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The neural basis for understanding imitation-induced musical meaning: The role of the human mirror system

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Abstract

Music can convey meanings by imitating phenomena of the extramusical world, and these imitation-induced musical meanings can be understood by listeners. Although the human mirror system (HMS) is implicated in imitation, little is known about the HMS's role in making sense of meaning that derives from musical imitation. To answer this question, we used fMRI to examine listeners' brain activities during the processing of imitation-induced musical meaning with a cross-modal semantic priming paradigm. Eleven normal individuals and 11 individuals with congenital amusia, a neurodevelopmental disorder of musical processing, participated in the experiment. Target pictures with either an upward or downward movement were primed by semantically congruent or incongruent melodic sequences characterized by the direction of pitch change (upward or downward). When contrasting the incongruent with the congruent condition between the two groups, we found greater activations in the left supramarginal gyrus/inferior parietal lobule and inferior frontal gyrus in normals but not in amusics. The implications of these findings in terms of the role of the HMS in understanding imitation-induced musical meaning are discussed.

Keywords: fMRI, musical meaning, inferior frontal gyrus, inferior parietal lobule, congenital amusia

1 Introduction

Like language, music is unique to humans. Before language emerged, ancient human ancestors were assumed to communicate with each other using gestures, facial expressions, and songlike vocalizations [1], which imitated animal movements, animal calls, and sounds of the natural world [2]. Being imitative in nature, musical vocalizations are also thought to precede spoken words in human evolution [2-5]. A similar case has also been observed in infant development, during which prelinguistic infants are able to make music-like sounds that are imitations of maternal utterances [6, 7]. Thus, imitation has been playing a critical role in human communication, evolution, and development.

Similarly, people nowadays also convey intentions and meanings through music [8]. Musical meaning can emerge from the imitation of phenomena in the extramusical world, including the sounds of creatures (e.g., birds), the qualities of objects (e.g., trains), and even the representations of abstract concepts (e.g., wideness) [9-11]. As proposed by the mimesis theory [12], music is an imitation or expression of the phenomena in our environment, and this imitation or expression can be readily captured by listeners [13, 14]. Although understanding the intentions of a composer or performer is a critical component in musical meaning processing [15], little is known about the neural correlates underlying the understanding of musical meaning that derives from the imitation of phenomena.

The human mirror system (HMS) consists of a core parietofrontal network of regions in the inferior parietal lobule (IPL) and inferior frontal gyrus (IFG)/premotor cortex (PMC), and it has been suggested that mirror neurons are fired during imitation of actions [16-19]. Substantial evidence has revealed that the HMS is activated by both action observation and execution [20-24] and motor imagery [22, 25-27]. Listening to human action sounds, including speech sounds [28-31] and action-related sounds such as tearing paper, screaming and kicking a football [32-35], also causes increased activations in the HMS. More importantly, the HMS is also engaged in processing semantic information of action-related sentences [36]. Taken together, previous studies indicate that imitation leads to the activation of the HMS, where mirror neurons automatically map observed or heard actions onto a motor program [37].

Although the HMS has also been assumed to be associated with imitation in music [38], very few experimental studies have investigated this relationship directly. Previous studies have shown that the HMS can be recruited by musical activities such as watching piano performances [39, 40], tapping to rhythms [41], and making emotional judgments of songs [42]. Furthermore, prior studies have also shown the engagement of a network of activity resembling the HMS during reproducing melodies [43] and rhythmic patterns [44, 45]. However, these musical activities are irrelevant to music (or musical structure) *per se*. Music itself can convey meanings by imitating the phenomena in the extramusical world [9-11]. However, none of the previous studies has investigated the HMS's role in making sense of imitation-induced musical meaning.

To address this issue, we used event-related fMRI techniques to investigate whether the HMS is implicated in processing musical meaning derived from imitation. Using a cross-modal semantic priming paradigm, a widely used design for studies of meaning processing in music [e.g., 46, 47], we presented participants with melodic sequences (primes) that were followed by pictures (targets). The melodic sequences contained a series of notes with either an upward or a downward direction, and the target pictures portrayed either a simple upward or downward movement, with the effect of picture complexity on brain activity controlled for [48]. Thus, the target pictures were either semantically congruent or incongruent to the musical primes. We hypothesized that, if the listeners were able to process the semantic relationship between the primes and targets by showing a priming effect, it would indicate that they had understood the link between the musical imitation (through melodic sequences) and the natural phenomena (as depicted by the pictures).

Apart from normal participants, we also tested individuals with congenital amusia (hereafter amusia), a neurodevelopmental disorder of musical processing [49]. Individuals with amusia not only have difficulty discriminating fine-grained pitch differences [50-53], but also show deficits in perceiving pitch direction [50, 51, 54, 55] and melodic contour [51, 56], which has led to the "melodic contour deafness hypothesis" by Patel [57]. Given that melodic contour is a building block for musical melodies, deficits in melodic contour perception may affect the understanding of musical meaning in amusia. Indeed, our previous study showed that amusics failed to elicit an N400 effect to musical meaning represented by the direction of pitch change, even though the pitch distances between the first and last notes of the melodic sequences exceeded their pitch direction discrimination thresholds [47]. Thus, by including both normal and amusic individuals as participants, we would be able to reveal the core brain regions that are necessarily required for effective processing of musical meaning, as compared to dysfunctional processing in amusia. Given the role of the HMS in imitation [e.g., 16, 18], we predicted that the parietofrontal regions including the IPL and IFG/PMC would be activated during the understanding of musical meaning in normal but not in amusic individuals.

2 Materials and methods

2.1 Participants

Twelve amusic and 12 normal individuals took part in the experiment. The Montreal Battery of Evaluation of Amusia (MBEA), consisting of six subtests—scale, contour, interval, rhythm, meter, and memory, was used to assess musical abilities of these participants [58, 59]. Participants were identified as amusics if they scored 65 or below on the melodic composite score (sum of the scores on the scale, contour, and interval tests) [54], and below 78% correct on the MBEA global score [59]. Furthermore, participants' pitch change detection and pitch direction discrimination thresholds were measured using a two-alternative forced choice AXB paradigm [50], in which a sequence of three stimuli (A, X, and B) were presented in each trial and the second one (X) was either the same as the first (A) or last (B). In particular, on each trial of the pitch change detection threshold task, three pure tones (A, X, and B) were presented consecutively, among which tone X was identical to either tone A or B. Participants were required to judge whether tone X had the same pitch as tone A or B. On each trial of the pitch direction discrimination threshold task, three 2-tone pairs (A, X, and B) were presented, where pair X was identical in pitch direction to either pair A or B. Participants were required to indicate whether the pitch direction of pair X was the same as that of pair A or B. Experimental trials were presented with an adaptive staircase procedure, in which the initial pitch difference was four semitones and was then varied with a "two-down, one-up" staircase procedure. The procedure terminated after 16 reversals, and the threshold was computed based on the average pitch difference of the last six reversals. For more details please refer to ref. [50]. After the fMRI experiment, one amusic participant and one matched control participant were excluded from further analysis based on a head motion criterion of 3 mm of translational and 3° of rotational movement across the session. As a result, the final sample consisted of 11 participants in each group.

