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Review

Impaired short-term memory for pitch in congenital amusia

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ABSTRACT

Congenital amusia is a neuro-developmental disorder of music perception and production. The hypothesis is that the musical deficits arise from altered pitch processing, with impairments in pitch discrimination (i.e., pitch change detection, pitch direction discrimination and identification) and short-term memory. The present review article focuses on the deficit of short-term memory for pitch. Overall, the data discussed here suggest impairments at each level of processing in short-term memory tasks; starting with the encoding of the pitch information and the creation of the adequate memory trace, the retention of the pitch traces over time as well as the recollection and comparison of the stored information with newly incoming information. These impairments have been related to altered brain responses in a distributed fronto-temporal network, associated with decreased connectivity between these structures, as well as in abnormalities in the connectivity between the two auditory cortices. In contrast, amusic participants' short-term memory abilities for verbal material are preserved. These findings show that short-term memory deficits in congenital amusia are specific to pitch, suggesting a pitch-memory system that is, at least partly, separated from verbal memory.

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Contents

1. Introduction

Congenital amusia (also sometimes referred to as tone deafness) has been described as a deficit in music processing, affecting both perception and production (Peretz, 2003, 2013; Peretz and Hyde, 2003; Tillmann et al., 2015; Williamson and Stewart, 2013). Individuals affected by this neurodevelopmental disorder, which is suggested to have a hereditary component (Peretz et al., 2007), report difficulties detecting when someone sings out of tune (including themselves), recognizing familiar tunes without lyrics, detecting wrong or out-of-tune notes, and memorizing (even short) melodies (Ayotte et al., 2002; Peretz et al., 2003). This latter deficit is also reflected in subjective complaints, such as for example, “I try to hold on the melody to remember it later on, but it just vanishes and disappears”.

Unlike acquired amusia following brain damage (Clark et al., 2015; Peretz et al., 1997; Tillmann et al., 2007), congenital amusia occurs without obvious brain injury or hearing loss (see Peretz, 2013). This disorder also occurs despite normal performance in tests investigating low-level auditory processing, cognitive processing (including memory), and language processing (e.g., see Ayotte et al., 2002; Foxton et al., 2004; Peretz et al., 2002 for extensive testing).

While this kind of congenital musical disorder has been described for a long time (Allen, 1878), it has been systematically studied only recently (e.g., Peretz et al., 2002), thanks to the development of a test battery providing common ground for diagnosis, the Montreal Battery for the Evaluation of Amusia, MBEA (Peretz et al., 2003). The MBEA tests listeners' capacity of music perception and memory, notably regarding the pitch dimension and the time dimension and also includes an incidental memory test. Four of the six subtests require short-term memory: participants listen to a short melody (from 7 to 21 tones), followed by a short silent retention delay (3 s) and then a second melody, which is either an exact repetition or contains a one-note-change (introducing a change of tonality, contour, interval or rhythm in four separated subtests). Participants have to indicate whether the two melodies are identical or different. The main deficit of individuals failing in the MBEA relates to the pitch dimension, thus detecting changes related to the insertion of an out-of-key tone, an altered contour or interval. In particular, the failure in the first subtest (see Fig. 1A), which requires detecting a change to a different tone that is out-of-key, has been described as having particularly strong diagnostic power (Peretz et al., 2008). The pronounced failure in the scale subtest of the MBEA might be due to the accumulation of amusics' impaired pitch discrimination, impaired pitch memory (see below) as well as impaired knowledge of the regularities of the Western tonal system. In contrast to the clear deficit on the pitch dimension subtests of the MBEA, the deficits in the time dimension seem to affect only half of the detected amusics (Peretz et al., 2003; see also Fig. 1A).

In the following, we will first review findings about pitch-related deficits as observed with psychoacoustic tasks in congenital amusia and then discuss experimental evidence showing that congenital amusics present a pitch short-term memory deficit, which might be central in the genesis of the disorder.

1.1. *Impaired processing of pitch in music, speech and psychoacoustic tasks based on tones*

In the research domain of congenital amusia, the proposed main hypothesis for the primary core deficit eliciting the amusic condition is a deficit of the processing of pitch. Processing impairments have been observed for different pitch-related materials (music, speech as well as tones presented out of musical contexts, as in psychoacoustic paradigms) and different experimental tasks (e.g., pitch change detection, pitch direction discrimination/identification, short-term memory tasks). These observations imply the possibility of impairments of pitch processing at different processing levels, notably from the extraction of pitch periodicity to mental representations of the tone information as well as of tonal structure. As pitch is a major form-bearing dimension in music (McAdams, 1989) and is used in Western tonal music with the minimal difference between tones of one semitone (i.e., 100 cents), a pitch-processing deficit might lead to the observed music-processing deficits, including the failure to acquire normal knowledge of the tonal system via mere exposure, as observed for non-musician listeners who are not amusic (e.g., Peretz and Hyde, 2003; Bigand and Poulin-Charronnat, 2006).

Congenital amusics' pitch-processing deficit is not restricted to musical contexts, which require tonal knowledge, but is also observed in tasks testing pitch processing out of musical contexts. Deficits have been shown when participants were asked to detect whether the pitch of one tone was changed in a sequence of (five) otherwise identical and isochronous piano tones, a task referred to as pitch change detection (Albouy et al., 2015a; Hyde and Peretz,

