Current Advances in the Cognitive Neuroscience of Music

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The study of music perception and cognition is one of the oldest topics in experimental psychology. The last 20 years have seen an increased interest in understanding the functional neuroanatomy of music processing in humans, using a variety of technologies including fMRI, PET, ERP, MEG, and lesion studies. We review current findings in the context of a rich intellectual history of research, organized by the cognitive systems underlying different aspects of human musical behavior. We pay special attention to the perception of components of musical processing, musical structure, laterality effects, cultural issues, links between music and movement, emotional processing, expertise, and the amusias. Current trends are noted, such as the increased interest in evolutionary origins of music and comparisons of music and language. The review serves to demonstrate the important role that music can play in informing broad theories of higher order cognitive processes such as music in humans.

Key words: **music; language; emotion; structure; evolutionary psychology; expertise**

Introduction

The field of music cognition traces its origins to the 4th century BCE, long before the establishment of experimental psychology itself, through the ideas of Aristoxenus, an Aristotelian philosopher. Contrary to the Pythagoreans of that time, Aristoxenus argued that musical intervals should be classified by their effects on listeners as opposed to merely examining their mathematical ratios (Griffiths 2004; Levitin 1999). This notion brought the scientific study of music into the mind, followed by the first psychophysics experiments at the dawn of experimental psychology, which mapped changes in the physical world onto changes in the psychological world (e.g., Fechner 1860; Helmholtz 1863/1954). Indeed, many of the earliest studies in experimental psychology concerned music, and the Gestalt psychology movement was formed in part to address questions about part—whole relationships in music and melody (Ehrenfels 1890/1988).

The past decade has seen an exponential increase in studies of music cognition. Musical behaviors that are typically studied include listening, remembering, performing, learning, composing, and, to a lesser extent, movement and dancing. The largest paradigm shift has been the increased use of neuroimaging and neural case studies to inform theories about the brain basis for musical behaviors. A second theme over the past decade has been an increased interest in the origins of music and its connection with language, both evolutionarily and functionally.

In cognitive neuroscientific studies of language, mathematical ability, or visual perception, one rarely encounters a definition of the capacity being studied, yet the question of just what is music (and by implication, what it is not) is one that emerges more often in this field of inquiry than in the others. Those who study music cognition often rely on the theorist Leonard Meyer, who defined it as a form of emotional communication, or on the definition of the composer Edgar Varése,

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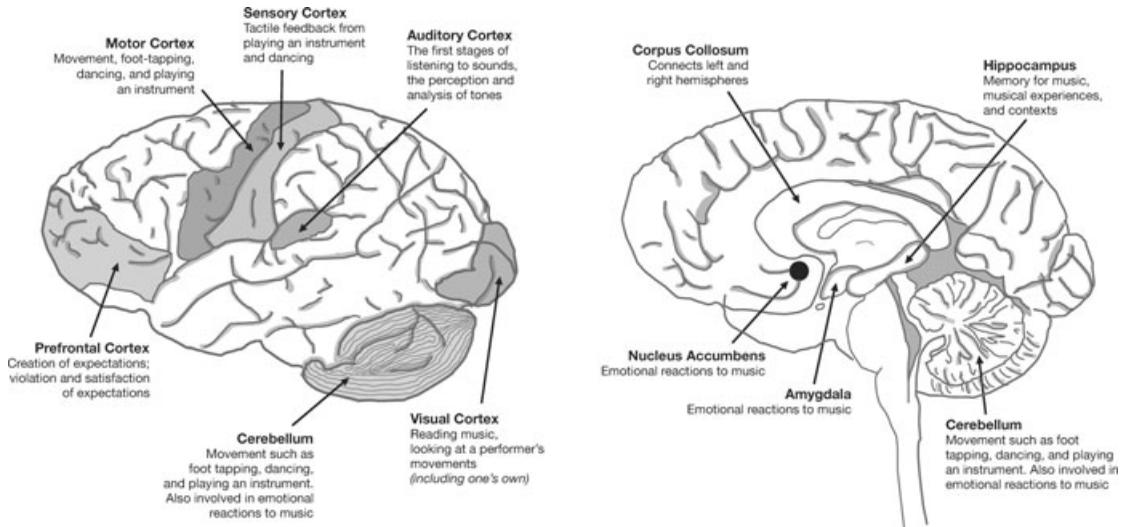
Figure 1. Core brain regions associated with musical activity. Based on Tramo 2001 and updated in 2006 (from Levitin 2006).

who famously defined it as "organized sound." Music can be seen as a form of artistic expression, communication, self-expression and self-discovery, or as an auditory art form. Music most typically involves variations in pitch and rhythm that are composed or improvised with the purpose of inducing emotional responses in the listener. However, these are neither necessary nor sufficient conditions, and one is usually left with a Wittgensteinian conclusion that a new exemplar can be considered music if it bears a "family resemblance" to other examples that are generally agreed to be "music."

As studied in the laboratory, researchers typically examine variations in one musical attribute while holding the others constant so as to maintain experimental control. A review of the literature can be parsed in at least three ways: by the discipline of those who study it (e.g., psychology, neuroscience, musicology, music theory, sociology, anthropology, biology); by the attribute of the musical signal studied (rhythm, pitch, melody, timbre); or by those mental processes involved. Here, we choose to organize this review using the latter, cognitive–systematic approach, with a brief opening discussion of the origins of music. We limit our discussion to music in humans.

The Origins of Music

At the annual meeting of the Society of Music Perception and Cognition (SMPC) held at M.I.T. during the summer of 1997, the cognitive scientist Steven Pinker made a now famous declaration that music cognition is "not worth studying" because, he said, it is "auditory cheesecake," an evolutionary byproduct of the adaptation for human language. The phrase *auditory cheesecake* derives from a rhetorical challenge to evolutionary theory: If evolution selects those behaviors that are maximally adaptive, how do you explain that many of us like fats and sweets (as in cheesecake, for example), which can actually lead to obesity, diabetes, and other clearly maladaptive outcomes?