As shown in Table 1, the two groups were matched in age, sex, and education, but the amusic group showed worse performance on the MBEA and higher pitch thresholds than the control group. All participants were right-handed as assessed by the Edinburgh Handedness Inventory [60]. All had normal hearing and reported to have normal or corrected-to-normal vision. None had reported history of neurological or psychiatric diseases. None of the controls received formal musical training or played any musical instruments. One amusic participant had one year of singing lessons and another had one year of piano lessons. Ethical approval was granted by Shanghai Normal University in China, and all participants gave written informed consent and were paid for their participation.

Table 1 Characteristics of participants

Variable	Amusics	Controls	Group-statistic	*d* (95% CI)
Demographic variable				
Age in years	22.91 (2.55)	23.09 (0.94)	$t(12.69) = -0.22, p = .828$	-0.09 (-0.93, 0.74)
Sex (male: female)	3:8	3:8	—	—
Handedness	11R	11R	—	—
Education in years	15.64 (2.11)	16.36 (1.12)	$t(15.22) = -1.01, p = .329$	-0.43 (-1.27, 0.43)
Mean scores of MBEA				
Scale	18.27 (2.72)	27.91 (1.22)	$t(13.86) = -10.71, p < .001$	-4.57 (-6.43, -2.67)
Contour	19.00 (3.29)	28.27 (0.90)	$t(11.51) = -9.02, p < .001$	-3.85 (-5.59, -2.07)

Interval	18.00 (3.90)	27.64 (1.50)	$t(12.90) = -7.65, p < .001$	-3.26 (-4.74, -1.74)
Rhythm	19.73 (3.88)	26.91 (1.64)	$t(13.47) = -5.66, p < .001$	-2.41 (-3.62, -1.16)
Meter	18.45 (5.05)	27.18 (2.79)	$t(20) = -5.02, p < .001$	-2.14 (-3.19, -1.06)
Memory	20.36 (5.08)	28.00 (1.48)	$t(11.69) = -4.78, p < .001$	-2.04 (-3.19, -0.85)
Melodic score	55.27 (7.21)	83.82 (2.86)	$t(13.06) = -12.20, p < .001$	-5.20 (-7.33, -3.05)
Global score (%)	63.23 (5.90)	92.17 (3.10)	$t(15.12) = -14.40, p < .001$	-6.14 (-8.45, -3.81)
Pitch perception threshold				
Pitch change detection	1.40 (1.04)	0.27 (0.12)	$t(10.27) = 3.57, p = .005$	1.52 (0.44, 2.56)
Pitch direction discrimination	4.02 (1.32)	0.48 (0.22)	$t(10.57) = 8.76, p < .001$	3.74 (1.94, 5.49)

Note. R = right-handed; MBEA = Montreal Battery of Evaluation of Amusia. MBEA scores are expressed as the number of correct responses out of 30. Pitch perception thresholds are in semitones. Standard deviation values are shown in parentheses.

2.2 Stimuli

A total of 84 short melodic sequences were created as potential prime stimuli, which consisted of 15 quarter notes with either an upward or a downward pitch direction. Half of the sequences were constructed with a small pitch distance no more than two semitones between two consecutive tones, whereas the other half were constructed with a large pitch distance of more than four semitones. Because all sequences had an ascending or a descending direction, the pitch distances between the first and last tones ranged from 12 to 28 semitones. Each sequence lasted four seconds. All notes were generated by Overture 4.1 (GenieSoft Inc.) and played with a grand piano sound using Pianissimo 1.0 (Acoustica Inc.). Using Adobe Audition CS6 (Adobe Systems Inc.), these sequences were normalized to have the same sound intensity level (-3 dB) and 400 ms fade-out ramps.

Target pictures were two schematic representations, one with an upward movement and the other with a downward movement. Each prime was paired with a target picture to form semantically congruent or incongruent conditions (see Fig. 1), thus resulting in 168 prime-target pairs.

Insert Figure 1, about here.

A behavioral pretest was conducted in order to select paired stimuli for the formal fMRI experiment. An independent group of 17 musically untrained participants were asked to rate each prime-target pair for their congruency on a 9-point scale from 1 = *strongly incongruent in meaning* to 9 = *strongly congruent in meaning*, resulting in two ratings for each prime. The pairs with ratings below 4 and above 6 were considered to be incongruent and congruent, respectively. For each prime, paired *t*-tests were conducted to determine whether the two ratings were significantly different from each other. In the end, 96 prime-target pairs (congruency ratings on 48 congruent pairs: $M = 7.28$, $SD = 0.67$; congruency ratings on 48 incongruent pairs: $M = 2.84$, $SD = 0.60$; $t(47) = 31.58$, $p < .001$) were selected for the fMRI experiment. Among these pairs, primes comprised of 24 upward and 24 downward melodic sequences with 12 small and 12 large pitch distances, respectively. As in the pretest, each prime was used twice: in one trial, the prime was semantically congruent to the target picture; and in the other trial, the prime and target were incongruent.

2.3 Procedure

Before performing the fMRI experiment, participants were first trained on the task using a personal computer. They repeatedly practiced six trials outside the scanner until they became fully familiarized with the task. Inside the scanner, foam pads were used, and explicit verbal instructions were given to the participants in order to limit their head motion. Using the E-prime 2.0 software (Psychology Software Tools Inc.), visual stimuli were presented and projected onto a screen at the front of the scanner. Participants viewed these stimuli through a mirror attached to the head coil. Auditory stimuli were presented via MR-compatible headphones. Participants wore foam earplugs to reduce the effect of ambient scanner noise. Before scanning, the sound volume was adjusted to a comfortable listening level for each participant.

During the scanning session, participants were asked to keep their body still and their eyes open, directing toward the middle of the screen. They were first given the same six trials for practice. Each trial started with a black fixation cross (with a random duration of 2 s, 4 s, or 6 s) at the center of the white screen. When the fixation cross disappeared, the prime was presented with a black screen background (4 s), followed by the visual presentation of a target picture (2 s). After the target picture had disappeared, a response screen (2 s) appeared and participants were asked to indicate whether the meaning expressed by the prime-target pair was congruent or incongruent by pressing one of the two response buttons with their thumbs. Half of the participants responded to the congruent trials with the right thumb and the incongruent trials with the left thumb, and the other half did the opposite. The next trial began 2 s after the previous trial, no matter whether the participants made their response within 2 s or not. The 96 trials were presented in pseudo-randomized order with a maximum of three congruent or incongruent trials in a row. These trials were divided into two sessions with a break in between. The order of presentation was counterbalanced across participants.