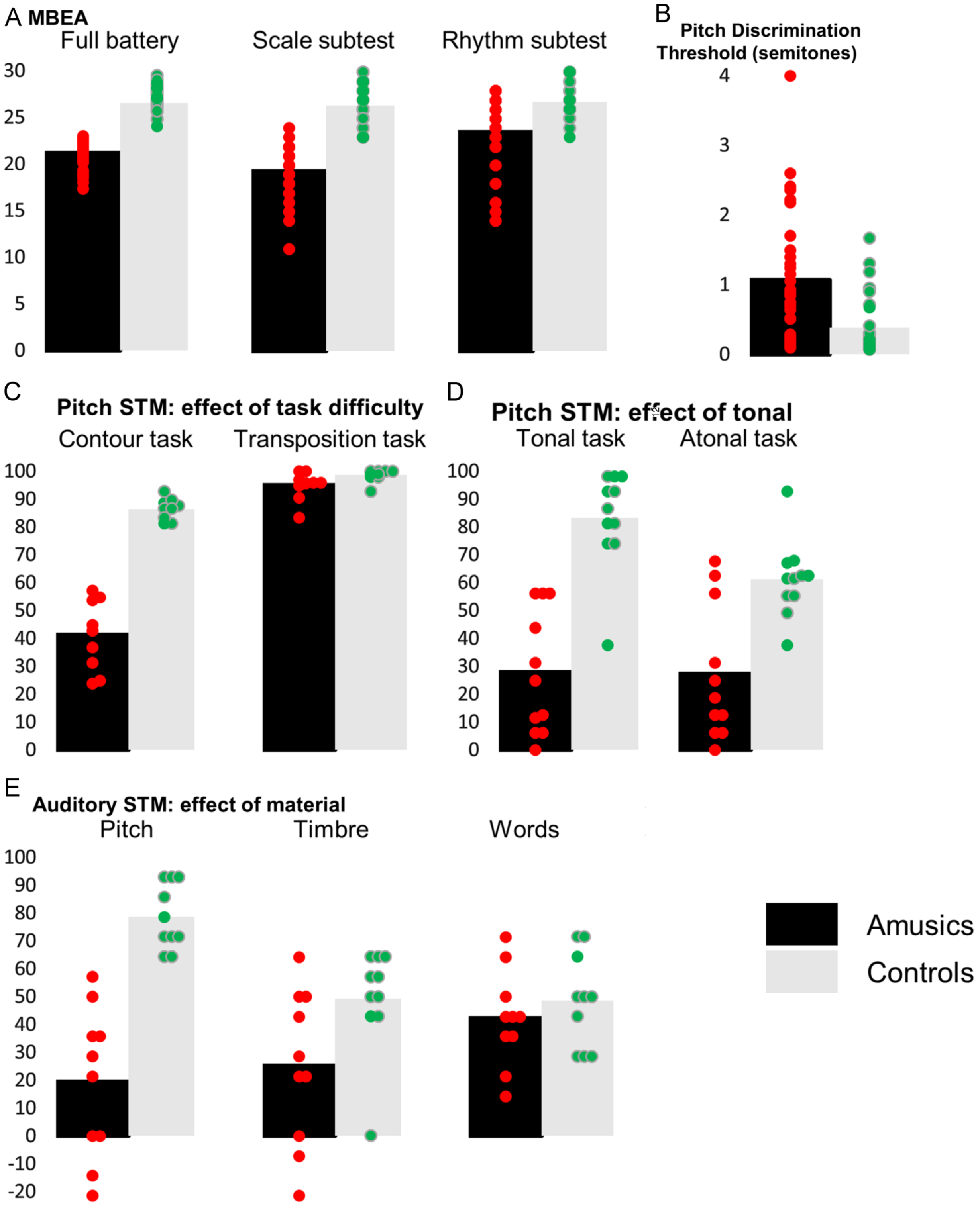

Fig. 1 – Group data for amusic and control participants presented together with individual data points (red: amusics, green: controls) for the following tests: (A) MBEA (Peretz et al., 2003), expressed as numbers of correct responses (maximum score = 30). Scores are presented for the entire battery (cut-off for amusia diagnosis = 23/30) and two of the six subtests (scale and rhythm, maximum score = 30 in each case). (B) Pitch Discrimination Thresholds (as measured in Tillmann et al., 2009) in semitones (for the same participants as in Fig. 1A). (C) Performance (presented in terms of percentage of Hits-False Alarms) in pitch Short-Term Memory tasks (data from Albouy et al., 2013a): a difficult task with only a single note changing in the second melody, creating a melodic contour change; and an easy task with a full transposition of the second melody. (D) Performance (presented in terms of percentage of Hits-False Alarms) in pitch short term memory tasks (data from Albouy et al., 2013b) with tonal and atonal melodies. (E) Performance (presented in terms of percentage of Hits-False Alarms) in auditory short-term memory tasks for pitch (melodies), musical timbre, and word materials (data from Tillmann et al., 2009). Data in A and B have been collected in Lyon over the last ten years (N_amusics = 34, N_controls = 34). N = 9 in each group in C, N = 11 in each group in D, and N = 10 in each group in E.

2004; Tillmann et al., 2011b). While controls performed at ceiling for a to-be-detected pitch change of a quarter of a semitone (25 cents), amusics needed a pitch change of 2 semitones (200 cents) to reach performance that was statistically significantly different from controls' performance (Hyde and Peretz, 2004). Psychophysical paradigms, which are using adaptive tracking paradigms with 2-down-1-up staircase methods (usually tested with two-interval forced-choice paradigms where participants have to report which of the intervals contained a pitch change, for example), have provided more fine-grained measurements, but congruently revealed that amusic individuals' thresholds for pitch change detection are increased (i.e., worse) in comparison to that of control participants (e.g., Cousineau et al., 2015; Foxton et al., 2004; Liu et al., 2010; Tillmann et al., 2009).

The deficit has also been observed in psychoacoustic tasks requiring the processing of pitch direction and measuring the thresholds of the minimum pitch difference necessary to be able to do the task (Foxton et al., 2004; Jiang et al., 2013; Liu et al., 2010, 2012, 2015), e.g., discriminating which of two (or three) pitch paires (or glides) is not in the same direction. Some studies have shown a stronger deficit for a pitch direction discrimination task rather than a pitch change detection task (e.g., reporting which tone pair contained a change) (Liu et al., 2010, Williamson et al., 2012, Foxton et al., 2004). This has led to the more specific proposition of the “melodic contour deafness hypothesis” (Patel, 2008; Liu et al., 2012), which states that reduced melodic contour perception (or impaired perception of the direction defined by the pitch intervals, that is up vs. down, for example) in congenital amusia may have prevented amusics from learning musical intervals and perceiving melodic structures. Liu et al. (2012) compared thresholds of pitch direction identification in discrete tones and in gliding tones[1] (for both verbal stimuli and complex tones): amusics showed higher thresholds in discrete stimuli than in gliding stimuli, suggesting that contour processing is not the only processing step that is impaired in congenital amusia. Furthermore, as some congenital amusics have pitch direction discrimination thresholds that are in the range of control participants' thresholds, Stewart (2011) suggested that the observed contour deficits might also include a deficit in short-term memory for pitch. She quotes one of the amusic individuals of her participant pool to introduce this hypothesis: “When the music finished, the sound was always gone – as though it had never happened. And this bewildered me with a sense of failure to hold on to what I had just heard” (page 631).

Beyond music, pitch contains relevant information also for speech material; this can be related to intentional and emotional prosody as well as to meaning (in tonal languages, such as Mandarin). In contrast to first reports having suggested intact speech processing (Peretz et al., 2002; Ayotte et al., 2002), more recent reports about congenital amusia have revealed pitch-processing deficits also for language materials, including syllables/words or sentences (Nan et al., 2010; Thompson et al., 2012; Tillmann et al., 2015), even though the deficit is less strong for verbal materials than for non-verbal (tonal) materials (Tillmann et al., 2011a, 2011b).

