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The Role of Brain Connectivity in Musical Experience

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Human beings of all ages and all cultures have been creating, enjoying, and celebrating music for centuries, yet how the experiences of music are instantiated in the human brain is only beginning to be understood. To gain a full understanding of the neuroscience of positive experiences, one of the goals of positive neuroscience must entail examining how the brain subserves music appreciation. The central thesis of this chapter is that structural and functional networks in the human brain enable musical behaviors that are exceptional, resourceful, and rewarding. Here I will describe studies that characterize how the human brain implements varieties of human perceptual, cognitive, and emotional abilities that surround musically relevant behaviors. Two parallel lines of these studies investigate special populations—people with absolute pitch and synesthesia—that possess exceptional abilities in perceptual categorization and association, respectively. Another line of studies examines how the general population can learn the structure that underlies musical systems from mere exposure, and identifies neural substrates of this learning process. A third line of studies tackles neural structures that give rise to uniquely personal, intense emotional responses to music. Finally, I propose a view that music furthers our understanding of the fundamental organizational structure of the brain as an interlocking set of networked highways, and I close with speculations on what the present studies could mean for positive neuroscience and to psychology and neuroscience more generally.

ABSOLUTE PITCH—A CASE OF HYPERCONNECTIVITY

Absolute pitch (AP) is the enhanced ability to categorize musical pitches without a reference. The ability can be tested with a pitch categorization task, easily done on a piano or with computerized testing (we have implemented one such test at musicianbrain.com/aptest). In a typical trial of such a pitch categorization test, a tone is played and the subject's task is to identify the pitch class of the tone (A, B-flat, B, C, etc.). While the vast majority of the population—non-AP possessors—perform almost at chance, AP possessors are robustly able to label pitches above chance. AP is thought to be rare, ranging from 0.01% to 1% of the population (Ward, 1999), but it is relatively common among several special populations. Among the "best" Western classical composers as identified by *The New York Times* (Tommasini, 2011), more than half are AP possessors as identified by historical evidence. This high occurrence of AP among great composers has led some to suggest that AP may be a sign of genius, musical creativity, and/or exceptional ability in the musical domain (Levitin & Rogers, 2005; Ward, 1999). Despite this association with exceptional ability, however, AP is also linked to neurodevelopmental disorders. High-functioning individuals with autism perform above controls in pitch discrimination and categorization (Bonnel et al., 2003), and musicians with AP are more likely to possess autism traits than musicians without AP (Dohn, Garza-Villarreal, Heaton, & Vuust, 2012). Furthermore, individuals with Williams syndrome, a neurogenetic disorder resulting in developmental delay coupled with strong language and social skills, out-perform controls in pitch categorization tasks despite impaired general cognitive ability, suggesting that the development of AP within its critical period may be extended in children with neurogenetic disorders such as Williams syndrome (Lenhoff, Perales, & Hickok, 2001). In addition to associations with a neurogenetic disorder, evidence for genetic contributions to AP include familial aggregation of AP ability even after controlling for musical training (Baharloo, Service, Risch, Gitschier, & Freimer, 2000). People of East Asian descent are much more likely to have AP (Gregersen, Kowalsky, Kohn, & Marvin, 1999), and more recently a genome-wide linkage study has identified several loci of genetic linkage to AP, including chromosomes 8q24.21, 7q22.3, 8q21.11, and 9p21.3 (Theusch, Basu, & Gitschier, 2009).

There is also abundant evidence for developmental contributions to AP. People who speak tone languages, as well as people with early musical training, are more likely to have AP (Deutsch, Dooley, Henthorn, & Head, 2009). Furthermore, the type of musical training influences the accuracy of AP: People who train in high-pitched instruments, such as the violin, are more likely to have AP in high registers; people who train in low-pitched instruments, such as the cello, are more likely to have AP in low registers; and pianists are more likely to have AP for white keys than black keys on the piano (Miyazaki, 1989). Due to its interactions with genetic and environmental contributions, AP has been described as a new model for investigating the effects of genes and development on neural and cognitive function (Zatorre, 2003).

