Corrections

NEUROSCIENCE

Correction for "Mars 520-d mission simulation reveals protracted crew hypokinesis and alterations of sleep duration and timing," by Mathias Basner, David F. Dinges, Daniel Mollicone, Adrian Ecker, Christopher W. Jones, Eric C. Hyder, Adrian Di Antonio, Igor Savelev, Kevin Kan, Namni Goel, Boris V. Morukov, and Jeffrey P. Sutton (first published January 7, 2013; 10.1073/pnas.1212646110).

The authors note that Fig. 2 appeared incorrectly. The authors unintentionally labeled the ordinate of Fig. 2A "cumulative wake activity ($\times 10^4$)" instead of "cumulative wake activity (counts/min $\times$ 10^7)," and they unintentionally labeled the parenthetical metric on the ordinate of Fig. 2D as "(h $\times$ 10^2)" when it should have been "($\times 10^2$)".

The corrected figure and its legend appear below. These errors do not affect the conclusions of the article.
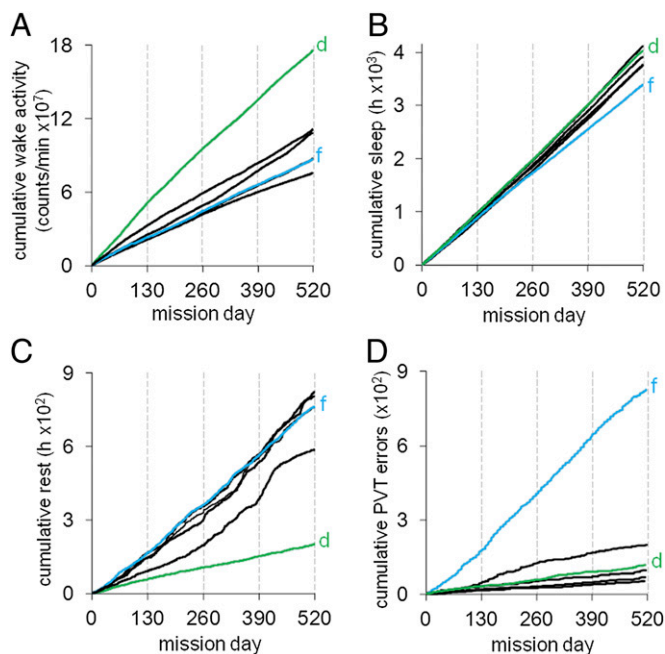

Fig. 2. Cumulative functions over 520 d of mission confinement for each crewmember's waking activity levels (A), time spent in sleep (B) and rest (C), and PVT-B error rate (D). Examination of data from crewmembers d and f illustrate the interindividual differences among the crew in reaction to the prolonged mission confinement.

PSYCHOLOGICAL AND COGNITIVE SCIENCES

Correction for "Reduced sensitivity to emotional prosody in congenital amusia rekindles the musical protolanguage hypothesis," by William Forde Thompson, Manuela M. Marin, and Lauren Stewart, which appeared in issue 46, November 13, 2012, of *Proc Natl Acad Sci USA* (109:19027–19032; first published October 29, 2012; 10.1073/pnas.1210344109).

The authors note that two column headings in Table 3 appeared incorrectly. "F0 (Hz)" should instead appear as "Log F_0 (ST)" measured as $12*\log_2(F_0)$, or the number of semitones from 1 Hz, where middle C (261.626 Hz) has an approximate value of 96. "*SD* F0" should instead appear as "*SD* (ST)". Statistical analyses of the fundamental frequency of speech stimuli were also based on $12*\log_2(F_0)$. The corrected table appears below. This error does not affect the conclusions of the article.

Table 3. Acoustical features of the Macquarie Battery of Emotional Prosody

Emotion	Log F_0 (ST)	SD (ST)	Contour changes	Slope	Duration (s)	Intensity (dB)
Happy						
M	93.44	3.92	8.13	5.00	2.85	73.99
SEM	1.17	0.22	0.30	7.74	0.12	0.39
Tender						
M	86.99	3.34	6.50	−13.51	3.24	68.76
SEM	1.94	0.33	0.27	4.45	0.15	0.39
Afraid						
M	93.46	1.69	7.56	−17.54	2.31	74.80
SEM	1.97	0.13	0.34	3.77	0.08	0.56
Irritated						
M	91.98	2.97	5.63	−30.15	2.43	73.76
SEM	1.12	0.24	0.44	9.00	0.08	0.83
Sad						
M	87.49	2.88	6.94	−11.98	3.10	68.76
SEM	1.75	0.42	0.40	3.31	0.13	0.89
No Emotion						
M	87.01	2.64	6.81	−15.30	2.90	71.66
SEM	1.65	0.22	0.29	4.25	0.11	0.72

ST, semitones from 1 Hz, or $12*\log_2(F_0)$; *M*, mean; *SD*, standard deviation; *SEM*, standard error of the mean.

MICROBIOLOGY

Correction for "Evolution of the receptor binding properties of the influenza A(H3N2) hemagglutinin," by Yi Pu Lin, Xiaoli Xiong, Stephen A. Wharton, Stephen R. Martin, Peter J. Coombs, Sebastien G. Vachieri, Evangelos Christodoulou, Philip A. Walker, Junfeng Liu, John J. Skehel, Steven J. Gamblin, Alan J. Hay, Rodney S. Daniels, and John W. McCauley, which appeared in issue 52, December 26, 2012, of *Proc Natl Acad Sci USA* (109:21474–21479; first published December 10, 2012; 10.1073/pnas.1218841110).

The authors note that on page 21474, within the Data Deposition footnote, the URL "http://platform.gisaid.org/epi3/" should instead appear as "http://gisaid.org/".

IMMUNOLOGY

Correction for "Essential role of MALT1 protease activity in activated B cell-like diffuse large B-cell lymphoma," by Stephan Hailfinger, Georg Lenz, Vu Ngo, Anita Posvitz-Fejfar, Fabien Rebeaud, Montserrat Guzzardi, Eva-Maria Murga Penas, Judith Dierlamm, Wing C. Chan, Louis M. Staudt, and Margot Thome, which appeared in issue 47, November 24, 2009, of *Proc Natl Acad Sci USA* (106: 19946-19951; first published November 6, 2009; 10.1073/pnas.0907511106).

