Musical and verbal semantic memory: two distinct neural networks?

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Abstract

Semantic memory has been investigated in numerous neuroimaging and clinical studies, most of which have used verbal or visual, but only very seldom musical material. Clinical studies have suggested that there is a relative neural independence between verbal and musical semantic memory. In the present study, "musical semantic memory" is defined as memory for "well-known" melodies without any knowledge of the spatial or temporal circumstances of learning, while "verbal semantic memory" corresponds to general knowledge about concepts, again without any knowledge of the spatial or temporal circumstances of learning. Our aim was to compare the neural substrates of musical and verbal semantic memory by administering the same type of task in each modality. We used high-resolution PET H_2O^{15} to observe 11 young subjects performing two main tasks: 1) a musical semantic memory task where the subjects heard the first part of familiar melodies and had to decide whether the second part they heard matched the first, and 2) a verbal semantic memory task with the same design but where the material consisted of well-known expressions or proverbs. The musical semantic memory condition activated the superior temporal and the inferior and middle frontal areas in the left hemisphere and the inferior frontal area in the right hemisphere. The verbal semantic memory condition activated the middle temporal region in the left hemisphere and the cerebellum in the right hemisphere. We found that both verbal and musical semantic processes activated a common network throughout the left-sided temporal neocortex. In addition, there was a material-dependent topographical preference within this network, with the activation predominating anteriorly during semantic musical and posteriorly during semantic verbal tasks.

Keywords: semantic memory; music; verbal memory; temporal cortex; prefrontal cortex; PET

Introduction

Over the last few decades, neuropsychological studies of brain-damaged patients have revealed the compartmentalization of the musical and verbal domains of the brain (Luria et al. 1965; Signoret et al. 1987).

Specific abilities to perceive music may be selectively impaired in cases of amusia without aphasia (Eustache et al. 1990; Lechevalier et al. 1995). Moreover, the left hemisphere appears to be specialized for both rhythm, syntax and access to musical semantic representations (i.e. identification and recognition of melodies) (Peretz 1990; Platel et al. 1997; Patel et al. 1998) whereas the right hemisphere appears to be specialized for melodic (e.g. pitch contour) and timbre perception (Zatorre et al. 1992; Platel et al. 1997). In contrast with clinical and neuroimaging studies of music perception, there have been very few studies of musical memory and, rather surprisingly, the similarity and differences between language and music are mainly studied in the syntactic processing (Koelsch et al. 2002; Patel 2003) and rarely discussed for memory (Platel et al. 2003) .

The aim of the present study was to investigate if the musical semantic memory is sustained by a specific neural network; in other words, we looked for the neural substrates of the musical lexicon. As defined by Tulving back in 1972, "Semantic memory is the memory necessary for use of language. It is a mental thesaurus, organized knowledge a person possesses about words and other verbal symbols, their meaning and referents, about relations among them, and about rules, formulas, and algorithms for manipulations of these symbols, concepts, and relations. Semantic memory does not register perceptible properties of inputs, but rather cognitive referents of input signals." Nowadays, semantic memory in general is defined as the memory for concepts, regardless of the spatial or temporal circumstances of learning (Tulving 1985 ; Tulving 2001), while musical semantic memory in particular serves to register "well-known" melodies, but not the spatial or temporal circumstances of learning. This form of semantic memory enables us to identify songs and melodies or to have a strong feeling of knowing them.

Peretz (1996) reported the observation of a patient (CN) with bilateral temporal lesions who was able to learn verbal material, but not new musical tunes. This clinical case argues for the existence of a long-term memory system devoted to musical material. Starting from neuropsychological dissociations observed in clinical cases, Peretz et al., (1994) proposed a cognitive model of the access to musical lexicon. In this model, the recognition of a musical tune is based both on a melodic and a temporal dimension. This model postulates the

existence of a verbal and a musical lexicon. They are independent but still have a privileged relationship. Musical semantic memory, as considered in our study, can be assimilated to Peretz's musical lexicon. Both of these concepts (musical semantic memory or musical lexicon) differ from Koelsch et al.'s conception of the meaning of music (Koelsch et al. 2004). Actually, these authors considered that "aspects of musical meaning might comprise: (i) meaning that emerges from common patterns or forms; (ii) meaning that arises from the suggestion of particular mood; (iii) meaning arising from extra-musical associations and (iv) meaning arising from combinations of formal structures that create tension" (Koelsch et al. 2004). In fact, they referred to associations between musical perception and semantic meaning through sounds association with verbal concepts, but not to the idea of a musical lexicon *per se*.

Whereas numerous functional imaging studies have already examined the neural basis of semantic memory using mainly verbal and visual material (Cabeza and Nyberg 2000; Cappa 2008), only a handful of authors have studied semantic memory using very familiar musical material (Besson and Schon 2001; Platel et al. 2003; Satoh et al. 2006; Plailly et al. 2007). Besson and Schön (2001) argued that a distinction should be made between the long-term memory systems for music and language. Using the event-related brain potentials (ERP) method, they recorded differential ERP effects for semantic processing when subjects focused all their attention on either the lyrics or the music of opera excerpts. Halpern and Zatorre (1999) examined the cerebral network involved during a musical imagery task and suggested a right frontal lobe implication during the retrieval from musical semantic memory. Nevertheless, this last result could more reflect the musical episodic memory retrieval, as found in our previous study (Platel et al. 2003). Actually, the participants heard the melodies just before the experiment and had to judge their rate of familiarity. This reminder of familiar melodies could allow some subjects to refer to this melodies listening context when they imagined the following of the melodies.