"We enjoy strawberry cheesecake, but not because we evolved a taste for it," Pinker argues. "We evolved circuits that gave us trickles of enjoyment from the sweet taste of ripe fruit, the creamy mouth feel of fats and oils from nuts and meat, and the coolness of fresh water. Cheesecake packs a sensual wallop unlike anything in the natural world because it is a brew of megadoses of agreeable stimuli which we concocted for the express purpose of pressing our pleasure buttons" (Pinker 1997,

p. 525). Moreover, in the quantities that fats and sweets would have been available to our hunter—gatherer ancestors, they posed no threat.

Pinker argues that music exploits circuits that evolved for spoken language: that language was the evolutionary adaptation, music the byproduct or spandrel. He feels similarly about literature and the other arts, that the pleasures afforded by them are incidental (cf. Carroll 1998). Michael Gazzaniga (2008) and others (e.g., Tooby & Cosmides 2001) believe that artistic thinking in general would have been essential to early human development. An ability to engage in and enjoy fictional thinking would have conferred an evolutionary advantage to our ancestors. They could consider hypothetical scenarios and plan their responses to them ahead of time, without having to try various alternatives during a moment of imminent danger, such as a confrontation with a predator. Music, and indeed all art, derives from three abilities that are hallmarks of human cognition: theory of mind, recursion, and abstract representation (Levitin 2008, see also Cosmides & Tooby 1995).

Music composition and improvisation can be seen as a preparatory activity for training cognitive flexibility—arranging and rearranging the elements of pitch and rhythm over time is now believed to exercise attentional networks (or more generally, executive function; H. J. Neville, personal communication, November, 2006) and from an evolutionary standpoint can be seen as an "honest signal" for mental and emotional flexibility and fitness (Cross & Woodruff, in press, Miller 2000; Sluming & Manning 2000). Moreover, our primitive ancestors who could sing and dance for hours on end, creating variations on themes, were indicating to potential mates their cognitive and physical flexibility and fitness—skills that could come in handy if the food supply ran out or one needed to hastily build a new shelter or escape from a predator. Music-dance, among other cognitive displays, would have indicated the presence of the creative mind as well as physical fitness and

motor coordination (because in evolutionary time frames music was usually accompanied by dance).

Perception and Musical Structure

Music is characterized by eight perceptual attributes, or dimensions, each of which can be varied independently: pitch, rhythm, timbre, tempo, meter, contour, loudness, and spatial location (Levitin 1999; Pierce 1983). Perceptual grouping in music occurs as a function of principles similar in some ways to those for grouping in vision. Grouping by similarity of timbre and loudness has been demonstrated, as has grouping by proximity of pitch or onset time, and by good continuation of pitch (Bregman 1990). Temporal grouping of tones into subsequences gives rise to the perception of meter (common meters in Western music are based on groupings of 2, 3, or 4 primary beats). The points over time at which one would naturally tap a foot or snap a finger to accompany music are called the *tactus*, the underlying beat or pulse.

Each human culture develops its own traditions for the ways in which the eight perceptual attributes are employed to create music. The system of rules or conventions by which sounds are strung together in a given culture can be thought of as the grammar for that music (Lerdahl & Jackendoff 1983; Lerdahl 2001) and as reflecting a musical style. Musical and linguistic grammar allow for the generation of a theoretically infinite number of songs or sentences through combinations and rearrangements of elements. Tonality occurs as a function of either the simultaneous or sequential sounding of tones. In Western tonal music, major and minor tonalities are the principal distinctions. Other musical traditions use different conceptions; we restrict our discussion here to Western tonal music.

Early reports (e.g., Bever & Chiarello 1974) stated that music is predominantly a right-hemisphere activity and language, left (in neurologically intact right-handed listeners).

This is now considered to be an oversimplification, in part because of the distributed nature of specialized processing mechanisms acting on the individual musical attributes listed above. It is now known that music listening, performing, and composing engage regions throughout the brain, bilaterally, and in the cortex, neocortex, paleo-, and neocerebellum (Peretz & Zatorre 2003; Platel et al. 1997; Sergeant 1993; Tramo 2001). Laterality effects do exist, however. For example, magnetic encephalography (MEG) responses to deviations in the memorized lyrics of tunes are stronger in the left hemisphere, while the perception of violations of expected notes are governed by the right hemisphere (Yasui et al. 2008). The act of learning music causes a left hemisphere shift (Ohnishi et al. 2001), particularly as naming processes become involved (such as naming musical intervals, chords, etc.; Zatorre et al. 1998).

Evidence supports the differential specialization of the left and right mesial temporal lobes in learning new melodies (Wilson & Saling 2008). When presented with a learning task for novel melodies in tonal and atonal contexts, patients with either left- or right-sided mesial temporal damage were impaired in interval recognition compared to normal controls. However, when memorizing melodies within a tonal context, individuals with right mesial temporal damage in particular were unable to use implicit knowledge of Western musical tonality to aid their memory.

While our subjective experience of music may seem complete and seamless, this phenomenological unity belies the fact that the perceptual components are processed separately. Primary auditory cortex in both cerebral hemispheres in most mammals contains a tonotopic map—a map of pitches running from low to high, which mirrors the neuronal pitch map in the cochlea (Bendor & Wang 2005) and allows for the encoding of pitch height (that dimension of pitch perception that correlates with frequency). Human perception of music relies on pitch relations as well as absolute pitch infor-

mation (Dowling 1978; Narmour 1990; White 1960), which suggests that human music perception may be qualitatively different from that of most animal species. There has been a history of debate in the animal learning literature regarding whether animals' mental representations are relational or absolute (Hanson 1959; Kohler 1918/1938; Reese 1968; Spence 1937). Even most bird species do not recognize their own songs in transposition (Hauser & McDermott 2003). In human listeners the absolute values of a tone's pitch and duration are processed, and when there is more than one tone present it is the processing of tonal relations that gives rise to the appreciation of melody (Dowling & Harwood 1986). To some extent tonal relations are computed even when only a single tone is presented—the listener is aware, for example, that the presented tone is higher or lower, or longer or shorter, than a conceptual average tone encountered across the course of a lifetime.