The authors note that data reported in this article have been deposited in the Gene Expression Omnibus (GEO) database, www.ncbi.nlm.nih.gov/geo (accession no. GSE41034).

Reduced sensitivity to emotional prosody in congenital amusia rekindles the musical protolanguage hypothesis

William Forde Thompson[a,1], Manuela M. Marin[b], and Lauren Stewart[c]

[a]ARC Centre of Excellence in Cognition and its Disorders, Macquarie University, Sydney, NSW 2109, Australia; [b]Department of Basic Psychological Research and Research Methods, University of Vienna, 1010 Vienna, Austria; and [c]Department of Psychology, Goldsmiths, University of London, New Cross, London, SE14 6NW, United Kingdom

A number of evolutionary theories assume that music and language have a common origin as an emotional protolanguage that remains evident in overlapping functions and shared neural circuitry. The most basic prediction of this hypothesis is that sensitivity to emotion in speech prosody derives from the capacity to process music. We examined sensitivity to emotion in speech prosody in a sample of individuals with congenital amusia, a neurodevelopmental disorder characterized by deficits in processing acoustic and structural attributes of music. Twelve individuals with congenital amusia and 12 matched control participants judged the emotional expressions of 96 spoken phrases. Phrases were semantically neutral but prosodic cues (tone of voice) communicated each of six emotional states: happy, tender, afraid, irritated, sad, and no emotion. Congenitally amusic individuals were significantly worse than matched controls at decoding emotional prosody, with decoding rates for some emotions up to 20% lower than that of matched controls. They also reported difficulty understanding emotional prosody in their daily lives, suggesting some awareness of this deficit. The findings support speculations that music and language share mechanisms that trigger emotional responses to acoustic attributes, as predicted by theories that propose a common evolutionary link between these domains.

auditory | pitch | contour | intonation | impairment

Emotional communication is fundamental to social interaction. Within the auditory domain, emotional meaning can be powerfully communicated in both music and language (1). Based on evidence that there is a common acoustic code for emotional communication, researchers have speculated that the emotional signals evident in music and speech are decoded using shared processes (2, 3) and may reflect a common evolutionary origin (4–10). According to Darwin (5), language and music evolved from an earlier precursor or "musical protolanguage" that was used in courtship and territoriality and in the expression of emotion (6). More recently, several theorists and researchers have elaborated on this hypothesis and emphasized the importance of emotional communication in protolanguage (4, 7, 8, 10, 11), which may have been crucial for maintaining social and parent–infant bonds. These models make testable empirical predictions about the partially overlapping nature of emotional processes underlying music and spoken language.

The most basic prediction of the musical protolanguage hypothesis is that sensitivity to music—a channel specialized for emotional communication—should be correlated with sensitivity to emotion conveyed by speech. If the capacity to process and interpret music is enhanced by training, then sensitivity to emotional speech prosody should also be enhanced (12, 13). Conversely, if the capacity to process and interpret music is impaired, then sensitivity to emotional speech prosody should also be impaired.

In this investigation, we examined whether a group of amusic individuals—characterized by an abnormally poor ability to perceive, appreciate, and remember music—exhibit reduced sensitivity

to emotional prosody in speech. Amusia can arise following acquired brain injury (14), but may also occur congenitally in individuals who otherwise have normal auditory and intellectual abilities (15, 16). Like specific language impairment, congenital amusia emerges early in life and continues throughout adulthood. Up to 17% of individuals suspect that they are tone-deaf (17), but the prevalence of true congenital amusia is estimated to be much lower (18, 19).

Structural neuroimaging data reveal subtle differences in the brains of individuals with congenital amusia in the inferior frontal cortex and superior temporal areas, variously in the left hemisphere (20, 21) or the right (22). The finding of morphological differences outside the temporal cortex is congruent with findings from functional imaging studies showing activation of frontal and temporal areas when pitch information must be integrated or compared over time (23–26). A subsequent study using diffusion tensor imaging (27) suggests that individuals with amusia have reduced structural connectivity in the right superior branch of the arcuate fasciculus—a large fiber bundle connecting temporal and frontal areas.

The behavioral manifestations of brain anomalies associated with congenital amusia have been the subject of intense investigation. In general, the disorder is characterized by difficulties with singing in tune, responding rhythmically to music, detecting pitch errors in melodies, and recognizing melodies without lyrics (28). These anomalies have implications for emotional and aesthetic responses to music. Many amusic individuals report fewer changes in their emotional state when listening to music, and do not incorporate music into their daily activities to the extent reported by most people (29). Whereas 100% of a sample of nonamusic individuals reported that they "like" or "love" listening to music, only 43% of a sample of amusic individuals felt the same (29). Consonant and dissonant excerpts of music have highly dissimilar aesthetic connotations for most listeners, but individuals with congenital or acquired amusia perceive them to be aesthetically similar (15, 30).

It has been argued that behavioral manifestations of congenital amusia can be traced to impaired pitch perception (31, 32). Specifically, amusic individuals have difficulty perceiving pitch direction (33, 34) and detecting pitch deviations smaller than one semitone within tone sequences (32) and tone pairs (31). Other evidence suggests that amusia is associated with short-term memory deficits for pitch (35–37) and timbre (38) in the absence of memory deficits for verbal materials. Given the important role of pitch in music, it is no surprise that such pitch deficits are associated with impaired music perception and experience. Amusic

individuals can still perceive other acoustic attributes of music at normal levels, such as tempo and intensity. Such attributes can be used to make basic judgments including whether music sounds happy or sad (15).

A central question surrounding congenital amusia is whether the impairment is restricted to music perception or whether it extends to other domains such as speech processing. Pitch is not only an important attribute for music; it also carries syntactic and emotional information in speech (2, 3, 39). For example, pitch contour can be used in speech to differentiate a statement from a question, or a sad emotion from a happy emotion. More generally, music and speech are both auditory signals that acquire meaning through changes in attributes such as pitch, timing, intensity, and timbre. Prosody refers to all suprasegmental changes that occur in the course of an utterance (40, 41). Linguists generally differentiate between two prosodic phenomena, namely linguistic prosody, which belongs to the language itself, and emotional prosody, which depends on the emotional state of the speaker.