Our previous PET study of the neural substrates underlying the semantic and episodic components of musical memory suggested the existence of a neural distinction between these two kinds of memory (Platel et al. 2003). Semantic memory for musical material seems to involve the left anterior temporal cortex. Satoh et al. (2006) studied cerebral blood flow by means of H_2O^{15} PET scanning during the recognition of familiar melodies. They observed the activation of the anterior part of both temporal lobes, the middle part of the left superior temporal gyrus and the medial frontal cortices. Using fMRI, Plailly et al. (2007) investigated the neural bases of the familiarity-based processing of music and odors. They reported

involvement of the left-sided frontal (e.g. inferior frontal gyrus) and parieto-occipital areas, for both types of stimuli. This result suggests that it is a multimodal neural system that contributes to the feeling of familiarity.

Contrary to neuropsychological studies of brain-damaged patients, neuroimaging studies of semantic memory have failed to demonstrate a clear-cut distinction between the neural networks involved in semantic retrieval processes for verbal and musical semantic memory. Thus, the question of independence between the musical and verbal lexicons remains open. Moreover, no neuroimaging study has so far directly assessed neural activity during comparable musical and verbal semantic memory retrieval tasks. The comparisons between language and music mainly focused on syntactic processing and suggested a common network as regards prefrontal brain areas and different structural representations in the posterior brain regions (Patel 2003; Koelsch 2006). Based on previous studies of musical syntax (Minati et al. 2008), musical semantic memory (Platel et al. 2003), and language (Vigneau et al. 2006), we hypothesized that there is a partial neural distinction between verbal semantic memory and musical semantic memory. This neural specificity for musical semantic memory would appear to be present throughout the temporal cortex and prefrontal areas. Tasks with musical material, i.e. nonverbal material, have usually been found to involve the anterior part of the temporal cortex, whereas tasks with verbal material tend to produce more posterior activations (Drury and Van Essen 1997; Platel et al. 2003 ; Vigneau et al. 2006). We therefore predicted that musical semantic processes would induce more anterior activations than verbal semantic processes, notably in the temporal cortex.

Subjects and methods

Subjects

Twelve healthy men (mean age = 23.6 years, range 20-27 years, S.D. = 1.96) were selected from a population of university students (mean educational level = 15.6, S.D. = 1.11) to take part in this study. All were right-handed (as determined by the Edinburgh Handedness Inventory, Oldfield, 1971) and had normal hearing.

Because musicians may develop specific cognitive strategies due to musical expertise, we purposely enrolled non-musicians (none had received music lessons or participated in musical performances) so that our findings could be generalized to most people. Our subjects also had to meet two additional criteria. First, they had to be "common listeners" (i.e. not music lovers, who tend to listen to one specific type of music only), and second, they had to score normally on two tests of pitch perception : (1) comparison of two sequences of notes varying exclusively in term of pitch difference of one note, 2) comparisons of pitch between two notes). Throughout the study, all participants were told that the experiment in which they were taking part related to the perception of music, but they were never informed that the musical and verbal components of semantic memory were being specifically studied, in order to avoid their memorizing melodies or very familiar French proverbs and popular sayings before the experiment. All gave written informed consent prior to participation and the research protocol was approved by the regional ethics committee.

Nature of the musical and verbal material

The musical material was drawn from a pre-experimental study featuring 31 "familiar"[1] tunes (data not shown). These were short tonal melodies (5s) (no lyrics) taken from both the classical and modern repertoires and played on a single instrument (flute). Popular songs and melodies associated with French lyrics were avoided so as to minimize verbal associations, as were those which might spontaneously evoke autobiographical memories, such as the "Wedding March" or melodies used in popular TV commercials. During the post experimental debriefing, we have verified that no one had looked for lyrics during the experiment. All melodies were rated as "very familiar" by more than 70% of subjects in a

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[1] Here are some examples of selected familiar tunes: Vangelis, "Conquest of Paradise"; E. Grieg, excerpts from the "Peer Gynt Suite".

pilot study of 50 subjects matched with the experimental sample. For the musical reference condition, we used 32 pairs of tonal sequences of notes (5s duration) played with the same instrument as those in the semantic musical task. The melodies used in this reference condition were real melodies, extracted mainly from the classical repertory, which were rated as "completely unknown" by more than 80% of the same pre-experimental sample. After completing the study, no participant declared having found any melody to be familiar to him. The sequences in one given pair were either the same or differed by the pitch of a single note. All musical stimuli were played by using a synthesizer set to flute-tone without orchestration and had a short length (between 5-7 seconds). The verbal semantic memory task used 35 "familiar" French proverbs or popular sayings[2] of approximately 4 seconds duration also drawn from a pre-experimental study. The sentences were uttered by a female speaker with as neutral a prosody as possible, in order to minimize their emotional contents. All were rated as "very familiar" by more than 70% of subjects in a pilot study of 50 subjects matched with the experimental sample. For the verbal reference condition, we constructed 35 "pseudo-sentences" of the same duration made up of non-words. We had chosen to use "pseudo-sentences" of non-words for the verbal reference task to avoid automatic semantic memory access, inevitable if we had used a lexical task with real words. Thus, the construction of the experimental material of our two reference tasks was guided by the two following objectives: 1] to obtain verbal and musical materials which were acoustically the nearest possible of the stimuli presented in the semantic tasks, with an aim of withdrawing the maximum of perceptual processes in the memory conditions; 2] to use stimuli not inducing automatic research in semantic memory, consequently unknown of the subjects (for the musical material), and not referring to words of the mother tongue (for the verbal material).