2.4 Data acquisition and analysis

Participants were scanned on a 3T Siemens Magnetom Trio Tim System (Siemens, Erlangen, Germany) with a 12-channel head coil. Functional images were acquired using a gradient echo-planar imaging sequence with the following parameters: repetition time = 2 s, echo time = 30 ms, field of view = 192 mm, flip angle = 90°, matrix size = 64 × 64 mm, voxel size = $3 \times 3 \times 3$ mm^3, 37 axial slices, slice thickness = 3 mm, and inter-slice gap = 0.6 mm.

The analysis of the fMRI data was performed using the DPABI 3.0 [61] and SPM 12 toolboxes (Wellcome Trust Center for Neuroimaging, London, UK) run in Matlab R2016a (MathWorks Inc, Natick, MA, USA). The two toolboxes offer complementary functions. Compared to SPM, DPABI requires less manual operations, making preprocessing less time-consuming with a reduced risk of inadvertent mistakes [61, 62]. However, SPM, but not DPABI, provides further statistical analyses (e.g., GLM analysis) for task-based fMRI data [61]. Since DPABI also calls SPM functions in preprocessing data [62], it is convenient to perform the GLM analysis using SPM based on the preprocessed data by DPABI [61]. Therefore, the functional imaging data were first preprocessed in DPABI. For preprocessing, blood oxygen level dependent (BOLD) images were realigned to the first functional image in order to correct for head movement. The realigned volumes were normalized to the EPI template in the Montreal Neurological Institute (MNI) space. Each normalized image was then smoothed with a 6-mm full-width at half-maximum isotropic Gaussian kernel. Statistical analyses based on the general linear model were then carried out in SPM. At the first level, neural activity during the presentation of the target was modeled by a canonical hemodynamic response function and its temporal derivative. For each participant, four conditions were modeled separately: congruent trials with correct responses, congruent trials with incorrect and omitted responses, incongruent trials with correct responses, incongruent trials with incorrect and omitted responses. Additionally, we included six regressors modeling head movement parameters. To reduce low frequency drifts, a high-pass filter was set at 128 s. An autoregressive AR(1) model was applied to account for temporal autocorrelation intrinsic to the fMRI time-series. Individual contrast images for the conditions "incongruent against congruent trials with correct responses" and "congruent against incongruent trials with correct responses" were generated. One-sample *t*-tests were performed to evaluate whether the observed differences were significantly different from zero within each group separately. Regions consisting of a cluster size of at least 10 voxels that exceeded an uncorrected voxel threshold of $p < .001$ were considered reliable. At the second level, two-sample independent *t*-tests were used to investigate the effect of group. Considering the role of the HMS in imitation, we included the combined regions of interest (ROIs; i.e., the bilateral IPL, supramarginal gyrus, IFG, and precentral gyrus) for small volume correction analysis. All anatomical ROIs were constructed using the Talairach Daemon option of the WFU PickAtlas 3.0.5 toolbox [63]. Statistical significance was set at voxel-level uncorrected $p < .001$ and cluster-level false discover rate (FDR) corrected $p < .05$ with $k > 10$ voxels. Anatomical labels for activated regions were provided by the SPM Anatomy toolbox version 2.2c [64, 65] and if unavailable, then provided by the xjView 9.6 toolbox (http://www.alivelearn.net/xjview/).

Bivariate correlations were computed between MBEA scores, behavioral data, and beta values of the ROIs. For each ROI demonstrating a significant group effect, the MarsBaR 0.44 toolbox (http://marsbar.sourceforge.net/index.html) was used to extract each participant’s mean BOLD parameter estimate value (beta value) from a 6 mm radius sphere around peak activations.

3 Results

3.1 Behavioral results

To eliminate the contribution of response bias, we adopted the sensitivity measure from the signal detection theory [66] as an accuracy index. A “yes” response to a congruent trial was defined as a hit whereas a “yes” response to an incongruent trial was defined as a false alarm. To avoid the biasing effect of extreme hit or false-alarm proportions of zero or one on d' values, we adopted the strategy of adding 0.5 to all data cells in the two-by-two contingency table [67, 68].

The values of d' were submitted to a two-way repeated-measures ANOVA with group (amusics, controls) as a between-subjects factor and pitch direction (upward, downward) as a within-subjects factor. Neither the main effect of pitch direction, $F(1, 20) = 0.92$, $p = .349$, $\eta_p^2 = .04$, nor the interaction between group and pitch direction, $F(1, 20)= 1.15$, $p = .296$, $\eta_p^2 = .05$, was significant. Therefore, the data were collapsed across pitch direction. The two-sample t-test showed that controls ($M = 2.84$, $SD = 0.99$) performed better than amusics ($M = 0.85$, $SD = 0.77$), $t(20) = -5.26$, $p < .001$, $d = -2.24$, 95% CI [-3.31, -1.14], on judging semantic congruency between the primes and targets.

3.2 Neuroimaging results

As can be seen in Table 2, when comparing incongruent with congruent trials, amusics showed more activation in the left extra-nuclear and right sub-gyral, caudate nucleus, and the brainstem. Controls, by contrast, only showed increased activation in the left supplementary motor area (Boersma, #3817). SMA is a relevant area with regard to sensorimotor interactions. A possible interpretation for this activation is that it may be a stimulus driven motor representation rather than an intention driven representation.

Table 2 Differential brain activations from the within-group and between-group analyses (incongruent > congruent)

			MNI coordinates			
Region of activation	BA	No. of voxels	*x*	*y*	*z*	*z* score
Amusics						
R Sub-gyral		20	24	-18	27	3.91
R Caudate nucleus			18	-18	21	3.63
L Extra-nuclear		10	-6	-36	3	3.69
R Brainstem			3	-33	0	3.49
Controls						
L Supplementary motor area	6	11	-3	3	57	4.01
Controls > Amusics						
L Supramarginal gyrus*	40	19	-48	-45	30	4.05
L Inferior frontal gyrus*	45	21	-48	27	15	3.70
L Inferior frontal gyrus*			-51	33	12	3.50
Amusics > Controls						
no significant clusters						

Note. L = left; R = right. * Small volume-corrected *p*s = .036 (FDR corrected).

When comparing the incongruent > congruent contrast between groups, we found that controls yielded a greater activation in the left supramarginal gyrus/IPL and IFG than amusics (see Fig. 2). No activated region was found in amusics relative to controls.

Insert Figure 2, about here.

The results from the opposite comparison of congruent > incongruent trials are presented in Table 3. For the within-group analysis, neither amusics nor controls showed more clusters for congruent than incongruent trials. These results may be explained by fMRI adaptation, according to which unrelated stimuli elicit enhanced neural activation compared to related stimuli while related stimuli reduce BOLD responses relative to unrelated or novel stimuli [69, 70]. For the between-group analysis, amusics showed more clusters in the left IPL and IFG for congruent than incongruent trials compared to controls. In other words, amusics showed reduced BOLD responses to incongruent trials in the left IPL and IFG, while controls demonstrated increased responses to incongruent trials in these regions. These results were consistent with those obtained by comparing incongruent with congruent trials in Table 2.