Initial evidence on linguistic prosody perception in congenital amusia suggested that the disorder is domain specific. In one study, a group of 11 adults diagnosed with congenital amusia was assessed for impairments in music and linguistic prosody (15). Amusic individuals were at normal levels in their ability to classify spoken utterances as questions or statements. The impairment only extended to speech stimuli when pitch changes from spoken utterances were extracted and presented in the absence of linguistic information. Based on such evidence, Peretz and her colleagues concluded that the disorder is largely restricted to the musical domain. Other studies showed that most amusic individuals can identify stressed words in sentences and can differentiate between declarative and interrogative sentences (39, 42). When subtle intonational pitch contrasts are used, however, amusic individuals are found to be impaired in the discrimination, identification, and imitation of statements and questions that differ in the pitch direction of the final word (43). This finding suggests that impaired pitch processing in congenital amusia may not be domain specific (44, 45, 46).

One reason the impairments observed in congenital amusia are largely restricted to music is that fine-grained changes in pitch are highly meaningful in music, whereas speech prosody often involves coarse-grained changes in pitch. The most common pitch change in Western melodies is a single semitone (47), whereas the rising pitch that occurs at the end of a question is typically larger than seven semitones in French and English (48). As such, the impairment underlying congenital amusia may be highly relevant to music because of the reliance of music on fine-grained pitch movements. Supporting this hypothesis, a recent investigation revealed that amusic individuals can correctly identify unambiguous examples of questions and statements, but exhibit deficits with subtle exemplars (49).

Whereas previous studies of amusia have focused on sensitivity to linguistic prosody (39, 42–45), the present study examines the perception of emotional prosody in this population. There are several reasons to suspect that impairments associated with congenital amusia may extend to the ability to decode emotional prosody, even though their ability to differentiate statements from questions is often minimally affected. First, questions and statements have well-defined meanings in speech but have no clear parallel in musical contexts. In contrast, both music and speech prosody communicate emotion. Second, questions and statements are distinguished by large changes in pitch that are well above the threshold of the pitch discrimination ability of amusic individuals, whereas subtle shifts in pitch and timing can significantly alter the emotional connotations of speech. Third, evidence suggests that the same acoustic cues are used in music and speech prosody to convey the same emotional messages (1), and researchers have argued that emotional signals in the two domains are decoded using shared brain circuitry (2, 3, 12). Fourth, recent neuroimaging

studies indicate that the amusic brain can be described by anomalies of the right hemisphere (50, 51), which has also been found to be crucial for emotional-speech-prosody processing in healthy brains (52). For example, neuroimaging studies suggest that the right mid-superior temporal gyrus adjacent to the superior temporal sulcus plays an important role in the processing of emotional prosody (52–56). For these reasons, we predicted that individuals with congenital amusia would exhibit reduced sensitivity to emotional prosody in speech.

Results

For each of the six emotional prosody categories (happiness, sadness, fear, irritation, tenderness, and no emotion), we calculated the percentage of correct judgments out of the 16 spoken phrases. These data were subjected to a two-way mixed-design ANOVA with Group (amusic versus control) as the between-subjects factor and Emotion as the within-subject factor (six emotion categories). There was a main effect of Group, as predicted, $F(1, 22) = 9.11$, $P = 0.006$, $\eta^2 = 0.29$. Classification of emotions conveyed by the prosodic stimuli was less accurate in the amusic group ($M = 77.87\%$, $SEM = 2.42$) compared with the control group ($M = 88.19\%$, $SEM = 2.42$). The findings confirm that impairments associated with congenital amusia are not restricted to music but extend to one of the most basic skills of social interaction: the capacity to interpret emotional connotations in speech.

We also observed a significant main effect of Emotion, $F(5, 110) = 25.82$, $P < 0.0001$, $\eta^2 = 0.50$. Across groups, classification was less accurate for prosodic stimuli intended to convey tenderness than prosodic stimuli intended to convey other emotions (all $P < 0.05$). Finally, there was a significant interaction between Emotion and Group, $F(5, 110) = 3.51$, $P = 0.006$, $\eta^2 = 0.07$. This interaction is illustrated in Fig. 1. Planned contrasts (one-tailed) indicated that the amusic group was significantly poorer than the control group at classifying prosodic stimuli intended to convey happiness, $t(22) = 3.82$, $P = 0.0009$; sadness, $t(22) = 2.14$, $P = 0.024$; tenderness, $t(22) = 2.42$, $P = 0.012$; and irritation, $t(22) = 1.75$, $P = 0.047$. Correct classification by the two groups was not reliably different for prosodic stimuli intended to convey fear or no emotion.

The overall performance on the emotional prosody battery for the 24 participants was significantly correlated with pitch direction thresholds, $r(22) = -0.41$, $P = 0.049$. Consistent with this finding,
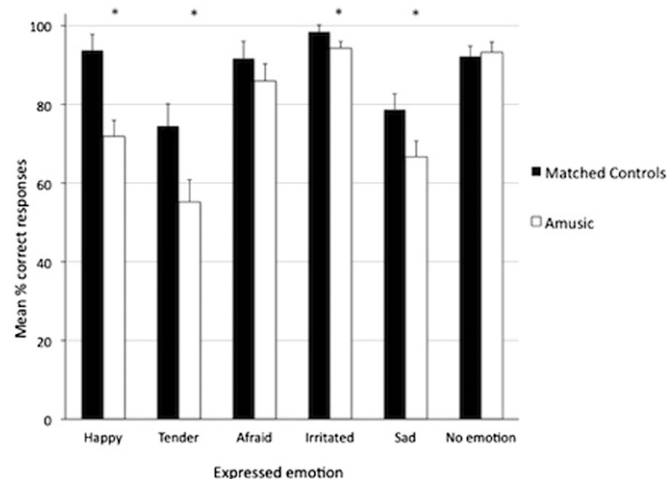

Fig. 1. The percentage of correctly decoded prosodic stimuli intended to convey each of six emotional categories by amusic and control groups. Error bars denote SEMs. Significant differences ($P < 0.05$) are indicated with an asterisk.

participants were most likely to confuse emotional categories that were similar to each other in the average slope of the vocal pitch contour. Across the fifteen unique pairs of emotion categories, a smaller pairwise difference in the average slope of utterances was associated with increased confusions for amusic, $r_s(13) = -0.45$, $P = 0.047$, and (marginally for) control participants $r_s(13) = -0.42$, $P = 0.059$. Overall performance was not significantly correlated with any of the matching variables or performance on the pitch-detection threshold task.