Paradigm

During the PET study, the participant was placed in a supine position on an adjustable table. An intravenous catheter was placed in the left arm for the administration of H_2O^{15}. Headphones were positioned on the subject's head, so that he could hear both the stimuli and instructions. He had to perform two similar categories of semantic memory tasks, one musical (hereafter called "MusSem") and one verbal ("VerbSem"). In the former, the subject heard the

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[2] Here are some examples of selected familiar French proverbs: "Strike while the iron's hot= Il faut battre le fer pendant qu'il est chaud"; "The more you get the more you want = L'appétit vient en mangeant"; "Every cloud has a silver lining = Après la pluie, le beau temps".

beginning of a well-known tune, followed by a short silence and a beep tone (mean interval 800ms), then either the next part of the melody or a different familiar melody. He had to decide whether the second part matched (i.e. was the end of) the first or not. If not, the second part belonged to another familiar melody (corresponding to 36.6% of stimuli). To highlight any specific activation brought about by musical semantic memory processes, the semantic memory task was contrasted with the perceptual control condition (the musical reference task or "MusRef") in which the subject was asked to indicate whether or not two original sequences of notes were similar. This task was supposed to call on decisional and motor processes to the same extent as the experimental task, but not on musical semantic memory since the musical sequences were unknown to the participant.

In the verbal semantic memory task, the subject listened to the beginning of a French proverb or popular saying, followed by silence and a beep tone (mean interval 800ms), and then by either the right or a wrong ending (which then belonged to another proverb). He had to decide whether or not the second part matched the first. This verbal semantic memory test was contrasted with the perceptual control condition (the verbal reference task or "VerbRef") in order to subtract the brain activation produced by decisional and motor processes. In this task the subject had to indicate whether or not two meaningless sequences of syllables (non-words respecting French phonological rules) were similar.

To resume the instructions: - for the semantic tasks, the participant had to press on the left button of a computer mouse (right index) if the continuation of the melody or proverb was the good one, and on the right button (right middle finger) if the continuation of the melody or proverb was not that expected. For the perceptual references tasks, the subject had to press on the left button of the mouse (right index), when the second melody or pseudo-words series was identical to the first sequence, and on the right button (right middle) when there was, in the second sequence, at least a note with a different pitch, or a different syllable in the second series of pseudo-words.

The difficulty of the verbal and musical semantic tasks was tested and adjusted during the pilot study. Each subject underwent 10 consecutive scans (injection of H_2O^{15}) during a single PET session lasting 1½ hours, including 2 repetitions of 4 different experimental conditions and 2 resting scans (see Fig 1). The musical task was given prior to the verbal task in order to reduce any possible verbal contamination during the musical task (i.e. by remembering or thinking of proverbs). During each scan, the subject was instructed to keep his eyes closed. The height of the table and the mouse location were adjusted for each subject to achieve the most comfortable position. Each task lasted 2 minutes and consisted of 15-18 stimuli

(depending on conditions) of 5 seconds duration. The response interval between two stimuli was set at 3 seconds in order to minimize automatic subvocal naming or episodic memory processes during this time.

Data acquisition

Behavioral data acquisition

Sound stimuli were presented at a comfortable loudness level using an E-Prime software. The responses and reaction times were recorded using a specific module written in E-Prime.

PET data acquisition

Measurements of the regional distribution of radioactivity were performed using a Siemens ECAT HR+ PET camera with full-volume acquisition allowing for the reconstruction of 63 planes. Transmission scans were obtained with a ^{68}Ga source prior to emission scans. The duration of each emission scan was 90 s. Approximately 6 mCi of H_2O^{15} were administered as a slow bolus in the left antecubital vein, using an automatic infusion pump. Each experimental condition began 30 s before data acquisition and continued until scan completion. This process was repeated for each of the 10 scans, for a total injected dose of ≈60mCi. The interval between injections was 6 min. 40 s. The head was gently immobilized in a dedicated headrest. Head position was aligned transaxially to the orbitomeatal line with a laser beam. The position of the head was checked with the laser beam prior to each injection.

Image handling and transformation

All calculations and image transformations were performed on Unix System workstations. First of all, the 10 scans of each subject were realigned, using AIR 3.0 software. For subsequent data analysis, we used Statistical Parametric Mapping software (SPM5, Wellcome Department of Cognitive Neurology) implemented in the MATLAB environment. The images were nonlinearly transformed into a standard space, i.e. the MNI PET template of SPM5. They were smoothed using a 12-mm Gaussian filter. As the images were scaled to an overall CBF grand mean of 50ml/100g/min., we shall refer to "adjusted rCBF" hereafter. We used a

gray matter threshold of 80% of the whole brain mean and covariates were centered before inclusion in the design matrix. We then used the same procedure as that described in Hubert et al. (2007;2008). An ANCOVA (analysis of covariance), with global activity as a confounding covariate, was performed on a voxel-by-voxel basis. The results of the t statistic (SPM {t}) were then transformed into a normal standard distribution (SPM {z}). The significant cut-off was set at the $p<0.001$ uncorrected for all multiple comparisons. The anatomical/cytoarchitectonic location of significant activation was based on the SPM5 MNI template. All the coordinates listed in the sections below are SPM5 coordinates.

Data analysis

Behavioral data analysis

We performed a repeated-measures ANOVA on performance and response time, and Tukey's post-hoc analyses.

PET scan analysis

Twelve sets of scans were acquired but only 11 were analyzed. One subject was excluded because of his poor experimental performance due to non-compliance with the instructions in one of the tasks.

Subtraction analyses: Using t-tests, two planned comparisons of means were carried out between each of the two semantic tasks and rest 'musical semantic – rest' (named hereafter MusSem-Rest) and 'verbal semantic – rest' (named hereafter VerbSem-Rest), in order to unravel the cerebral rCBF changes associated with perceptual, motor and semantic processes. The comparisons between each reference task and rest (MusRef-Rest) and (VerbRef-Rest) were realized to highlight the components related to acoustic processing, working memory and motor decision.

Similar analyses were conducted between each semantic task (verbal/musical) and its corresponding reference task 'Musical semantic – musical reference' (named hereafter MusSem-MusRef) and 'Verbal semantic – verbal reference' (named hereafter VerbSem-VerbRef). Hit rates were added as a covariate, to avoid possible confounding effects of any difference between musical and verbal subjects' performances (which was, indeed, the case, see Behavioral data below).

