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Characterizing congenital amusia

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The ability to make sense of the music in our environment involves sophisticated cognitive mechanisms that, for most people, are acquired effortlessly and in early life. A special population of individuals, with a disorder termed congenital amusia, report lifelong difficulties in this regard. Exploring the nature of this developmental disorder provides a window onto the cognitive architecture of typical musical processing, as well as allowing a study of the relationship between processing of music and other domains, such as language. The present article considers findings concerning pitch discrimination, pitch memory, contour processing, experiential aspects of music listening in amusia, and emerging evidence concerning the neurobiology of the disorder. A simplified model of melodic processing is outlined, and possible loci of the cognitive deficit are discussed.

Keywords: Music; Perception; Congenital amusia; Pitch; Contour.

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The study of acquired disorders of musical processing, following brain injury, has a long history in the neurological literature (for a review, see Critchley & Henson, 1977) but consideration of musical deficits arising developmentally has been a relatively recent focus of enquiry. Investigations conducted over the past decade have established that some individuals experience lifelong problems in the perception and production of music. This developmental disorder—termed congenital amusia (Peretz et al., 2003) manifests as a difficulty with singing in tune, dancing or tapping along with music, detecting anomalous pitches in familiar and unfamiliar melodies, judging dissonance in musical excerpts, and recognizing and memorizing melodies without lyrics (Ayotte, Peretz, & Hyde, 2002; Dalla Bella, Giguere, & Peretz, 2009; Dalla Bella & Peretz, 2003). Importantly, these problems cannot be accounted for by deficits in peripheral auditory processing, a lack of exposure to music, or a general learning impairment (Ayotte et al., 2002). Counterintuitively, individuals who self-label as "tone-deaf" rarely fall into this category: The use of this term is typically associated with an inability to sing in tune, while perceptual abilities tend to be normal (Cuddy, Balkwill, Peretz, & Holden, 2005; Pfordrescher & Brown, 2008; Wise & Sloboda, 2008).

The identification of such individuals would once have been considered no more than an anecdotal curiosity. But research into the cognitive architecture of musical processing demonstrates that, regardless of musical training, the majority of humans display a sophisticated knowledge of the rules of musical structure, even from early life (Hannon & Trainor, 2007; Winkler, Háden, Ladinig, Sziller, & Honing, 2009). Such knowledge is not dependent on formal musical training; rather it is implicitly acquired through exposure to the statistical regularities of the musical environment (Saffran, Johnson, Aslin, & Newport, 1999). Congenital amusia is therefore interesting in at least three respects: First, the disorder provides a window onto the cognitive architecture of normal musical processing and its neural substrate; second, it provides a means for establishing whether musical deficits impact upon processing in non-musical domains; and finally, the opportunity to investigate the disorder at all levels allows the possibility of tracing connections from the level of the gene through to the development of brain structure and the emergence of a complex cognitive ability. In this paper, I review the state of current knowledge of the disorder and propose a simplified scheme of melodic processing, in order to advance hypotheses concerning the possible locus of the deficit(s) at the cognitive level.

Diagnosis

The presence of congenital amusia is typically ascertained using the Montreal Battery for the Evaluation of Amusia (MBEA; Peretz et al., 2003), originally developed to investigate acquired deficits in neurological patients (Peretz, 2001). This battery requires participants to discriminate between novel tunes, lasting four bars in length. Each of the five main subtests employs a systematically different type of manipulation, to probe a distinct aspect of musical perception—namely, key, contour, interval, rhythm, and metre. The subtests are scored out of 30, and the results of the individual subtests can be summed to give a global score. In the first group study of congenital amusia, Peretz and colleagues appealed for individuals to come forward who self-reported lifelong musical difficulties. In comparison with the global scores of 160 adults who reported no such problems, 89% of these self-reported amusics scored more than two standard deviations from the mean global score of the normative sample (Peretz et al., 2003). These individuals were consistently impaired on the three pitch-based subtests, while more variability was seen on the tests involving changes to temporal structure. Subsequent testing confirmed their difficulties in recognizing well-known tunes (except via lyrics), as well as their inability to sing in tune, of which they were unaware (Ayotte et al., 2002).

