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The neural substrates of musical memory revealed by fMRI and two semantic tasks

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ABSTRACT

Recognizing a musical excerpt without necessarily retrieving its title typically reflects the existence of a memory system dedicated to the retrieval of musical knowledge. The functional distinction between musical and verbal semantic memory has seldom been investigated. In this fMRI study, we directly compared the musical and verbal memory of 20 nonmusicians, using a congruence task involving automatic semantic retrieval and a familiarity task requiring more thorough semantic retrieval. In the former, participants had to access their semantic store to retrieve musical or verbal representations of melodies or expressions they heard, in order to decide whether these were then given the right ending or not. In the latter, they had to judge the level of familiarity of musical excerpts and expressions. Both tasks revealed activation of the left inferior frontal and posterior middle temporal cortices, suggesting that executive and selection processes are common to both verbal and musical retrievals. Distinct patterns of activation were observed within the left temporal cortex, with musical material mainly activating the superior temporal gyrus and verbal material the middle and inferior gyri. This cortical organization of musical and verbal semantic representations could explain clinical dissociations featuring selective disturbances for musical or verbal material.

Introduction

Semantic memory refers to memory for general knowledge, unrelated to specific experiences or the type of material used (e.g. words, faces or music). Clinical studies have revealed that patients sometimes retain musical abilities despite severe cognitive impairments such as aphasia or amnesia (Signoret et al., 1987; Cuddy and Duffin 2005; Samson et al., 2009). Based on neuropsychological dissociations reported in clinical studies, Peretz and colleagues (Peretz and Coltheart 2003; Peretz et al., 2009) have developed a cognitive model of the cortical organization of music recognition. This views the musical semantic memory system as a purely musical lexicon, which interacts with the verbal lexicon. In this study, musical semantic memory is defined as the long-term storage of familiar melodies or musical excerpts. It is musical semantic memory that allows us to experience a strong feeling of knowing when listening to music (reflecting familiarity processes) and gives us the ability to hum or whistle the subsequent notes of a melody, or in some cases retrieve the title, composer or performer of a particular excerpt (corresponding to identification) (Platel and Eustache, 2000). Whereas numerous clinical studies have supported the idea that musical knowledge and verbal knowledge are cognitively autonomous (for review, see Peretz 2008), few authors have investigated this issue using neuroimaging methods. The neural substrates of semantic memory have been unraveled using a variety of experimental paradigms in neuroimaging studies (Cabeza and Nyberg 2000; Binder et al., 2009). Semantic memory retrieval requires the activation of a large neural network, mainly located in the temporal and frontal cortices of the left hemisphere. When verbal material is used, semantic memory relies mainly upon the middle and inferior temporal and inferior frontal gyri in this hemisphere (for review, see Binder et al., 2009). The situation appears to be less clear-cut for musical material, however. Neuroimaging studies featuring this type of material have reported the involvement of the anterior part of the temporal lobes, either in the left hemisphere (Platel et al., 2003) or in both (Satoh et al. 2006), with activation of the middle part of the left superior temporal gyrus and the medial frontal cortices for recognition tasks (Satoh et al., 2006) and mainly of the left inferior frontal gyrus for familiarity tasks (Plailly et al., 2007). However, these studies did not allow direct comparisons to be made between music and language, and some of them used stimuli, such as nursery songs, which may also have elicited verbal processes.

In a previous H_2O^{15} PET study, we found that the verbal and musical sets of material used in a semantic congruence task drew on two close but partially distinct networks, located mainly in the left temporal cortex (Groussard et al., 2010). In this study, participants had to decide whether the second part of a familiar melody (musical congruence condition) or a French proverb (verbal congruence condition) was the right or wrong ending. They therefore had to access their semantic store in order to retrieve musical or verbal

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representations of the melodies or expressions they heard in order to decide whether they were then given the right ending or not. The post-experiment debriefing suggested, however, that the congruence task involved syntactic processes as well (i.e. corresponding to the detection of irregularities within the harmonic, melodic, rhythmic or metric structure), particularly for incongruent items.

In order to clarify this issue and to highlight the brain regions mainly involved in the as pure semantic retrieval process as possible, we chose to administer the same semantic tasks in the present study, using fMRI. In fact, using an event-related analysis, this makes it possible to exclude incongruent items which could involve syntactic processes.