Table 3 Differential brain activations from the within-group and between-group analyses (congruent > incongruent)

			MNI coordinates			
Region of activation	BA	No. of voxels	*x*	*y*	*z*	*z* score
Amusics						
no significant clusters						
Controls						
no significant clusters						
Controls > Amusics						
no significant clusters						

Amusics > Controls						
L Supramarginal gyrus*	40	19	-48	-45	30	4.05
L Inferior frontal gyrus*	45	21	-48	27	15	3.70
L Inferior frontal gyrus*			-51	33	12	3.50

Note. L = left; R = right. * Small volume-corrected *p*s = .036 (FDR corrected).

We also analyzed the correlations among MBEA scores, accuracy in congruency judgment and the associated brain activations, but not the correlations between pitch thresholds and these measures, because the pitch distances between the first and last notes of the melodic sequences exceeded participants' thresholds for pitch perception. For amusics, neither the MBEA scores nor the behavioral measures of performance were significantly correlated with the beta values of the IPL (*p*s > .555) or IFG (*p*s > .504). Similarly, none of the correlations was significant for controls (all *p*s > .200). The lack of correlation between these measures might be because we had a limited sample of participants with homogeneous characteristics, which might have underestimated the true degree of relationship between these variables [71, 72]. When the data from the two groups were pooled, all correlations were significantly positive ($r(20) > .44$, ps < .042), due to the between-group differences.

4 Discussion

Using fMRI, we investigated the neural correlates underlying the understanding of musical meaning that derives from the imitation of natural phenomena in our environment. While amusic individuals showed a dysfunctional HMS in the understanding of musical meaning, normal individuals showed significantly increased activations in the left IPL and the left IFG during comprehension of musical meaning. These findings reveal for the first time the HMS as the prime agent for understanding musical meaning that derives from imitation and extend its role to abstract representation of meaning in music.

The first main finding of our study is that the left HMS is activated in normal individuals during the understanding of musical meaning that derives from the imitation of phenomena. In the HMS, the IPL is mostly implicated in motoric descriptions of actions [19, 20, 73], while the IFG is more concerned with the goal or intention of actions [74-76]. In our study, when listening to an upward or a downward melody, the listeners needed to map the kinematic pattern of the heard pitch movement onto an internal motor representation of the same movement. Consistent with the IPL's role in sensorimotor transformation [77-79], we observed stronger BOLD responses to incongruent than congruent trials in the IPL. In addition, the ascending and descending melodic sequences in the present study cued the intentions of upward and downward movements (e.g., going upstairs or downstairs). To judge the semantic congruency between the picture and the melody, participants had to infer the intentions of the movements of the primes and targets. Therefore, the activation of the IFG in normal individuals reflected the understanding of these intentions.

Although the PMC is often activated during imitation [23, 80-82], no significant activation in the PMC was observed in our study. However, after using a more liberal threshold of uncorrected $p < .001$ and cluster size of $k = 0$ voxels, we observed activity changes in the middle frontal gyrus ($x = -48$, $y = 6$, $z = 54$, z score = 3.37, $p < .001$, $k = 1$, BA 6) and supplementary motor area ($x = -3$, $y = 6$, $z = 57$, z score = 3.26, $p = .001$, $k = 2$, BA 6). There are two possible interpretations for the less robust activation of the PMC in the present study. One possibility may lie in the fact that our participants were not familiar with the experimental stimuli and task. Indeed, previous studies have reported that the PMC and supplementary motor area are significantly more active for familiar than unfamiliar stimuli, such as music [83-86] and visual pictures [87, 88]. In the present study, although walking up or down the stairs as depicted in the target pictures could be considered as familiar actions, the melodic sequences that were composed specifically for the current experiment could be unfamiliar to our participants. This might have resulted in the nonsignificant activation of the PMC in our study. Future studies are required to further explore this possibility. Another possibility is related to the modality of stimulus presentation. It has been suggested that the premotor activity is based on unimodal (visual, auditory, or tactile) attention shifts [89-92], which are tightly coupled to the motor program [93]. However, our study involved crossmodal attention shifts from auditory cues to visual targets, which resulted in decreased activation of the PMC. Indeed, behavioral research has confirmed that the processing of unimodal auditory cues and targets is coupled to the motor program, which is not the case for crossmodal auditory cues and visual targets [94].

The activation of the HMS is confined to the left hemisphere in our study, which is consistent with previous evidence that action sounds are associated with the activation of the left HMS [32, 95, 96]. However, it is contradictory to the finding that bilateral HMS is involved during action observation and imitation [21, 97]. This discrepancy may be attributed to the difference in stimuli across different studies. The stimuli used in the present study were both auditory and visual stimuli (i.e., the musical primes and target pictures), whereas the stimuli in those previous studies [21, 97] were visual stimuli only. It has been shown that the left hemisphere of the human brain has a multimodal (visual, auditory) HMS [19] and may code actions at a more abstract level or in an amodal manner [98], while the right hemisphere only has a visual HMS [19]. Thus, the activation of the left HMS in our study may reflect the multimodal (visual, auditory) stimuli used.

The second main finding of our study is that the HMS is involved in the abstract representation of musical meaning. Previous fMRI data have indicated that the HMS is implicated in the processing of action-related information, such as executing actions [22], perceiving actions [e.g., 23, 28, 35], and imagining actions [e.g., 22, 25]. Some evidence also suggests that a mirror-like system is implicated in producing musical stimuli [43-45]. Our study extends these results by suggesting the role of the HMS in understanding meaning in music. Particularly, in the present study, each melody with an upward or a downward pitch direction was paired with a picture with an upward movement and another with a downward movement. In order to judge whether the meaning of the target picture was congruent or incongruent with the meaning of the prime, the participants had to extract the meanings from both the prime and the target. Thus, the activation of the HMS reflected the extraction of abstract meaning. On the other hand, what we manipulated was the semantic relations between musical primes and target pictures. This design ruled out the possibility that the HMS was activated by musical primes or target pictures alone. Indeed, the IPL and IFG share cognitive functions, especially in semantic integration [99-101], possibly due to the anatomical connections between the two [102, 103]. Consequently, the activation of the HMS reflected semantic integration processes. In short, the HMS in the present study is involved in the understanding of abstract meaning in music.