These genetic and developmental behavioral differences suggest that AP possessors may have structural differences in the brain even in utero, as well as functional differences that may either (a) emerge as a consequence of these structural differences or (b) develop as a compensatory mechanism or strategy around the structural differences. Using diffusion tensor imaging, a magnetic resonance imaging (MRI) technique that allows visualization and quantification of major white matter connections in the brain, we found larger white matter volumes of structural connectivity in a segment of the arcuate fasciculus—specifically the segment connecting the superior and middle temporal gyri—in AP subjects relative to well-matched controls (Loui, Li, Hohmann, & Schlaug, 2011a). Left-hemisphere connectivity was especially robustly enhanced in the AP subjects, with the volume of identified tracts being significantly and positively correlated with behavioral accuracy in pitch categorization tasks (Loui et al., 2011a).

In addition to structural differences in the AP brain, differences in brain function at rest and during the processing of musical sounds may provide further insight into the neural mechanisms of exceptional perceptual categorization. To investigate the functional underpinnings of enhanced perceptual categorization abilities, we conducted a functional MRI (fMRI) study using the sparse temporal sampling design (Hall et al., 1999) in 15 AP possessors and 15 controls matched for age, sex, ethnicity, linguistic background, and age of onset and number of years of musical training.[1] Subjects listened to short musical segments and rated the levels of emotional arousal in music, compared to a rest condition. fMRI during emotional judgments of musical stimuli showed higher activations in multiple regions in the AP group. Increased activity was observed in the left superior temporal gyrus and left postcentral gyrus, regions involved in auditory and somatosensory processing, respectively. Additionally, increased activity was observed in bilateral hippocampus, amygdala, and substantia nigra/ventral tegmental area in the AP group, regions important in emotion and reward processing. These distributed increases in auditory, sensory integration, and emotion and reward processing regions may suggest intrinsic enhancements in the functional brain network of the AP group.

What do we mean by intrinsic enhancements of a functional brain network? To motivate ideas on brain networks, consider the social networks that are familiar to human society. You might have friends from elementary school, friends from high school, friends from college, and friends from graduate school. Occasionally a friend from graduate school might also know your friend from high school, in a situation many refer to as "small-world" phenomenon (Watts & Strogatz, 1998). The ways in which we describe the small-world network of our social circles can also be applied to descriptions of the human brain (Reijneveld, Ponten, Berendse, & Stam, 2007; Sporns, Tononi, & Kötter, 2005).

The newly emerging field of connection science has produced tools for describing network properties of the human brain using graph theory and small-world networks (e.g., Rubinov & Sporns, 2010), tools that can describe network properties of the human brain as a network with nodes of brain regions (or groups of functionally defined brain regions) and edges of connections that represent significant structural or functional connections between the nodes. When applied to fMRI data, such a network analysis entails obtaining time-series data from each region in the brain (as defined, in this case, using an anatomical atlas; Tzourio-Mazoyer et al., 2002), and then performing correlations between every pair of these time-series to obtain a pairwise connection matrix to describe the connection properties of each brain region. This pairwise connection matrix can yield statistics to describe the whole brain network—the sum total of all nodes and edges in the brain. These network properties include degree (number of significant connections in the network), strengths (of significant connections), clustering (proportion of nodes connected to each node that are also connected to each other), global and local efficiency (how efficiently information exchange happens in all or part of the network—related to clustering and inversely related to the path length between two nodes; Latora & Marchiori, 2001). Applying graph theory to fMRI data in AP subjects and controls, we saw that the AP group showed increased network connectivity, especially in the left superior temporal gyrus (Figure 12.1). Specifically, fMRI data from the AP group showed increased degrees and increased clustering throughout the brain, with effects centering around the left superior temporal gyrus. These differences in network degree and clustering remained the same even when the analysis was repeated only in the silent rest condition data, suggesting that network differences in AP brain were intrinsic, rather than tied to the task of music listening per se (Loui, Zamm, & Schlaug, 2012b). The intrinsic differences of network connectivity in the AP brain may explain the phenomenon of AP possessors hearing pitch categories even in nonmusical situations, such as environmental sounds (some AP possessors report, for example, hearing that the washing machine is a G-sharp, or that the wind is an F).