Fine-grained pitch discrimination

Pitch has been argued to be a fundamental building block of music in all known cultures (McDermott & Hauser, 2005). In Western music, most melodies are constructed with small intervals between consecutive tones; 70% of intervals are either repeated pitches or 1 or 2 semitones (Vos & Troost, 1989). Thus, an inability to discriminate adjacent pitches would probably have far-reaching consequences for the representation of higher order musical features such as contour (the pattern of ups and downs of a melody) and key (the set of hierarchically related pitches from which the melody is composed).

While individual case studies of congenital amusia have pointed to fundamental deficits in pitch discrimination (Allen, 1878; Peretz et al., 2002), threshold-based testing in cohorts has yielded a mixed picture: Hyde and Peretz (2004) found that individuals with congenital amusia failed to detect a pitch change of a semitone when presented within the context of a five-item sequence that was otherwise monotonic and isochronous, while controls achieved ceiling performance for changes as small as 0.25 semitones. Foxton, Dean, Gee, Peretz, and Griffiths (2004) used forced-choice methods to assess thresholds, separately for the detection of a pitch change and the discrimination of pitch change direction. They found individuals with congenital amusia to be significantly worse at both tasks, but particularly for the discrimination of pitch direction, where only 2 of the 10 amusics tested had thresholds of less than one semitone. As shown in Figure 1, recent psychophysical testing from our group shows that, barring a single outlier within the congenital amusia group, all participants have thresholds below one semitone for the simple detection of a pitch difference, but approximately half the group have thresholds for the discrimination of pitch *direction* that approach or exceed one semitone (Liu, Patel, Fourcin, & Stewart, 2010; Williamson & Stewart, 2010). Variability in measured thresholds across different studies can be expected owing to cohort effects, as well as differences in methodology and stimuli (e.g., the use of forced-choice versus non-forced choice methods; the use of spectrally complex versus pure tones). However, reaching a consensus on this issue will be important, since the extent to which pitch discrimination is impaired has a critical bearing on the inferences that can be drawn about how these fundamental pitch discrimination processes may impact upon the representation of higher order musical structure.

Contour discrimination

"Contour" relates to the shape of a melody, governed by the changes in pitch over time, and can be considered to constitute the "global" structure of a melody, while its "local" structure is governed by the precise intervals and absolute pitches of which the melody is comprised. This global level of structure has been demonstrated to be cognitively salient, since listeners are better able to detect a difference between two pitch patterns (shifted in overall pitch) when the difference alters, as opposed to retains, the contour of the original pattern (Dowling & Fujitani, 1971). Patient studies provide support for a hierarchy of processing, with contour processing preceding the more local, intervallic level of representation (Liégeois-Chauvel, Peretz, Babaï, Laguitton, & Chauvel, 1998; Peretz, 1990). The diagnostic test of congenital amusia (the MBEA) includes subtests that explicitly distinguish between these two types of difference (contour violated; contour maintained) although individuals with congenital amusia do poorly on both (Peretz et al., 2003).

These higher level difficulties may emerge from the more fundamental deficit in discriminating pitch direction, since pitch direction must be viewed as a key building block of contour. However, poor contour discrimination cannot be improved simply by stretching the pitch range such that constituent intervals are several times the measured pitch detection thresholds (Foxton et al., 2004). It may be that the arrested development of a sensitivity to pitch direction in early life has profound and long-lasting effects on the development of contour perception such that the latter could not be improved no matter how salient the constituent intervals become.

Domain specificity of the contour deficit

Aspects of spoken language also comprise pitch contours, which convey different communicative meanings, including emotion, emphasis, and sentence type (e.g., statement/question; Xu, 2005).

