Neural correlates of absolute pitch: A review

Jiancheng Hou
The Ohio State University and Florida International University, USA

Andrew CN Chen
Capital Medical University, China

Bei Song
East China Normal University and Music Conservatory of Harbin, China

Changan Sun
Suzhou University of Science and Technology, China

Theodore P. Beauchaine
The Ohio State University, USA

Abstract

Absolute pitch (AP) is the ability to identify and/or produce specific music notes without a reference tone from the Western tonal system. Functional imaging studies show that AP is subserved by a network of interconnected neural structures including the left posterior dorsolateral frontal cortex (DLFC), the bilateral planum temporale (PT), and other brain regions. Neurophysiological studies show that AP possessors do not always require context updating during pitch identification due to possible "tonal templates", and that AP appears to emerge at a late processing stage that is associated with multiple cognitive strategies and is facilitated by music training at early ages. Morphometry studies show decreased cortical thickness and gray matter concentration among those with AP, which may reflect increased efficiency of AP skill. Graph theoretical analyses of cortical thickness covariations show involvement of higher-order auditory processing, working memory, and semantic memory processes. Diffusion tensor imaging studies provide evidence for a neural pathway between the left posterior DLFC and the left PT, which establishes retrieval and manipulation of verbal-tonal associations. Compared to AP musicians, quasi-AP (QAP) musicians have an extensive right hemisphere network implicated in auditory working memory and show the bilateral structural characteristics of PT morphometry. Future research should confirm the definition of PT boundary and the role of (bi)lateralization of PT in AP ability, develop a standard AP test, identify genetic bases of AP, and describe relations between AP, tonal languages, and associated neural functions and structures among non-musicians with AP ability.

Corresponding author:
Jiancheng Hou, Department of Psychology, Florida International University, AHC4 Room 426, 11200 SW 8th Street, Miami, FL 33199, USA.
Email: jihou@fiu.edu

Absolute pitch (AP) is the ability to identify and/or produce specific music notes with high accuracy and quick response speed, without the benefit of a reference note from the Western tonal system (Deutsch, 2013; Levitin, 1999; Parncutt & Levitin, 2001). AP is quite rare, with a prevalence of about 0.01% in the general population (Bachem, 1955; Hirose et al., 2002). Among professional musicians, the prevalence of AP is 10–15% (Baharloo, Johnston, Service, Gitschier, & Freimer, 1998; Gregersen, Kowalsky, Kohn, & Marvin, 1999, 2001; Hirose et al., 2002). AP appears to be conferred by the interaction of a genetic predisposition with early music training during a sensitive developmental period (Baharloo et al., 1998; Gregersen et al., 1999, 2001; Wilson, Lusher, Wan, Dudgeon, & Reutens, 2009; Zatorre, 2003). AP appears to exist along a continuum, which is sometimes parsed into several subtypes, including weak-, quasi-, and pseudo-AP (Bermudez & Zatorre, 2009; Levitin, 2008; Miyazaki, 1989; Wilson et al., 2009). Our objective in writing this review is to explore what is known about neural correlates of AP, and to consider possible future research directions.

Functional correlates of AP

Functional imaging

Functional imaging is a technique for estimating regional brain activation through measurement of changes in blood oxygenation that occur to support neural activity. An early study by Zatorre, Perry, Beckett, Westbury, and Evans (1998) determined that during pitch naming, there is activation in the left posterior dorsolateral frontal cortex (DLFC), which facilitates associative learning and memory among AP musicians, who can readily retrieve associations between pitch and verbal labels. This result has since been confirmed by other studies (Bermudez & Zatorre, 2005; Ohnishi et al., 2001; Schulze, Gaab, & Schlaug, 2009; Wengenroth et al., 2014; Zatorre, Chen, & Penhune, 2007). The role of the left posterior DLFC in associative learning and memory has also been verified in nonhuman primate studies (Bermudez & Zatorre, 2005; Katsuki, Saito, & Constantinidis, 2014; Petrides, 1990; Petrides, Alivisatos, Evans, & Meyer, 1993; Qi et al., 2010).

Another important region for AP ability is the planum temporale (PT), located in the posterior portion of the superior temporal gyrus (STG) (Clark, Boutros, & Mendez, 2010). Functional neuroimaging studies yield positive correlations between the left PT activation and AP proficiency among AP musicians during pitch naming (Wilson et al., 2009; Zatorre et al., 1998). The PT is implicated in auditory processing, including perception of phonemes (units of speech; Griffiths & Warren, 2002). Phonemic categories of speech are similar to music pitch categories, which are important to AP ability (Burns & Campbell, 1994).