While some studies have reported strong deficits in pitch discrimination tasks for all tested amusics (Peretz et al., 2002; Hyde and Peretz, 2004), other studies have reported an overlap in pitch thresholds between amusic and control groups for pitch change detection and/or pitch direction judgments (Albouy et al., 2013a, 2013b, 2015a; Foxton et al., 2004; Jiang et al., 2013; Jones et al., 2009; Liu et al., 2010; Omigie et al., 2013; Tillmann et al., 2009; Williamson et al., 2012), showing that some amusics have thresholds within the range of control participants (see Fig. 1B).

1.2. *The hypothesis of impaired short-term memory of pitch*

While some amusics exhibited normal pitch thresholds in psychoacoustic tasks, they all showed impaired short-term memory for pitch (Albouy et al., 2013a, 2013b; Tillmann et al., 2009; Williamson et al., 2010; Williamson and Stewart, 2010) (see Fig. 1C: Contour Task, Fig. 1D: Tonal Task, and Fig. 1E: Pitch Task). These observations have led to the hypothesis of impaired short-term memory of pitch in congenital amusia.

In a standard auditory short-term memory paradigm, participants are presented with two sound sequences S1 and S2 (e.g., pitch sequences forming simple melodies) separated by a retention interval (delay), and are asked to compare the two sequences, which might for example differ in a single note, in order to judge whether the two sequences are the same or different.

Recent studies (Jiang et al., 2013; Peretz, 2013; Vuvan et al., 2015) have suggested that perceptual impairments, as revealed by pitch discrimination tasks (testing either pitch change or pitch direction), can influence short-term memory deficits in congenital amusia. Indeed, amusics' pitch memory performance improves as the distance between a standard and a comparison element becomes larger (Albouy et al., 2013a; Jiang et al., 2013; Tillmann et al., 2009). Amusics' performance was better when the change in the second melody of the pair created a contour violation or involved a larger pitch interval change than when it preserved the contour or involved a smaller pitch interval change (Albouy et al., 2013a, 2013b; Tillmann et al., 2009). However, this influence is similar to the one observed for control participants (except in conditions where ceiling performance was reached). Most importantly, amusics' deficit in memory performance persists for amusics who have pitch discrimination thresholds that are in the range of control participants' thresholds as well as when the to-be-detected pitch changes (in the memory paradigm) are larger than the pitch discrimination thresholds of each amusic individual (i.e., tailored individually) (e.g., Foxton et al., 2004; Tillmann et al., 2009 (see Fig. 1E); Williamson et al., 2010). These findings thus exclude perceptual, low-level explanations as the sole explanation of the impaired memory performance.[2] Further

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[1] Tone pairs were presented and participants were requested to identify the pitch direction with the following questions: “Which pitch pattern did you hear (high-low or low-high)? » for discrete stimuli, and “which pitch pattern did you hear (rising-falling or falling-rising)?” for gliding stimuli.

[2] These findings also contradict the conclusion of Jiang et al. (2013) who claimed that pitch memory deficits simply reflect amusics' impaired pitch discrimination. However, in Jiang et al. (2013), as a consequence of their rather difficult threshold

support for a pitch memory deficit in amusia has been provided by the observation of a stronger destructive effect of interference (i.e., additional tones presented during the delay) as well as of increased retention delay in amusia in comparison to controls, results suggesting weak, unstable memory traces in amusia (Williamson et al. 2010, Gosselin et al. 2009).

It is important to point out that amusics' impaired short-term memory for pitch cannot be explained by a general deficit of short-term memory. Amusic participants do not show any deficits for short-term memory with verbal materials, such as the classical forward/backward span tasks (Albouy et al., 2013b; Marin et al., 2012; Williamson and Stewart, 2010) or the short-term memory task (S1 – delay – S2, requiring a same/different judgment) with words (Fig. 1E, Tillmann et al., 2009). Note however that timbre memory is also deficient in amusia, even though less strongly (Fig. 1E, Tillmann et al., 2009; Marin et al., 2012), suggesting the use of spectral pitch information in timbre (i.e., frequency-related information) for timbre memory and/or some shared neural resources for pitch and timbre memory.

These data patterns have led us to propose the hypothesis that the main deficit underlying the amusic condition lies in the short-term memory for pitch information (Tillmann et al., 2009, 2015). Impaired pitch memory would lead to low performance scores not only in the MBEA, but also in pitch change detection tasks, and pitch direction discrimination or identification tasks. Indeed, any psychophysical paradigm testing pitch change detection requires keeping in memory the stimulus of one presentation interval and comparing it with the other(s) presentation interval(s). Similarly, pitch-direction judgments (whether discrimination or identification) require a memory trace of the previous tone(s) and its comparison with the pitch of the current tone (Demany and Semal, 2008)[3]. This observation highlights that auditory perception and its investigation also involve memory, in particular due to the sequential nature of the stimulus presentation. Depending on the severity of the short-term memory deficit, the comparisons and judgments in psychophysical paradigms testing pitch change detection and/or pitch direction might be impaired because of a weakened or faulty memory trace. This hypothesis based on one common underlying deficit might explain the data patterns reported in previous research. For example, amusics with normal pitch discrimination thresholds might have a less severe memory deficit, allowing them to perform normally after a very short delay (as in psychophysical tasks), but leading them to fail as soon as longer retention delays are used, such as in classical short term memory tasks or the MBEA. However, in cases of a more severe memory deficit, amusics might also fail in tasks requiring comparisons over shorter time spans as used in psychoacoustic tasks. Currently, we cannot separate this hypothesis from the possibility that there might be different subtypes of congenital amusia: amusic individuals with pitch memory deficit with or without associated pitch discrimination deficits (Tillmann et al., 2015). Here, we focus on the first, more parsimonious hypothesis, postulating one underlying mechanism (with a deficit of different degrees in pitch memory) explaining the various data patterns.

In the following, we review studies that have investigated amusics' short-term memory of pitch information. For that aim, we regroup the findings according to three processing steps that are relevant in short-term memory: 1) encoding (processes whereby information is registered); 2) storage or retention (maintenance of information over time); and 3) retrieval or recollection (accessing information by recall or recognition).

This presentation structure was chosen for clarification, even though there is some overlap because results might be due to impaired processing in more than one of the processing steps. This research domain also benefits from the advantages of acquiring neurophysiological recordings, which allow for investigating the three processing steps. The overall data suggest impairments in all three processing steps; starting with the encoding of the pitch information and the creation of the adequate memory trace, the retention of the pitch traces over time as well as the recollection and comparison of the information. It remains to be investigated in how far the deficits in the first step might cause deficits in the next steps or whether these deficits might be based on independent impairments of the system.