Although the direct comparison between the musical and the verbal semantic tasks seemed the more relevant contrast, this direct comparison allowed exclusively highlighting the more significant amplitude changes between the two tasks, including perceptual, executive and memory processes. Given that we had built these two memory tasks with very similar semantic processing, the more significant difference between them was produced in large part by the perceptual processes. Thus, to reveal brain activation specifically associated to musical semantic memory processes, excluding both the effects of perceptual activity and contamination by semantic verbal components, we performed the direct comparison between the two semantic tasks after the subtraction of the respective reference tasks [MusSem-MusRef] – [VerbSem-VerbRef]. We have also reported the results of the reverse comparison ([VerbSem-VerbRef] – [MusSem-MusRef]) that is expected to highlight the neural substrates of verbal semantic memory. These comparisons were carried out, using an explicit mask (p< 0.001 uncorrected for multiple comparisons), within the brain areas activated in the previous contrasts MusSem-MusRef and VerbSem-VerbRef, so as to remove differences that would result from deactivations.

Conjunction analysis: To identify the cerebral substrates involved in both the verbal semantic task vs. rest (VerbSem-Rest) and musical semantic task vs. rest (MusSem-Rest) comparisons, and thus to pinpoint the cerebral network associated with perceptual, motor and semantic processes, we used a conjunction analysis based on the recently proposed "valid conjunction inference with the minimum statistic" (Nichols et al., 2005). In this test, each comparison in the conjunction was individually significant, corresponding to the valid test for a "logical AND".

All activations are reported at *p<0.001* (uncorrected). This threshold was chosen in light of empirical studies showing that such a threshold protects against false positives (Bailey et al. 1991). Only activations involving clusters with more than 50 voxels are reported.

RESULTS

Behavioral data

The mean accuracy of performances was 85.45% (S.D.=9.74) for the musical semantic task, 98.39% (S.D.=2.60) for the verbal semantic task, and 95.24% (S.D.=5.50) and 98.17%

(S.D.=3.15) for the musical and verbal reference tasks respectively. The accuracy was lower for the musical semantic task than for either the verbal semantic or any of the reference tasks ($p<0.001$). These performances were not significantly different from those of the subjects in our pre-experimental population.

PET data

Semantic versus Rest

Comparing the musical semantic memory task with the resting state (MusSem-Rest) revealed bilateral activation of the superior temporal lobe (extending into the middle temporal lobe). When compared with rest (VerbSem-Rest), the verbal semantic memory task elicited bilateral activation of the middle temporal area, though this was more extensive on the left than on the right (Table1 and Fig.2). Using 2x2 repeated-measures ANOVA (on mean cluster values of each subject), we observed an interaction between the stimulus type and the side of activation. The temporal activation triggered by verbal material was mainly left-sided, whereas with musical material the temporal activation was mainly right-sided ($p< 0.001$ uncorrected).

Conjunction Semantic versus Rest

The conjunction analysis revealed activation in the bilateral middle and superior temporal lobe extending into the superior temporal pole and inferior frontal area (BA 11/22), and right activation in the angular (BA 39) and superior frontal areas (BA 11) (Table 1 and Fig. 2).

Reference versus rest

The comparison between musical reference task with the resting state (MusRef-Rest) involved bilateral activations of the superior temporal area (BA 22) (extending into the middle temporal region), right activation of the inferior and superior frontal gyri (BA 45/11), bilateral activations of the cerebellum structures and right activations of the inferior parietal area (BA 39) (Table 2 and Fig. 3). Verbal reference versus rest (VerbRef-Rest) revealed extensive activation of the bilateral superior and inferior temporal areas (BA 22), bilateral activation of the orbital part of the superior frontal region (BA 11), and right activation of the parahippocampal, amygdala (BA 48) and superior parietal area (BA 7).

Semantic versus Reference

Comparing the musical semantic with the musical perceptual reference task (MusSem-MusRef) revealed extensive activation of anterior part of the left superior temporal areas (extending into the superior temporal pole) and *pars triangularis* of the inferior and middle frontal areas (BA 38/47/48), as well as of the right inferior frontal (BA 44) and middle and

anterior cingulate areas (BA 32) (Table 3 and Fig. 4). Comparing the verbal semantic and verbal perceptual reference tasks (VerbSem-VerbRef) revealed activation of the posterior part of the left middle temporal area (BA 21) and right cerebellum (Table 3 and Fig. 4).

Musical versus Verbal

The comparison between musical and verbal semantic tasks ([MusSem-MusRef] – [VerbSem-VerbRef]) showed activation of the left inferior frontal areas (extending into the superior temporal pole) (BA 38/44) and the *pars triangularis* and orbital of the inferior frontal areas (BA 47) (Table 3 and Fig. 5).

Verbal versus Musical

The direct comparison between verbal semantic and musical semantic ([VerbSem-VerbRef] – [MusSem-MusRef]) implicated activation of the right cerebellum (verbal semantic task) (Table 3 and Fig. 5). Using a less conservative threshold for this comparison, we found an additional activation of the left posterior part of the middle temporal lobe.

DISCUSSION

The neural distinction between music and language has already been suggested in the neuroimaging literature of syntactic and semantic processing as in the synthetic model of the localization of music and language in the brain proposed by Brown and colleagues (2006). Nevertheless, this distinction had never been shown with direct comparisons between music and language using comparable semantic memory tasks.