If reduced emotional decoding by amusics stems from a pitch-perception deficit, then it can be suggested that these individuals may rely heavily on non-pitch cues such as intensity and duration to determine an emotion category. This hypothesis predicts that amusics should have considerable difficulty differentiating emotion categories that are associated with similar intensity and duration values. This indeed appears to be the case: amusic participants were more likely than control participants to confuse emotion categories that were similar to each other in the intensity and duration of exemplar utterances. Five pairs of emotion categories in our stimulus set were relatively dissimilar to each other in the intensity and duration of exemplar utterances (based on a median split of difference scores); conversely, six pairs of emotion categories were relatively similar to each other in both attributes (four other pairs were similar in one attribute and dissimilar in the other). For pairs with dissimilar intensity and duration values (tender/afraid, sad/afraid, tender/irritated, sad/irritated, afraid/no emotion), the percentage of confusions was low for amusic ($M = 11.67\%$, $SEM = 2.41$) and control ($M = 8.33\%$, $SEM = 1.72$) participants, $t(22) = 1.13$, not significant. For emotion pairs with similar intensity and duration values (sad/tender, irritated/afraid, happy/no emotion, happy/irritated, sad/no emotion, and tender/no emotion), confusions were significantly more common for amusic participants ($M = 42.59\%$, $SEM = 6.87$) than for control participants ($M = 19.91\%$, $SEM = 2.26$), $t(22) = 3.14$, $P = 0.005$. A mixed-design ANOVA confirmed the reliability of this interaction, $F(1, 22) = 10.03$, $P = 0.004$, $\eta^2 = 0.31$.

Results of the questionnaire on participants' ability to perceive emotional prosody in the context of their daily lives revealed that responses of amusic individuals and controls differed significantly for all three statements. First, mean ratings for statement 1 were significantly higher for the amusic group ($M = 2.83$, $SEM = 0.24$) than for the control group ($M = 2.08$, $SEM = 0.23$), $t(22) = 2.26$, $P = 0.017$ (one-tailed test), indicating that amusic individuals reported greater difficulty than matched controls understanding how people feel merely by listening to them speaking. Second, mean ratings for statement 2 were significantly higher for the amusic group ($M = 3.50$, $SEM = 0.23$) than for the control group ($M = 2.58$, $SEM = 0.29$), $t(22) = 2.49$, $P = 0.01$, indicating that amusic participants rely more heavily than matched controls on facial expressions and gestures when interpreting the moods and feelings of people with whom they are speaking. This reliance on non-auditory cues would be expected among individuals who have reduced capacity to perceive emotion from speech prosody. Third, mean ratings for statement 3 were significantly higher for the amusic group ($M = 2.58$, $SEM = 0.19$) than for the control group ($M = 1.83$, $SEM = 0.24$), $t(22) = 2.43$, $P = 0.012$, indicating that amusic participants believe that they have more difficulty than matched controls with interpreting subtle aspects of speech prosody (such as sarcasm).

Discussion

The results of this investigation confirm that amusic individuals are less accurate than matched controls at classifying emotions conveyed by speech prosody, supporting the hypothesis that music and speech are associated with shared resources for decoding acoustic signals of emotions. In particular, our amusic sample was significantly worse than matched controls at decoding the emotions of happiness, tenderness, sadness, and irritation

conveyed through speech prosody. Amusic participants also reported difficulty interpreting emotional speech in the context of their daily lives, suggesting some awareness of their deficit.

Other investigations have reported that amusic individuals have elevated thresholds for pitch-change detection and pitch-direction discrimination (34) along with impaired sensitivity to subtle pitch changes derived from speech stimuli (39, 42–45, 49). For example, individuals with amusia who speak a tone language have reduced ability to discriminate individual words that differ only in tone, and reduced sensitivity to pitch sequences derived from questions and statements (34). The current results corroborate findings of elevated thresholds for pitch-direction discrimination and its association with prosody perception, but extend earlier reports in two crucial respects.

First, the current study examined the capacity of individuals with amusia to distinguish nuances of emotional meaning in speech. Previous research on congenital amusia uncovered only subtle problems outside of the domain of music because it focused on linguistic prosody rather than emotional prosody (43–45, 49, 57). Indeed, existing research implies that the perception of linguistic prosody in everyday contexts is largely spared in congenital amusia. According to the melodic-contour deafness hypothesis, a pattern of severe impairment for music with largely spared linguistic prosody perception arises because reduced sensitivity to pitch direction has a more noticeable impact on music perception than speech perception (39). More generally, "a degraded pitch-perception system may compromise music perception but leave other domains, such as speech intonation in which meaningful pitch variations are coarse, relatively unaffected. Yet, the same pitch-tracking mechanisms may subserve both domains" (see p. 250 in ref. 15). The current findings reveal that impairments associated with amusia can have significant consequences for the perception of emotional prosody in speech. Whereas amusic individuals have little or no difficulty with most aspects of speech perception in everyday contexts, they have significantly reduced sensitivity to the emotional connotations of speech—one of the most basic skills of social interaction.

Second, the findings illustrate that amusic individuals exhibit reduced sensitivity to emotional prosody even though prosodic stimuli contain multiple and redundant sources of relevant information (58). This finding contrasts with evidence that pitch-perception deficits have little effect on emotional decoding because other acoustic cues such as tempo and loudness are available (59). Under normal conditions, speakers convey emotional intentions using a range of prosodic attributes including pitch, pace, timing, timbre, and intensity (58). These attributes act as perceptual cues that collectively signal an emotional intention. No single acoustic attribute unambiguously signals an emotional intention. Rather, perceivers form hypotheses about the most likely intentions based on available evidence from a range of acoustic attributes (58, 60, 61). For individuals with congenital amusia, an impairment of pitch processing means that the evidence available for emotional decoding is reduced, and that they may rely heavily on non-pitch cues such as duration and intensity when decoding emotional prosody. Our finding that amusic participants were most likely to confuse emotion categories that are similar in the duration and intensity of exemplar utterances supports the latter possibility. For tasks that involve differentiating a small number of highly distinctive emotions, the reduced evidence available to individuals with amusia may have no detectable effect on decoding (59). However, our findings suggest that reduced emotional decoding becomes evident when amusic individuals are required to categorize a larger array of emotional connotations.