1.3. *Impaired encoding of pitch information*

A set of behavioral and neuroimaging studies suggest that amusic individuals show impaired functioning of the early steps of memory processing (encoding and building of the pitch memory traces), which thus might lead (or contribute) to the impaired performance in pitch-related tasks, whether requiring pitch discrimination (in psychoacoustic tasks involving short delays between stimuli that change in pitch or direction) or short-term memory with an introduced, longer delay.

Behavioral evidence comes from two recent studies investigating amusics' pitch encoding abilities as a function of the duration given to encode the auditory information presented in a pitch discrimination task or a memory task (Albouy et al., submitted for publication; Cousineau et al., 2015). Psychoacoustic studies in typical listeners have revealed that the building of optimal pitch traces might take up to a few hundred milliseconds (Demany and Semal, 2005; Massaro and Idson, 1977; Massaro and Loftus, 1996). Albouy et al. (submitted for publication) showed that while amusic individuals exhibit decreased performance as compared to controls when time to encode the information was short, they were performing as well as controls when the duration of the to-be-encoded material was sufficiently long (more than 350 ms per note, Fig. 2). Moreover, the benefit of increasing the time available to encode pitch information was present in both

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(*footnote continued*)
paradigm, the pitch changes seem to have overcorrected amusics' deficit as amusics actually performed better than control participants. It is further worth noting that overall performance was close to or even at chance level in their memory paradigms.

[3] This also applies for gliding tones, which requires comparing information across different time points. The involvement of memory might be further enhanced when tested in psychoacoustic paradigms that require the comparison of different stimuli (e.g., "is the first or second sound going up?" (Foxton et al., 2004); "did you hear rising–falling or falling–rising?" (Liu et al., 2012); or determining the "odd-one out", the first or last sound of three sequentially presented sounds (Liu et al., 2010).

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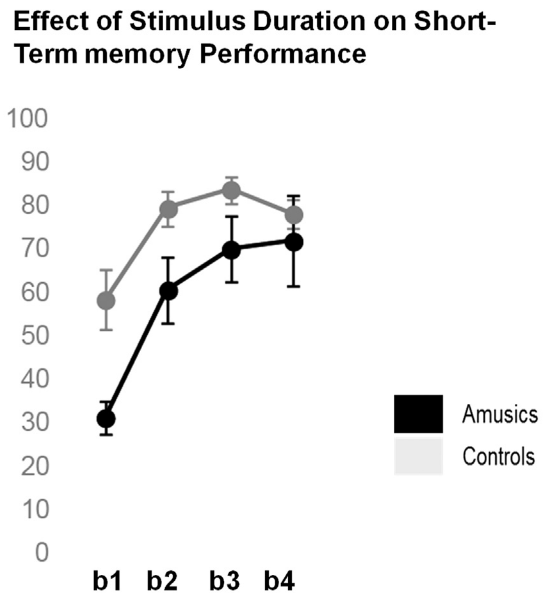

Characteristics	b1	b2	b3	b4
Tone duration (d) in ms	100	100	350	350
Inter Tone Interval (ITI) in ms	0	250	0	350
Stimulus Onset asynchrony (SOA) in ms	100	350	350	700

Fig. 2 – Amusics' and controls' performance for a short-term memory task in which participants were required to compare two 4-tone Sequence presented with a 2-s delay. When the melodies were different, only one tone changed in the second melody and created a contour change. Data are presented in terms of percentage of Hits-FAs as a function of different blocks varying in stimulus duration. Stimulus characteristics are presented the table. Black circles, amusics; grey circles, controls. Error bars indicate the standard errors of the means, SEM. Adapted from Albouy et al. (submitted for publication).

participant groups, but stronger in amusics than in controls, thus suggesting that the time constraints for pitch encoding differed between the two groups. Amusics would thus need more time than controls to properly encode the sounds (i.e., to construct a proper memory trace). These findings suggest that increasing the duration of the to-be-encoded material (by increasing tone duration, adding an inter-tone interval, and/or increasing stimulus onset asynchrony) would allow for more reliable representations of pitch to be formed in the amusic brain, and would in turn lead to increased discrimination (and memory) performance.

The hypothesis of impaired, or delayed, encoding of pitch in the amusic brain has also received support in a MEG study investigating short-term memory for pitch in congenital amusia (Albouy et al., 2013a). During the encoding of melodies, the amusic brain elicited abnormal (decreased and delayed) N100m components in bilateral Inferior Frontal Gyri (pars opercularis, BA 44) and auditory regions (Heschl's Gyrus, Superior Temporal Gyrus). These altered responses were interpreted as reflecting impaired and delayed encoding of pitch information (see Fig. 3A). Furthermore, these abnormal responses were associated with abnormal connectivity: Dynamic Causal Modeling (David et al., 2006) revealed decreased intrinsic connectivity in both auditory cortices, associated with increased lateral connectivity between left and right auditory cortices as well as decreased right fronto-temporal backward connectivity in amusics relative to controls (Fig. 3B) (Albouy et al., 2013a; see also Hyde et al., 2011; Lévêque et al., submitted for publication, for converging fMRI data). These findings were consistent with the involvement of temporo-frontal regions (bilateral, although with an asymmetry in favor of the right hemisphere) in pitch and melody processing and memory, as observed in normal participants with functional cerebral imaging (Gaab et al., 2003; Griffiths, 1999; Janata et al., 2002; Koelsch et al., 2009; Peretz and Zatorre, 2005; Schulze et al., 2009; Tillmann et al., 2003, 2006; Zatorre et al., 1994) and were congruent with anatomical anomalies observed along the temporo-frontal pathway in the amusic brain (Hyde et al., 2006, 2007; Loui et al., 2009; Mandell et al., 2007). The hyper-connectivity between the two auditory cortices has been interpreted as either a marker of the primary deficit or an attempt to compensate for impaired right auditory cortex functioning, during both passive listening (Hyde et al., 2011) and when performing a memory task (Albouy et al., 2013a).

1.4. *Impaired maintenance of pitch information*

Both behavioral and neurophysiological studies have provided evidence for impaired retention of pitch information in amusics' short-term memory. Up to now, both investigation methods have been applied to short-term memory tasks requiring only the maintenance of the previously presented information, but have not yet investigated the manipulation of the to-be-retained information during the delay period, as would be required in more classical working memory tasks (Baddeley, 1990). However, we can make the hypothesis that amusics would be impaired also in this more complex processing type involving working memory of pitch.