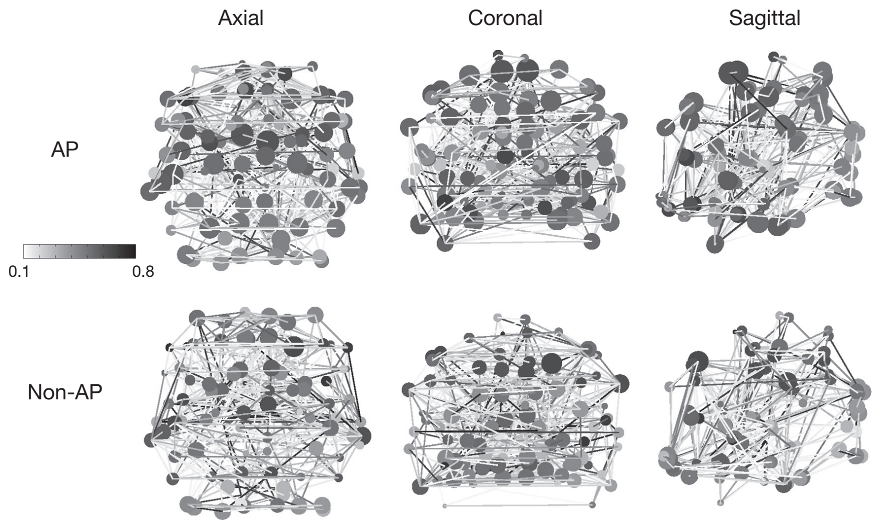

Figure 12.1 Small-world network of absolute pitch (AP) and non-AP functional magnetic resonance imaging data: Each node (circle) denotes one brain region (as defined by an atlas), and each edge (line) represents a connection, defined as a significant correlation at the $r > .5$ threshold. The size of each node denotes the degree (number of connections), whereas the shading of each node denotes the clustering coefficient (proportion of a node's connected nodes that are also connected with each other). Shading of the edges corresponds to strength of connections, with black lines denoting highest correlations. The larger nodes and darker hubs in the AP group from these visualizations show that the AP brain is an enhanced network; that is, it has more degrees and higher clustering.

SYNESTHESIA—ANOTHER CASE OF ENHANCED CONNECTIVITY

Having seen that AP is characterized by heightened structural and functional connectivity, especially in regions of the brain that subserve auditory perception, a possible follow-up question concerns which other groups or special populations might also possess similar modes of enhanced connectivity. One candidate population of increased connectivity is people with synesthesia. While AP is a neurological phenomenon where sound stimuli are perceived as belonging to categories of pitch classes, synesthesia is another neurological phenomenon where perceptual stimuli trigger concurrent perceptual sensations in other modalities. In grapheme-color synesthesia, letters and numbers trigger percepts of color, whereas in colored-music synesthesia, musical sounds (pitches, chords, timbres) trigger percepts of color. Like AP, the possession of synesthesia is sensitive to both genetic and environmental contributions: It runs in the family and is eight times more common in people in the creative industries, such as artists, composers, and poets (Ramachandran & Hubbard, 2001). Existing models posit two classes of neural mechanisms that may give rise to synesthesia: hyperconnectivity and disinhibition. Models of hyperconnectivity describe increased connectivity (both structural and functional), increased binding, or cross-wiring/cross-activation between regions involved in processing the relevant trigger and concurrent sensations (Ramachandran & Hubbard, 2001). In contrast, models pertaining to disinhibition posit that regions that normally inhibit the cross-wiring or cross-activation between trigger and concurrent processing are not in place among synesthetes (Grossenbacher & Lovelace, 2001). While most of the cognitive neuroscience literature on synesthesia has focused on grapheme-color synesthesia, studying colored-music synesthesia may be an optimal model to disentangle these competing hypotheses. This is because the regions mainly involved in color processing (visual association cortices in the occipital lobe) and in musical sound processing (auditory association cortices in the temporal lobe) are relatively distal in the brain; thus, any enhanced connections between these processing regions would be expected to bridge the clearly definable processing regions in the auditory and visual systems.