Although the amusic group was worse than the control group at decoding fear, this difference was not statistically reliable. One interpretation of this finding is that prosodic signals of fear were largely decoded using acoustic attributes other than pitch direction,

Table 1. Amusic and control participant characteristics I

Group	Age (y)	Sex	Handedness	Musical training (y)	Education (y)	NART	Digit span
Amusic							
M	49.58	7 F	11 R	1.00	16.58	40.83	20.17
SD	13.57	5 M	1 L	2.13	2.75	4.67	4.06
Control							
M	46.33	7 F	11 R	1.83	16.50	43.96	21.58
SD	10.12	5 M	1 L	1.99	1.83	4.06	3.55
t tests							
t	0.665			0.989	0.087	1.75	0.909
p	0.513			0.333	0.931	0.094	0.373

F, female; L, left; M, male; *M*, mean; R, right; *SD*, standard deviation; *t*, test statistic of the independent samples *t* test.

and individuals with congenital amusia were able to process those attributes at normal levels. Decoding by amusic and control participants was also similar for the no-emotion category. This finding is less surprising given that we would not necessarily expect impaired music perception to result in a deficit in the ability to detect the absence of an emotional connotation. More generally, the association between congenital amusia and emotional prosody perception was more evident for some emotions than for others (the significant group by emotion interaction remained significant when the no-emotion category was excluded from the data).

One implication of our results is that individuals with congenital amusia may need to draw from nonprosodic cues of emotion when engaged in social interactions that depend on vocal communication. Because emotional decoding impairments are relatively minor, social implications are unlikely to be evident in contexts where nonprosodic cues are available, such as semantic content or cues arising from facial expressions and gestures. Social implications may be more evident in contexts that do not permit nonprosodic cues, such as speaking on the telephone. In such contexts, it may be possible for amusic individuals to attend carefully to contextual cues, eliminating any detectable impairment in the perception of emotional speech prosody that may be associated with this disorder.

To conclude, impairments associated with congenital amusia are not restricted to music, but include significantly reduced capacity to decode emotional connotations from speech prosody, especially for certain emotions. As such, the findings provide further support for the claim that music and speech share a common acoustic code for emotional communication. They also lend support to early speculations by Darwin, elaborated upon by several contemporary theorists, that emotional communication is a fundamental link between these domains and reflects their common evolutionary origin (4–10).

Materials and Methods

Participants. Twenty-four participants (12 amusic individuals and 12 matched controls) took part in the investigation in return for a small monetary compensation. Participants were recruited by means of an online test based on the scale and rhythm subtests of the Montreal Battery of Evaluation of Amusia (MBEA) (62) (www.delosis.com/listening/home.html). The MBEA tests for potential impairments in pitch perception (scale, contour, interval) and rhythm perception (grouping, meter), as well as musical memory. For pitch and rhythm subtests, pairs of brief melodies are presented and participants must indicate whether they are same or different. For most people, even slight differences between the two melodies (in pitch or timing) are highly noticeable and performance on the MBEA is close to ceiling. However, individuals with congenital amusia have difficulty comparing the melodies, leading to significantly reduced performance.

Participants were invited for further testing if they completed the online test twice and scored below 22/30 on the scale subtest on two consecutive occasions. All participants provided informed consent and testing was approved by the Goldsmiths Research Ethics Committee, University of London. On-site testing included four MBEA subtests (scale, contour, interval, and rhythm) to assess the presence or absence of congenital amusia. A composite score was calculated based on the three pitch-based subtests, and those scoring 65 or below out of 90 were classed as having congenital amusia. The emphasis on pitch-based subtests for diagnosis reflects the fact that amusic individuals are highly variable in their performance on the rhythm subtest, with up to 50% of amusic individuals scoring in the normal range (62).

Amusic and control participants were matched on age, sex, handedness, number of years of education, years of musical training, performance on the National Adult Reading Test (NART) (63), and performance on the digit span test (64). Two additional pitch threshold tasks were also conducted: a pitch-change detection task and a pitch-direction discrimination task (for details, see refs. 37 and 43). Table 1 provides background information on the two groups; Table 2 displays scores on the MBEA subtests and pitch thresholds. The two groups performed significantly differently on all three MBEA pitch-based subtests, the MBEA rhythm subtest, and the pitch-direction discrimination test. The groups performed similarly on the pitch-change detection task.

All participants confirmed that they had no neurological or psychiatric disorder. Hearing tests were also administered to eliminate the possibility

Table 2. Amusic and control participant characteristics II

Group	MBEA scale	MBEA contour	MBEA interval	MBEA rhythm	Pitch composite	Detection threshold	Direction threshold
Amusic							
M	19.67	20.17	17.75	25.25	57.58	0.19	0.89
SD	2.96	2.69	1.86	3.62	6.27	0.08	0.84
Control							
M	27.50	28.50	27.75	28.92	83.75	0.16	0.16
SD	2.20	1.09	2.01	0.79	4.43	0.07	0.08
t tests							
t	7.36	9.95	12.65	3.34	11.80	1.14	2.96
p	<0.001	<0.001	<0.001	0.002	<0.001	0.265	0.007

M, mean; *SD*, standard deviation; *t*, test statistic of the independent samples *t* test. The pitch composite score is the mean score based on the scale, contour, and interval subtests of the MBEA.

that poor performance on the MBEA was caused by hearing impairment. Pure-tone thresholds were determined using a manually operated Amplivox 2160 pure-tone diagnostic audiometer and following a standardized procedure for the measurement of hearing thresholds. Participants were required to have a mean hearing level, in at least one ear, of less than or equal to 20 dB, as measured at 250, 500, 1,000, and 2,000 Hz. These frequencies cover the range of frequencies used in the listening tasks. One amusic and one control participant did not fulfill this criterion. However, data inspection revealed that these two participants were not outliers in any of the tasks, so they were not excluded from the sample and the main analysis.