When testing short-term memory with delayed-sample-to-standard matching paradigms, a set of behavioral data has revealed amusics' difficulty in maintaining pitch information over the retention interval. Amusic participants were more sensitive than controls to increased memory load, added interference, and increased retention delay. A weaker and more unstable memory trace was suggested by stronger performance decrease for increased memory load in amusics: when the to-be-remembered tone sequence was increased from three to five tones, performance was only slightly affected for controls, but decreased significantly for amusics (Gosselin et al., 2009). When the retention interval was either silent or filled with irrelevant tones, congenital amusics showed a stronger interference effect and performed worse than controls when irrelevant tones were inserted between the to-be-compared tones (Gosselin et al., 2009). When increasing the duration of a silent retention period between the to-be-compared tones from 0 to 15 s, amusic participants showed faster decline in performance with increased retention delay than did controls (Williamson et al., 2010).

Oddball paradigms have also been used to study the decay of sound memory traces in auditory sensory memory with active behavioral paradigms and/or neurophysiological recordings. The repetition of a standard tone sets up a reference in sensory memory, which constitutes a basis for developing

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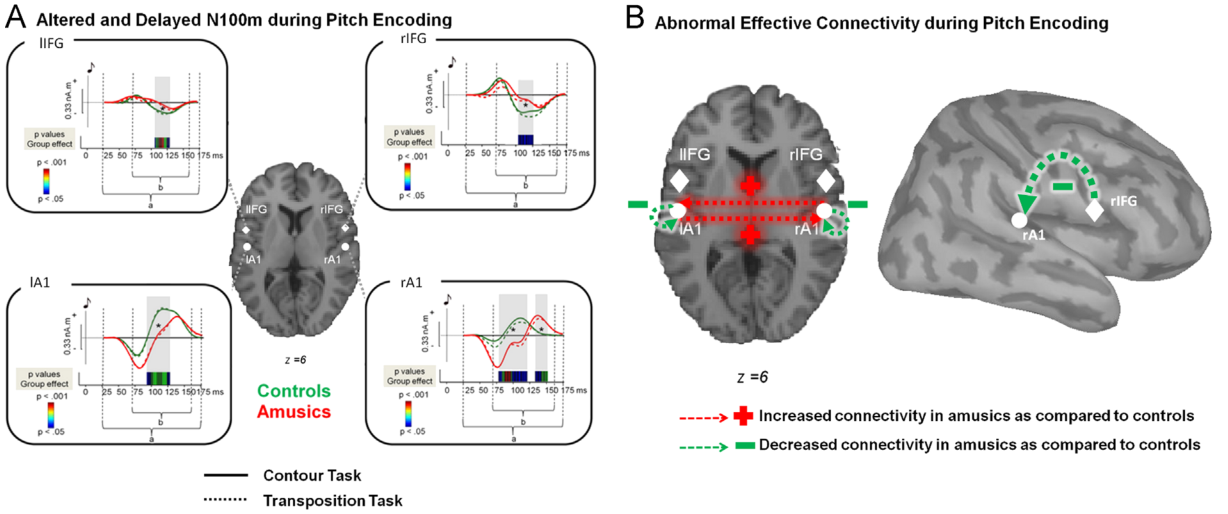

Fig. 3 – (A) Source reconstruction of the brain responses evoked during the encoding of S1 in a short-term memory task (S1, delay, S2, see Albouy et al. (2013a) for details, and Fig. 1C for behavioral data). Coordinates of the peaks of activations are displayed on the single subject T1 image provided by SPM8 for four regions: the bilateral auditory cortices as well as the bilateral pars opercularis of the Inferior Frontal Gyrus. The surrounding panels correspond to the grand average of source data for each region and for the time window where the inversion was performed (25–175 ms after the tone onset, as indicated by a) for the control group (green) and amusic group (red), for the contour task (CT) (full lines) and the transposition task (TT) (dotted lines). For the N100m analysis, ANOVAs were performed at each time sample and for each region on source amplitude in the 70–160 ms time window (as indicated by b) in the two groups of participants. *p*-values for the main effects are reported across time below source amplitudes. Note that only effects lasting longer than 15 ms were reported. Color bar represents the *p*-values for the Group effect with blue for $p<.05$; green for $p<.01$; and red for $p<.001$. Adapted from Albouy et al. (2013a). (B) Results of the Dynamic Causal Modeling analysis for the encoding of melodies in a short-term memory task (S1, delay, S2). Dashed arrows indicate connections that significantly differ between between controls and amusics (in green: controls > amusics; in red: amusics > controls).

predictions, and to which each new auditory input is automatically compared. When the input does not match with this memory trace (prediction-error), a Mismatch Negativity (MMN) is automatically generated. The results of Moreau et al. (2013) using this type of protocol with EEG have suggested normal responses to deviant sounds in amusic individuals, even with a small deviance size (25 cents). The used Stimulus Onset Asynchrony (SOA) was relatively short (500 ms). Under the hypothesis that memory traces are weaker and/or more prone to decay with time in amusics than in controls, a larger SOA should alter behavioral deviant detection (and the MMN) more strongly in amusics than in controls. We thus presented series of complex tones and asked amusic and matched control participants to detect deviant tones within these series (Lévêque et al.,; we present here a subset of the behavioral data of this study testing 11 amusic individuals and 11 control participants). Two SOAs were tested: 500 ms and 1500 ms. Deviants were 200 cents above the standard tone (1047 Hz), and occurred with a probability of 15%. As a control condition, blocks with intensity deviants (i.e., a deviance of 20 dB) were added (also with a deviant probability of 15%). Results revealed that, even though amusic participants were able to detect all of the (fairly large) deviants as well as control participants in both SOA conditions, reaction times of amusic participants were more negatively affected by the increased SOA than were reaction times of control participants (as reflected in an interaction between participant groups and SOAs, $p=.038$; see Fig. 4). This finding shows that even when a deviant is properly detected by amusic participants, its trace in sensory memory seems to decline faster or to be less rapidly accessible to consciousness after a silent period of 1400 ms. The cerebral signatures of these behavioral effects as well as the observation that this effect was similar for frequency and intensity deviants warrant further investigation.

Recording the MEG signal during the retention interval of short-term memory tasks has further revealed functional anomalies in the amusic brain, notably by analyzing the oscillatory activities in two frequency bands (Albouy et al., 2012, 2013a): activities in the gamma range, which were expected to be high in regions involved in short-term memory processing (Kaiser et al., 2008), and activities in the alpha-band, which were expected to be stronger in brain areas specialized in processing that is unrelated to the task (Klimesch et al., 2007). These analyses were done for two pitch memory tasks (see behavioral data Fig. 1C): a difficult task, where the changed melody S2 concerned only one note (introducing a contour change), and an easy task, that amusics were able to perform as well as controls, where the change of S2 involved a complete transposition (7 semitones above/below S1).