The third main finding of our study is that unlike normals, amusics demonstrated a dysfunctional HMS in the understanding of musical meaning, which is in agreement with our prior EEG study that reported the absence of an N400 effect in processing musical meaning in amusia [47]. The failure to derive musical meaning from pitch change direction confirmed that amusia is indeed a pitch-related disorder, including pitch perception [e.g., 50, 51, 104], tonal functional cognition [105-107], and emotion perception [108-111]. Although impaired pitch discrimination and memory in amusia is related to abnormal activity changes in the right IFG as well as decreased functional connectivity between the right IFG and the right auditory cortex [112-114], our study further indicates that impaired musical meaning understanding in amusia is associated with aberrant brain activity in the left parietofrontal cortices. These results imply that functional anomalies in the amusic brain may depend on task demands. Moreover, given that the HMS is an innate endowment [e.g., 115, 116], our findings confirm the assumption that the pitch-based deficit of amusia is likely to be present at birth [117, 118]. Indeed, it has been suggested that amusia has a genetic basis [119, 120]. From this perspective, one could speculate that the brain function for understanding musical imitation may be hardwired in the brain of neurotypical individuals, but not in that of amusic individuals.

In sum, the present data show that the HMS plays an important role in understanding musical meaning that derives from the imitation of phenomena, providing new insight into the neural representation of musical meaning in the HMS. It is worth noting that we used the direction of pitch change to imitate an upward or a downward movement, which reflects a creative intention. Interestingly, Steinbeis and Koelsch [15] manipulated experimental instructions (that is, whether participants were informed that the piece of music was written by a composer or generated by a computer), and found that understanding the composer's intentions activated the anterior medial frontal cortex, superior temporal sulcus/middle temporal gyrus/IPL, temporal pole, IFG, and middle occipital gyrus in listeners. Therefore, it is reasonable to assume that the HMS may be involved in the understanding of musical meaning, regardless of whether they are derived from imitation or not. Taken together, our findings provide functional imaging evidence in support of the mimesis theory that music is an imitation of phenomena, and imitation-induced musical meaning can be readily understood by normal listeners [12-14].

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Declarations of interest

None.

References

[1] I. Cross, Music and cognitive evolution, in: R. Dunbar, L. Barrett (Eds.), The Oxford Handbook of Evolutionary Psychology, Oxford University Press, New York, NY, 2007, pp. 649-667.

[2] S.J. Mithen, The Singing Neanderthals: The Origins of Music, Language, Mind, and Body, Weidenfeld & Nicolson, London, UK, 2005.

[3] C. Darwin, The Descent of Man and Selection in Relation to Sex, John Murray, London, UK, 1871.

[4] B.G. Levman, The genesis of music and language, Ethnomusicology 36(2) (1992) 147-170.

[5] J. Blaking, How Musical Is Man, University of Washington Press, Seattle, WA, 1973.

[6] N. Masataka, Pitch characteristics of Japanese maternal speech to infants, J. Child Lang. 19(2) (1992) 213-223.

[7] C.E. Snow, Imitativeness: a trait or a skill?, in: G.E. Speidel, K.E. Nelson (Eds.), The Many Faces of Imitation in Language Learning, Springer, New York, NY, 1989, pp. 73-90.

[8] D.J. Hargreaves, R. MacDonald, D. Miell, How do people communicate using music, in: D. Miell, R. MacDonald, D.J. Hargreaves (Eds.), Musical Communication, Oxford University Press, Oxford, UK, 2005, pp. 1-25.

[9] S. Koelsch, Brain and Music, John Wiley & Sons, West Sussex, UK, 2013.

[10] S. Koelsch, Towards a neural basis of processing musical semantics, Phys. Life Rev. 8(2) (2011) 89-105.

[11] S. Davies, Musical Meaning and Expression, Cornell University Press, New York, NY, 1994.

[12] M. Leman, Embodied Music Cognition and Mediation Technology, The MIT Press, Cambridge, MA, 2007.

[13] A. Cox, Music and Embodied Cognition: Listening, Moving, Feeling, and Thinking, Indiana University Press, Indiana, IN, 2016.

[14] A. Cox, The mimetic hypothesis and embodied musical meaning, Music. Sci. 5(2) (2001) 195-212.

[15] N. Steinbeis, S. Koelsch, Understanding the intentions behind man-made products elicits neural activity in areas dedicated to mental state attribution, Cereb. Cortex 19(3) (2009) 619-623.

[16] G. Rizzolatti, L. Craighero, The mirror-neuron system, Annu. Rev. Neurosci. 27 (2004) 169-192.

[17] H.M. Hobson, D.V.M. Bishop, The interpretation of mu suppression as an index of mirror neuron activity: past, present and future, Royal Soc. Open Sci. 4(3) (2017).

[18] P. Molenberghs, R. Cunnington, J.B. Mattingley, Brain regions with mirror properties: a meta-analysis of 125 human fMRI studies, Neurosci. Biobehav. Rev. 36(1) (2012) 341-349.

[19] M. Iacoboni, M. Dapretto, The mirror neuron system and the consequences of its dysfunction, Nat. Rev. Neurosci. 7(12) (2006) 942-951.

[20] M. Iacoboni, R.P. Woods, M. Brass, H. Bekkering, J.C. Mazziotta, G. Rizzolatti, Cortical mechanisms of human imitation, Science 286(5449) (1999) 2526-2528.

[21] S. Caspers, K. Zilles, A.R. Laird, S.B. Eickhoff, ALE meta-analysis of action observation and imitation in the human brain, Neuroimage 50(3) (2010) 1148-1167.

[22] P.G. Simos, E. Kavroulakis, T. Maris, E. Papadaki, T. Boursianis, G. Kalaitzakis, H.E. Savaki, Neural foundations of overt and covert actions, Neuroimage 152 (2017) 482-496.

[23] K. Sakreida, S. Higuchi, C. Di Dio, M. Ziessler, M. Turgeon, N. Roberts, S. Vogt, Cognitive control structures in the imitation learning of spatial sequences and rhythms—an fMRI study, Cereb. Cortex 28(3) (2018) 907-923.

[24] D. Corbo, G.A. Orban, Observing others speak or sing activates spt and neighboring parietal cortex, J. Cogn. Neurosci. 29(6) (2017) 1002-1021.

[25] S. Hétu, M. Grégoire, A. Saimpont, M.-P. Coll, F. Eugène, P.-E. Michon, P.L. Jackson, The neural network of motor imagery: an ALE meta-analysis, Neurosci. Biobehav. Rev. 37(5) (2013) 930-949.

[26] M. Jeannerod, Neural simulation of action: a unifying mechanism for motor cognition, Neuroimage 14(1) (2001) S103-S109.

[27] F. Lui, G. Buccino, D. Duzzi, F. Benuzzi, G. Crisi, P. Baraldi, P. Nichelli, C.A. Porro, G. Rizzolatti, Neural substrates for observing and imagining non-object-directed actions, Soc. Neurosci. 3(3-4) (2008) 261-275.

[28] R. Jardri, D. Pins, M. Bubrovszky, P. Despretz, J.-P. Pruvo, M. Steinling, P. Thomas, Self awareness and speech processing: an fMRI study, Neuroimage 35(4) (2007) 1645-1653.

