and action-related conceptual features. This interpretation is additionally supported by our behavioral ratings which demonstrated higher relevance of visual and action-related features for musical instruments in musicians than in non-musicians.

Increased activation to musical instruments in musicians was additionally observed in precuneus, bilateral angular gyrus and superior frontal gyrus. Both angular gyrus (Hoenig and Scheef, 2009; Mashal et al., 2009; Obleser and Kotz, 2010) and precuneus (Hoenig and Scheef, 2009; Mashal et al., 2009; Whitney et al., 2009) are commonly associated with semantic processing, particularly at the word level. Functional imaging studies in the language domain suggest that activation in these brain regions reflect task-dependent retrieval strategies (Binder et al., 2009; Bookheimer, 2002; Price, 2000, 2010), with the angular gyrus being most likely related to constraining the notoriously ambiguous meaning field of almost every word, and precuneus increasing the allocation of attention during semantic constrain (Hoenig and Scheef, 2009; Lawrence et al., 2008). Increased activation in superior frontal gyrus—as well as in precuneus—have been reported for various kinds of semantic decisions (Birn et al., 2010; Kouider et al., 2010; Sharp et al., 2010; Whitney et al., 2009) suggesting a more decisional executive role of these brain areas in, but not only, semantic processing. Alternatively, within the language domain, the medial superior frontal cortex has also recently been implicated in conceptual processes supporting speech production (Birn et al., 2010) or volitional effort in terms of strategic demands during word retrieval (Tremblay and Gracco, 2010).

Single parameter estimates of the four conditions ($\mathrm{MI}_{\mathrm{musicians}}$, $\mathrm{CO}_{\mathrm{musicians}}$, $\mathrm{MI}_{\mathrm{non\text{-}musicians}}$, $\mathrm{CO}_{\mathrm{non\text{-}musicians}}$) that were entered in the interaction analysis between group and object class showed that the interaction effects within right angular gyrus (and to some degree also in the left angular gyrus)—might be driven by differences in relative deactivation, such that musicians show slightly less deactivation for musical instrument than for control objects. This activity pattern was different in pSTG/MTG, inferior temporal and inferior parietal cortex, which showed in musicians more activation for musical instruments. Interestingly, these brain regions showing differences in relative deactivation are also central components of the so-called default-mode network (Gusnard et al., 2001b; Raichle et al., 2001). Activation differences within these default-mode areas might therefore alternatively reflect a differential recruitment of mental resources in terms of conscious focusing. This interpretation would be in good agreement with an increase in self-referential mental activity in musicians while processing musical instruments (Gusnard et al., 2001a). In line with this reasoning, a recent meta-analysis in the context of episodic memory retrieval reported increased activity in nodes of the default mode network during remembering (recollection) (Kim, 2010).

In the perceptual task, auditory perception of real sounds recruited STG including the temporal plane as well as parts of MTG, bilaterally in both groups. In musicians, the posterior portion of this right-hemisphere auditory perception area functional–anatomically overlapped with the activation cluster obtained for conceptual processing of musical instruments in musicians. Hence, auditory perception of real sounds and conceptual processing of visually presented musical instruments share a common neural substrate in right pSTG/MTG in musicians, but not in non-musicians.

Accumulating neuroscientific evidence demonstrates an involvement of the posterior superior temporal gyrus as well as adjacent areas in superior temporal sulcus and middle temporal gyrus in various forms of higher-level sound processing including processing of human voices, sound recognition, and music imagery (Belin et al., 2000; Kraemer et al., 2005; Lewis et al., 2004; Maeder et al., 2001; Wheeler et al., 2000), and sound recognition deficits ensue from lesions in this region (Clarke et al., 2000) (Fig. 8). Evidence from electrophysiological stimulation and recording work (Creutzfeldt et al., 1989; Ojemann et al., 1988) also suggests that STG and neighboring areas in MTG may be made up of multiple functional areas, each engaged in different aspects of complex acoustic processing. Most interestingly, electrical activity in posterior STG and to some extent also in adjacent MTG has been shown to reflect some general phonetic aspects of spoken language demonstrating