To identify potential differences in patterns of structural connectivity between synesthetes and controls, we compared diffusion tensor images of 10 colored-music synesthetes and 10 controls who were matched for age, sex, ethnicity, IQ (as determined by Shipley scores), and number of years and age of onset of musical training. We found that people with colored-music synesthesia have different hemispheric asymmetry and increased structural connectivity in the white matter tracts connecting visual and auditory association areas to the frontal lobe (Zamm, Schlaug, Eagleman, & Loui, 2013). Results are driven by enhanced white matter connectivity among synesthetes in the right hemisphere inferior frontal occipital fasciculus (IFOF—shown in three views in Figure 12.2), a white matter pathway that connects visual association regions in the occipital lobe, through auditory association regions in the temporal lobe, to attention binding or top-down modulation regions in the frontal lobe. Furthermore, fractional anisotropy (a measure of white matter integrity) of the right IFOF of the synesthete group correlated with the consistency of audiovisual synesthetic associations as defined by the Synesthesia Battery (Eagleman, Kagan, Nelson, Sagaram, & Sarma, 2007). A search within the IFOF for most significant brain–behavior correlations revealed that white matter underlying the right fusiform gyrus correlated most strongly with behavioral performance on the Synesthesia Battery, further pinpointing the role of IFOF in audiovisual associations toward white matter within the right fusiform gyrus (shown by the arrow in Figure 12.2).

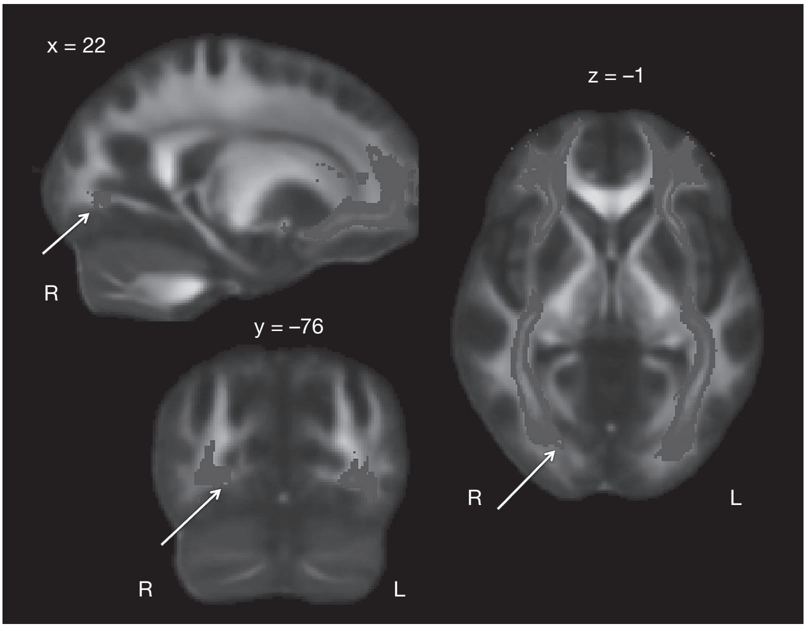

Figure 12.2 The inferior-frontal occipital fasciculus (IFOF): A pathway connecting occipital lobe to frontal lobe through the temporal lobe is shown as activated cluster. We found that colored-music synesthetes have higher white matter integrity in this pathway in the right hemisphere, with the association between white matter integrity and synesthetic behavior being highest in the fusiform gyrus, identified by the arrow.