Materials. *MBEA.* The MBEA is currently the most widely used test for diagnosing amusia (62). It is theoretically motivated, reliable upon retest, highly sensitive, correlated with Gordon's Musical Aptitude Profile (65), and satisfies important psychometric properties. The present study used four of the six subtests from the battery: scale, contour, interval, and rhythm. These subtests each consisted of thirty trials, where a trial comprised two short musical phrases that were either identical or differed at a single point (the nature of the difference differed according to the subtest). Participants reported whether the phrases were the same or different.
Macquarie Battery of Emotional Prosody. To create stimuli that varied in emotional prosody, we recorded four male and four female adults speaking semantically neutral phrases such as: "The broom is in the closet and the book is on the desk." Each phrase consisted of 14 syllables and was spoken with the intention to communicate each of six emotions: happy, sad, tender, irritated, afraid, and neutral. These emotions were selected because they vary in decoding difficulty and involve a range of acoustic cues to emotion. During the recording session, an experienced recording engineer provided continuous coaching and feedback to the speakers, and speakers could repeat any spoken phrase until they were satisfied that they had effectively communicated the target emotion. The final stimulus set consisted in 96 spoken phrases (16 spoken phrases per emotion category), which can be downloaded from the first author's website (www.psy.mq.edu.au/me2). The spoken phrases were recorded with a sample rate and bit depth of 44.1 KHz/16 bit—mono in an acoustically controlled recording booth in the department of media, music, and cultural studies at Macquarie University. Participants spoke into a K2 Condenser Microphone (Røde Microphones) and were recorded with Cubase SX 4 (Prochak).

Acoustic analyses were conducted using Praat (version 5.2.11) (66) to determine how the acoustic attributes of the spoken phrases were affected by the intended emotion. Table 3 summarizes the results of the analysis. Each acoustic attribute was subjected to a one-way ANOVA comparing means across the six emotion categories. The analyses revealed that the intended emotion significantly affected numerous acoustic attributes in the speech samples, including variables related to fundamental frequency, timing, and intensity.

First, there was a significant difference in the average fundamental frequency (in hertz) depending on the intended emotion, $F(5, 90) = 3.88$, $P = 0.003$, $\eta^2 = 0.18$. The average frequency was higher for speech that conveyed happiness ($M = 93.44$, $SEM = 1.17$), fear ($M = 93.46$, $SEM = 1.97$), and irritation ($M = 91.98$, $SEM = 1.12$) than for speech that conveyed sadness ($M = 87.49$, $SEM = 1.75$), tenderness ($M = 86.99$, $SEM = 1.94$), or no emotion ($M = 87.01$, $SEM = 1.65$). Second, there was a significant difference in the variability of the fundamental frequency in spoken phrases (SD of hertz) depending on the intended emotion, $F(5, 90) = 7.30$, $P < 0.0001$, $\eta^2 = 0.29$. The average variability in frequency was highest for spoken phrases that conveyed happiness ($M = 3.92$, $SEM = 0.22$) and tenderness ($M = 3.34$, $SEM = 0.33$), and lowest for spoken phrases that conveyed fear ($M = 1.69$, $SEM = 0.13$). Third, there was a significant difference in the number of contour changes in the spoken phrases depending on the intended emotion, $F(5, 90) = 6.22$, $P < 0.0001$, $\eta^2 = 0.26$. The average number of contour changes was highest for spoken phrases that conveyed happiness ($M = 8.13$, $SEM = 0.30$) and lowest for spoken phrases that conveyed irritation ($M = 5.63$, $SEM = 0.44$). Fourth, the rising or falling trend of fundamental frequency in spoken phrases differed as a function of the intended emotion, as measured by the slope of the regression (trend) line across each spoken phrase. A positive slope indicated a global increase in fundamental frequency across the phrase. A negative slope indicated a global decrease in fundamental frequency across the phrase. There was a significant difference in the average slope of spoken phrases depending on the intended emotion, $F(5, 90) = 3.77$, $P = 0.004$, $\eta^2 = 0.17$. Slopes were highest for phrases intended to convey happiness ($M = +5.00$, $SEM = 7.74$) and lowest for phrases intended to convey irritation ($M = -30.15$, $SEM = 9.01$). Fifth, there was a significant difference in the duration of spoken phrases depending on the intended emotion, $F(5, 90) = 10.28$, $P < 0.0001$, $\eta^2 = 0.36$.

Table 3. Acoustical features of the Macquarie Battery of Emotional Prosody

Emotion	F0 (Hz)	SD F0	Contour changes	Slope	Duration (s)	Intensity (dB)
Happy						
M	93.44	3.92	8.13	5.00	2.85	73.99
SEM	1.17	0.22	0.30	7.74	0.12	0.39
Tender						
M	86.99	3.34	6.50	−13.51	3.24	68.76
SEM	1.94	0.33	0.27	4.45	0.15	0.39
Afraid						
M	93.46	1.69	7.56	−17.54	2.31	74.80
SEM	1.97	0.13	0.34	3.77	0.08	0.56
Irritated						
M	91.98	2.97	5.63	−30.15	2.43	73.76
SEM	1.12	0.24	0.44	9.00	0.08	0.83
Sad						
M	87.49	2.88	6.94	−11.98	3.10	68.76
SEM	1.75	0.42	0.40	3.31	0.13	0.89
No emotion						
M	87.01	2.64	6.81	−15.30	2.90	71.66
SEM	1.65	0.22	0.29	4.25	0.11	0.72

M, mean; SD, standard deviation; SEM, standard error of the mean.