Tonal relations, or musical intervals (as opposed to large-scale musical structure), have been shown to be predominantly served by networks in the right temporal region (Liégeois-Chauvel et al. 1998; Zatorre 1985) and in the left dorsolateral prefrontal and right inferior frontal cortex (Zatorre et al. 1998), with particular deficits noted following lesions of the right anterolateral part of Heschl's gyrus (Johnsrude et al. 2000; Tramo et al. 2002; Zatorre 1988). Neuroimaging studies have shown that a hierarchy of pitch processing operations seems to exist. Fixed pitches and noise are processed in Heschl's gyrus bilaterally (Patterson et al. 2002). Posterior regions of secondary auditory cortex process pitch height, and anterior regions process pitch chroma (pitch class) (Warren et al. 2003). Intervals, contour, and melody activate the superior temporal gyrus (STG) and planum polare (PP) (Patterson et al. 2002).

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2003; see also (Tervaniemi & Huotilainen 2003) for converging evidence from the event-related potential, or ERP).

An examination of blood oxygenation level-dependent (BOLD) responses using functional magnetic resonance imaging (fMRI) revealed that major and minor tonalities recruit the bilateral inferior frontal gyri, medial thalamus, and the dorsal cingulate cortex (Mizuno & Sugishita 2007). The authors suggest that the frontal and thalamic regions are implicated in judging tonality, while the cingulate may be recruited for the resolution of mental conflict in response when the participant differentiates modality. Minor, compared to major chords, shows selective activation in the amygdala, retrosplenial cortex, brain stem, and cerebellum (Pallesen et al. 2005), and in a separate study of mode melodies, activation was found in left parahippocampal gyrus, bilateral ventral anterior cingulate, and left medial prefrontal cortex (Green et al. 2008). (We note that in this and subsequent fMRI studies reported in this review the relation between neural activation to a stimulus and neural deactivation is an area of current inquiry and much work remains to be done on this issue. Not all papers report deactivation, and in those that do, the clear interpretation of deactivations has not been established.)

Rhythm perception and production invoke regions in the cerebellum and basal ganglia (Ivry & Keele 1989; Janata & Grafton 2003), as well as several motor areas such as the premotor cortex and supplemental motor area (Halsband et al. 1993). Timing, synchrony, and entrainment may be subserved by a system of hierarchically controlled oscillators in the cerebellum (Ivry & Hazeltine 1995; Ivry & Schlerf 2008; Sternberg et al. 1982) that contribute to our sense of tempo (Levitin & Cook 1996). One recent experiment (Grahn & Brett 2007) investigated the perception and production of both regular (small integer ratios) and irregular (complex integer ratios) rhythmic groupings in monotonal (same pitch) sequences. The perception of an accented tone, or beat, was

thus induced by the temporal context created by the stimuli rather than the perception of a prominent tone created by deviations in pitch or volume; these rhythmic sequences were created as metrically simple, metrically complex, and nonmetric. Metrically simple rhythms were more accurately reproduced by the participants. Furthermore, both simple and complex rhythms generate activity in several areas as measured by fMRI, including motor areas such as the supplemental motor area, basal ganglia, and cerebellum. However, specific to rhythms in which accents arise at regular intervals (which give the feeling of a simple beat), the basal ganglia, pre-SMA/SMA, and the anterior superior temporal gyri showed greater activation. These areas may subserve the internal, intuitive, "beat-based" timer in both musicians and nonmusicians. The increased performance ability for simple, perceptually salient rhythms suggests the existence of a metrically regular, internal timer; such a timer in adults may preferentially support the processing of small-integer ratio temporal intervals typical of Western music (cf. Ivry & Hazeltine 1995; Poppel 1997; Sternberg et al. 1982).

The aforementioned neuroanatomical studies suggest a theoretical model of functional architecture whereby distinct neural circuits for music grouped into pitch organization and temporal organization represent an interactive system of music processing (Peretz & Coltheart 2003). Although the extent to which pitch and rhythm processing are separable or constitute Fodorian modules (Fodor 1983) is not entirely understood, double-dissociation evidence from patient populations strongly suggests independence of pitch and rhythm processing (Ayotte et al. 2000; Di Pietro et al. 2004; Liégeois-Chauvel et al. 1998; Peretz 1990; Peretz & Kolinsky 1993; Piccirilli et al. 2000; Vignolo 2003). The prevailing view is thus that pitch, rhythm, and loudness are processed separately and then come together later (where "later" in neural processing time may be 25–50 ms later) to give us the impression of a fully realized musical object or phrase.

The perception of certain tonal and rhythmic structures (such as octave equivalence) appears to be innate, pointing to a possible evolutionary function (as mentioned earlier). During the first year of life, infants prefer pleasing to displeasing musical intervals (Trainor et al. 2002). Infants are also capable of perceiving violations in complex meter, a feature that characterizes much non-Western music, a capacity that declines at the end of the first year of life (Hannon & Trehub 2005). This suggests that maturation involves becoming sensitive to the music of one's culture during the first year of receiving musical input, and that humans may be born with the capacity to learn any of the world's music forms. By the age of 5 years children demonstrate an adultlike electrophysiological response called the "early right anterior negativity" response or ERAN, and a negative voltage response approximately 500 ms after the event, known as the N5, to violations of musical syntax for the music of their culture (Jentschke et al. 2008).

The now well-known idea put forth by Chomsky (1965) was that humans enter the world equipped with a "language acquisition device" (LAD). That is, given proper input, we have the cognitive equipment to automatically acquire language. Because of the presence of precocious perceptual abilities of infants, a nativist position is held by the majority of researchers in this field. Our intrinsic capacity for music is seen as leaning to nature, while the learning of specific musical forms relies on nurture—specifically on exposure during a sensitive or critical period of development (Trainor 2005). This strong nativist position in the literature on early musical capacities suggests that a counterpart in music to the LAD indeed exists, which we will call the "music acquisition device".