For the difficult contour task, oscillation power in the gamma band in the right dorsolateral prefrontal cortex was stronger in controls than in amusics (see also Kaiser et al., 2008). Conversely, for the easier transposition task, for amusics, we observed stronger contralateral recruitment (left IFG) and a stronger involvement of the right temporo-parietal junction than in controls (Fig. 5A). This pattern of results highlights right frontal anomalies in congenital amusia,

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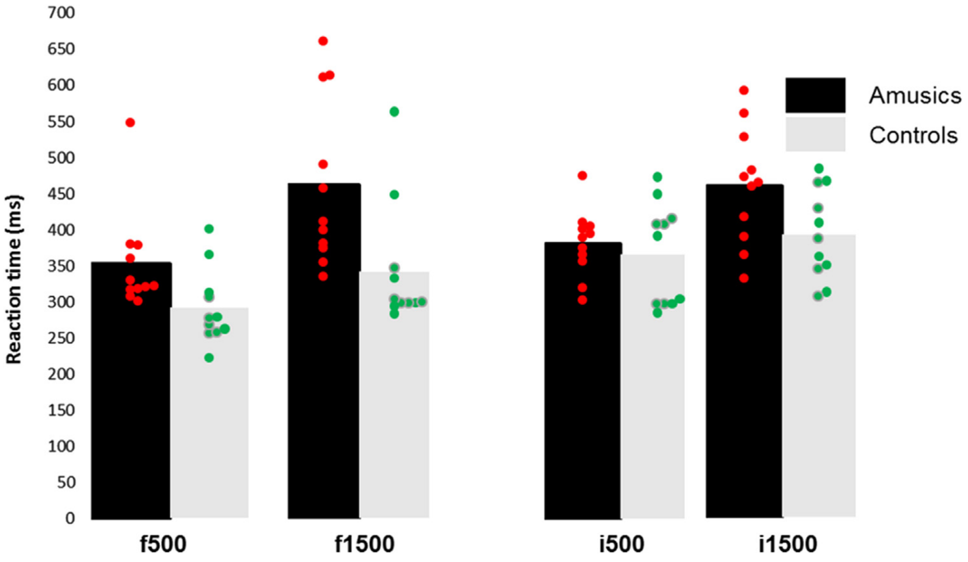

Fig. 4 – Reaction times (ms) for the amusic group ($N=11$) and the control group ($N=11$) for detecting frequency (f) or intensity (i) changes in oddball sequences, presented as a function of the SOA (500 or 1500 ms). See main text for details.

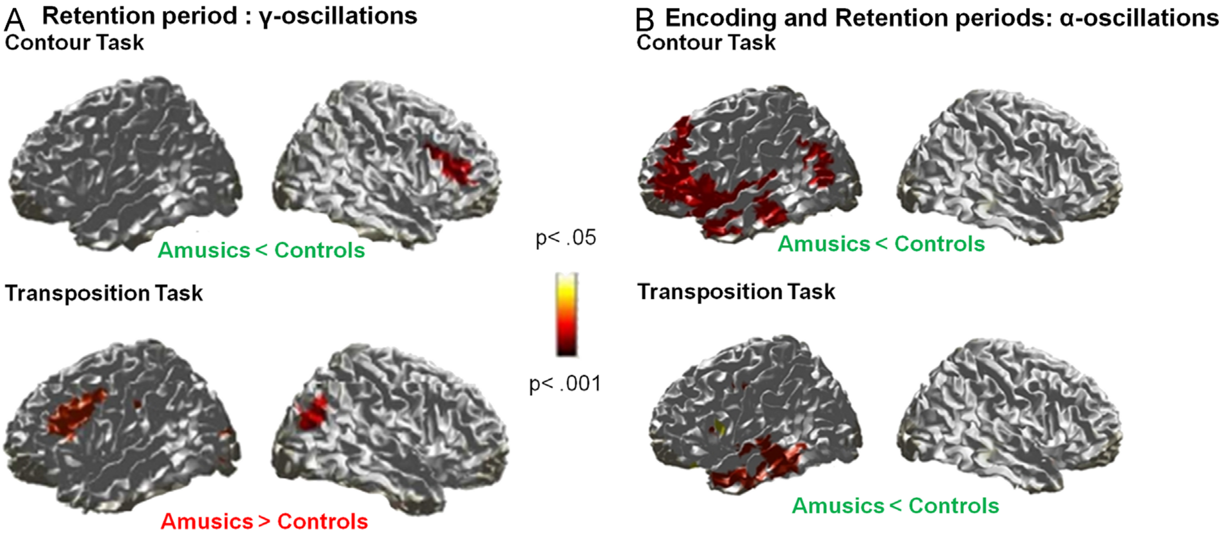

Fig. 5 – (A) Cortical meshes showing regions where gamma-power was significantly different between groups during the retention period of two short-term memory tasks (upper panel, Contour Task; lower panel, Transposition task- see Fig. 1C). *p*-values (two sided *t*-tests corrected for multiple comparisons using cluster-level statistics) for the Group effect are color-coded with yellow for $p<.05$; red for $p<.01$; and black for $p<.001$. Adapted from Albouy et al. (2013a). (B) Cortical meshes showing regions where alpha-power superior in controls in comparison to amusic individuals for both S1 and the retention delay. Red regions represent significant *p*-values (two sided *t*-tests corrected using cluster-based multiple comparison) in controls (upper panel) and amusic individuals (lower panel). Adapted from Albouy et al. (2012).

which might be, in the case of the easy task, compensated by a recruitment of other auditory-related areas normally less involved in pitch memory, such as the contralateral left IFG and right temporo-parietal regions.

Furthermore, during the retention period, amusic individuals did not show the task-related modulation of oscillatory activations in the alpha band that was observed for the controls (see Fig. 5B). In particular, for control participants, during both S1 and the retention delay, enhanced alpha-oscillations were observed in cortical areas that are specialized in processing stimuli that are unrelated to the task, that is the left fronto-temporal pathway and bilateral visual cortical areas (see also Obleser et al., 2012 for data of typical individuals). This finding again suggests an atypical involvement of the two hemispheres in pitch memory tasks in congenital amusia.

1.5. *Impaired retrieval of pitch information*

Behavioral data cannot easily disentangle the three involved steps in short-term memory paradigms using recognition tasks: amusic individuals show decreased performance, but the observed performance levels cannot indicate whether there is an alteration of the retrieval step in particular. For

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that aim, recall tasks would need to be adapted for musical material, but this has not been done yet for amusic participants (see Williamson et al., 2010, for an attempt with musician and non-musician participants).