The finding of increased IFOF connectivity in colored-music synesthetes required manual selection of regions of interest (ROIs), by coders blinded to the group assignment of each subject, that were the neuroanatomical landmarks or endpoints of the IFOF. This manual selection process, although time consuming, ensured the highest reliability in adhering to individual differences in sulcal and gyral anatomy of each individual brain, while eschewing bias by ensuring similar sizes and locations of ROIs between the synesthete and control groups. However, scaling up the manual selection of ROIs to more regions in the brain can be costly. Thus, in a follow-up diffusion tensor imaging study, we explored the use of pairwise probabilistic tractography applied on ROIs that were defined by applying the Harvard-Oxford atlas across each brain and constraining the resultant ROIs to voxels within white matter. Pairwise tractography across all 111 seed regions, as defined by the Harvard-Oxford atlas, resulted in a 111 x 111 matrix expressing the strength of all connections between any pair of regions in the brain. This bottom-up pairwise tractography result enables another application of the small-world network analysis pipeline toward structural connectivity data, as opposed to functional connectivity data, as discussed earlier in this chapter. A whole-brain comparison between synesthetes' and control subjects' structural brain networks revealed that the synesthetes' brain network had more degrees and higher strengths of connections relative to controls. Region-specific comparisons between the connectivity values from each ROI showed significantly more connections (Bonferroni-corrected for 111 ROIs) in the synesthetes' brain network in the bilateral superior and middle temporal gyri, inferior lateral occipital cortex, supracalcarine cortex, and frontal medial cortex—regions involved in auditory association, visual association, and top-down modulation that are also traversed by the IFOF (Loui, Zamm, & Schlaug, 2013).

To investigate functional differences in synesthetes hand in hand with the structural differences, we applied the previously discussed sparse-temporal sampling fMRI paradigm of emotional judgment of musical stimuli to colored-music synesthetes. Preliminary fMRI results showed shared enhancements between AP and synesthetes relative to controls, in auditory processing regions in the superior temporal lobe as well as regions responsible for top-down control in the frontal lobe. In addition, synesthetes showed higher activations in the right superior temporal gyrus, a way station of auditory perception, coupled with increased activations in bilateral color-sensitive visual association regions in the lingual gyrus of the occipital lobe, during the perception of musical stimuli that were rated by the synesthetes as highly arousing (Loui, Zamm, & Schlaug, 2012a). These functional results converge with structural differences observed in the synesthete brain in showing domain-specific enhancements in auditory and visual association, coupled with a general network of auditory and cognitive processing during music perception that is shared with the nonsynesthete control population.

In sum, exceptional audiovisual associations may be subserved by the integrity of white matter that connects visual and auditory association regions to top-down modulatory regions in the frontal lobe. The synesthete's enhanced perceptual experience of seeing colors when hearing sounds may involve both domain-general (top-down) and domain-specific (bottom-up) enhancements in structural connectivity in white matter, as well as functional connectivity in gray matter. These results offer a link between synesthesia and other populations characterized by enhanced local white matter connectivity, such as AP possessors (Loui et al., 2011a) and individuals with high cognitive intelligence, high emotional intelligence, and exceptional creativity (Chiang et al., 2009; Jung et al., 2010; Takeuchi et al., 2011), as well as in patients with auditory verbal hallucinations and autistic spectrum disorders (Fletcher et al., 2010; Hoffman & Hampson, 2011).