Comparisons with rest:

Compared with the resting-state condition (Fig. 2), the musical and verbal semantic tasks triggered activation in similar temporal areas. These contrasts reflected both memory and perceptual processes. The left verbal semantic activation produced by the verbal semantic task was that which is habitually found in semantic processing, whereas the right posterior temporal activation produced by the verbal semantic task is classically involved in the processing of the human voice (Kriegstein and Giraud 2004; Alho et al. 2006). This activation was more bilateral during the musical semantic task than during the verbal one. Consistent with previous studies, we found predominant right hemispheric involvement for music, induced by the music perception processes and related mainly to tonal pitch perception (Limb 2006; Zatorre et al. 2007). The conjunction analysis between verbal and musical semantic tasks vs. rest (Fig. 2) revealed activation in the bilateral middle and superior temporal lobe

extending into the superior temporal pole and the inferior frontal area, as well as the right angular and superior frontal cortex. This activation reflects the common neural network involved in perceptual and semantic processes, whatever the nature of the material (verbal or musical).

Regarding our present results (Fig. 2 and 3) compared with rest and the comparison of cerebral activity in the reference musical vs. rest tasks, we observed bilateral activation restricted to the temporal area, with right hemisphere dominance. It seems likely that the right temporal activation was partly associated with perceptual processes, whereas the left temporal lobe seems to be more dedicated to semantic processes (Cabeza and Nyberg 2000; Thompson-Schill 2003) and feeling of familiarity (Plailly et al. 2007).

Comparisons with reference tasks:

When contrasting the participants' performances at the musical semantic vs. musical reference and verbal semantic vs. verbal reference tasks, the musical semantic task appeared to be more difficult than both the verbal semantic task and perceptual reference tasks, as already found in the pre-experimental study. This may be because in everyday life, non-musicians use words far more frequently than notes, and semantic verbal tasks are therefore comparatively easier than musical ones. As explained before, this bias was overcome by adding hit rates as a covariate in comparing the verbal and musical semantic tasks to each other.

Semantic Musical

Compared with the reference task, the musical semantic memory task was associated with a relative rCBF increase in the left superior temporal cortex, including its foremost part, the middle and *pars triangularis* both inferior frontal areas, as well as the right inferior frontal and middle and anterior cingulate areas. According to Copland et al. (2007), the right anterior cingulate is involved in the successful detection of a prime-target relationship. In our study, activation of the right anterior cingulate could be associated with the successful detection of the relationship between the beginning and the end of a melody, as our subjects had to decide whether or not the second part was the correct following. Whereas activations obtained in the left inferior frontal gyrus (BA 44/48, also named "Broca's area") seem to be associated to musical syntactic processing, as proposed by Koelsch et al. (2004). Therefore, these frontal activation could be linked to the detection of incongruity, producing a syntactic process (Tillman et al. 2003), particularly for the stimuli in which the second part of the melody does not match the first one. On the other hand, we think that activation in the left ventral frontal

area (BA 47) and in the temporal pole (BA 38) imply more specifically semantic processes (Greenberg et al. 2005; Satoh et al. 2006). In our musical semantic memory task, participants had to access their semantic memory to retrieve musical representations (knowledge) of the melodies they heard in order to decide if the following part was the correct one or not. During debriefing, all participants confirmed a semantic memory access to solve the task. Moreover, they were not able to recall the first time they heard a particular melody. Thus, activation of the left *pars triangularis* of the inferior frontal area, extending into the superior temporal pole, has previously been observed in studies of musical memory (Platel et al. 1997; Platel et al. 2003). Regarding the left inferior frontal area, similar results have been obtained with different musical material and experimental paradigms (Satoh et al. 2006; Plailly et al. 2007). Satoh et al. (2006) observed activation of the left inferior frontal gyrus during a recognition task of familiar music (compared to musical reference task). Plailly et al. (2007) also recorded activation of the left inferior and middle frontal gyrus prompted by feelings of familiarity for musical but also olfactory items (compared to unfamiliar items). Considering that in the musical semantic vs. perceptual reference task comparison the most of the common perceptual processes between the two conditions was subtracted, we think, therefore, that in our study, activation of the inferior and middle frontal gyrus could specifically reflect the feeling of familiarity for musical material (Kikyo et al. 2002; Kikyo and Miyashita 2004; Satoh et al. 2006; Plailly et al. 2007). These results are confirmed by the direct comparison between verbal and musical semantic processing (Fig.5). The left inferior frontal areas (extending into the superior temporal pole, BA 38) and the pars triangularis and orbital of the inferior frontal areas (BA 47) activate during the musical, but not during the verbal semantic memory task. This suggests they may be predominantly involved in the musical semantic processing.

In addition, left superior temporal pole activation has previously been demonstrated during the retrieval of specific or unique semantic information (for example: the Eiffel Tower in the "towers" category or concepts at a subordinate level) (Rogers et al. 2006; Patterson et al. 2007), abstract concepts (Fliessbach et al. 2006), personal semantic information (Svoboda et al. 2006), person identity information (Tsukiura et al. 2007), emotional material (Olson et al. 2007) and famous faces and buildings (Gorno-Tempini and Price 2001). Some authors have suggested that the left anterior temporal region may contribute to the processing of specific or unique semantic information (Martin and Chao 2001; Rogers et al. 2006; Tsukiura et al. 2007). As early as 1987, Jackendoff proposed in his semantic/conceptual structure theory a differentiation of knowledge for unique entities/categories terms. On the basis of these