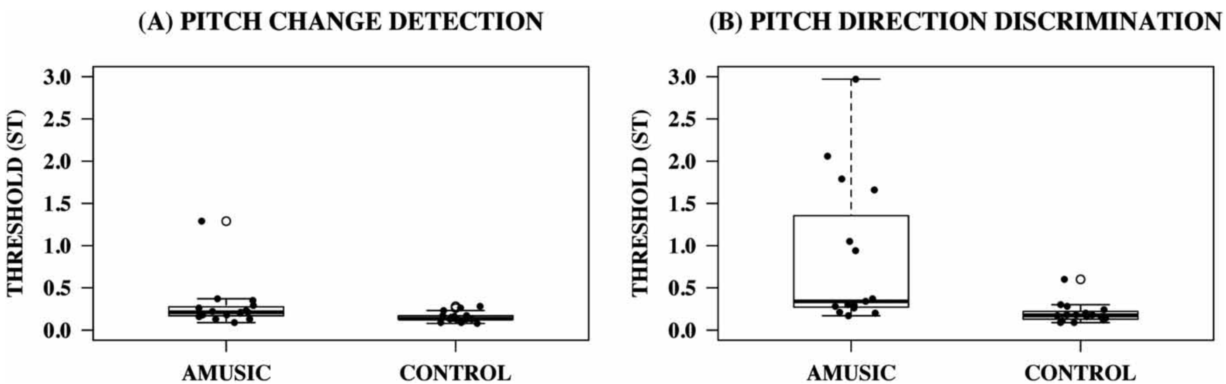

Figure 1. *Boxplots of pitch thresholds for two psychophysical tasks: (A) pitch change detection, and (B) pitch direction discrimination. From "Intonation Processing in Congenital Amusia: Discrimination, Identification and Imitation", by F. Liu, A. Patel, A. Fourcin, and L. Stewart, 2010, Brain, 133(6), p. 1688. Copyright 2010 by the Name of Copyright Holder. Reprinted with permission.*

Investigating whether individuals with congenital amusia experience difficulties with speech intonation is therefore of theoretical importance, since a dissociation in performance has implications for theories of domain specificity (Peretz & Coltheart, 2003). Ayotte et al. (2002) reported that individuals with congenital amusia were able to perform just as well as controls on tests of focus identification and discrimination based on salient pitch accents (e.g., "Go in *front* of the bank, I said" versus "Go in front of the *bank*, I said") as well as on tests of statement/question identification and discrimination (e.g., "He speaks French." versus "He speaks French?"). However, they performed poorly on analogous tests that used nonspeech tone analogues that were based on the intonation patterns of the speech stimuli. This dissociation in contour processing (intact processing for speech but not for melodies) cannot be explained on the basis of coarser pitch contrasts in the speech and nonspeech versions, since a subsequent study (Patel, Foxton, & Griffiths, 2005), using focus-shift pairs, replicated the dissociation when the tone analogues exactly mirrored the pitch trajectories of the speech stimuli. However, as pointed out by Patel (2008), this apparent dissociation may not necessarily reflect a genuine sparing of contour processing in a linguistic context but rather the differential use of a "semantic-recoding" strategy in the two conditions. In the speech version, salient pitch changes can be "tagged" according to the syllable on which they occur, so that it is unnecessary to encode the entire pitch pattern for comparison with the second. In the tone analogue condition, salient pitch changes are divorced from any lexical information, and comparison must be made between the two pitch patterns in their entirety. This argument, which relates specifically to the results obtained using focus-shift pairs and their analogues, suggests that performance differences using such stimuli may depend on the extent to which the speech and nonspeech versions rely on pitch memory.

A recent study in our laboratory revisited the question of whether individuals with congenital amusia would show intact discrimination of contour in a linguistic context, taking care to consider the issues mentioned above (Liu et al., 2010). Our tone-analogues exactly mirrored the intonation patterns in speech; we used statement–question, as opposed to focus-shift sentence pairs, in order to remove any possibility of a semantic-recoding strategy being utilized in the speech condition, and we ensured that the speech stimuli (and thus the tone analogue stimuli) employed a range of pitch contrasts, including some that were more subtle than those that had been used in previous studies. As shown in Figure 2, individuals with congenital amusia were impaired at discrimination and identification of contours, in both speech and nonspeech contexts. A comparison of correct versus incorrect trials revealed that incorrect responses were more likely for stimuli with a smaller pitch excursion. Finally, performance on these tests correlated significantly with psychophysically derived thresholds, particularly those ascertained for the discrimination of pitch direction. Such findings suggest that contour deficits observed in congenital amusia do indeed extend to the speech domain, particularly when pitch contrasts are subtle. Only 2 of the 16 individuals with congenital amusia reported difficulties in everyday communication, such as mistaking a question as a statement or vice versa, which probably reflects the influence of additional cues (visual, contextual) in conveying communicative intent in everyday speech.