Other studies reveal increased right hemispheric auditory domination among AP musicians. For example, Wengenroth et al. (2014) found increased activations of the right PT and left posterior DLFC (including the left Broca's area) during pitch labeling. Right rather than left PT activation was associated with AP perception, whereas the posterior DLFC and the left Broca's area were activated during pitch labeling. Zatorre (2003) divided AP ability into two phases. The first involves precognitive perceptual processes, and the second involves cognitive labeling. Pitch perception relies on a referencing process in which incoming auditory signals are compared to a

pre-stored template, which may be based on an absolute scale among AP musicians (Levitin & Rogers, 2005; Wengenroth et al., 2014). In considering functional dominance of the right Heschl's gyrus and the right PT among AP musicians, Wengenroth et al. (2014) speculated that referencing to the postulated AP template might take place in the right hemisphere. Results implicating different regions across studies might be explained by task differences (e.g., passive listening vs. pitch-naming), or by a lack of consistent measurement of AP ability.

Wengenroth et al. (2014) also identified a right hemisphere network for AP perception, including the right premotor and secondary somatosensory cortices, the right inferior frontal gyrus, and the right middle temporal gyrus. These function together with the right PT, the left posterior DLFC, and the left Broca's area – regions that are instrumental for pitch labeling. The premotor cortex is responsible for direct and indirect sensorimotor transformations, and auditory imagery (Zatorre et al., 2007). The secondary somatosensory cortex is involved in enhanced multisensory and sensorimotor integration among musicians, and subserves kinesthetic and proprioceptive awareness (Wengenroth et al., 2014). The inferior frontal gyrus (Platel, Baron, Desgranges, Bernard, & Eustache, 2003) and the middle temporal gyrus (Binney, Parker, Lambon-Ralph, 2012; Oechslin, Meyer, & Jäncke, 2010) subserve language functions, especially semantics. The left posterior DLFC is involved in conditional association pitch memory, among other functions (Bermudez & Zatorre, 2005; Zatorre et al. 1998). Finally, the left Broca's area is implicated in motor aspects of speech performance (Wengenroth et al., 2014). Overall, it seems that AP is associated with integration across multiple brain regions that together form a complex, functionally interconnected network.

Other neuroimaging studies demonstrate that bilateral regions besides the left posterior DLFC are activated among AP musicians during pitch naming, including the superior temporal gyrus (Zarate & Zatorre, 2008) and the middle frontal gyrus (Wilson et al., 2009). Both the right inferior frontal and right occipital gyri are also activated (Zatorre et al., 1998). The superior temporal gyrus is implicated in auditory processing, including perception of phonemes (units of speech; Griffiths & Warren, 2002; Oechslin, Imfeld, Loenneker, Meyer, & Jäncke, 2010). Superior temporal gyrus activation during pitch naming is correlated positively with AP proficiency (Ohnishi et al., 2001; Wilson et al., 2009; Zatorre et al., 1998). The inferior frontal gyrus subserves semantic functions (Platel et al., 2003), the middle frontal gyrus is implicated in sensorimotor functions with auditory signals (Wan & Schlaug, 2010), and the occipital gyrus subserves vision and visual imagery functions (Schmithorst, 2005). This suggests a potential functional network including the left posterior DLFC and additional regions, since the DLFC is linked to other implicated brain regions, and lesions to it impair acquisition of arbitrary associations between stimuli and responses (Petrides, 1990). Thus, activation of the left posterior DLFC among AP vs. non-AP musicians may reflect engagement of an associative mechanism that occurs spontaneously and forms the basis for AP ability.

The bilateral PT and the left posterior DLFC may also form a functional pathway that is implicated in AP. The PT (as well as the posterior portion of the superior temporal gyrus) comprises part of the auditory association cortex, which projects directly to the left posterior DLFC (Petrides & Pandya, 1988). AP ability may result in part from interactions between the PT/posterior DLFC and a network of other brain regions that are implicated in retrieval and manipulation of various types of associations with pitch (Zatorre et al., 1998), including verbal-tonal associations (Ohnishi et al., 2001; Petrides & Pandya, 1988). The PT-DLFC functional pathway may depend on structural organization between the PT and DLFC, since structure often constrains patterns of functional activity, both locally and globally (see Wang, Dai, Gong, Zhou, & He, 2014).