The average duration (in seconds) was longest (slower speech) for spoken phrases that conveyed sadness ($M = 3.10$, $SEM = 0.13$) and tenderness ($M = 3.24$, $SEM = 0.15$) and shortest (faster speech) for spoken phrases that conveyed fear ($M = 2.31$, $SEM = 0.08$). Sixth, there was a significant difference in the average intensity of spoken phrases depending on the intended emotion, $F(5, 90) = 16.53$, $P < 0.001$, $\eta^2 = 0.48$. The average intensity (in decibels) was highest for spoken phrases that conveyed fear ($M = 74.80$, $SEM = 0.56$) and lowest for spoken phrases that conveyed sadness ($M = 68.76$, $SEM = 0.89$).
Emotional Prosody Questionnaire. A short questionnaire was developed to collect data on participants' ability to perceive and produce emotional prosody in the context of their daily lives. Participants were asked to indicate their agreement with three statements: (*i*) When speaking on the telephone, I cannot tell how someone feels just by listening to their voice; (*ii*) When talking to people, I mostly rely on their facial expressions to understand their mood and feelings; and (*iii*) When people are talking to me, I do not realize when they are being sarcastic. The statements probed participants' perceived ability to decode emotional speech prosody when it is not supplemented by facial expressions and gestures (statement 1); their reliance on facial expressions and gestures when such visual cues are available (statement 2); and their perceived ability to decode subtle aspects of speech prosody (statement 3). Ratings were assigned on a 5-point scale with the following response options: strongly disagree, disagree, unsure, agree, and strongly agree.

Procedure. Amusic and control participants were tested individually in a sound-attenuated booth and heard all stimuli through Sennheiser headphones HD 202 at a comfortable fixed loudness level, or ∼70 dB as measured at the headphones. Sounds were presented through an external sound card (Edirol UA-4FX USB audio capture). The emotional prosody experiment was created and administered using Experiment Creator, a software application available from W.F.T.'s website. The 96 spoken utterances were presented in an order that was randomized independently for each participant. After each presentation, participants used a computer mouse to identify the intended emotion from a list of the six emotion categories that was displayed on the computer screen. Matlab (MathWorks) was used to control stimulus presentation and data collection for all other tests. The questionnaire was administered after the experiment.