Results presented so far suggest that AP and synesthesia are plausible models of exceptional behavior that lie on the high end of a spectrum of individual differences in connectivity. It remains to be seen what other types of exceptional behavior fall under this category of hyperconnectivity syndromes. Mottron et al. (2013) describe savant syndrome, hyperlexia, and hypergraphia as more examples of enhanced perceptual functioning in addition to AP and synesthesia. While these special populations may possess heightened connectivity in brain structure and function, what remains to be seen is the degree to which any enhanced connectivity patterns in these special populations, if observed, may be shared with or distinct from each other.

THE HUMAN BRAIN IS RESOURCEFUL—STATISTICAL LEARNING OF MUSICAL STRUCTURE

Results presented thus far have pertained to rare populations of humans who have unusual giftedness or impairments in musical functions. What about the rest of us? What are the bases of brain connectivity that enable the learning and liking of music within our society? Here we describe the use of a novel musical system to investigate the brain connectivity substrates for learning new music in humans.

The new musical system is a finite state grammar based on the Bohlen-Pierce scale, an artificial musical scale that uses a 3:1 frequency ratio instead of the 2:1 ratio (octave) found around the world. Detailed descriptions of this new musical system exist elsewhere (Loui, 2012a, 2012b; Loui, Wessel, & Hudson Kam, 2010) and therefore will not be repeated here, but important for present purposes we note that using an artificial musical system, we can generate thousands of new melodies that can be presented to subjects, giving us high precision and experimental control in the investigation of how learning occurs in humans. After hearing a large set of (400) melodies in one of two possible artificial finite-state grammar systems only once each, participants could not only recognize the melodies they had heard but also could generalize their knowledge of the underlying grammar toward new melodies that had not been heard before, suggesting that humans exploit the statistical properties of their sound environment to acquire sensitivity toward grammatical structure when confronted with a new musical system (Loui, 2012a, 2012b; Loui et al., 2010). Event-related potential data showed two negative waveforms, the first reflecting sensory processing in the superior temporal lobe and the second reflecting further cognitive analysis in the frontal lobe, that increased after learning to differentiate statistically frequent instances of the new musical system, suggesting that the human brain rapidly and flexibly acquires musical structure by capitalizing on frequency and probability of sound events—statistical resources that are available within the auditory environment (Loui, Wu, Wessel, & Knight, 2009).

In further studies we asked which anatomical connections in the brain might be allowing this rapid statistical learning system. As the arcuate fasciculus is a major white matter pathway that connects the temporal lobe and frontal lobe structures and is diminished in people who lack musical ability (Loui, Alsop, & Schlaug, 2009), it was a prime candidate for a neuroanatomical correlate of individual differences in new music learning. We tested the possibility that the structure and morphology of the arcuate fasciculus might reflect individual differences in learning the Bohlen-Pierce scale: We correlated the volume of the arcuate fasciculus, as defined by probabilistic tractography from diffusion tensor imaging data, with individual scores in the generalization test for learning the Bohlen-Pierce scale. Results showed that the ventral branch of the right arcuate fasciculus, connecting the right middle temporal gyrus (MTG—the ventral portion of Wernicke's area) with the right inferior frontal gyrus (IFG—the Broca's area), was significantly correlated with generalization scores (Loui, Li, & Schlaug, 2011b). Control tasks showed that this correlation was specific to music learning, and not to individual differences in memory or intellectual functioning. Furthermore, white matter integrity in the turning point of the arcuate fasciculus, in white matter underlying the supramarginal gyrus, was most highly correlated with learning accuracy. This suggests that individual differences in arcuate fasciculus morphology, specifically the extent to which the arcuate fasciculus descends into the temporal lobe, may be predictive of individual differences in learning ability. This is consistent with work by Flöel and colleagues (Flöel, de Vries, Scholz, Breitenstein, & Johansen-Berg, 2009), which showed an association between white matter integrity in tracts from the Broca's area and success in learning an artificial grammar. Taken together, by combining a new learning paradigm with neuroimaging techniques that enable the visualization and comparison of individual differences in white matter pathways, we were able to identify anatomical connections in the brain that may be required for music learning.