Even if contour-processing deficits rarely impact upon speech comprehension in everyday life in a nontonal language such as English, their consequences may be more significant for speakers of a tonal language, such as Cantonese or Mandarin, where recognition of the subtle pitch changes that characterize different lexical tones is critical for semantic comprehension. Alternatively, it can be argued that acquisition of a tonal language in early life may mitigate against the development of congenital amusia (Peretz, 2008). To test this hypothesis in its fullest form, a cross-language comparison of the prevalence of congenital amusia would be needed. Nevertheless, two separate cohorts of Chinese individuals have been diagnosed with congenital amusia, using the MBEA, suggesting that

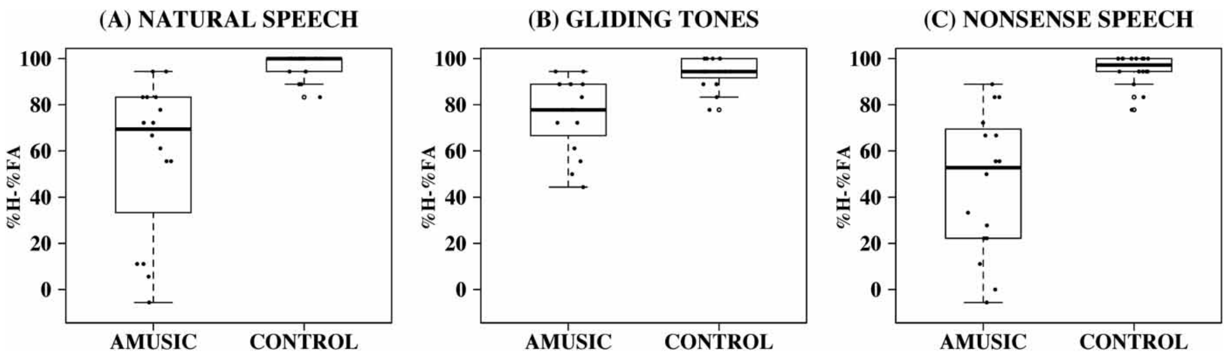

Figure 2. *Boxplots of the %H (hits) − %FA (false alarms) scores of the amusic and control participants on the three discrimination tasks: (A) natural speech, (B) gliding tones, and (C) nonsense speech. From "Intonation Processing in Congenital Amusia: Discrimination, Identification and Imitation", by F. Liu, A. Patel, A. Fourcin, and L. Stewart, 2010, Brain, 133(6), p. 1686. Copyright 2010 by the Name of Copyright Holder. Reprinted with permission.*