The way in which pitches and, to a lesser degree, rhythms may be lawfully strung together constitutes the grammar of a given musical style or culture. It has been shown that infants at the age of 9 months are sensitive to particular characteristics of the scales of their own musical culture (Trehub et al. 1999). The ability that children have in detecting changes in key and harmony in their native music appear between the ages of 5 and 7 years (Trainor & Trehub 1994). The processes of acquiring knowledge of one's musical culture can be viewed as involving statistical learning (Saffran et al. 1996; Saffran et al. 1999). Native listeners of their musical system, after exposure to thousands of tonal sequences, implicitly learn which tones and chords are mostly likely to complete a musical sequence. Composers sometimes reward and sometimes violate listener expectations (Narmour 1990) but do so within this system of legal tones for their culture's music. Rarely if ever does one encounter a tone from outside one's musical system. Even upon hearing a relatively complex piece for the first time—say by Schoenberg or Reich—one would not suddenly encounter a tone from an Indian Raga or a pygmy scale.

Experiments that introduce stimuli violating the rules of musical grammar have been employed to investigate how the human brain processes musical structure. When presented with a violation in a chord sequence, an ERP response called ERAN is elicited (Koelsch et al. 2007). This response is not due to acoustic variation in the chord sequence, but to the irregularity of its musical grammar or violation of expectation (the so-called oddball paradigm). We return to this topic under Music and Language below, as numerous studies using this paradigm have been conducted to discern possible associations and dissociations between grammar processing in music and language.

Musical context has been found to be crucial to music perception. For example, in classic probe-tone studies (cf. Krumhansl & Kessler 1982) participants judged the perceptual congruence of chords after being primed by particular musical scales, creating in them a perceptual space for chord stability that was found to be substantially the same as Western music theory would predict; in other words, the average listener implicitly internalizes the rules of Western tonal music. In a recent study investigating

the neuromagnetic response to the probe-tone method (Otsuka et al. 2008), the contextual modality (major or minor mode) as well as perceptual priming affected the perception of chord tonality, as measured by activation at the level of the auditory cortex.

Internalizing the rules of one's musical culture naturally makes the processing of tonal structures in that music more automatic and efficient. This doesn't mean that one can't enjoy music from outside one's culture, but suggests that doing so may carry additional cognitive costs. Nan et al. (2008) studied this by examining the differences in neural activation for native and non-native music. They found that native music engages the ventro-medial prefrontal cortex (VMPC), an area known to activate when an individual processes information with ease, or a "feeling of knowing," as well as motor regions typically found to activate during music listening. Moreover, the same study investigated the presence and absence of phrase boundaries in native and non-native music. This implicated the planum temporale (PT), an integratory mechanism in the temporal lobe just posterior to Heschl's gyrus in the center of Wernicke's area. The PT was increasingly activated as phrase boundaries became more difficult to identify in native music. PT has also been implicated in studies of absolute pitch (a larger leftward asymmetry is associated with AP possession, Keenan et al. 2001; Schlaug et al. 1995) and it has been likened to a "computational hub" (Griffiths & Warren 2002).

The extraction of phrase boundaries is an essential preparatory operation for memory encoding: In order for an event to be stored it needs to be temporally segmented into a beginning and end. The neural basis for such event segmentation in musical phrase transitions was investigated using fMRI and found to involve distinct, dissociable dorsal and ventral fronto-temporal structures (Sridharan et al. 2007). In particular, a ventral fronto-temporal network, including the ventrolateral prefrontal cortex (vlPFC, BA 47, and BA44/45) and posterior temporal cortex (pTC, BA 21/22), was active during the early part of each transition, and a dorsal fronto-parietal network, including the dorsolateral prefrontal cortex (dlPFC, BA9) and posterior parietal cortex (PPC, BA 40), was active during the later part. These activations were predominantly right lateralized.

Prediction and anticipation are truly at the heart of the musical experience. Even nonmusicians are actively engaged, at least subconsciously, in tracking the ongoing development of a musical piece and forming predictions about what will come next. Typically in music, when something will come next is known, due to music's underlying pulse or rhythm (what musicians call the "tactus"), but less known is what will occur next. There is an important link between such predictive processes and the formation of event boundaries: In music the VLPFC has been consistently implicated in the detection of violations in musical expectancies or predictions (such as violations in chord and harmonic expectancies), even in musically untrained listeners.

Music, Movement, and Synchronization

Humans are the only species capable of synchronizing movement to sound (Patel 2007; Sacks 2007; although see Patel et al. in press, for new data that suggest such behavior may be found in *Cacatua galerita eleanora*). Although other animals (chimpanzees, elephants) can keep a steady tempo, when one animal is doing so, a conspecific that joins in will not be able to keep the beat or play in time.

The well-known association between music and movement both behaviorally and neurally (across cultures and throughout history) suggests an ancient evolutionary connection between music and dance, or more generally, between sound and movement. In fact, the motor theory of speech of speech perception (Liberman 1982; Liberman & Mattingly 1985) argues that we learn to speak by observing the mouth and lip movements of others. The recent discovery of mirror neurons (Rizzolatti et al. 1996)

and the evidence of their presence in Broca's area (Heiser et al. 2003; Johnson-Frey 2003; Lametti & Mattar 2006) suggests a plausible neuroanatomical substrate for the motor theory of speech perception—and the connection between music and dance. Listening to music may activate mirror neurons that cause us to think (at least unconsciously) about those motor movements that would be required to make the music. Dance can be conceived as an extension or complementary correlate of the movements required to create music. It has been widely observed that infants are readily able to sing back melodies that they hear—taking input from one sense (hearing) and producing output with another sense (vocal—motor) seamlessly. Broca's area may well be the seat of this ability as well. If so, the connection between music and dance can be thought of as an extension of the movements required for vocalizing simply applied to other body regions. The voluntary motion of the limbs to music, which characterizes dancing, activates the precuneus, a region of the parietal lobe (Brown & Parsons 2008).