EMPATHIZING VIA INTENSELY PLEASURABLE MUSIC—REWARDS OF THE MUSICAL EXPERIENCE

While statistical learning mechanisms in the brain are crucial for the learning of musical structures, most people do not report music learning as a primary reason for their avid consumption—even to the point of addiction—of music in their culture. Music is a multi-billion-dollar industry: People who have no formal musical training regularly enjoy intense emotional experiences at concerts where the music that is played often has only minimal structural complexity. Yet the emotional rewards of music are intensely personal and profound. What causes strong emotional responses to music?

In a recent study (Sachs, Ellis, Schlaug, & Loui, 2014), we asked if there were any structural connectivity characteristics in people who consistently experience strong emotional responses to music, compared to people who rarely experience such emotions to music. In a large sample (N = 237) of adult college-aged subjects, we administered the Aesthetic Responses to Music Questionnaire, which asked for subjects' personalities (using the Ten-Item Personality Inventory), history of music training, and demographic information, as well as their preferences for various genres of music, the frequency with which music gave them various strong emotional experiences such as chills, goosebumps, feelings of awe, tears, feelings in the pit of the stomach, and heart palpitations. Subjects also listed their favorite pieces of music and the ones that elicited these strong sensations. From these survey data we identified the 10 most emotional responders—those who consistently and reliably experienced chills and other strong emotional sensations according to their self-report—and the 10 least emotional responders—those who reportedly never experienced chills or any other strong emotional experience, despite similar age, sex, intellectual functioning, and amount and intensity of musical training (Sachs et al., 2014). These 20 individuals were brought into the lab for behavioral ratings of emotional arousal and psychophysical recordings of heart rate and skin conductance to confirm subjective reports of arousal, as well as structural neuroimaging to identify possible differences in the brain that are associated with strong emotional responses to music. We compared people who get chills from music and people who do not get chills, controlling for differences in personality, musical training, and musical exposure. Results showed greater volume of white matter connectivity between auditory regions in the superior temporal gyrus and emotion-processing regions in the insula and medial prefrontal cortex (MPFC). This three-node network of superior temporal gyrus, insula, and MPFC traverses white matter fasciculi that include the aforementioned arcuate fasciculus, which connects the superior temporal lobe to the lateral prefrontal cortex, and the uncinate fasciculus, which connects the anterior temporal lobe to the MPFC. The effects of increased white matter volume in the chill perceivers were bilateral, but stronger in the right hemisphere, consistent with existing literature showing bilateral but rightward-leaning activations during strongly emotional aesthetic responses to music (Salimpoor, Benovoy, Larcher, Dagher, & Zatorre, 2011; Trost, Ethofer, Zentner, & Vuilleumier, 2011).

The MPFC is activated by intensely pleasurable responses (Blood & Zatorre, 2001) and mental imagery of autobiographically relevant music (Janata, 2009; Janata et al., 2002; Kleber, Birbaumer, Veit, Trevorrow, & Lotze, 2007).

It is more generally engaged in emotional processing (Phan, Wager, Taylor, & Liberzon, 2002), specifically activated in self-referential mental activity (Gusnard, Akbudak, Shulman, & Raichle, 2001) and empathic accuracy—the tracking of attributions about other individuals' internal emotional state (Zaki, Weber, Bolger, & Ochsner, 2009). Recent fMRI studies also showed increased MPFC function accompanied by decreased lateral PFC function during creative improvisation, such as jazz improvisation (Limb & Braun, 2008) and freestyle rapping (Liu et al., 2012). The ventral MPFC is impoverished in connectivity among psychopathic criminals (Motzkin, Newman, Kiehl, & Koenigs, 2011). Because the MPFC plays a crucial role in creativity as well as with emotionally empathizing with others, our finding of increased auditory-to-MPFC activity in people who get chills from music may relate creativity in music to empathy, thus informing theories about the evolutionary function of music. Perhaps the reason that humans have evolved to create music is to identify emotionally with each other via an auditory mode of communication.