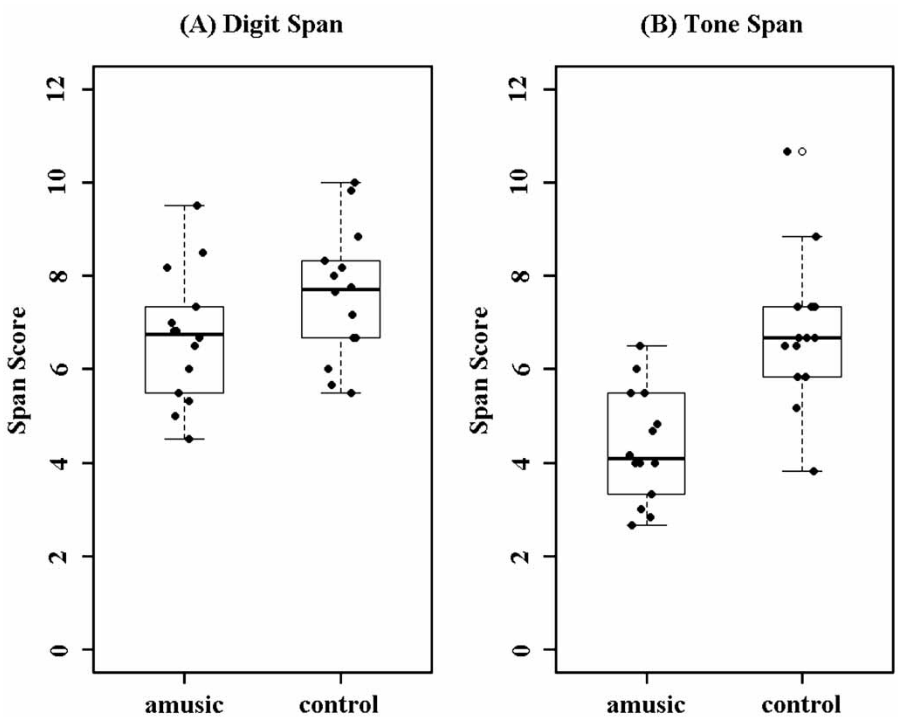

Figure 3. *Boxplots showing digit and tone spans for amusics and controls. From "Memory for Pitch in Congenital Amusia: Beyond a Fine-Grained Pitch Discrimination Problem", by V. Williamson and L. Stewart, 2010, Memory, 18(6), p. 662. Copyright 2010 by Psychology Press Ltd. Reprinted with permission.*

language background does not always (if ever) mitigate against the development of the disorder (Jiang, Hamm, Lim, Kirk, & Yang, 2010; Nan, Sun, & Peretz, 2010). Like the cohort reported in Liu et al. (2010), these individuals did not report difficulties with spoken communication, while laboratory tests of pitch processing with lexical tones revealed deficits relative to controls.

Pitch memory

As argued above, elevated thresholds for the discrimination of pitch direction are likely to have a role in the higher level contour deficits observed. But they are almost certainly not the whole story, since some individuals, diagnosed with congenital amusia, have pitch direction discrimination thresholds in the normal range. For these individuals, a different explanation is clearly warranted. A selective deficit in short-term memory for pitch seems a possible candidate, especially considering remarks such as the following, made by one amusic individual we have worked with:

> When the music finished, the sound was always gone—as though it had never happened. And this bewildered me with a sense of failure to hold on to what I had just heard. I have no idea what people mean when they say "I have a tune going round in my head". I have never had a tune tell out its music in my head, let alone repeat itself!

The suggestion that the experience of music is a transitory one for those with congenital amusia finds support in a several recent studies of pitch memory. Williamson, McDonald, Deutsch, Griffiths, and Stewart (2010) used a standard tone comparison task (as in Deutsch, 1970), in which participants compared two tones, presented immediately after each other, or with a time interval of 1, 5, 10, or 15 s later. When different, the second tone was a tone higher or lower than the first. While controls showed no decrement in performance as time interval increased, individuals with congenital amusia showed a significant decline in performance over time.

Extending this line of enquiry to memory for pitch patterns, Williamson and Stewart (2010) established a measure of pitch "span" in individuals with congenital amusia and matched controls. Participants discriminated pairs of pitch sequences, starting with sequences of two items, and sequence length was altered in accordance with performance (sequence length increased by one item following two correct trials and decreased by one item following one incorrect trial). As Figure 3 shows, individuals with congenital amusia had an average span of around 4 items, compared with 7 items for controls. Both groups had equivalent performance on an analogous task with spoken digits, suggesting that this short-term memory deficit is not a general auditory memory problem.

Our findings are congruent with those of Tillmann, Schulze, and Foxton (2009), who showed memory deficits for sequences of pitch and, to a lesser extent, timbral items, but not word lists. Importantly, the findings of neither study can be directly related to a simple inability to discriminate the constituent pitches, since intervals were either suprathreshold for the discrimination of pitch direction (Williamson & Stewart, 2010) or individually calibrated according to the measured detection thresholds of each participant (Tillmann et al., 2009), but further work will be needed to determine whether deficits in pitch direction and pitch memory could constitute separate routes to the amusic phenotype.