It is worth noting that music cannot exist without movement. Because sound is transmitted via vibrating molecules, some physical motion is required to set those molecules vibrating in the first place—hitting, plucking, bowing, blowing, or forcing air through the vocal cords (Levitin et al. 2002). Even when lying perfectly still, listeners in fMRI studies show activation in those regions of the brain that would normally orchestrate motor movement to music, including the cerebellum, basal ganglia, and cortical motor areas—it is as though movement is impossible to suppress (Levitin 2008; Levitin & Menon 2003). Tapping in synchrony to the pulse of a musical sequence (by humans) engages the presupplementary motor area, the supplemental motor area, the dorsal premotor cortex, the dorsolateral prefrontal cortex, the inferior parietal lobule, and lobule VI of the cerebellum, as measured by the BOLD response (Chen et al. 2008).

A generalized motor theory can account for this connection between sound and movement.

When listening to music many people report that it is difficult to avoid moving their bodies, whether it is a simple head nod to the beat, a body sway or a foot tap. This movement is processed via the medial geniculate nucleus, a subcortical auditory relay station (Brown & Parsons 2008); the absence of communication to cortical structures following automatic, synchronous movement to music can therefore be interpreted as biologically (as well as behaviorally) unconscious (cf. Levitin et al. 2003; Levitin & Menon 2003). When young adults were prompted to describe activities associated with the songs of their past, one of the most common activities recalled was dancing (Janata et al. 2007).

The connection between music and movement shows up also in studies of visual perception of musical performances. Watching a musical performance, even with the sound turned off, conveys a great deal of structural and emotional information, further supporting evolutionary connections between music and movement (Chapados & Levitin 2008; Davidson 1993; Vines et al. 2005, 2006).

The connection between auditory and kinesthetic senses was explored in a series of studies with both infants and adults (Phillips-Silver & Trainor 2005, 2007, 2008). Participants either bounced themselves (adults) or had themselves bounced (infants) to an unaccented rhythm either in a duple (march) or triple (waltz) meter. The meter biased the perceptual representation and subsequent recall of the sequences. In effect, the movement itself created the (cross-modal) accented beat. This interactive process was found to be mediated by the vestibular system: Although full body movement is the most effective in engendering the movement—sound interaction, head movement alone is capable of producing it, while body movement alone is not (Phillips-Silver & Trainor 2008). Additional data implicate the dorsal premotor cortex (dPMC) in rhythmic synchronization. Participants tapped to rhythmic sequences of varying levels of metric difficulty; greater difficulty was correlated

with increased dPMC activation (Chen et al. 2008).

Emotion

Music represents a dynamic form of emotion (Dowling & Harwood 1986; Helmholtz 1863/1954; Langer 1951). The conveying of emotion is considered to be the essence if not the purpose of music (Meyer 1956; Nietzsche 1871/1993) and the reason that most people report spending large amounts of time listening to music (Juslin & Sloboda 2001). Somewhat paradoxically, the cognitive and structural aspects of music have been the most extensively studied, perhaps because methods of studying them have been part of the standard cognitive psychology paradigms for decades. Advances in affective neuroscience as well as new links between neurochemistry and cognition have only recently made it possible to study emotion in music rigorously (Blood & Zatorre 2001; Blood et al. 1999; Panksepp 2003).

Historically, studies in affective neuroscience have focused almost exclusively on the processing of negative emotions (LeDoux 2000). The few existing studies of positive emotions have tended to use drugs of addiction to induce positive emotions artificially (Berridge 2003), and only recently have more naturalistic and ecologically valid studies of positive emotion been conducted (Kringlebach et al. 2003; Small et al. 2001). Listening to classical music is known to evoke strong emotions, including feelings of pleasure (Krumhansl 1997; Sloboda & Juslin 2001). Further, this experience is often accompanied by physical responses (Panksepp 1995), such as thrills, chills, shivers, and changes in heart rate that can be blocked by nalaxone, a known opioid antagonist (Goldstein 1980). The experience of pleasant, or consonant, music activates orbitofrontal, subcallosal cingulate, and frontal polar cortical areas (Blood et al. 1999). Chills have been shown to correlate with activity in the left ventral striatum, an area "responsible for" approaching reward, the dorsomedial midbrain, and deactivation in the amygdala (Blood & Zatorre 2001). Opioid transmission in the NAc has been associated with dopamine release in the ventral tegmental area (VTA) (Kelley & Berridge 2002), and together they are involved in mediating the brain's responses to reward. During music listening the VTA mediates activity in the NAc, hypothalamus, insula, and orbitofrontal cortex; this network represents the neural and neurochemical (via dopaminergic pathways) underpinnings of the anecdotal reports of pleasurable music (Menon & Levitin 2005). In addition, the hippocampus has been found in positron emission tomography (PET) studies to activate during pleasant music, and the parahippocampul gyrus, also implicated in emotion processing, has been found to activate during dissonant music (Koelsch et al. 2006). This network of structures, which includes the amygdala and the temporal poles, is thought to be the neurological basis for the emotional processing of music (Koelsch et al. 2006).

Complementary to the study of the neurological underpinnings of chills in response to music is a recent study on the physiological and psychological aspects, as well as the characteristics of the music that engenders this emotionally driven response (Grewe et al. 2007). Psychologically, individuals who experience chills are not necessarily thrill-seekers; they tend toward greater sensitivity to sensory stimulation. Those who experience chills are more likely to depend on rewards from the environment, in a sense being more vulnerable to the response's occurrence; are highly familiar with classical music (a genre included as part of the stimuli in the experiment); identify strongly with their musical preferences; and often listen to music in isolation. Psychoacoustically, there was no specific pattern that emerged in most of the chill-inducing excerpt, but a small portion included peaks in loudness, sharpness, and fluctuation. The contextual aspects of what induced chills were the entry of a voice, loudness, the entrance of a specific theme, and the auditory experience of two contrasting voices. These are the unique

musical contexts considered by the researchers to represent increases in attention, bringing on an emotional experience, of which the physical reaction of a chill is a consequence (Grewe et al. 2007). The listener is thus considered to be an active participant in not only responding, but creating an emotional experience with music through attention, leading to a chill as an induced side effect.