As this review suggests, AP arises from a complex neural network. Evidence also suggests that it is distributed along a continuum (Bermudez & Zatorre, 2009; Itoh, Suwazono, Arao,

Miyazaki, & Nakada, 2005; Levitin, 2008; Wilson et al., 2009). Compared to AP, quasi-AP (QAP) musicians generally show lower accuracy and greater variability in pitch naming performance. For example, Wilson et al. (2009) found that about half of QAP musicians report regular use of reference tones, and that most QAP musicians show more accurate identification of spectral notes (pitch chroma) C, G, and A compared with all other notes. This pattern is not evident among AP musicians. QAP musicians also require more time to summon musical pitches, whereas reactions of AP musicians are immediate (Rakowski, 2008). During pitch naming, QAP musicians show significant activation in the right hemisphere network, including the right superior and middle temporal gyri and the right dorsolateral prefrontal cortex (Wilson, Lusher, Wan, Dudgeon, & Reutens, 2006). The superior and middle temporal gyri subserve long-term semantic memory (Binder, Desai, Graves, & Conant, 2009; Johnson et al., 2011), whereas the dorsolateral prefrontal cortex is involved in working memory, among many other functions (Grimault et al., 2009). During pitch naming, activation of an extensive right hemispheric network including the right anterior-posterior superior temporal gyrus, the right middle and inferior frontal gyri, and the right cerebellum, has also been observed among AP musicians (Wilson et al., 2009). The middle frontal gyrus subserves motor and sensorimotor perception functions (Poldrack et al., 2005; Wan & Schlaug, 2010), the inferior frontal gyrus is implicated in semantics (Platel et al., 2003), and the cerebellum is involved in early auditory encoding (Schulze et al., 2009), working memory (Baddeley, 2003), and multimodal encoding (Stewart et al., 2003). Semantic, motor, and sensorimotor perceptions and multimodal encoding are necessary for QAP and AP (Hsieh & Saberi, 2008; Wilson et al., 2009; Zatorre & Beckett, 1989). These findings support behavioral results suggesting that QAP musicians adopt strategies such as timbre, semantics, performing, and visual imagery during pitch naming tasks (Wilson et al., 2009). Wilson et al. (2009) also reported (1) a left hemisphere advantage among AP musicians, and (2) engagement of the right hemisphere with working memory function, indicative of increased pitch processing load, among individuals with lower AP skill. This suggests that regular use of reference tones serves as an anchor from which interval judgments are made to identify remaining tones among QAP musicians, which is not the case for AP musicians (Wilson et al., 2009).

Neurophysiology

Both electroencephalography (EEG) and magnetoencephalography (MEG), two neurophysiological techniques, have been used to evaluate AP ability among musicians.

Electroencephalography. Event-related potentials (ERPs), which are electroencephalographically-derived measures of electrical activity across the scalp, can capture responses to specific external events/stimuli. ERPs are advantageous because they detect neural responses with much higher temporal resolution than fMRI, and can therefore be used to determine what stage(s) of cognition is/are affected by specific experimental manipulations (Blackwood & Muir, 1990). Most studies have used the auditory oddball paradigm to test how AP musicians process musical stimuli, and how their responses differ from those of non-AP musicians and non-musicians. Many of these studies show that AP musicians have decreased P300 (positive voltage change that peaks at about 300 ms) amplitudes and latencies compared to both non-AP musicians and non-musicians (see Crummer, Walton, Wayman, Hantz, & Frisina, 1994; Klein, Coles, & Donchin, 1984; Renninger, Granot, & Donchin, 2003; Wayman, Frisina, Walton, Hantz, & Crummer, 1992). The P300 usually reflects stimulus evaluation and category, as well as updating of working memory (WM). P300 amplitudes correlate negatively with WM function,