previous findings, we can consider that each familiar melody refers to an unique semantic representation, just as face identity memory does (Gorno-Tempini and Price 2001). In other words, each individual melody is highly specific compared with other items in the same category and, as already postulated by Sacks (2006), memories for familiar melodies are specifically related to earlier personal events, encounters or states of mind evoked by listening to them. The anterior-posterior distinction hypothesis was postulated only for the left hemisphere. This view is not in disagreement with the clinical observations of pitch discrimination impairment following posterior temporal excisions (Liégeois-Chauvel et al. 1998) or with the results obtained by Halpern and Zatorre (1999) in their musical imagery task. These last authors observed, during a musical imagery task, activation in the right inferior frontal area and assumed that it reflected the involvement of these regions in the retrieval of familiar musical information but perhaps contaminated by episodic memory. In addition, considering the recent work of Peretz et al. (2009) regarding the cortical organization of the musical lexicon, we hypothesize that our right-sided activation preferentially refers to the storage in perceptual memory of the melodic traces for familiar tunes, as previously proposed by Samson and Peretz (2005) regarding the patients with temporal lesions (consistent with the idea of a participation of posterior temporal regions in musical perceptual processes, as found in the musical reference vs rest contrast, Fig 3). Whereas left-sided activation is linked to access to semantic attributes or associations (knowledge of style or personal information relating to a particular melody) involved in the explicit retrieval of melodies. Our PET findings are in good accord with this proposition: we found most right-lateralized activation in the MusSem-Rest contrast (Fig. 2) and MusRef-Rest (Fig. 3), reflecting certainly perceptual memory processes, and most left-lateralized activation for the MusSem-MusRef (Fig. 4), more specifically reflecting semantic memory associations. However, our participants were non-musicians, unlike those of Halpern and Zatorre who had an average of 9.5 years of musical education, and it is possible that bilateral (predominantly right) activations elicited by musical imagery were linked to the musical expertise during the musical information retrieval process.

Semantic Verbal

The verbal semantic memory task was associated with the activation of the left middle temporal area and right cerebellum. These temporal and cerebellar regions are usually highlighted in studies of semantic memory (Cabeza and Nyberg 2000; Thompson-Schill 2003) and are known to be particularly dedicated to language comprehension in general (Price 2000) and auditory comprehension in particular (Jobard et al. 2007). The middle temporal

gyrus was known to be the locus of lexical representation storage (Lau et al. 2008). The results of our study suggest that the verbal semantic memory of French proverbs and popular sayings draws on a more posterior part of the temporal cortex than does music. This finding is consistent with previous knowledge about the antero-posterior distribution of semantic representations across the left temporal lobe, with unique semantic information being more anteriorly represented than general semantic information (such as superordinate level concepts, as animals) (Martin and Chao 2001; Rogers et al. 2006). The verbal memory task used in our study probably referred to more general semantic representations than the musical memory task did. The verbal stimuli we used probably had little emotional and personal specificity compared with the musical ones, and the activation they brought about may reflect a category-specific effect (shared by everybody and associated with several concepts) rather than an item-specific one.

The right cerebellum activation observed during the verbal semantic task, in the 'Verbal semantic – verbal reference' comparison (Fig. 4) and in the direct semantic verbal comparison ([VerbSem-VerbRef] – [MusSem-MusRef]) (Fig. 5), is not surprising, given that this area has been shown to be involved in several cognitive processes, such as semantic memory or language comprehension and production. Right-sided cerebellar activation during semantic processing has been associated with the amplification and improvement of representations to facilitate correct decision-making (Booth et al. 2007). Our results are also consistent with the fact that the right cerebellum has reciprocal connections with the left lateral temporal cortex.

In summary, consistent with our previous studies (Platel et al. 1997; Platel et al. 2003), we observed activation throughout the left temporal and prefrontal cortex for musical semantic processes. In light of direct comparisons between language and music, we propose that our results are consistent with the hypothesis of antero-posterior temporal organization for semantic concepts, with musical semantic retrieval involving the anterior temporal lobe more than verbal semantic retrieval. To specify the nature of this neural distribution, we suggest that musical material may be associated with the retrieval of unique semantic representations (such as faces or famous buildings) involving left anterior temporal regions, whereas verbal material may be associated with the retrieval of more general semantic representations involving more posterior temporal regions.

To conclude, our results show that verbal and musical semantic memory processes mostly activate a left temporal and prefrontal neural network, previously described for semantic and syntax processing. However, within this left common network, it appears that

musical semantic processes involve to a greater extent the left anterior temporal areas and produce more bilateral activations than the verbal semantic ones. Consistent with clinical dissociations (Eustache et al. 1990), we found that verbal and musical material draw on two different networks, suggesting that the musical lexicon (Peretz and Coltheart 2003; Platel et al. 2003; Peretz et al., 2009) is sustained by a largely distributed bilateral temporo-prefrontal cerebral network involving right cerebral regions for the retrieval of melodic traces in perceptual memory, whereas left cerebral areas are linked to access to the verbal and non-verbal semantic attributes and knowledge of familiar tunes.