Experiential aspects of music listening

Given the aforementioned difficulties with contour perception and pitch memory, individuals with congenital amusia may be expected to display, at best, a level of ambivalence towards music. Indeed, comments made by some of our participants refer to feelings of either intense boredom or aversion. However, a questionnaire study (McDonald & Stewart, 2008), which drew on the published literature regarding the uses of music (Juslin & Laukka, 2004; North, Hargreaves, & Hargreaves, 2004; Sloboda, O'Neill, & Ivaldi, 2001) and its psychological functions (DeNora, 2000; Juslin & Laukka, 2004; Sloboda et al., 2001) in everyday life, presented a more nuanced picture. Individuals with congenital amusia, as a group, used music in fewer everyday situations such as while driving, doing household chores, or during exercise, and they identified with fewer psychological functions, such as the use of music to match or change mood. However, a subgroup of individuals, constituting a third of the cohort, were indistinguishable from controls in both these regards. Interrogation of the behavioural data of this subgroup revealed their perceptual deficits to be equally profound according to MBEA performance. In some senses, this echoes cases from the neurological literature in demonstrating an apparent dissociation between perception and emotional response to music (Griffiths, Warren, Dean, & Howard, 2004; Peretz, Gagnon, & Bouchard, 1998). However, it is important to acknowledge that the emotional response to music is complex and multifaceted (Juslin & Västfjäll, 2008), encompassing everything from the acoustic experience of consonance/dissonance to the recognition of happy/sad emotions in music (primarily conveyed through changes in tempo and key) and the transformative experience of having a "shiver down the spine". While the first neuropsychological case mentioned above (Griffiths et al., 2004) related to the loss of "shivers" down the spine in the presence of intact musical perception, the second (Peretz et al., 1998) reports intact recognition of emotion in music (e.g., "happy" versus "sad"), in the presence of severely degraded perception. Both "shivers" and the recognition of emotion in music—using cues such as tempo or key—are rather distinct from the aspect of musical appreciation that drives the individual to seek out, purchase, and listen to music during daily life. The rewarding aspect of music listening is likely to hinge, at least partly, on the capacity of the listener to build expectations from musical structure (Huron, 2006; Meyer, 1956), based on internalized regularities that have been implicitly acquired over a lifetime of musical listening (Saffran et al., 1999). According to these

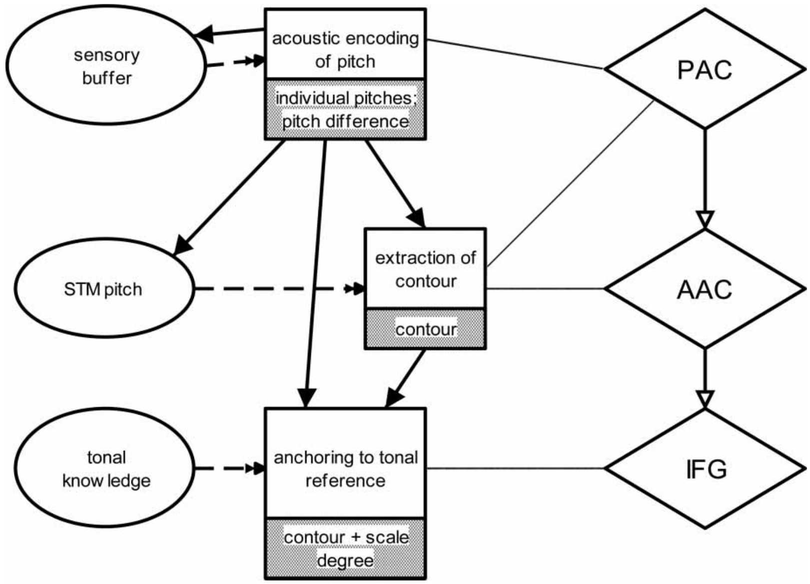

Figure 4. *Simplified model of melodic processing in the normal listener. PAC = primary/secondary auditory cortex; AAC = auditory association cortex; IFG = inferior frontal gyrus; STM = short term memory. See text for details.*