whereas P300 latencies correlate positively (see Christopher, Adam, & Robert, 2006; Polich, 2007; Rawdon et al., 2013; Steiner, Barry, & Gonsalvez, 2013). Because AP musicians presumably possess an internally fixed and long-term tonal template in which tone names are attached to given frequencies, they are able to name tones without references (Hirose et al., 2002; Levitin & Rogers, 2005; Siegel, 1974; Takeuchi & Hulse, 1993). Decreased P300 amplitudes and latencies among AP musicians suggest less WM deployment with tone reference (Klein et al., 1984; Wayman et al., 1992). These studies do not identify the neural source generator of the P300 or any other ERP. However, other studies on attention, memory capacity, and face recognition show that P300s are generated by the superior temporal plane, mesial temporal region, inferior parietal lobe, and hippocampus (Desimone, 1996; Friederici et al., 2001; Guerin & Miller, 2009; Itier & Taylor, 2004; Levy & Goldman-Rakic, 2000; Nishitani et al., 1999; Yamaguchi & Knight, 1991), all of which have WM functions.

There are also some null findings in comparisons of P300 amplitudes and latencies between AP musicians and non-AP musicians. For example, Hirose et al. (2002) asked all participants who listened to pure target tones and non-target tones to count the targets. All participants correctly counted almost all targets, and P300 responses were evident in both groups, with no differences. This suggests that WM was employed and tonal context was updated among AP musicians. This null result suggests that AP possessors not only employed AP ability while listening to tones, but also counted targets with updated WM, as indicated by P300 responding. Previous studies required participants to discriminate or label tones, which may have required AP possessors to refer to their tonal templates, so context updating occurred less, resulting in no discernable P300.

At least two separate processing stages have been proposed for AP ability. The first is an early phase of pitch encoding that is subserved by the auditory cortex ("pitch memory"). The second is a conditional associative memory mechanism that categorizes pitches with verbal labels and/or other abstract codes. This occurs in frontocentral sites ("pitch labeling") (Deutsch, Kuyper, & Fisher, 1987; Levitin, 1994; Levitin & Rogers, 2005; Rogenmoser, Elmer, & Jäncke, 2014; Schulze, Mueller, & Koelsch, 2013; Zatorre, 2003; Zatorre & Beckett, 1989). In a recent ERP study with pure sine tone category manipulations, nonsignificant differences in mismatch negativity (MMN; a negative ERP to an unexpected stimulus in a series of stimuli) waveforms were observed between AP and non-AP musicians, but there was significantly reduced frontal P3a (a positive ERP that is a subcomponent of the P300 and occurs at 250–280 ms in response to novel stimuli) amplitude among AP musicians (Rogenmoser et al., 2014). MMN indexes an early stage of automatic auditory processing and is sensitive to auditory pre-attention manipulations at a sensory memory level (Garrido, Kilner, Stephan, & Friston, 2009; Picton, Alain, Otten, Ritter, & Achim, 2000). The nonsignificant between-groups MMN difference suggests that AP is not necessarily driven by differential pitch encoding by the auditory cortex (Rogenmoser et al., 2014). This study also supports results reported by Elmer, Hanggi, Meyer, and Jäncke (2013), who found no group difference between AP and non-AP musicians in neurophysiological indicators of early sensory processing during passive listening of spectral tones. However, reduced P3a likely reflects less WM involvement (Berti & Roeber, 2013; Ruhnau, Wetzel, Widmann, & Schroger, 2010; Schomaker & Meeter, 2014), and associations with multiple cognitive functions that are sensitive to verbal, auditory imagery, and sensorimotor cues (Escera, Alho, Winkler, & Naatanen, 1998; Roeber, Berti, & Schroger, 2003; Schroger & Wolff, 1998; Wetzel & Schroger, 2007). These findings are consistent with the assertion that AP possessors use multiple cognitive strategies (e.g., verbal coding [Siegel, 1974], semantic memory [Hsieh & Saberi, 2008], auditory, kinesthetic, visual, and spatial imagery [Zatorre & Beckett, 1989]) during AP tasks. Indeed, Siegel (1974) found that AP musicians retained pitch

information by using verbal labels to remember tone information. Zatorre and Beckett (1989) found that AP musicians can encode music pitches verbally. In addition, music pitches can be coded by emotions, spatial positions, and visual imagery. For example, the pitch "F#" can be coded with emotional words such as "unnatural sensation, poignancy, ache, or bitterness" (Hsieh & Saberi, 2008). Such findings are supported by neuroimaging studies described below. P3a responses also correlate positively with age of commencement of music training (Rogenmoser et al., 2014). In fact, early music training during a developmentally sensitive period may be crucial for AP formation (Baharloo et al., 1998; Gregersen et al., 1999, 2001; Levitin, 1999, 2008; Levitin & Rogers, 2005; Wilson et al., 2009; Zatorre, 2003). Therefore, the later-occurring, cognitively-based multidimensional processing stage is a crucial mediator of AP, and its efficiency depends in part on early music training.