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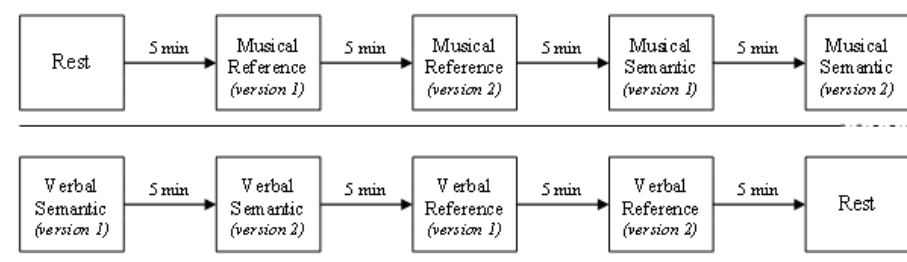
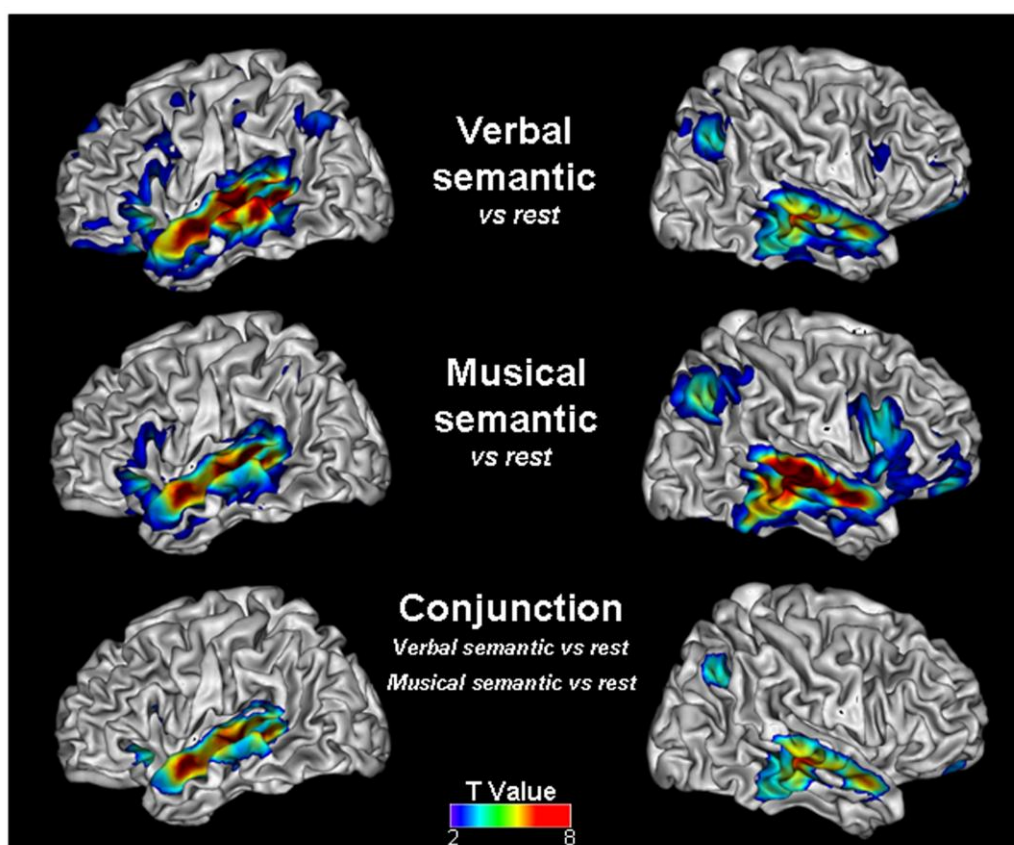*Fig. 1: Overall design of the experimental paradigm*

Fig. 2: PET scan comparisons: brain activations in the musical semantic tasks versus rest; and conjunction analysis of musical semantic versus rest and verbal semantic versus rest. Significantly activated regions with an uncorrected p-value threshold of 0.001, with multiple-comparison correction.
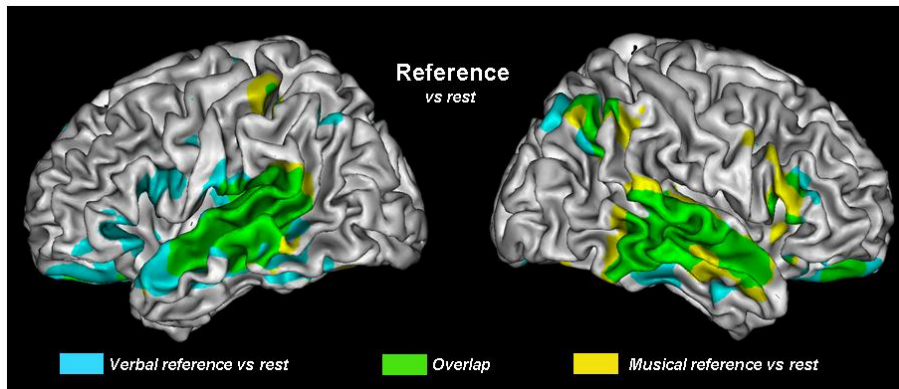
Fig. 3: PET scan comparisons: brain activation in the musical reference versus rest (yellow), verbal reference versus rest (blue) and overlap (green). Significantly activated regions with an uncorrected p-value threshold of 0.001, with multiple-comparison correction.
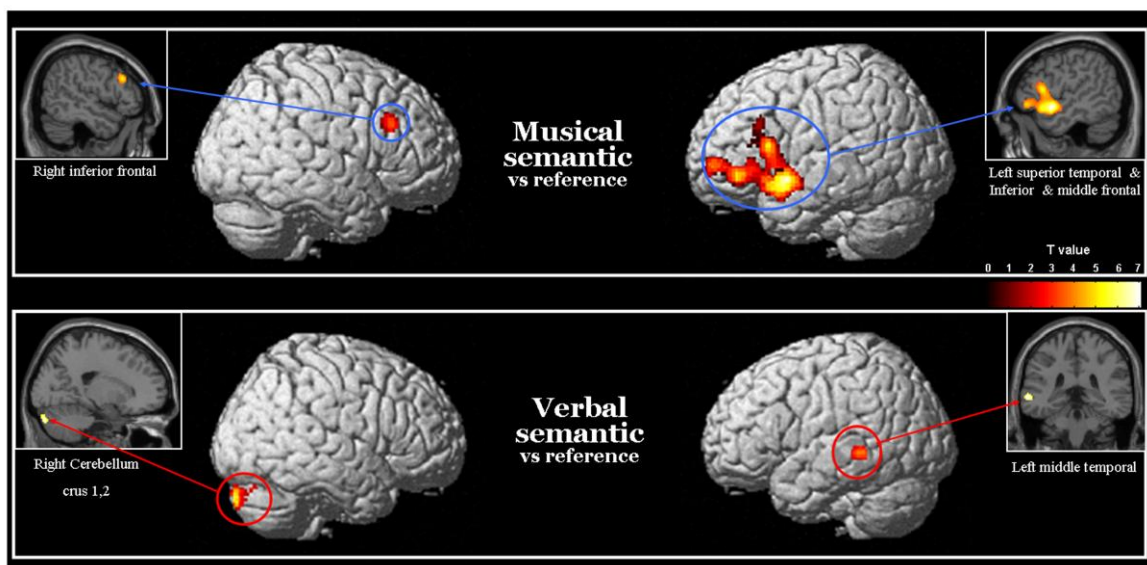

Fig. 4: PET scan comparisons: brain activation in the musical semantic versus musical reference tasks and verbal semantic versus verbal reference tasks (adding hit rates as a covariate). Significantly activated regions at the p-value threshold of 0.001 uncorrected for multiple comparisons.