theories, there is a close coupling between the resolution—or even thwarting—of our expectations and activation of the brain's reward circuitry (Huron, 2006). Those with degraded perception of music—owing to a lack of sensitivity to pitch direction and/or a truncated window over which musical events can be integrated—may well be limited in the extent to which they can derive expectations from pitch. However, expectations can also be derived from temporal information (Hannon & Trehub, 2005), which is often preserved in congenital amusia (Hyde & Peretz, 2004). Alternatively, the extent to which appreciation of music is possible in the face of perceptual deficits may relate to whether or not there are accompanying deficits in the processing of timbre—a perceptual attribute concerning the quality of a sound. Timbre is the perceptual attribute that differentiates, for instance, a violin from a clarinet, and it relates to several acoustic properties, including spectral and temporal features (McAdams & Cunible, 1992). Several cases in the neurological literature suggest that deficits in pitch pattern perception are often accompanied by timbral deficits, such that music may sound distorted ("like an out-of-tune child's dulcimer"; Griffiths et al., 1997). The MBEA does not test for timbral processing deficits, but one possibility is that many individuals with amusia have both a pitch and a timbral impairment, making musical appreciation unlikely. The subgroup of amusics who use music just as much and for similar functions as controls may be those whose deficits are restricted to the pitch domain. There are currently no published studies of timbral perception in amusia (though see Tillmann et al., 2009, for findings concerning timbral memory), and this is a current focus of investigation in our laboratory.

In tune but not aware?

Recently, it has been suggested that congenital amusia might be conceived of as a disorder of awareness, rather than perception. Preliminary evidence for this comes from behavioural and functional imaging studies. In particular, a recent paper demonstrated that individuals with congenital amusia could reproduce the direction of a pitch change even when they were at chance in reporting whether the change went up or down (Loui, Guenther, Mathys, & Schlaug, 2008). Similarly, studies of singing reveal that individuals with congenital amusia, though inaccurate in their production, nevertheless produce responses that are reasonably well correlated with the target pitches (R^2 values between .66 and .85), often with a systematic downward shift (Hutchins, Zarate, Zatorre, & Peretz, 2010). Neuroimaging studies have also shown evidence of an intact electrophysiological response to anomalous or deviant pitches in amusia, even when behavioural measures indicate an absence of detection (Braun et al., 2008; Moreau, Jolicoeur, & Peretz, 2009; Peretz, Brattico, Jarvenpaa, & Tervaniemi, 2009). This has led to the suggestion that representations of pitch may be accessible for action-based processing (e.g., singing) but are unavailable to conscious awareness, inviting parallels with the phenomenon of blindsight in the visual system (Loui et al., 2008). However, a study of singing from long-term memory (Dalla Bella et al., 2009) yielded mixed results, with 6 of the 11 tested making errors at both an interval and a contour level. Such findings are not easy to reconcile with the hypothesis of intact representation of pitch for action in amusia across the board and hint at the likely existence of a subgroup of individuals for whom this characterization may hold true.

Biological basis

Structural neuroimaging data reveal subtle differences in the brains of individuals with congenital amusia, in inferior frontal cortex and superior temporal areas, variously in the left hemisphere (Hyde et al., 2007; Hyde, Zatorre, Griffiths, Lerch, & Peretz, 2006) or the right (Mandell, Schulze, & Schlaug, 2007). An understanding of how these biological differences relate to the behavioural deficits previously mentioned is currently far from clear, but the finding of morphological differences outside the temporal cortex are congruent with findings from functional imaging studies showing activation of frontal and temporal areas when pitch information must be integrated or compared over time (Gaab, Gaser, Zaehle, Jancke, & Schlaug, 2003; Koelsch et al., 2009; Levitin & Menon, 2003; Zatorre, Evans, & Meyer, 1994). A recent study using diffusion tensor imaging (Loui, Alsop, & Schlaug, 2009) suggests that individuals with amusia have reduced structural connectivity in the right superior branch of the arcuate fasciculus—a large fibre bundle connecting temporal and frontal areas. A functional magnetic resonance imaging (fMRI) study (Hyde, Zatorre, & Peretz, 2011) involving passive listening to sequential pitch changes of varying excursion size found that amusics showed an abnormal reduction in activation in the right inferior frontal cortex. Functional connectivity analyses indicated a reduced temporofrontal interaction, though in contrast to Loui et al. (2009), this was restricted to the ventral, as opposed to dorsal, stream.