As mentioned above, AP has a distinctive functional-anatomical architecture in the left auditory cortex, which may facilitate an optimized early "categorical perception", and the left DLFC, which is responsible for "pitch labeling" based on associative memory (Jäncke, Langer, & Hanggi, 2012; Loui, Li, Hohmann, & Schlaug, 2011). Based on this, Elmer, Rogenmoser, Kuhnis, and Jäncke (2015) used EEG to evaluated resting-state intracranial functional connectivity between the left auditory cortex and the left DLFC among a sample of musicians with and without AP. Results demonstrated increased left-hemispheric theta phase synchronization among AP musicians, which explained ~30% of variance in pure sine absolute-hearing. Based on these results, Elmer et al. proposed that among AP participants, tonal inputs and corresponding mnemonic representations are coupled tightly, such that a distinctive EEG signature can be detected during short resting-state periods.

Similar to QAP studies, Itoh et al. (2005) selected high-, middle-, and low-AP subgroups, as well as an untrained group, to execute a vocal pitch-naming task. Findings included (1) decreased P3b (a positive ERP that is also a subcomponent of the P300 and occurs at 250–500 ms in response to improbable events) amplitudes in the parietal cortex in the high-AP group compared to the other three groups; (2) a parietal positive slow wave (ppSW), which appeared at about 450 ms in the parietal cortex, immediately followed the P3b, in all but the high-AP group; (3) a frontal negative slow wave (fnSW) following the P3b in the low-AP and untrained groups; and (4) a left posterior temporal negativity (also known as AP negativity) in the high-AP group.

The P3b also reflects WM function (Berti & Roeber, 2013; Ruhnau et al., 2010), so decreased P3b in the high-AP group likely indicates less WM involvement due to their reliance on tonal templates (see above; Hirose et al., 2002; Levitin & Rogers, 2005; Siegel, 1974; Takeuchi & Hulse, 1993). The ppSW represents processing of given verbal labels to pitches as identified and stored in WM (Itoh et al., 2005; Zatorre et al., 1998; Wilson et al., 2006, 2009). Evoked ppSW in the mid-AP, low-AP, and untrained groups may indicate relative pitch (RP) or WM referencing during pitch naming. This would be expected if pitches are held in memory to serve as references in coming trials among these groups compared with the high-AP group (Itoh et al., 2005). The fnSW primarily reflects cortical processing for RP that is calibrated permanently in terms of pitch relations among notes on the musical scale (a moveable template; Levitin & Rogers, 2005). It is essential for those who have little or no AP and those who have no music training, because large fnSW is elicited only for exceptionally high cognitive loads that require effortful retention in WM (Ruchkin, Johnson, Canoune, & Ritter, 1990). The left posterior temporal negativity (AP negativity) may be triggered automatically by pitch input, and appears to be an index of specificity of high-level AP ability (Itoh et al., 2005).

It should be noted that RP refers to the ability to make pitch judgments about their relations, for example, within a musical interval (see Zatorre et al., 1998). Some AP subtypes may have a

wide range of RP abilities (Itoh et al., 2005; Miyazaki, 1992; Wengenroth et al., 2014). On the other hand, excellent RP listeners may have AP ability due to the fact that they derive "temporary AP cues" by memorizing an external reference tone, so it needs a systematic separation of AP and RP cues essential for accurate AP ability (Wengenroth et al., 2014).

These studies examined distinct processing stages, as reflected by EEG components, and are consistent with possible tonal templates among AP possessors, who do not need to move in and out of WM, so context updating is not always required. Divergence for AP from non-AP individuals mainly exists at a late processing stage that is associated with available multiple cognitive strategies and the age of commencement of music training, rather than at the early stage at sensory memory level.