Many listeners report using music for mood regulation and may find comfort in sad music (Chamorro-Premuzic & Furnham 2007). One might assume that sad people would be uplifted by happy music, but this is not always the case. Huron (2006) offers an explanation. Prolactin, a tranquilizing and consoling hormone, is produced by the anterior pituitary gland when we're sad (Panksepp 2006). The evolutionary purpose of sorrow is to aid in energy conservation and allow for reassessment of priorities for the future following a traumatic event. Prolactin is released after orgasm, after birth, and during lactation in females. A chemical analysis reveals that prolactin is not always present in tears—it is not released in tears of lubrication of the eye, or when the eye is irritated, or in tears of joy; it is only released in tears of sorrow. Huron speculates that sad music allows us to "trick" our brain into releasing prolactin in response to the safe or imaginary sorrow induced by the music, and the prolactin then reverses our mood. Aside from the neurochemical story, there is a more psychological or behavioral explanation for why we find sad music consoling. When people feel sad or suffer from clinical depression, they often sense being cut off from other people, feeling as though no one understands them. Happy music can be especially irritating because it makes them feel even less understood. Sad music is consoling because it connects the listener to others who seem to be experiencing a similar affective state.

As the field of music cognition advances, its investigators are acquiring deeper, empirically driven understanding of the complexity of emotion, manifested as a contextual process. For example, the amygdala shows increased activation when music is presented concurrently with an audio-visual stimulus providing context (Eldar et al. 2007). No such activation is found when positive or negative music is presented alone, suggesting that real-world context aids in building a more meaningful emotional representation, capable of differentially engaging the amygdala. Presumably, the adaptive quality of the amygdala (central to the mammalian fear and avoidance, fight-or-flight network) is increased by the corroboration of a potential danger from another sensory modality.

The neuroanatomical substrates of emotion regulation in music were studied in a group of postoperative epileptics (Khalfa et al. 2008) with temporal lobe resections (including the amygdala). Patients with right-hemisphere resection showed reduced recognition of sad music (and overidentification of happy music) while patients with left-hemisphere resections showed reduced recognition of both happy and sad music. These findings must be interpreted with caution because the experiment did not evaluate the preservation of lower level perceptual function in the patients following surgery; that is, pitch or contour deficits could conceivably underlie the participants' judgment of emotion in the music.

There exists a widespread belief in Western culture that major keys are intrinsically associated with positive affect while minor keys are related to negative affect. This turns out to be largely a product of exposure and learning and is thus culturally dependent. It has been shown that other musical systems (e.g., Middle Eastern, Indian) do not share these associations (Balkwill & Thompson 1999; Balkwill et al. 2004; Trehub 2003).

Consistent with findings on state-dependent memory (see Bower 1981), mood affects memory for music played in different modalities. It has been reported that when induced with a positive mood, Western listeners are more likely to recognize a melody played in a major key than a minor key (Houston & Haddock 2007), indicating that strong associations are made to

music that is congruent with (culturally defined) transient mood states.

Happy classical music (mentioned above in the context of strong feelings of pleasure and chills) has been associated with activity in the bilateral ventral and left dorsal striatum, left anterior cingulate, left parahippocampul gyrus, and auditory association areas in listeners unselected for musical background (Mitterschiffthaler et al. 2007). In contrast, the emotional state induced by sad music activates the hippocampus/amygdala and auditory association areas; emotionally neutral classical music is processed in the insula and auditory association areas.

Electrophysiological data confirm that musicians process the emotional content of music, as indexed by its mode, differently than do nonmusicians. Specifically, when perceiving melodies that are similar in length, tempo, and rhythm, but different in mode, musicians display a late positive component ERP (P3) to the onset of a note in minor mode melodies (Halpern et al. 2008). Interestingly, neither musicians nor nonmusicians showed a late positive component to music in the major mode. The authors argue that the absence of this effect in musicians is likely due to an enculturation effect of the preponderance of music in the major mode. As a consequence, the minor mode acts as an oddball stimulus, which requires additional information processing.

Music and Language

The last several years have seen an increased focus on studies of music and spoken language, due in part to advances in digital recording and signal processing technology, and to the increased recognition that music and language both represent complex, higher-order cognitive processes that invoke a large number of subsystems including attention, categorization, memory, and feature detection. Music and language share many attributes. Both are primarily auditory-based forms of communication. (Ex-

ceptions to auditory transmission include that both can be written down, felt through bone conduction or other tactile means, and that lip readers can understand speech without an auditory signal.) In both music and language the sensory input evolves over time in a coherent structure. Theories of structure in both domains are in fact theories of temporal coherence and how elements are grouped over time (Cooper & Meyer 1960; Cooper & Paccia-Cooper 1980; Krumhansl 1990, 1991; Lerdahl 2001; Lerdahl & Jackendoff 1983; Patel 2007; West et al. 1985; Zatorre et al. 2002). A second parallel concerns the specific order of constituents in revealing meaning. The sentences of all human languages (spoken and signed) are composed of words in a certain linear order (Akmajian et al. 1980). Although some languages display considerable freedom of word order, in no human language may the words of a sentence occur in a random order. This is also the case with music: Musical phrases are composed of notes and/or chords, but these are not randomly ordered and a reordering of elements produces a different melody (Lerdah 2001; Patel 2003).

Based on the existence of such commonalities, Patel (2003) introduced the "shared syntactic integration resource hypothesis" (SSIRH), which proposes that syntax in language and music share a common set of circuits instantiated in frontal brain regions. SSIRH is based as well on empirical findings implicating frontal regions in the processing of harmonic structure (Janata et al. 2002; Tillman et al. 2003) and, in particular, the processing of harmonic anomalies (Koelsch et al. 2002; Maess et al. 2001).

Evidence for the SSIRH comes from several studies that co-locate musical and linguistic operations. When musical structure is disrupted, areas of the brain implicated in linguistic syntax—Brodmann area (BA) 47 and the adjoining anterior insula—play a role in the perception of that disruption (Levitin & Menon 2003, 2005). Violations of musical expectations also invoke BA 47 (Koelsch et al. 2000) and Broca's area (Koelsch et al. 2002).