Debates on the evolutionary function of music have lasted for centuries, and while the current debate surrounds whether music can be an evolutionary adaptation or exaptation (Trainor, 2006), I believe these results from the study on chills can inform this debate by bringing the evolutionary function of music into a social context. If emotional experiences to music involve areas of the brain that are important for empathizing with other people, then perhaps the purpose of music is to arouse emotional responses that resonate with other minds. Music, then, is a social artifact for empathy.

The view of music as a social artifact for empathy is also supported by a recent controlled study in which children who learned to play music together significantly improved in emotional empathy, relative to an untrained control group (Rabinowitch, Cross, & Burnard, 2012). While further studies are needed to test for control interventions, this training study converges with our neuroimaging results in implicating networks of emotional response to music that are shared with social-emotional processing.

CONCLUSION

The studies presented in this chapter touch on the multiple dimensions of musical experience: pitch perception, sound production, sound categorization, audiovisual association, grammar learning, and emotional and aesthetic reception. In each of these dimensions we show that structural and/or functional connectivity plays an important role. One of the conclusions that emerge from these data is that music is a powerful tool for examining myriad brain functions, ranging from primary cortical functions (auditory perception) to the more mystical and elusive subjective experiences (aesthetic response). Music recruits a fronto-temporal network that allows sound perception, production, and categorization. This network engenders musical knowledge, which is acquired via statistical exposure. Aspects of the frontotemporal network are also implicated in creativity and emotional communication.

If studying the brain can inform our understanding of music, one might ask the inverse question: What can music teach us about the organization of the brain? Recently there has been a debate on what, if anything, might be the fundamentally unifying structure of the brain. In 2012, Wedeen et al. published in *Science* findings from diffusion spectral imaging, concluding that the brain is organized in grid-like structures, like a woven fabric or like the streets of Manhattan. This claim was criticized by Catani et al. (2012), who contended that the findings were due to the imaging technique used rather than to the intrinsic structure of the brain per se, and that if anything, the unifying structure of the brain is as a series of small paths that might enlarge due to use and reuse, thus resembling the streets of Victorian London.

How can the findings here contribute to such a debate? Is there anything that music and neuroimaging research is telling us about the unifying structure of the brain that is separate from all the neuroimaging methods we use? My view is that if musical function must rapidly, flexibly, and resourcefully recruit entire continua of mental operations, from the most basic pitch discrimination functions to the most intensely personal subjective experiences such as aesthetics, then perhaps the structure of the brain that enables music is as an interlocking set of networked highways and byways that connect regions that subserve various functions. Certainly the arcuate fasciculus plays a prominent role as a superhighway linking perception and action operations, but the entrances and exits from such a superhighway may interface with other highways such as the inferior frontal occipital fasciculus and the uncinate fasciculus, which correlate with top-down modulation of audiovisual associations and social-emotional processing, respectively. A comprehensive model of musical experience, then, must incorporate most if not all of the principal structures and functions of the human brain. Future work will continue to characterize components of musical experience that may be engendered by networks and clusters within the connectome, defined as a sum total of all connections in the brain. By relating the varieties of exceptional, resourceful, and rewarding human experiences, as instantiated in musical behavior, to systems and networks of the human brain, the neuroscience of music perception and cognition addresses the core goal of positive neuroscience in advancing our understanding of human flourishing.

NOTE

1. Sparse temporal sampling refers to the temporally sparse (e.g., once every 15 seconds, as opposed to once every 2 seconds in a regular design) acquisition of functional magnetic resonance images in an environment where auditory presentations are important to the experiment. Auditory stimuli are presented in silence, and as the brain's hemodynamic response associated with the auditory event is recruited, which typically requires 4 to 8 seconds, the functional magnetic resonance images are acquired, thus allowing the presentation of auditory stimuli in silence.

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