Magnetoencephalography. Magnetoencephalography (MEG) records magnetic fields produced by electrical currents that occur naturally in the brain, using very sensitive magnetometers. To date, few studies have used MEG to examine AP performance. However, using a passive listening paradigm, Wengenroth et al. (2014) found that the right P1 (the net current that gives rise to a magnetic field) was localized 10 mm further behind in the right Heschl's gyrus, and that the late P2a was localized 15 mm further behind in the right PT among AP musicians. Furthermore, the posterior shift of right P2a correlated with AP proficiency. Averaged MEG source waveforms in response to auditory stimulation showed no significant differences across groups between auditory evoked fields adjusted to the early P1 component in the bilateral Heschl's gyrus. However, the amplitude of right P2a in PT was higher among AP musicians compared with the left hemisphere, and in comparison with non-AP musicians. In addition, the integral of right P2a amplitude was correlated with AP proficiency. Alterations of auditory evoked fields, especially amplification of P2 component and/or the N1–P2 complex, have been reported in response to acoustical, musical, and speech training among children and adults (Kuriki, Kanda, & Hirata, 2006; Tremblay, Kraus, McGee, Ponton, & Otis, 2001). This may reflect very short-term neuroplastic changes at the functional level (Wengenroth et al., 2014), and it is consistent with functional imaging findings that the right PT is associated with AP perception (see above).

Structural correlates of AP

Brain structure can be assessed in several ways, including measurement of gray matter volume, gray matter concentration, cortical thickness, surface area, and white matter connectivity. Although brain structure does not fully constrain brain function, except in the most severe cases of neural insult (see, e.g., Vigneau-Roy, Bernier, Descoteaux, & Whittingstall, 2012), structural architecture can influence patterns of functional activity across brain regions. Therefore, structural measurements may be relevant to understanding AP.

Morphometry

Previous studies demonstrate stronger left surface asymmetry in PT among AP musicians (Griffiths & Warren, 2002; Schlaug, Jäncke, Huang, & Steinmetz, 1995). This asymmetry may be driven by a smaller right PT surface rather that a larger left surface (Keenan, Thangaraj, Halpern, & Schlaug, 2001). AP musicians also exhibit larger left PT volumes, which are associated with increased AP accuracy. This is not the case for the right PT (Zatorre et al., 1998).

There is still controversy regarding the role of PT asymmetry in AP. For example, Zatorre (1989) found that AP ability was unchanged after surgical excision of the left PT, which implies that the right PT may play a role in AP ability. Indeed, Wengenroth et al. (2014) found that,

compared to non-AP musicians, AP musicians have larger volumes of right Heschl's gyrus, but smaller volumes of the right PT. Whether this Heschl's gyrus and PT asymmetry are a consequence or a cause of AP acquisition remains to be resolved.

In another study, Wilson et al. (2009) found no left PT asymmetry between AP and QAP musicians, but AP musicians still had smaller right PT volumes than QAP musicians. Combined with findings presented above, this suggests the importance of left PT morphometry for AP musicians, in contrast to bilateral PT morphometry for QAP musicians and lower AP possessors.

Bermudez, Lerch, Evans, and Zatorre (2008) found decreased cortical thickness and concentration among AP musicians compared to non-AP musicians. Most notably, thinner cortex volumes were observed in the bilateral posterior dorsal frontal region, which, as noted above, subserves aspects of conditional associative memory. This is consistent with fMRI studies showing that the posterior dorsolateral frontal cortex is most effective when AP possessors identify single notes (Petrides et al., 1993; Zatorre et al., 1998). AP performance is also associated with other thinner cortex and reduced gray matter concentration findings, including the right ventral premotor cortex, which is responsible for sensorimotor transformation and hierarchical processing of music functions (see Koelsch, 2011; Tillmann et al., 2006); the right pars opercularis, which is implicated in various aspects of auditory-motor transformation (see Zatorre et al., 2007); the right inferior parietal lobule, which subserves phonological functions (see Bermudez et al., 2008; Bermudez & Zatorre, 2005; Lai et al., 2014); and the left postcentral gyrus, which is involved in multisensory integration and emotional memory (see Loui et al., 2011). Reasons underlying decreased cortical thickness are not yet clear, as many factors could be responsible for the effects, such as cell size, number, packing density, and number of connections, and extent of myelination, all of which interact with MRI acquisition, the resultant signal, and subsequent processing (Bermudez et al., 2008; Eickhoff et al., 2005; Gittins & Harrison, 2004). However, thinner cortices and reduced gray matter concentrations may reflect greater efficiency and automaticity for AP musicians. In fact, James et al. (2014) showed that reduced gray matter concentrations among musicians are beneficial to increased working efficiency for musical perception and performing skills.