An additional link between language and music comes from an experiment with children with specific language impairment (SLI) (Jentschke et al. 2008). Four- and 5-year olds with SLI presented a particular ERP pattern when they listened to the final chord in a sequence that violated harmonically lawful musical syntax. This response pattern deviates from that of children and adults who develop language typically, in that the SLI response elicited did not include an early right anterior negativity (ERAN) or the N5. Jentschke and colleagues (2008) further suggest that musical training may be a means of early intervention for children at risk for developing SLI.

Music theorists and philosophers at least from the time of Nietzsche have struggled with the question of whether music has meaning apart from the formal, syntactic structures that constitute the rules of a musical system or style. To invoke parallels with distinctions made by linguists for the analysis of natural languages (e.g., Fromkin & Rodman 1993), it has been suggested that all musical semantics are inseparable from considerations of musical pragmatics (Ashley 2007). In language, *pragmatics* refers to the level of analysis concerned with how people actually use sentences and the intentions of the speaker apart from the actual words used (irony and sarcasm fall in this domain). Ashley argues that in effect musical semantics or meaning derives from musical pragmatics or intentions. Nevertheless, a recent study found neural evidence for two distinct processes, one syntactic and the other semantic (which Ashley would interpret as semantic−pragmatic).

The N5 electrophysiological response is associated with failures of a musical sequence to meet harmonic expectations (Koelsch et al. 2000). Steinbeis and Koelsch (2008) reasoned that if the N5 were in fact elicited by processes governing meaning, a simultaneously presented linguistic−semantic anomaly ought to reduce the N5 but not the ERAN. This was in fact what they found (see also Koelsch et al. 2007). This result indicates that the structure of music itself can be one path to the construction of

meaning in music and reinforces the idea that language and music are based on shared neural underpinnings.

Most spoken languages employ pitch variation (as a component of linguistic prosody) to convey meaning and to disambiguate utterances. In tonal languages (such as Thai, Mandarin, and Cantonese) pitch variation within a word can completely alter the meaning of the word (e.g., different pitch trajectories for the word /ma/ in Cantonese can give the word the meanings "mother" or "gun powder"). The extent to which bona fide musical operations are involved in processing tonal languages are a topic of current interest. Western, nontonal language speakers were played excerpts from tonal languages. The processing of pitch information in those tonal language utterances was found to be more accurately coded by musicians than nonmusicians, as measured by pitch encoding at the subcortical level of the inferior colliculus (Wong et al. 2007), perhaps associated with musicians increased usage or attention to the pitch attributes of an auditory signal. This is the first study to demonstrate superior subcortical pitch processing in musicians (although the direction of causality is unknown—do people with superior subcortical pitch processing become musicians? or does musical experience exert this effect?). A conceptually related study examined the ability of French musicians versus nonmusicians to detect prosodic variation in a structurally similar and related language, Portuguese (Marques et al. 2007). Although musicians and nonmusicians were equally capable of detecting strong prosodic incongruities in foreign sentences, musicians were significantly better at identifying the more subtle incongruities.

A number of studies have examined music and language by studying children during language acquisition. There is evidence that low-level auditory processing at the level of the brain stem is related to literacy skills in children; those individuals who respond to speech sounds in an early or intermediate fashion display higher achievement in reading than those individuals who are delayed in their responses

(Abrams et al. 2006; Banai et al. 2005; Kraus & Banai 2007). Although it stands to reason that auditory processing in the linguistic domain would be related to literacy, there are also recent findings that link musical discrimination abilities to reading ability. In a series of studies with school-aged children, Forgeard et al. (2008) found that the ability to discriminate melodies is predictive of phonological skills, particularly phonemic awareness (sensitivity to the sounds of language), which is a prerequisite for reading ability. Moreover, they find that children with specific reading disability (dyslexia) are impaired in both melodic and rhythmic tasks, indicating impairment that extends beyond melodic discrimination to a more pervasive deficit in music processing.

Second language pronunciation ability in children was positively associated with musical aptitude test. In addition, greater ERP activation to mistuned variants of musical chords was observed in those with better pronunciation skills (Milovanov et al. 2008). Although common neural underpinnings between music and language constitute a likely explanation of the congruence between linguistic and musical skills in the domains of language and music, other factors possibly accounting for the relationship noted by Milovanov and colleagues (2008) are executive functions (such as attention), as well as the maturity level of the temporal lobes, sensitivity to the musicality of language, and basic sound processing.

Amusia

The term *amusia* is generally applied to individuals with a supposed deficit in one or more aspects of music processing. The lay term *tone deafness* is seen as an equivalent. Scientists now make a distinction between acquired amusias (typically following brain injury) and congenital amusia. The term *musicality* has been described in several ways, from a universal human attribute to the ability to attain high levels of musical expertise, or even simply the ability to enjoy music (Shuter-Dyson 1999). There is considerable debate among scientists, musicians, and the population at large as to whether musicality is based on talent, experience, or some combination of both (Howe et al. 1998). A complicating factor is that "musicality" can manifest itself in diverse—and sometimes nonoverlapping forms: One can be expert in compositions, performances, improvisations, listening, editing, etc. Within a given subdomain, expertise can exist primarily for rhythm, pitch, or timbre. Despite these diverse definitions, certain individuals describe themselves as "musical," while others do not.

As we described above, musical processes can be parsed into different components which are subserved by different areas of the brain. This leads to the prediction that brain damage should selectively impair only affected components. Dozens of case studies have borne this out (e.g., Ayotte et al. 2000; Di Pietro et al. 2004; Peretz et al. 2004; Piccirilli et al. 2000).