Figure 5: PET scan comparisons: brain activation in the musical semantic versus verbal semantic [MusSem-MusRef] – [VerbSem-VerbRef] and verbal semantic versus musical semantic [VerbSem-VerbRef]-[MusSem-MusRef] (using an explicit mask). Significantly activated regions at the p-value threshold of 0.001 uncorrected for multiple comparisons. The plots represent the relative contribution of the different conditions of our paradigm, according to the "effect of interest", for selected peaks. The first column corresponds to the musical reference condition and the 2nd, 3rd, and 4th columns correspond selectively to the musical semantic, verbal semantic and verbal reference conditions.

Contrast and anatomical location	Cluster size (in pixels)	x	y	z	Z score
Musical semantic - Rest					
Right superior and middle temporal (Ba22)	7027	64	-20	0	> 7.80
Left superior and middle temporal (Ba22)	6010	-50	-20	0	> 7.80
Right angular (Ba39)	1192	40	-64	46	5.57
Right middle and superior frontal (Ba11)	553	18	48	-22	4.93
Right middle and anterior cingulate (Ba 32)	161	6	32	28	4.52
Left cerebellum crus I & II	387	-10	-82	-28	4.18
Right cerebellum	98	30	-62	-26	3.98
Verbal semantic - Rest					
Left middle and superior temporal (Ba22)	7755	-62	-20	0	> 7.80
Right superior and middle temporal (Ba22)	3890	58	-26	2	6.46
Right superior frontal (Ba11)	754	6	52	-20	5.02
Right angular (Ba39)	447	44	-62	42	4.98
Left superior frontal (Ba11)	405	-18	28	-20	4.32
Left inferior frontal (Ba48)	93	-38	12	28	3.93
Right cerebellum crus II	70	18	-88	-32	3.71
Left angular (Ba7)	88	-40	-70	42	3.61
Conjunction *(MusSem – Rest and VerbSem –Rest)*					
Left middle and superior temporal (Ba11)	5571	-52	-24	-2	7.33
Right middle and superior temporal (Ba22)	3767	58	-26	2	6.46
Right angular (Ba39)	441	44	-62	42	4.98
Right superior frontal (Ba11)	161	16	52	-18	3.83

Table 1. Brain regions activated during the musical semantic and verbal semantic tasks vs rest; and conjunction analysis of musical semantic vs. rest and verbal semantic vs. rest. Areas significantly activated at p<0.001 uncorrected.

Contrast and anatomical location	Cluster size (in pixels)	x	y	z	Z score
Musical reference - Rest					
Right superior temporal (Ba22)	4956	72	-30	6	>7.80
Left superior temporal (Ba22)	4159	-48	-22	0	7.44
Right inferior frontal (Ba45)	170	52	22	6	4.03
Right superior frontal (Ba11)	91	18	46	-22	3.97
Right cerebellum (Ba19)	147	28	-64	-22	3.90
Right cerebellum	63	16	-68	-50	3.75
Left cerebellum	79	-22	-86	-28	3.61
Right inferior parietal (Ba39)	93	48	-56	46	3.49
Verbal reference - Rest					
Left superior temporal (Ba22)	6265	-50	-20	0	7.77
Right superior temporal (Ba22)	3504	64	-16	-2	6.30
Left superior frontal (Ba11)	860	-18	32	-20	4.82
Right superior frontal (Ba11)	290	18	48	-22	4.36
Right parahippocampal/amygdale (Ba48)	131	22	10	-14	3.91
Left inferior temporal (Ba20)	135	-52	-46	-16	3.60
Right superior parietal (Ba7)	54	32	-78	46	3.59
Right superior frontal (Ba11)	77	12	28	-24	3.57

Table 2. Brain regions activated during in the musical reference vs. rest), verbal reference vs rest. Areas significantly activated at p<0.001 uncorrected, for all comparisons.

Contrast and anatomical location	Cluster size (in pixels)	x	y	z	Z score
Musical semantic - Musical reference					
Left pole superior temporal and inferior frontal (Ba38/47/48)	1774	-50	6	-10	5.81
Right inferior and middle frontal (Ba44)	135	52	26	30	4.41
Right anterior and middle cingulate (Ba32)	142	8	30	26	3.89
Verbal semantic – Verbal reference					
Right cerebellum crus I & II	320	24	-70	-30	4.26
Left middle temporal (Ba21)	54	-62	-38	0	3.70
Musical semantic					
Left inferior frontal, pole and superior temporal (Ba38/44)	299	-50	6	-10	4.54
Left inferior frontal (Ba47)	52	-40	40	-2	3.58
Verbal semantic					
Left cerebellum crus I	85	24	-70	-30	3.83

Table 3. Brain regions activated during the musical semantic vs. musical reference tasks and verbal semantic vs. verbal reference tasks (adding hit rates as a covariate). Verbal semantic corresponded to the [VerbSem-VerbRef] – [MusSem-MusRef] comparison and Musical semantic corresponded to the [MusSem-MusRef] – [VerbSem-VerbRef] comparison.). Areas significantly activated at p<0.001 uncorrected, for all comparisons.