Regarding the literature, it is now well established that both the difficulty and nature of the semantic task have an impact on the pattern of activation (Mummery et al., 1996; Muller et al., 1997; Cabeza and Nyberg 2000). Thus, in order to take our direct comparison of musical and verbal semantic tasks a stage further, we decided to administer a "semantic familiarity task" as well, requiring a more thorough semantic memory search to rate the level of familiarity of musical excerpts (musical familiarity condition) and French expressions (verbal familiarity condition) on a 4-point scale. In all the musical conditions, familiar musical stimuli were strictly selected (no excerpts with lyrics, and no excerpts which might spontaneously evoke autobiographical memories) in order to limit labeling and verbalization. These two tasks were highly complementary, in that the congruence task allowed us to explore musical semantic processing with as few verbal associations as possible but was also limited to an automatic search, whereas the familiarity task gave rise to more thorough semantic retrieval, but opened up the possibility of verbal labeling when the participants knew the melody extremely well, corresponding to identification (retrieving the title, composer or performer of the musical excerpt). The complementary aspects of these two tasks (i.e. congruence and familiarity tasks) investigating automatic and more thorough semantic retrieval, performed by the same participants, would allow us to increase the understanding of the functional organization of musical semantic memory and highlight the neural networks activated by verbal material, musical material or both. Previous studies have shown that semantic memory tasks with verbal or musical material activated the prefrontal and temporal areas mainly on the left side for verbal (Binder et al., 2009) and in both hemispheres for musical material (Platel et al., 1997, 2003; Satoh et al., 2006; Plailly et al., 2007). In addition, we recently proposed an anteroposterior organization within the left middle and superior temporal gyri (Groussard et al., 2010), such that there was predominantly anterior activation during the musical semantic task and predominantly posterior activation during the verbal one. Thus, comparing the performance of the same group of nonmusician participants on congruence and familiarity semantic tasks featuring verbal and musical materials, allows to examine more deeply these networks and the cognitive contribution of each cortical area.

Materials and methods

Participants

Twenty healthy right-handed volunteers (mean ± SD: 24.55 ± 3.80 years) were selected from a population of university students (mean education level ± SD: 16.35 ± 2.03 years) to take part in this study. All were nonmusicians (10 women and 10 men) with normal hearing and no history of neurological disease. Participants were selected according to stringent criteria: (1) none had taken music lessons or participated in musical performances (except for compulsory music classes at secondary school (1 hr per week)), (2) they were "common listeners" (i.e. not music lovers, who tend to listen to one specific type of music only), and (3) they scored normally on a test of pitch perception. All gave their written informed consent prior to taking part and the research protocol was approved by the regional ethics committee.

Stimuli and experimental procedure

All participants were tested on two memory tasks: a congruence task and a familiarity task. The order of these tasks was counterbalanced across participants.

Congruence task

In the congruence task, two similar categories of semantic memory tasks were performed: one using musical material (hereafter called "MusSem") and the other using verbal items ("VerbSem"). In the former, subjects heard the beginning of a well-known tune, followed by a short silence and a beep tone (mean interval 800 ms), then either the next part of the melody or a different familiar melody. They had to determine whether the second part matched (i.e. was the right ending to) the first one or not. This musical semantic memory task was contrasted with a perceptual reference condition ("MusRef") in which the subjects listened to two unfamiliar sequences of notes that were either identical or differed by one note, and then had to say whether or not they were the same. This task was designed to call on the same decisional, perceptual and motor processes as the experimental task, but not on musical semantic memory, since the musical sequences were unknown to the participants.

In the verbal semantic memory task, subjects listened to the beginning of a French proverb or popular saying, followed by a short silence and a beep tone (mean interval 800 ms), and then by either the right or wrong ending (one belonging to another proverb). They had to decide whether or not the second part matched the first one. This verbal semantic memory test was contrasted with a perceptual reference condition ("VerbRef") in order to subtract the brain activation produced by decisional, perceptual and motor processes. In this task, subjects had to indicate whether two meaningless sequences of syllables (nonwords respecting French phonological rules) were the same or if they differed by one syllable. The difficulty of the verbal and musical semantic tasks was tested and adjusted in a pilot study. The musical congruence task was designed to probe semantic processing with as few verbal associations as possible and thus, to make the contrast between melody and word processing as sharp as possible when comparing the activation results (no lyrics, and an instruction that did not involve trying to remember the title or composer of familiar melodies; see Supplementary material). For each task, subjects were instructed to respond by pressing the button with their right index finger if the response was "correct" (musical and verbal semantic tasks) or "similar" (musical and verbal reference tasks) and with their right middle finger if it was "incorrect" (musical and verbal semantic tasks) or "different" (musical and verbal reference tasks).

The musical and verbal stimuli were presented in two functional runs of sixteen 31–34 s blocks. Each run consisted of four blocks in each condition (alternating between musical reference, musical semantic, verbal semantic and verbal reference). The response interval between two stimuli was set at 3 s in order to minimize automatic subvocal labeling or episodic memory processes during this time.

Familiarity task

Like the congruence task, the familiarity task featured both musical and verbal materials. In this task, participants had to rate the level of familiarity of 60 excerpts of melodies and 60 French expressions on a 4-point scale (i.e. familiarity referring to the participants' life experience). Participants were instructed to press the button under the middle finger of their left hand if they were sure that they never had heard the melody or the expression before (Fam1), the button under the index finger of their left hand if they were not sure whether they had heard it before or not (Fam2), the button under the index