Many studies show that functional connections and anatomical structures of brain networks are organized in a highly efficient small-world manner at levels of degree, clustering, and local efficiency of functional correlations (Bullmore & Sporns, 2009; Loui, Zamm, & Schlaug, 2012). Graph theory analysis is often used to compare small-world properties of brain networks (Rubinov & Sporns, 2010). Jäncke et al. (2012) used graph theoretical analysis of cortical thickness covariations to examine whether AP musicians differ from RP musicians and non-musicians in small-world network characteristics. Although all participants demonstrated typical small-world features, AP musicians exhibited small-world alterations. AP musicians show significantly increased local connectivity in peri-sylvian language areas, including the right Heschl's gyrus, the right PT, right lateral aspects of the superior temporal gyrus, the right pars triangularis, the left planum polare, the left superior temporal sulcus, and the left pars opercularis. Moreover, interconnectedness is decreased globally, which may suggest that AP musicians possess diminished neural integration (less connectivity) across diffuse brain regions. All of these brain regions are involved in higher-order auditory processing, working memory, and semantic memory processes.

Diffusion tensor imaging

Diffusion tensor imaging (DTI) is a structural MRI technique that is often used to evaluate the integrity of white matter fiber tracts (Alexander, Lee, Lazar, & Field, 2007). AP musicians exhibit greater connectivity between the bilateral temporal lobes (including posterior superior temporal gyrus, pSTG, and posterior middle temporal gyrus, pMTG), and increased volumes of white matter

tracts connecting the leftward pSTG and pMTG compared with non-AP musicians (Loui et al., 2011; Oechslin, Meyer, et al., 2010). These findings are consistent with functional MRI studies demonstrating that the left superior temporal sulcus (STS) is a center for automatic and effortless categorization, and provides a way station along the left STG to left MTG pathway, which sends information from fine-grained, controlled perceptual representations to unconscious, automatic categories that are based on representations (Loui et al., 2012; Schulze et al., 2009).

AP musicians also exhibit more white matter fibers in the right hemisphere than non-AP musicians (Loui et al., 2011). For example, both the right STG and right MTG exhibit connections with the right frontal lobe (especially the right inferior frontal gyrus, IFG) via the arcuate fasciculus (AF, a portion in the superior longitudinal fasciculus), a fiber tract that connects temporal and frontal regions (Catani & Mesulam, 2008; Loui, Alsop, & Schlaug, 2009). The STG–IFG connection subserves perception, and the MTG–IFG connection subserves production–perception matching. The STG–MTG–IFG connection represents an important three-node network for language that is also responsible for music and auditory perception and categorization more generally among AP musicians (Loui et al., 2009; Loui et al., 2011).

The superior longitudinal fasciculus (SLF), which includes subregions of the AF, connects (1) the temporal lobe (involved in auditory processing such as music and language) with the frontal lobe, which involves with executive functions including working memory (Friederici, 2009; Glasser & Rilling, 2008; Oechslin, Meyer, et al., 2010), and (2) the frontal with the parietal lobes, which regulate motor behavior, and involves with visual and spatial functions (Makris et al., 2005). AP musicians exhibit enhanced SLF connectivity, with greater fractional anisotropy (FA; a measure of directionality of diffusion within a voxel) in the left SLF than the right compared with non-AP musicians and non-musicians. AP musicians also exhibit a positive correlation between AP acuity and left SLF construction (Oechslin, Meyer, et al., 2010). Thus, left AF and SLF architecture appear to provide structural evidence that supports functional findings of a coordinated network that includes the left posterior DLFC (closely adjacent to the left inferior frontal gyrus) and the left PT (located at the superior temporal gyrus), which establish retrieval and manipulation of verbal-tonal associations.

Taken together, these findings suggest that PT morphometry differences between AP and non-AP musicians facilitate categorization of tones and speech, and establish verbal-tonal associations. Further studies should examine to what extent the left vs. right PT may be involved in AP ability, or if bilateral PT might be crucial for AP proficiency. Divergences across extant studies may result from a number of methodological differences. For example, Zatorre et al. (1998) measured cortical volumes rather than surface areas due to their definition of PT boundaries. In addition, PT size depends strongly on PT boundaries (Wilson et al., 2009). Graph theoretical analysis of small-world networks show involvement of higher-order auditory processing, working memory, and semantic memory processes among AP musicians. AP musicians also exhibit differences in left AF and SLF architecture, which may confer an advantage in production–perception matching, and/or in music and auditory perception and categorization performance. In addition, QAP musicians show bilateral structural characteristics of PT morphometry. One hypothesis is that they may possess extensive dual-stream anatomy for pitch perception and production, but this needs further exploration.