[29] M. Tettamanti, G. Buccino, M.C. Saccuman, V. Gallese, M. Danna, P. Scifo, F. Fazio, G. Rizzolatti, S.F. Cappa, D. Perani, Listening to action-related sentences activates fronto-parietal motor circuits, J. Cogn. Neurosci. 17(2) (2005) 273-281.

[30] K. Watkins, T. Paus, Modulation of motor excitability during speech perception: the role of Broca's area, J. Cogn. Neurosci. 16(6) (2004) 978-987.

[31] M. Tettamanti, R. Manenti, P.A. Della Rosa, A. Falini, D. Perani, S.F. Cappa, A. Moro, Negation in the brain: modulating action representations, Neuroimage 43(2) (2008) 358-367.

[32] V. Gazzola, L. Aziz-Zadeh, C. Keysers, Empathy and the somatotopic auditory mirror system in humans, Curr. Biol. 16(18) (2006) 1824-1829.

[33] L.R. Engel, C. Frum, A. Puce, N.A. Walker, J.W. Lewis, Different categories of living and non-living sound-sources activate distinct cortical networks, Neuroimage 47(4) (2009) 1778-1791.

[34] E. Ricciardi, D. Bonino, L. Sani, T. Vecchi, M. Guazzelli, J.V. Haxby, L. Fadiga, P. Pietrini, Do we really need vision? How blind people "see" the actions of others, J. Neurosci. 29(31) (2009) 9719-9724.

[35] G. Di Cesare, F. Fasano, A. Errante, M. Marchi, G. Rizzolatti, Understanding the internal states of others by listening to action verbs, Neuropsychologia 89 (2016) 172-179.

[36] M. Ghio, M. Tettamanti, Semantic domain-specific functional integration for action-related vs. abstract concepts, Brain Lang. 112(3) (2010) 223-232.

[37] P. Molenberghs, R. Cunnington, J.B. Mattingley, Is the mirror neuron system involved in imitation? A short review and meta-analysis, Neurosci. Biobehav. Rev. 33(7) (2009) 975-980.

[38] I. Molnar-Szakacs, K. Overy, Music and mirror neurons: from motion to ’e’motion, Soc. Cogn. Affect. Neurosci. 1(3) (2006) 235-241.

[39] J. Hou, R. Rajmohan, D. Fang, K. Kashfi, K. Al-Khalil, J. Yang, W. Westney, C.M. Grund, M.W. O'Boyle, Mirror neuron activation of musicians and non-musicians in response to motion captured piano performances, Brain Cogn. 115 (2017) 47-55.

[40] B. Haslinger, P. Erhard, E. Altenmüller, U. Schroeder, H. Boecker, A.O. Ceballos-Baumann, Transmodal sensorimotor networks during action observation in professional pianists, J. Cogn. Neurosci. 17(2) (2005) 282-293.

[41] J.L. Chen, V.B. Penhune, R.J. Zatorre, Listening to musical rhythms recruits motor regions of the brain, Cereb. Cortex 18(12) (2008) 2844-2854.

[42] L.M. McGarry, J.A. Pineda, F.A. Russo, The role of the extended MNS in emotional and nonemotional judgments of human song, Cogn. Affect. Behav. Neurosci. 15(1) (2015) 32-44.

[43] G. Hickok, B. Buchsbaum, C. Humphries, T. Muftuler, Auditory-motor interaction revealed by fMRI: speech, music, and working memory in area Spt, J. Cogn. Neurosci. 15(5) (2003) 673-682.

[44] N. Konoike, Y. Kotozaki, H.J. Jeong, A. Miyazaki, K. Sakaki, T. Shinada, M. Sugiura, R. Kawashima, K. Nakamura, Temporal and motor representation of rhythm in fronto-parietal cortical areas: an fMRI study, PLoS One 10(6) (2015).

[45] N. Konoike, Y. Kotozaki, S. Miyachi, C.M. Miyauchi, Y. Yomogida, Y. Akimoto, K. Kuraoka, M. Sugiura, R. Kawashima, K. Nakamura, Rhythm information represented in the fronto-parieto-cerebellar motor system, Neuroimage 63(1) (2012) 328-338.

[46] S. Koelsch, E. Kasper, D. Sammler, K. Schulze, T. Gunter, A.D. Friederici, Music, language and meaning: brain signatures of semantic processing, Nat. Neurosci. 7(3) (2004) 302-307.

[47] L. Zhou, F. Liu, X. Jing, C. Jiang, Neural differences between the processing of musical meaning conveyed by direction of pitch change and natural music in congenital amusia, Neuropsychologia 96 (2017) 29-38.

[48] M.M. Bradley, S. Hamby, A. Löw, P.J. Lang, Brain potentials in perception: picture complexity and emotional arousal, Psychophysiology 44(3) (2007) 364-373.

[49] I. Peretz, J. Ayotte, R.J. Zatorre, J. Mehler, P. Ahad, V.B. Penhune, B.t. Jutras, Congenital amusia: a disorder of fine-grained pitch discrimination, Neuron 33(2) (2002) 185-191.

[50] C. Jiang, V.K. Lim, H. Wang, J.P. Hamm, Difficulties with pitch discrimination influences pitch memory performance: evidence from congenital amusia, PLoS One 8(10) (2013) e79216.

[51] J.M. Foxton, J.L. Dean, R. Gee, I. Peretz, T.D. Griffiths, Characterization of deficits in pitch perception underlying ‘tone deafness’, Brain 127(4) (2004) 801-810.

[52] C. Jiang, J.P. Hamm, V.K. Lim, I.J. Kirk, Y. Yang, Fine-grained pitch discrimination in congenital amusics with Mandarin Chinese, Music Percept. 28(5) (2011) 519-526.

[53] K.L. Hyde, I. Peretz, Brains that are out of tune but in time, Psychol. Sci. 15(5) (2004) 356-360.

[54] F. Liu, A.D. Patel, A. Fourcin, L. Stewart, Intonation processing in congenital amusia: discrimination, identification and imitation, Brain 133(6) (2010) 1682-1693.

[55] P. Loui, F.H. Guenther, C. Mathys, G. Schlaug, Action-perception mismatch in tone-deafness, Curr. Biol. 18(8) (2008) R331-R332.

[56] C. Jiang, J.P. Hamm, V.K. Lim, I.J. Kirk, Y. Yang, Processing melodic contour and speech intonation in congenital amusics with Mandarin Chinese, Neuropsychologia 48(9) (2010) 2630-2639.

[57] A.D. Patel, Music, Language, and the Brain, Oxford University Press, Oxford, UK, 2008.

[58] D.T. Vuvan, S. Paquette, G. Mignault Goulet, I. Royal, M. Felezeu, I. Peretz, The Montreal Protocol for Identification of Amusia, Beh. Res. Meth. 50(2) (2018) 662-672.