1. Juslin PN, Laukka P (2003) Communication of emotions in vocal expression and music performance: Different channels, same code? *Psychol Bull* 129(5):770–814.
2. Ilie G, Thompson WF (2006) A comparison of acoustic cues in music and speech for three dimensions of affect. *Music Percept* 23:319–329.
3. Ilie G, Thompson WF (2011) Experiential and cognitive changes following seven minutes exposure to music and speech. *Music Percept* 28:247–264.
4. Brown S (2000) The "musilanguage" model of music evolution. *The Origins of Music*, eds Wallin BMNL, Brown S (MIT Press, Cambridge, MA), pp 271–300.
5. Darwin C (1871) *The Descent of Man, and Selection in Relation to Sex* (John Murray, London), 1st Ed.
6. Fitch WT (2006) The biology and evolution of music: A comparative perspective. *Cognition* 100(1):173–215.
7. Mithen SJ (2006) *The Singing Neanderthals: The Origins of Music, Language, Mind and Body* (Harvard Univ Press, Cambridge, MA).
8. Dissanayake E (2000) Antecedents of the temporal arts in early mother-infant interaction. *The Origins of Music*, eds Wallin NL, Merker BH, Brown S (The MIT Press, Cambridge, MA), pp 389–410.
9. Jesperson O (1922) *Language: Its Nature, Development and Origin* (W. W. Norton, New York).
10. Fitch WT (2010) *The Evolution of Language* (Cambridge Univ Press, Cambridge, UK).
11. Trehub SE (2003) The developmental origins of musicality. *Nat Neurosci* 6(7):669–673.
12. Thompson WF, Schellenberg EG, Husain G (2004) Decoding speech prosody: Do music lessons help? *Emotion* 4(1):46–64.
13. Lima CF, Castro SL (2011) Speaking to the trained ear: Musical expertise enhances the recognition of emotions in speech prosody. *Emotion* 11(5):1021–1031.
14. Särkämö T, et al. (2009) Cognitive deficits associated with acquired amusia after stroke: A neuropsychological follow-up study. *Neuropsychologia* 47(12):2642–2651.
15. Ayotte J, Peretz I, Hyde K (2002) Congenital amusia: A group study of adults afflicted with a music-specific disorder. *Brain* 125(Pt 2):238–251.
16. Peretz I, Cummings S, Dubé MP (2007) The genetics of congenital amusia (tone deafness): A family-aggregation study. *Am J Hum Genet* 81(3):582–588.
17. Cuddy LL, Balkwill LL, Peretz I, Holden RR (2005) Musical difficulties are rare: A study of "tone deafness" among university students. *Ann N Y Acad Sci* 1060:311–324.
18. Kalmus H, Fry DB (1980) On tune deafness (dysmelodia): Frequency, development, genetics and musical background. *Ann Hum Genet* 43(4):369–382.
19. Henry MJ, Mcauley JD (2010) On the prevalence of congenital amusia. *Music Percept* 27:413–418.
20. Hyde KL, et al. (2007) Cortical thickness in congenital amusia: When less is better than more. *J Neurosci* 27(47):13028–13032.
21. Hyde KL, Zatorre RJ, Griffiths TD, Lerch JP, Peretz I (2006) Morphometry of the amusic brain: A two-site study. *Brain* 129(Pt 10):2562–2570.
22. Mandell J, Schulze K, Schlaug G (2007) Congenital amusia: An auditory-motor feedback disorder? *Restor Neurol Neurosci* 25(3-4):323–334.
23. Gaab N, Gaser C, Zaehle T, Jancke L, Schlaug G (2003) Functional anatomy of pitch memory—An fMRI study with sparse temporal sampling. *Neuroimage* 19(4):1417–1426.
24. Koelsch S, et al. (2009) Functional architecture of verbal and tonal working memory: An FMRI study. *Hum Brain Mapp* 30(3):859–873.
25. Levitin DJ, Menon V (2003) Musical structure is processed in "language" areas of the brain: A possible role for Brodmann Area 47 in temporal coherence. *Neuroimage* 20(4):2142–2152.
26. Zatorre RJ, Evans AC, Meyer E (1994) Neural mechanisms underlying melodic perception and memory for pitch. *J Neurosci* 14(4):1908–1919.
27. Loui P, Alsop D, Schlaug G (2009) Tone deafness: A new disconnection syndrome? *J Neurosci* 29(33):10215–10220.
28. Stewart L (2011) Characterizing congenital amusia. *Q J Exp Psychol (Hove)* 64(4):625–638.
29. McDonald C, Stewart L (2008) Uses and functions of music in congenital amusia. *Music Percept* 25:345–355.
30. Peretz I, Blood AJ, Penhune V, Zatorre R (2001) Cortical deafness to dissonance. *Brain* 124:928–940.
31. Peretz I, et al. (2002) Congenital amusia: A disorder of fine-grained pitch discrimination. *Neuron* 33(2):185–191.
32. Hyde KL, Peretz I (2004) Brains that are out of tune but in time. *Psychol Sci* 15(5):356–360.
33. Foxton JM, Dean JL, Gee R, Peretz I, Griffiths TD (2004) Characterization of deficits in pitch perception underlying 'tone deafness' *Brain* 127(Pt 4):801–810.
34. Liu F, et al. (2012) The mechanism of speech processing in congenital amusia: Evidence from Mandarin speakers. *PLoS ONE* 7(2):e30374.
35. Gosselin N, Jolicoeur P, Peretz I (2009) Impaired memory for pitch in congenital amusia. *Ann N Y Acad Sci* 1169:270–272.
36. Tillmann B, Schulze K, Foxton JM (2009) Congenital amusia: A short-term memory deficit for non-verbal, but not verbal sounds. *Brain Cogn* 71(3):259–264.
37. Williamson VJ, Stewart L (2010) Memory for pitch in congenital amusia: Beyond a fine-grained pitch discrimination problem. *Memory* 18(6):657–669.
38. Marin MM, Gingras B, Stewart L (2012) Perception of musical timbre in congenital amusia: Categorization, discrimination and short-term memory. *Neuropsychologia* 50(3):367–378.
39. Patel AD (2008) *Music, Language, and the Brain* (Oxford Univ Press, New York).
40. Banse R, Scherer KR (1996) Acoustic profiles in vocal emotion expression. *J Pers Soc Psychol* 70(3):614–636.
41. Grandjean D, Bänziger T, Scherer KR (2006) Intonation as an interface between language and affect. *Prog Brain Res* 156:235–247.
42. Patel AD, Foxton JM, Griffiths TD (2005) Musically tone-deaf individuals have difficulty discriminating intonation contours extracted from speech. *Brain Cogn* 59(3):310–313.
43. Liu F, Patel AD, Fourcin A, Stewart L (2010) Intonation processing in congenital amusia: Discrimination, identification and imitation. *Brain* 133(Pt 6):1682–1693.
44. Jiang C, Hamm JP, Lim VK, Kirk IJ, Yang Y (2010) Processing melodic contour and speech intonation in congenital amusics with Mandarin Chinese. *Neuropsychologia* 48(9):2630–2639.
45. Nan Y, Sun Y, Peretz I (2010) Congenital amusia in speakers of a tone language: Association with lexical tone agnosia. *Brain* 133(9):2635–2642.
46. Jiang C, Hamm JP, Lim VK, Kirk IJ, Chen X, Yang Y (2012) Amusia results in abnormal brain activity following inappropriate intonation during speech comprehension. *PLoS ONE*, 7(7):e41411.
47. Vos PG, Troost JM (1989) Ascending and descending melodic intervals: Statistical findings and their perceptual relevance. *Music Percept* 6:383–396.
48. Fitzsimons M, Sheahan N, Staunton H (2001) Gender and the integration of acoustic dimensions of prosody: Implications for clinical studies. *Brain Lang* 78(1):94–108.
49. Hutchins S, Gosselin N, Peretz I (2010) Identification of changes along a continuum of speech intonation is impaired in congenital amusia. *Front Psychol* 1:236.
50. Loui P, Schlaug G (2009) Investigating musical disorders with diffusion tensor imaging: A comparison of imaging parameters. *Ann N Y Acad Sci* 1169:121–125.
51. Hyde KL, Zatorre RJ, Peretz I (2011) Functional MRI evidence of an abnormal neural network for pitch processing in congenital amusia. *Cereb Cortex* 21(2):292–299.
52. Wiethoff S, et al. (2008) Cerebral processing of emotional prosody—Influence of acoustic parameters and arousal. *Neuroimage* 39(2):885–893.
53. Beaucousin V, et al. (2007) FMRI study of emotional speech comprehension. *Cereb Cortex* 17(2):339–352.
54. Ethofer T, et al. (2006) Cerebral pathways in processing of affective prosody: A dynamic causal modeling study. *Neuroimage* 30(2):580–587.
55. Grandjean D, et al. (2005) The voices of wrath: Brain responses to angry prosody in meaningless speech. *Nat Neurosci* 8(2):145–146.
56. Frühholz S, Ceravolo L, Grandjean D (2012) Specific brain networks during explicit and implicit decoding of emotional prosody. *Cereb Cortex* 22(5):1107–1117.
57. Patel AD, Wong M, Foxton J, Lochy A, Peretz I (2008) Speech intonation perception deficits in musical tone deafness (congenital amusia). *Music Percept* 25:357–368.
58. Thompson WF, Balkwill LL (2006) Decoding speech prosody in five languages. *Semiotica* 158:407–424.
59. Peretz I, Gagnon L, Bouchard B (1998) Music and emotion: Perceptual determinants, immediacy, and isolation after brain damage. *Cognition* 68(2):111–141.
60. Balkwill LL, Thompson WF (1999) A cross-cultural investigation of the perception of emotion in music: Psychophysical and cultural cues. *Music Percept* 17:43–64.
61. Thompson WF, Balkwill LL (2010) Cross-cultural similarities and differences. *Music and Emotion*, eds Juslin PN, Sloboda JA (Oxford Univ Press, Oxford, UK), 2nd Ed, pp 755–788.
62. Peretz I, Champod AS, Hyde KL (2003) Varieties of musical disorders. The Montreal battery of evaluation of amusia. *Ann N Y Acad Sci* 999:58–75.
63. Nelson HE, Willison JR (1991) *National Adult Reading Test (NART)* (NFER-Nelson, Windsor, UK).
64. Wechsler D (1997) *WAIS — III Administration and Scoring Manual* (The Psychological Corporation, San Antonio, TX), 3rd Ed.
65. Gordon EE (1965) Musical Aptitude Profile (GIA Publications, Chicago).
66. Boersma P, Weenink D (2009) Praat: Doing Phonetics by Computer (University of Amsterdam), Version 5.2.11.