In contrast to behavioral measurements, neurophysiological recordings provide some information related to the retrieval process, even though the neural correlates also include the encoding of the second melody (S2) of the pair in the recognition memory paradigm. Comparing cerebral activity when listening to S2 in same pairs and in different pairs allows for investigating anomalies during retrieval (Albouy et al., 2013a, 2015b). Indeed, encoding applies to both types of S2 (same, different), but the different trials (in contrast to the same trials) involve a mismatch between the encoded information and the retrieved information. Comparing the brain responses for same and different trials during S2 thus reflects a neuronal mismatch response that requires retrieval: if there were no memory involved, there would be no mismatch. Using the short-term memory recognition paradigm presented above, we studied the event-related fields time-locked to the onset of the changed tone in S2 (in different trials, after subtracting the response to same trials to minimize the effects of S2 encoding in the responses). In control participants, a clear response pattern emerged, with two large change-related ERFs (Fig. 6A), generated in bilateral STG and IFG, in areas similar to the ones recruited during pitch encoding (see Fig. 3A). However, in amusic participants, these responses, even for correctly detected melody changes, were greatly reduced (Fig. 6A). This might either reflect specific difficulties at retrieval or be the consequence of anomalies of the memory traces formed or maintained during prior processing steps (i.e., encoding, retention).

Dynamic causal modeling of ERFs during S2 further allowed us to characterize the processes at stake in this last stage of the short-term memory paradigm (Albouy et al., 2015b). In controls, change-specific responses were associated with an increased forward and backward connectivity between right auditory and frontal cortices (Fig. 6B). These results can be interpreted in a hierarchical predictive coding framework (Friston, 2005; Garrido et al., 2007; Lecaignard et al., 2015) where high-level areas provide predictions as to the incoming sounds to expect (here S2 can be predicted based on the retrieved S1 memory trace), and low-level sensory areas compare these predictions to the actual sounds, sending a prediction error in case of a discrepancy between the two. Control connectivity patterns during a change in S2 can then be interpreted as the auditory cortex sending a prediction error to frontal areas (i.e., the perceived sound does not match the prediction that was generated based on S1 memory traces), and the frontal areas sending a backward message to update predictions. Compared to controls, amusics showed increased forward connectivity from auditory to frontal areas for same trials, i.e., when S2 was identical to S1, suggesting that the auditory cortex was sending inappropriate error signals to the frontal cortex, as if the S2 melody were processed as a new melody, whereas S2 could entirely be predicted based on S1's memory trace (Fig. 6C). This could be the consequence of the poor memory trace of S1 maintained in the amusic brain.

1.6. *Impaired cerebral correlates of short-term memory for pitch*

The research reviewed above provides further knowledge about the phenomenon of congenital amusia and about pitch memory in general. Congenital amusics have repeatedly been found to exhibit deficits in pitch short-term memory tasks, which could be the foundation of other pitch-related deficits observed in this population. Because these pitch memory deficits arise without any deficit in auditory verbal memory, it suggests two (at least partly) separated auditory memory systems (Schulze and Koelsch, 2012; Schulze et al., 2011a; Tillmann et al., 2009).

Behavioral and electrophysiological evidence suggest that pitch-memory deficits in congenital amusia are subtended by anomalies in cerebral functioning during all three steps of the short-term memory paradigm: encoding, retention, and retrieval of the pitch information. For now, the relationship between the different types of anomalies remains elusive, and further work is needed to understand whether they derive from the first dysfunctional processing step(s) or whether several distinct deficits co-occur. Encoding anomalies were shown by a critical dependency of congenital amusics' performance on tone duration, and reduced and delayed cortical responses during melody encoding in fronto-temporal areas. During the retention delay, impaired functioning of amusics was shown by an increased cost of memory load, interfering material during the delay, and increased length of the delay, as well as by abnormal oscillatory activities observed with MEG. At retrieval, strongly reduced evoked responses were observed with MEG for a pitch change in a melody.

In all processing stages, cerebral anomalies (even though bilateral) appear to be more pronounced in the right fronto-temporal pathway, in agreement with the role of this pathway in pitch processing and memory in control participants previously reported in neuroimaging studies (Griffiths, 1999; Koelsch et al., 2009; Peretz and Zatorre, 2005; Schulze and Koelsch, 2012; Schulze et al., 2011a, 2011b; Zatorre et al., 1992). It is worth noting that abnormalities start as early as 100 ms post-stimulus onset in the auditory cortices, with delayed and reduced responses, and reduced intrinsic connectivity within auditory cortices (Albouy et al., 2013a). In pitch memory tasks, possible compensatory mechanisms involve the recruitment of the left hemisphere, with an over-connectivity of the two auditory cortices in amusia, and other right-hemispheric regions, such as temporo-parietal areas.

The results raise the question as to whether the reported anomalies could arise from anomalies related to lower-level, non-cortical processing. There are several arguments against this hypothesis, which however still remains to be further tested. First, measures of peripheral auditory functions have not revealed any deficits when tested behaviorally (Cousineau et al., 2015). In addition, auditory processing in the brainstem seems to be-at least to a large extent-preserved in congenital amusia: brainstem responses have been reported to be intact (Liu et al., 2014) or only delayed and altered for the processing of harmonics higher than H2 (but not for F0, for example) (Lehmann et al., 2015). This places the