[59] I. Peretz, A.S. Champod, K. Hyde, Varieties of musical disorders, Ann. N. Y. Acad. Sci. 999(1) (2003) 58-75.

[60] R.C. Oldfield, The assessment and analysis of handedness: the Edinburgh Inventory, Neuropsychologia 9(1) (1971) 97-113.

[61] C. Yan, X. Wang, X. Zuo, Y. Zang, DPABI: Data processing & analysis for (resting-state) brain imaging, Neuroinformatics 14(3) (2016) 339-351.

[62] C. Yan, Y. Zang, DPARSF: a MATLAB toolbox for "pipeline" data analysis of resting-state fMRI, Front. Syst. Neurosci. 4(13) (2010).

[63] J.A. Maldjian, P.J. Laurienti, R.A. Kraft, J.H. Burdette, An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets, Neuroimage 19(3) (2003) 1233-1239.

[64] S.B. Eickhoff, T. Paus, S. Caspers, M.-H. Grosbras, A.C. Evans, K. Zilles, K. Amunts, Assignment of functional activations to probabilistic cytoarchitectonic areas revisited, Neuroimage 36(3) (2007) 511-521.

[65] S.B. Eickhoff, K.E. Stephan, H. Mohlberg, C. Grefkes, G.R. Fink, K. Amunts, K. Zilles, A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data, Neuroimage 25(4) (2005) 1325-1335.

[66] N.A. Macmillan, C.D. Creelman, Detection Theory: A User's Guide, 2nd ed., Lawrence Erlbaum Associates, Inc., Mahwah, NJ, 2005.

[67] M.J. Hautus, Corrections for extreme proportions and their biasing effects on estimated values of d′, Behav. Res. Methods Instrum. Comput. 27(1) (1995) 46-51.

[68] M.J. Hautus, A. Lee, Estimating sensitivity and bias in a yes/no task, Br. J. Math. Stat. Psychol. 59(2) (2006) 257-273.

[69] K. Grill-Spector, R. Henson, A. Martin, Repetition and the brain: neural models of stimulus-specific effects, Trends Cogn. Sci. 10(1) (2006) 14-23.

[70] K. Grill-Spector, R. Malach, fMR-adaptation: a tool for studying the functional properties of human cortical neurons, Acta Psychol. (Amst.) 107(1) (2001) 293-321.

[71] B.H. Kantowitz, H.L. Roediger III, D.G. Elmes, Experimental Psychology, 10th ed., Cengage Learning, Stamford, CT, 2015.

[72] M.R. Leary, Introduction to Behavioral Research Methods, 7th ed., Pearson Education, Inc., New York, NY, 2017.

[73] T. Chaminade, A.N. Meltzoff, J. Decety, An fMRI study of imitation: action representation and body schema, Neuropsychologia 43(1) (2005) 115-127.

[74] F.P. de Lange, M. Spronk, R.M. Willems, I. Toni, H. Bekkering, Complementary systems for understanding action intentions, Curr. Biol. 18(6) (2008) 454-457.

[75] M. Iacoboni, I. Molnar-Szakacs, V. Gallese, G. Buccino, J.C. Mazziotta, G. Rizzolatti, Grasping the intentions of others with one's own mirror neuron system, PLoS Biol. 3(3) (2005) e79.

[76] L. Koski, A. Wohlschläger, H. Bekkering, R.P. Woods, M.-C. Dubeau, J.C. Mazziotta, M. Iacoboni, Modulation of motor and premotor activity during imitation of target-directed actions, Cereb. Cortex 12(8) (2002) 847-855.

[77] J. Pa, G. Hickok, A parietal–temporal sensory–motor integration area for the human vocal tract: evidence from an fMRI study of skilled musicians, Neuropsychologia 46(1) (2008) 362-368.

[78] F.C. Binkofski, J. Klann, S. Caspers, On the neuroanatomy and functional role of the inferior parietal lobule and intraparietal sulcus, in: G. Hickok, S.L. Small (Eds.), Neurobiology of Language, Academic Press, San Diego, 2016, pp. 35-47.

[79] K. Sakreida, I. Effnert, S. Thill, M.M. Menz, D. Jirak, C.R. Eickhoff, T. Ziemke, S.B. Eickhoff, A.M. Borghi, F. Binkofski, Affordance processing in segregated parieto-frontal dorsal stream sub-pathways, Neurosci. Biobehav. Rev. 69 (2016) 89-112.

[80] M. Belyk, P.Q. Pfordresher, M. Liotti, S. Brown, The neural basis of vocal pitch imitation in humans, J. Cogn. Neurosci. 28(4) (2016) 621-635.

[81] J. Jastorff, R.O. Abdollahi, F. Fasano, G.A. Orban, Seeing biological actions in 3D: an fMRI study, Hum. Brain Mapp. 37(1) (2016) 203-219.

[82] L.E. Marsh, G. Bird, C. Catmur, The imitation game: effects of social cues on ‘imitation’ are domain-general in nature, Neuroimage 139 (2016) 368-375.

[83] Y. Nan, T.R. Knösche, S. Zysset, A.D. Friederici, Cross-cultural music phrase processing: an fMRI study, Hum. Brain Mapp. 29(3) (2008) 312-328.

[84] A.M. Leaver, J. Van Lare, B. Zielinski, A.R. Halpern, J.P. Rauschecker, Brain activation during anticipation of sound sequences, J. Neurosci. 29(8) (2009) 2477-2485.

[85] R. Harris, B.M. de Jong, Differential parietal and temporal contributions to music perception in improvising and score-dependent musicians, an fMRI study, Brain Res. 1624 (2015) 253-264.

[86] C.S. Pereira, J. Teixeira, P. Figueiredo, J. Xavier, S.L. Castro, E. Brattico, Music and emotions in the brain: familiarity matters, PLoS One 6(11) (2011) e27241.

[87] J. Plata Bello, C. Modroño, F. Marcano, J.L. González–Mora, Observation of simple intransitive actions: the effect of familiarity, PLoS One 8(9) (2013) e74485.

[88] E. Tulving, H.J. Markowitsch, F.I.M. Craik, R. Habib, S. Houle, Novelty and familiarity activations in PET studies of memory encoding and retrieval, Cereb. Cortex 6(1) (1996) 71-79.

[89] L. Craighero, G. Rizzolatti, The premotor theory of attention, in: L. Itti, G. Rees, J.K. Tsotsos (Eds.), Neurobiology of Attention, Academic Press, Burlington, 2005, pp. 181-186.

[90] G. Rizzolatti, L. Craighero, Spatial attention: mechanisms and theories, in: M. Sabourin, F. Craik, M. Robert (Eds.), Advances in Psychological Science, Psychology Press, East Sussex, England, 1998, pp. 171-198.