Genetic studies of amusia suggest an inherited component to the disorder. An early twin study, using the Distorted Tunes Test (an early precursor to the MBEA) and comparing similarity of scores for monozygotic twin pairs (MZ; who share all their DNA) with those for dizygotic twin pairs (DZ; who share 50% of their DNA), reported a heritability of 71% (Drayna, Manichaikul, de Lange, Snieder, & Spector, 2001). A more recent study, using the MBEA, tested first-degree relatives of those with congenital amusia, as well as the first-degree relatives of controls matched to the probands. This indicated a risk rate of 39% for relatives of those with amusia, compared with 3% for those without (Peretz, 2007). DNA studies with pedigrees will be necessary to elucidate the candidate genes involved in amusia (Stewart, 2009). The structural and functional evidence discussed above implicates a gene or set of genes that may be involved in the early neuronal migration processes that underpin frontotemporal connectivity. Interestingly, such a suggestion has parallels with another developmental disorder—dyslexia—which has also been argued to be a disorder of neuronal migration (Galaburda, 2005), though the cortical regions affected by these migration anomalies are likely to be different in each of these disorders.

Potential loci of the deficit

As the above review indicates, new findings are rapidly emerging concerning the behavioural, cognitive, and biological aspects of congenital amusia. Ultimately, it will be necessary to propose a causal model of the disorder (Morton, 2004), in order to generate testable hypotheses concerning the nature of the deficit at each of these levels and how such deficits are linked. Such a model is beyond the scope of the present article but Figure 4 represents a schematic model of normal melodic processing, which permits tentative hypotheses to be advanced concerning possible loci of the deficit at the cognitive level. This simplified model proposes that melodic processing in the normal listener involves the following processing stages:

- *Acoustic encoding of pitch.* This is a process that operates in conjunction with the application of a sensory buffer, resulting in the representation of individual pitches and pitch differences between adjacent tones. This early encoding of pitch information involves the ascending auditory pathway, culminating at primary auditory cortex (Plack, 2005).
- *Extraction of contour.* This is a process that operates in conjunction with short-term pitch memory processes, resulting in a representation of contour, which, at the simplest level, may simply specify "up", "down", "same" as a description of the pitch of the incoming tone in relation to its predecessor, though a number of models of contour have been suggested in the literature that operate at a higher level of abstraction (e.g., Huron, 1996; Schmuckler, 1999; Zhu & Kankanhalli, 2003). Neuropsychological work indicates secondary auditory cortex as a neural substrate (Johnsrude, Penhune, & Zatorre, 2000).
- *Anchoring to a tonal reference.* This is a process that draws on stored knowledge of hierarchical pitch relationships in long-term memory, resulting in an output that represents incoming pitches in relation to a tonal reference. Evidence from functional imaging suggests the involvement of inferior frontal gyrus (Janata et al., 2002).

The deficits seen in congenital amusia could hypothetically arise at any or all of these processing stages. One account of the disorder suggests that amusia is a disorder of fine-grained pitch discrimination. This theory (Peretz et al., 2002) situates the locus of the disorder at an early stage (*acoustic encoding of pitch*) with cascade effects on later processing stages (e.g., *anchoring to a tonal reference)*. At least two alternative scenarios are also possible. One would be a deficit situated at an intermediate stage of processing—that is, in the extraction of contour, or in the short-term memory processes that operate in conjunction with this stage; the other would be situated at a relatively late stage in the processing hierarchy, relating either to the acquisition or to the use of tonal knowledge during the processing of pitch. The challenge now is to distinguish between these possibilities at the cognitive level and to determine how they relate to the genetic and neuroscientific findings on the one hand and the measured musical behaviours on the other. As with other developmental disorders, issues such as the likely existence of subgroups, the possibility of compensatory mechanisms, and the ameliorating and/or exacerbating effects of the environment will all have a role to play in accounting for the complex and often heterogeneous presentations of this disorder.

The investigation of disordered musical development sets in sharp relief the abilities that the rest of us take for granted. The characterization of this disorder at all levels—behavioural, cognitive, and biological—promises to yield important insights into the cognitive and neuroscientific basis of musical processing, as well as providing a model for understanding the relationship between genes, neural development, and the emergence of a complex and fundamental human behaviour.

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