Future directions

Studies of AP ability and brain function and structure have established a strong foundation for further investigations. In the near future, studies about AP ability could include the following promising directions. First, as mentioned above, there is still controversy over the role of PT

asymmetry in AP. On balance, it appears that right PT asymmetry plays a role in AP ability, but how the definition of PT boundary and whether (bi)lateralization of PT are consequences, correlates, or causes of AP remain unresolved.

In addition, the field lacks a standard test of AP ability. Researchers have selected AP participants based on tests developed within labs (e.g., Bermudez & Zatorre, 2009; Deutsch, Henthorn, Marvin, & Xu, 2006; Loui et al., 2011). In some studies, AP subtypes have a wide range of RP abilities (Itoh et al., 2005; Miyazaki, 1992; Wengenroth et al., 2014). Thus, lack of consistent measurement of AP and potential interactions with RP ability may contribute to at least some inconsistencies in the literature. Also, separation of AP from RP will be essential in future studies if we wish to improve our understanding of AP ability (Wengenroth et al., 2014).

Several studies document familial aggregation of AP, which suggests a genetic component (Baharloo, Service, Risch, Gitschier, & Freimer, 2000; Gregersen et al., 1999, 2001). Although early music training appears to facilitate AP acquisition (see above), it likely does so only among those who are predisposed genetically, reflecting a Gene × Environment interaction. This interpretation is consistent with findings confirming that AP ability is not simply the result of music training (Chin, 2003; Deutsch et al., 1987; Ross, Olson, & Gore, 2005; Ross, Olson, Marks, & Gore, 2004). Theusch, Basu, and Gitschier (2009) performed a genome-wide linkage study on a large number of AP families, genotyping 6090 single nucleotide polymorphisms (SNPs), and found that the strongest linkages for AP ability were on Chromosomes 8q24.21 and 7q22.3, although stratification by race was observed. In addition, Gregersen et al. (2013) found a peak on Chromosome 6q, as well as evidence of linkage on Chromosome 2 using a dominant model that established close phenotypic and genetic relationship between AP and synesthesia (the capacity for cross-modality sensory perception). Genes are known to influence brain function, structure, and behavior. All of these findings need to be replicated, since non-replications are quite common in molecular genetics research (see, e.g., Beauchaine, Gatzke-Kopp, & Gizer, in press). It is also likely that, like other complex human traits, AP is multifactorially inherited, with no single genetic locus being necessary or sufficient for skill acquisition. Future research should also evaluate brain function as a mediator between gene–AP relations.

Finally, AP ability is fostered by tonal language acquisition. In fact, the percentage of AP possessors who speak tonal languages (e.g., Mandarin, Cantonese, Thai, Vietnamese) is higher than among those who speak non-tonal languages (Bidelman, Hutka, & Moreno, 2013; Deutsch, Dooley, Henthorn, & Head, 2009; Deutsch, Henthorn, & Dolson, 2004; Deutsch et al., 2006; Dooley & Deutsch, 2010; Gandour, Wong, & Hutchins, 1998). Similar findings are observed among non-musicians who speak tonal languages. For example, Deutsch et al. (2004) found that among non-musicians who received minimal or no music training, the consistency in enunciating native word lists on different days among native speakers of Vietnamese and Mandarin was greater than among those who speak English. Although AP is often considered to reflect unusually strong long-term memory for pitch in special musicians, non-musicians with tonal-language speaking exhibit accurate long-term pitch memory (Deutsch et al., 2004). This may be because their everyday speech is dependent on AP ability (Braun, 2002; Levitin & Rogers, 2005). Non-musicians who speak tonal languages may be capable of labeling pitches to some degree, although not using specialized labels that musicians learn (Levitin & Rogers, 2005; Ross et al., 2004). Another reason may be that tonal language speakers retrieve speech pitch from a precognitive absolute memory for pitch (Braun, 2002). Many studies confirm a relation between brain function/structure and AP ability in musicians with non-tonal language speaking, but further studies should examine such relations among non-musicians with tonal language, ideally by applying neuroimaging. Taken together, such studies may further our understanding of music ability and human brain function in the future.

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