[91] G. Rizzolatti, L. Riggio, I. Dascola, C. Umiltá, Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention, Neuropsychologia 25(1) (1987) 31-40.

[92] G. Rizzolatti, L. Riggio, B.M. Sheliga, Space and selective attention, in: C. Umiltà, M. Moscovitch (Eds.), Attention and Performance 15, The MIT Press, Cambridge, MA, 1994, pp. 232-265.

[93] D.T. Smith, T. Schenk, The premotor theory of attention: time to move on?, Neuropsychologia 50(6) (2012) 1104-1114.

[94] L.M. Ward, Supramodal and modality-specific mechanisms for stimulus-driven shifts of auditory and visual attention, Can. J. Exp. Psychol. 48(2) (1994) 242-59.

[95] L. Aziz-Zadeh, M. Iacoboni, E. Zaidel, S. Wilson, J. Mazziotta, Left hemisphere motor facilitation in response to manual action sounds, Eur. J. Neurosci. 19(9) (2004) 2609-2612.

[96] J.W. Lewis, J.A. Brefczynski, R.E. Phinney, J.J. Janik, E.A. DeYoe, Distinct cortical pathways for processing tool versus animal sounds, J. Neurosci. 25(21) (2005) 5148-5158.

[97] L. Aziz-Zadeh, L. Koski, E. Zaidel, J. Mazziotta, M. Iacoboni, Lateralization of the human mirror neuron system, J. Neurosci. 26(11) (2006) 2964-2970.

[98] L. Aziz-Zadeh, R.B. Ivry, The human mirror neuron system and embodied representations, in: D. Sternad (Ed.), Progress in Motor Control: A Multidisciplinary Perspective, Springer, Boston, MA, 2009, pp. 355-376.

[99] T.-L. Chou, J.R. Booth, D.D. Burman, T. Bitan, J.D. Bigio, D. Lu, N.E. Cone, Developmental changes in the neural correlates of semantic processing, Neuroimage 29(4) (2006) 1141-1149.

[100] T.-L. Chou, C.-W. Chen, M.-Y. Wu, J.R. Booth, The role of inferior frontal gyrus and inferior parietal lobule in semantic processing of Chinese characters, Exp. Brain Res. 198(4) (2009) 465-475.

[101] E. Klepousniotou, V.L. Gracco, G.B. Pike, Pathways to lexical ambiguity: fMRI evidence for bilateral fronto-parietal involvement in language processing, Brain Lang. 131 (2014) 56-64.

[102] M. Catani, D.K. Jones, D.H. ffytche, Perisylvian language networks of the human brain, Ann. Neurol. 57(1) (2005) 8-16.

[103] J. Wang, L. Fan, Y. Zhang, Y. Liu, D. Jiang, Y. Zhang, C. Yu, T. Jiang, Tractography-based parcellation of the human left inferior parietal lobule, Neuroimage 63(2) (2012) 641-652.

[104] X. Lu, Y. Sun, H.T. Ho, W.F. Thompson, Pitch contour impairment in congenital amusia: new insights from the Self-paced Audio-visual Contour Task (SACT), PLoS One 12(6) (2017) e0179252.

[105] C. Jiang, F. Liu, W.F. Thompson, Impaired explicit processing of musical syntax and tonality in a group of Mandarin-speaking congenital amusics, Music Percept. 33(4) (2016) 401-413.

[106] D. Omigie, M.T. Pearce, L. Stewart, Tracking of pitch probabilities in congenital amusia, Neuropsychologia 50(7) (2012) 1483-1493.

[107] B.R. Zendel, M.-É. Lagrois, N. Robitaille, I. Peretz, Attending to pitch information inhibits processing of pitch information: the curious case of amusia, J. Neurosci. 35(9) (2015) 3815-3824.

[108] J. Ayotte, I. Peretz, K. Hyde, Congenital amusia: a group study of adults afflicted with a music-specific disorder, Brain 125(2) (2002) 238-251.

[109] N. Gosselin, S. Paquette, I. Peretz, Sensitivity to musical emotions in congenital amusia, Cortex 71 (2015) 171-182.

[110] C. Jiang, F. Liu, P.C.M. Wong, Sensitivity to musical emotion is influenced by tonal structure in congenital amusia, Sci. Rep. 7(1) (2017) 7624.

[111] M.M. Marin, W.F. Thompson, B. Gingras, L. Stewart, Affective evaluation of simultaneous tone combinations in congenital amusia, Neuropsychologia 78 (2015) 207-220.

[112] K.L. Hyde, R.J. Zatorre, I. Peretz, Functional MRI evidence of an abnormal neural network for pitch processing in congenital amusia, Cereb. Cortex 21(2) (2011) 292-299.

[113] P. Albouy, J. Mattout, R. Bouet, E. Maby, G. Sanchez, P.-E. Aguera, S. Daligault, C. Delpuech, O. Bertrand, A. Caclin, B. Tillmann, Impaired pitch perception and memory in congenital amusia: the deficit starts in the auditory cortex, Brain 136(5) (2013) 1639-1661.

[114] P. Albouy, J. Mattout, G. Sanchez, B. Tillmann, A. Caclin, Altered retrieval of melodic information in congenital amusia: insights from dynamic causal modeling of MEG data, Front. Hum. Neurosci. 9 (2015) 20.

[115] E. Nagy, H. Compagne, H. Orvos, A. Pal, P. Molnar, I. Janszky, K.A. Loveland, G. Bardos, Index finger movement imitation by human neonates: motivation, learning, and left-hand preference, Pediatr. Res. 58(4) (2005) 749-753.

[116] P. Nyström, T. Ljunghammar, K. Rosander, C. von Hofsten, Using mu rhythm desynchronization to measure mirror neuron activity in infants, Dev. Sci. 14(2) (2011) 327-335.

[117] I. Peretz, Musical disorders from behavior to genes, Curr. Dir. Psychol. Sci. 17(5) (2008) 329-333.

[118] I. Peretz, K.L. Hyde, What is specific to music processing? Insights from congenital amusia, Trends Cogn. Sci. 7(8) (2003) 362-367.

[119] I. Peretz, S. Cummings, M.-P. Dubé, The genetics of congenital amusia (tone deafness): a family-aggregation study, Am. J. Hum. Genet. 81(3) (2007) 582-588.

[120] D. Drayna, A. Manichaikul, M. de Lange, H. Snieder, T. Spector, Genetic correlates of musical pitch recognition in humans, Science 291(5510) (2001) 1969-1972.

Figure captions

Fig. 1. Design of the semantic priming paradigm. Melodic sequences with either upward or downward pitch direction changes were used as primes and pictures depicting upward or downward movements were used as targets.

Fig. 2. Significant activation areas in controls compared to amusics. The color scale reflects the *t* value for the contrast between incongruent and congruent conditions for voxels above the FDR-corrected threshold of $p < .05$; the more yellow a pixel is, the higher the *t* value is.