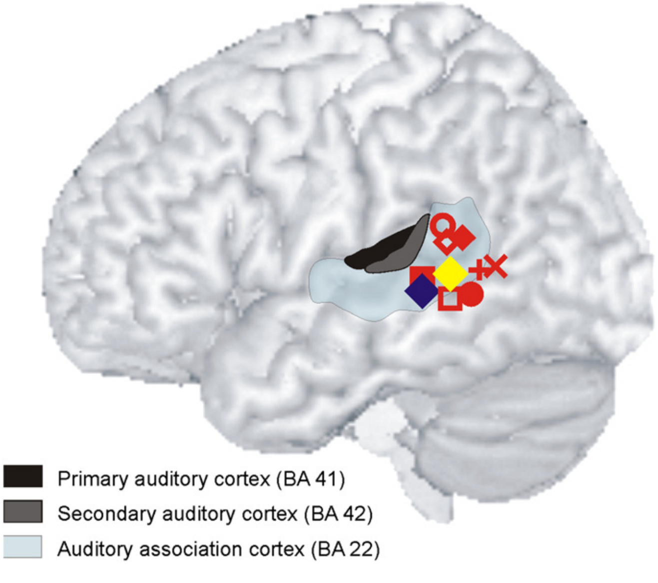

Fig. 8. The role of pSTG/MTG in sound processing based on previous imaging evidence. Peak activations (red symbols) are overlaid on the MNI reference brain. Posterior STG/MTG has been found activated during voice listening (Belin et al., 2000) (◊), sound recognition (Lewis et al., 2004; Specht and Reul, 2003), word recognition (Specht and Reul, 2003) (●), sound retrieval (Wheeler et al., 2000) (○), sound imagery (Zatorre et al., 1996) (♦, □), and sound verification (Kellenbach et al., 2001) (+). Both, the peak activation of acoustic conceptual processing from our previous study (blue diamond) (Kiefer et al., 2008) and the acoustic conceptual activation to musical instruments of the present study (yellow diamond) are located within this cluster of previously reported activations in pSTG/MTG. The gray-shaded areas schematically delineate the respective anatomical location of primary (BA 41) and secondary cortex (BA 42) as well as the blue-shaded area the location of auditory association cortex (BA 22).

that this region is involved in higher-level sound processing (Creutzfeldt et al., 1989). Anatomical connectivity analyses of the monkey brain suggest that the posterior part of the superior temporal gyrus (BA 22) belongs to the proximal auditory association cortex that receives input directly from the lower-level auditory areas (BA 41, 42) (Nieuwenhuys et al., 2008). In a lexical decision task, the left-hemisphere homologue of the pSTG/MTG has only recently been identified to code higher-level acoustic object information contributing to a concept (Kiefer et al., 2008).

It seems that concept formation in auditory association cortex differs with regard to hemisphere dominance. While pSTG/MTG of the left hemisphere is particularly important for coding acoustic features of everyday objects (e.g. telephone), it is the right hemisphere homologue that plays a crucial role for representing acoustic conceptual information of musical instruments. This striking shift in hemispheric lateralization is particularly supported by the eminent importance of the posterior temporal cortex of the right hemisphere for music perception. In line with this interpretation, deficits in conceptual recognition of musical instruments in musically naïve brain-lesioned subjects have been associated (among other areas) with a maximal lesion overlap in the posterior part of the middle temporal gyrus of the right hemisphere. Deficits in word retrieval, on the other hand, were rather associated with a maximal lesion overlap in posterior middle temporal gyrus of the left hemisphere (Damasio et al., 2004).

Musical hearing and comprehension has already been associated with alterations of the posterior two thirds of the first temporal convolution by early post-mortem examinations of the brains of outstanding musicians (Meyer, 1977). Today it is generally acknowledged that the perception of music ensues from a tightly woven interplay of temporal, parietal and frontal brain regions of both hemispheres (Tramo, 2001). The right auditory cortex, however, seems to be an essential prerequisite for music comprehension, particularly with respect to pitch perception of harmonic complex sounds—such as the sounds of musical instruments—as well as for processing other aspects like contour (melody) and color (timbre) (Halpern et al., 2004; Hyde et al., 2008; Liegeois-Chauvel et al., 1998; Parsons, 2001; Peretz, 1990; Platel et al., 1997; Schneider et al., 2005; Tramo and Bharucha, 1991; Zatorre et al., 1992) as well as the semantics of music (Koelsch et al., 2004; Koelsch and Siebel, 2005). Interestingly, given that some forms of music mimic prosodic gestures, this right hemisphere region is also relevant for processing speech prosody, i.e. paralinguistic aspects of vocal processing like speaker gender, age, and emotional state (Kotz et al., 2006; Schirmer and Kotz, 2006). Here, we showed for the first time that right pSTG/MTG is activated in response to conceptual processing of visually presented musical instruments only in musicians suggesting that right auditory association cortex codes conceptual sound features of musical instruments as a function of musical experience.