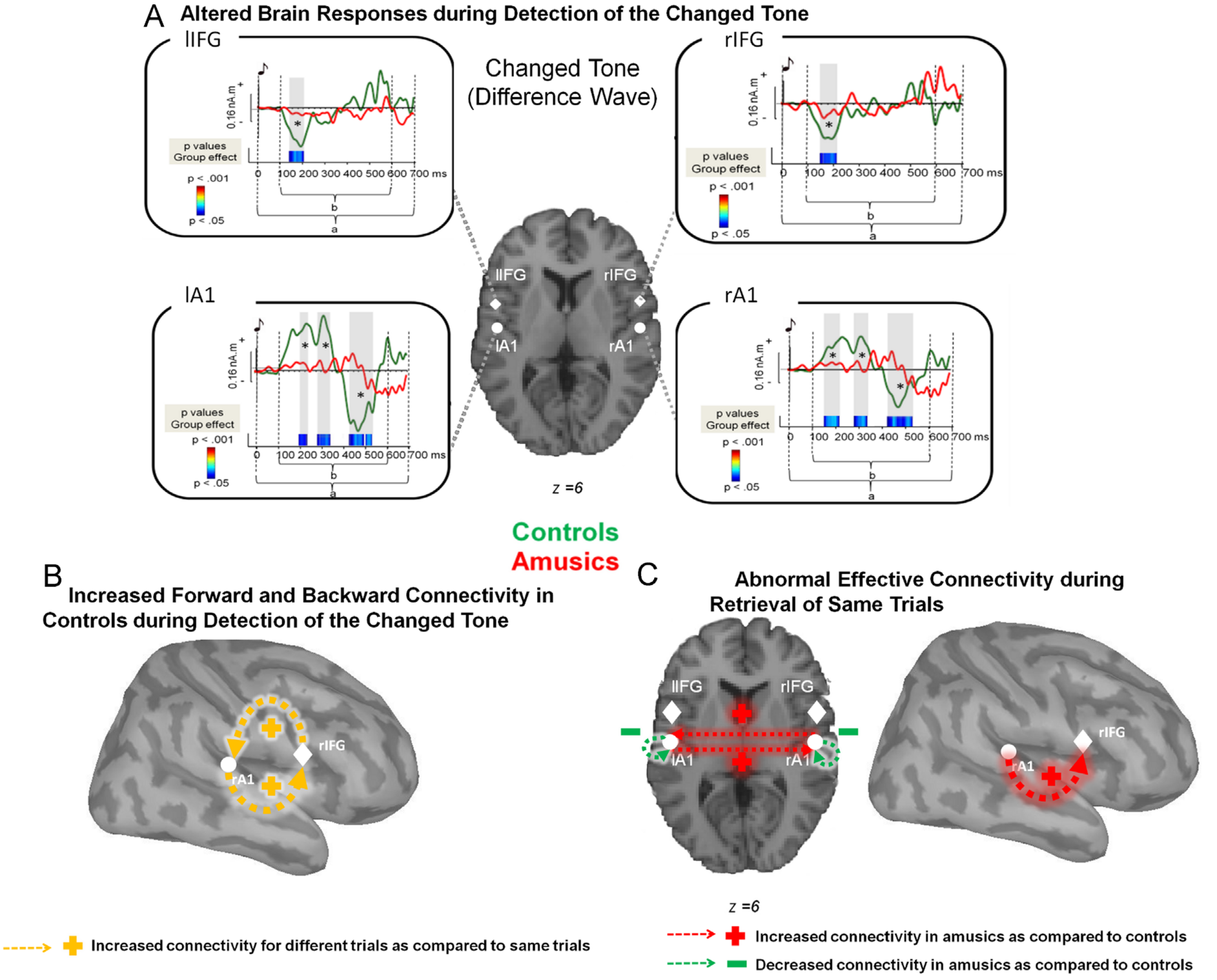

Fig. 6 – (A) Source reconstruction of the brain responses specifically evoked by the changed tone during retrieval (S2) in a short-term memory task. Coordinates of the peaks of activations are displayed on the single subject T1 image provided by SPM8 for four regions: the bilateral auditory cortices as well as the bilateral pars opercularis of the Inferior Frontal Gyrus. The surrounding panels correspond to the grand average of source data for each region and for the time window where the inversion was performed (0–700 ms after the changed tone onset, as indicated by a) for the control group (green) and the amusic group (red). Two sample *t*-tests were performed at each time sample and for each region on source amplitude in the 100–600 ms time window (as indicated by b) in the two groups of participants. *p*-values are reported across time below the source amplitudes with blue for $p<.05$; green for $p<.01$; and red for $p<.001$. Note that only effects lasting longer than 15 ms were reported. See Albouy et al. (2013a, 2015b) for details. (B) and (C) Results of the Dynamic Causal Modeling analysis for the retrieval of melodies in a short-term memory task. (B) "Different" vs. "Same" trials in S2 for controls. (C) Amusics vs. Controls comparison for same trials. Dashed arrows indicate connections that significantly differ between: "Different" trials and "Same" trials in controls for panel B (in yellow); controls and amusics (in green: controls > amusics; in red: amusics > controls) for panel C.

auditory cortex as the first impaired processing level of the auditory hierarchy. Second, in passive listening paradigms, the auditory cortex appeared to function fairly normally (Hyde et al., 2011), with even an accurate automatic detection of pitch abnormalities (Moreau et al., 2013; Peretz et al., 2009). Relatedly, in a recent study using fMRI, we observed normal differential responses between pitched material and narrow-band noises for individuals with congenital amusia in comparison to matched control participants (Norman-Haed submitted for publication; see Norman-Haignere et al., 2013, for details of the experimental paradigms).

Taken together, auditory processing seems to be preserved in congenital amusia up to the level of auditory cortices, where responses appear abnormal as soon as the task at hand depends on memory resources and/or more in-depth sound processing.

1.7. *Perspectives for remediation by exploiting implicit processes*

The here reviewed deficits in amusics' pitch memory might be enhanced by the use of investigation methods that require explicit judgments from the participants (e.g., “same vs. different”, “which pair is different?”; “did you hear high/low or low/high?”). Similarly to neuropsychological cases (e.g., Young et al., 1988; Tillmann et al., 2007), implicit processing might be more proficient than explicit processing also in congenital amusia. Some recent research has suggested that congenital amusia is also linked to altered consciousness regarding the processing of the pitch dimension (e.g., Omigie et al., 2012; Peretz et al., 2009; Tillmann et al., 2014). While neurophysiological recordings might be promising to further investigate the potential extent of amusics' memory deficit on an implicit level (e.g., without requiring explicit memory judgments), supporting evidence for less impaired pitch processing on an implicit level has already been provided by behavioral approaches. Improving our understanding of remaining functions in congenital amusia has implications for rehabilitation attempts, notably by encouraging training that exploits spared implicit processing resources (e.g., Kessels and de Haan, 2003)

For congenital amusia, implicit investigation methods have revealed better pitch processing and/or tonal structure processing than has been shown in explicit judgment tasks or memory tasks (Omigie et al., 2012; Peretz et al., 2009; Tillmann et al., 2012, 2014; Zendel et al., 2015). These data sets suggest that despite pitch processing deficits, some tonal structure knowledge has been acquired in individuals with congenital amusia. This knowledge has also been shown to influence short-term memory of pitch sequences, even though only by speeding up response times without improving performance per se (as in controls; see Fig. 1D) (Albouy et al., 2013b). Amusics' short-term memory for pitch thus benefits – even to a lesser extent than for controls – from tonal structure in the to-be-remembered material (Schulze et al., 2012). Increasing the strength of tonal structure in the to-be-memorized musical sequences (i.e., harmonized music instead of short five-tone sequences) might thus be beneficial also for amusics' short-term memory in terms of performance. Further benefits for amusics' short-term memory might be obtained by increasing available encoding time (Albouy et al., submitted for publication) or by adding a visual aid during encoding, as suggested by the beneficial effect of visual (uninformative) cues for pitch discrimination (Albouy et al., 2015a). Indeed, as performance in a pitch change detection task was improved by this visual cue thanks to audio–visual interactions enhancing the processing in the impaired modality, one might hypothesize that this improved processing also benefits for encoding and the creation of an improved memory trace. These results thus lay out some perspectives to build on material structure, timing, additional cues, and previously acquired knowledge aiming to develop training and rehabilitation programs for pitch-related processing deficits in congenital amusia.

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