Conceptual processing of acoustic features pertaining to musical instruments was found in higher-order auditory association cortex and adjacent areas, in close proximity but not encompassing primary or secondary auditory cortex. In contrast to conceptual sound processing, sound imagery also recruits primary and secondary auditory cortex similar to sound perception (Halpern et al., 2004; Kraemer et al., 2005; Zatorre and Halpern, 2005). The present finding of a considerable functional–anatomical overlap between conceptual and perceptual processing in auditory association cortex suggests that acoustic conceptual processing differs from both perceptual processing and auditory imagery with regard to the neural substrate (Kraemer et al., 2005; Zatorre et al., 1996). This difference in the neuroanatomical substrate may have a functional counterpart because conceptual processing of acoustic features naturally lacks the vividness of a sound experience that is typically present in sound perception and auditory imagery. Such a differentiation in terms of both neural substrate and phenomenological experience is not only well in line with the frequently reported distinction between conceptual processing and imagery (Hauk et al., 2006; Hauk et al., 2008; Kiefer et al., 2007; Kosslyn, 1994), but is also highly instrumental in preventing interfering processes from conceptually driven vivid sensory experiences on action planning during verbal communication and thought. There is growing evidence from imaging research that sensorimotor contributions during conceptual activation and explicit mental imagery do not only serve different functions at a computational level, but that these two also involve different cognitive processes and often—although not necessarily—engage different neural tissues (Willems et al., 2010). Furthermore, access to acoustic concept features and auditory imagery also differ with respect to their temporal dynamics: the earliest magnetoencephalographic activity associated with auditory imagery has been found with an average onset latency 170–250 ms in trained musicians who were presented with visual notes and explicitly instructed to imagine the corresponding sounds (Schurmann et al., 2002). By comparison, combined fMRI and ERP evidence has shown that acoustic conceptual features of everyday objects (like telephone) are recruited from the homologue left-hemisphere auditory areas (pSTG/MTG) as early as 150 ms within a word recognition task although this task did not require intentional retrieval of sound information (Kiefer et al., 2008).

It is well beyond doubt that neural activity—most likely reflecting auditory imagery—can occur in auditory cortex even in the absence of sound (Halpern et al., 2004). However, the invocation of an involuntary experience of auditory imagery by specific perceptual stimuli regardless of other cognitive activity is by no means obligatory (Hubbard, 2010), but rather crucially dependent on task demands (Zatorre and Halpern, 2005). For instance, visual presentation of animal pictures was not accompanied by auditory imagery of the animal sounds, unless the formation of such an auditory image had been explicitly instructed (Wu et al., 2006). Unlike earlier expertise studies on action understanding, the presently chosen well established visual conceptual task (picture–word matching) that does not require intentional retrieval of object sounds strongly discouraged any kind of imagery while allowing to test whether acoustic conceptual features are implicitly activated (Posner and Snyder, 1975). The present work therefore considerably substantiates the notion that experience through expertise and training leads to the establishment of conceptual memory traces in corresponding modality-specific association cortex. It confirms and extends pervious short-term training studies with novel objects (James and Gauthier, 2003; Kiefer et al., 2007; Weisberg et al., 2007) by demonstrating that experience-dependent conceptual plasticity in modality-specific cortex can also be found for real-world objects in real-life learning situations.

Conceptual knowledge emerges from the perception of and interaction with many single objects. These sensorimotor experiences are crucially important for the development of rich concepts about our natural and social world. The words, to which the concepts are tied, and their simple verbal associations and definitions convey only part of their content. Conceptual information essentially rests in our sensorimotor representations in the brain, through which we perceive, encode and store relevant object features. Hence, conceptual knowledge lies in many parts of the body which conceives the concept. We propose that the reinstatement of sensory and motor brain activity during conceptual processing is the cognitive basis for a rich and elaborated concept. In contrast, concepts lacking this grounding in perception and action remain vague, schematic, and largely depended on verbal associations (Barsalou et al., 2008). As the present study focused on object concepts and most specifically on musical instruments, the sensory and motor foundations of abstract concepts, functions words, and grammaticalized morphemes such as determiners were beyond the scope of this work (Barsalou and Wiemer-Hastings, 2005). Future studies will have to show whether an embodiment approach that assumes modality-specific conceptual representations generalizes to all types of concepts.

In conclusion, effects of learning experience—and particularly enhanced musical training—are profound and manifold in their influence on the deepest workings of the human brain (Altenmüller, 2001). The intensive experience of musicians with musical instruments establishes higher-level acoustic conceptual representations for musical instruments in and adjacent to auditory association cortex. The results of the present study therefore highlight the eminent importance of sensory and motor experience for enriched concepts of the environment. These findings are important contributions to our understanding of how experience entails plastic brain alterations that shape the way we conceive the world.

Supplementary materials related to this article can be found online at doi:10.1016/j.neuroimage.2011.02.065.

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