Sensitivity to pitch and time in music are considered fundamental to musical adeptness. Traditionally, tone deafness was conceived as a selective impairment in fine-grained pitch perception held by an estimated 4% of the population (Cox 1947; Joyner 1968). One definition states that individuals who are tone deaf are not able to discriminate pitches less than one semitone apart, but do not show associated deficits in time perception (Hyde & Peretz 2004). A more nuanced definition of amusia/tone deafness was proposed to include selective impairments in perception (of rhythm or melody, and perhaps not both), in production, and in song identification, arising from several distinct etiologies (Levitin 1999). A dissociation between the perception and production supports this (Loui et al. 2008). Also consistent with the expanded definition is recent evidence that amusia is not isolated to difficulties in pitch perception alone. Compared to a control group, individuals with amusia perform significantly worse on a mental rotation task, when controlling for sex differences in spatial processing (Douglas & Bilkey 2007). Similarly, enhanced

spatial capacities were found in orchestral musicians (Sluming et al. 2007). The mechanism driving improved spatial ability is argued to be related to experience in the sight reading of music (musical notation requires greater spatial acuity than text reading).

The Montreal Battery of Evaluation of Amusia (Peretz et al. 2003) is a test designed to screen for acquired amusia (resulting from brain injury) or congenital amusia (tone deafness). The tasks in the battery include tests of pitch, time and memory such as scale discrimination, contour, rhythm, and meter. Recently, Peretz et al. (2008) created an online version of the MBEA, which takes only 15–30 minutes to complete, composed of less than half the trials as the original MBEA. The test is seen as a reasonably precise and efficient diagnostic tool for congenital amusia, and the authors claim only a 7% error rate in detection. Particular subtests of the online version have been used to screen for individuals with potential amusia before bringing these individuals into the laboratory for a full diagnostic with the original MBEA, as in McDonald and Stewart (2008).

Neurologically, there do appear to be differences in the amusic brain, relative to controls. Individuals with congenital amusia have thicker cortex in the right inferior frontal gyrus (IFG) and the right auditory cortex (Hyde et al. 2007). This morphological difference at the cortical level is attributed to atypical cortical development, affecting the right frontotemporal tract known to play a role in the processing of musical pitch.

Evidence is mixed as to whether individuals with amusia have deficits that extend beyond the musical into the linguistic domain. For example, Ayotte et al. (2002) found that individuals with congenital amusia suffer from domain-specific musical impairment, consistent with the view of modularity in music processing (Peretz & Coltheart 2003), as their participants were unimpaired in a variety of linguistic tasks, including the processing of prosody in human speech. However, a study of French Canadian amusics by Lochy and colleagues (cited in

Patel et al. 2008) finds impairment in differentiation of statements and questions among amusic participants. A follow-up study to clarify these inconsistencies by the 2008 study of Patel et al. confirmed that approximately 30% of individuals in a British and French-Canadian sample had difficulty in sentence—statement differentiation. A possible confound in this study is that the stimuli presented to the British listeners were recorded in American English while the stimuli for the French-Canadian listeners were recorded in continental French, neither stimulus representing ecologically valid stimuli for the participants.

Individuals with congenital amusia also report fundamentally different experiences with music in their daily lives. In particular, controls listened to approximately 3 times as much music per week than individuals with amusia, less than half of an amusic sample claims to like or love music or use music in the context of setting the mood in a romantic encounter (McDonald & Stewart 2008). The most common psychological state induced by music in the amusics was nostalgia; however the majority attributed the nostalgia to cultural or lyrical associations to the music, rather than the music itself. Some individuals with amusia report an extremely negative form of arousal, described as aural irritation.

Expertise

Research in the domain of expertise comprises studies of how musical experience affects practice and performance, as well as evidence for skill transfer from music to other cognitive domains. Several studies attempt to shed light on the similarities and differences between the cognitive and auditory—perceptual processing capabilities of trained musicians versus nonmusicians.

Historically, it was believed that auditory perception was largely the result of automatic, bottom-up processes. It is now believed that auditory object formation and music perception

are the consequence of dynamic, interrelated processes involving cortical and subcortical regions, reflecting both bottom-up and top-down influences (Kraus & Banai 2007). In particular, the auditory system has shown itself to be plastic: What we think of as "auditory" cortex can become remapped for visual input in the congenitally deaf (Neville et al. 1998; Petitto et al. 2000). Musicians' better sensitivity to foreign tonal languages (as mentioned above, Wong et al. 2007) bolsters the argument that experience can exert an influence on low-level processing, even as far downstream as the inferior colliculus and brainstem.

Automaticity does not necessarily have to entail purely bottom-up processing, however. A recent ERP study (Brattico et al. 2006) found evidence that pitch processing—specifically recognition of "in-tuneness" and "in-keyness"—are automatic, preattentive processes reflecting overlearning of culturally dependent knowledge. In other words, attention is not required for recognizing violations of certain tonal expectations, as indexed by an early frontal negativity in the ERP signal. Automatic processing of pitch relations in the diatonic scale may mean that neural networks have acculturated themselves to that scale.

Another example of automatic processing in music is found in expert improvising musicians. Jazz musicians creating spontaneous musical performances, or improvisations, were studied using fMRI (Limb & Braun 2008). One might naïvely assume that improvisation requires focal activation in that region of the brain that is uniquely developed in humans—the prefrontal cortex (Gazzaniga 2008). In fact, strong patterns of deactivation were observed there, suggesting that conscious thought and volition needed to be suppressed. Activation was observed in neocortical sensory−motor areas that mediate organization and execution of musical performance. This pattern of activation conforms to subjective reports by musicians that improvisation relies on sub- or preconscious processes that are outside the domain of conscious control and awareness. The lack of con-

scious control represents overlearned and automatic processes characteristic of professional improvisers.

The most striking and obvious example of top-down influences on auditory perception comes from the phoneme acquisition trajectory in human babies. Born with the ability to discriminate all possible speech sounds, they eventually retain only those distinctions that are necessary for the language to which they are exposed during a certain critical or sensitive period (Kuhl 2004). Additional supporting evidence for the role of top-down influence in auditory perception comes from the finding that musicians' brains show greater sensitivity to the sounds of their own instruments versus others (Pantev et al. 2001). An electrophysiological study determined that when musicians (violinists in particular) listen to sounds of their own instrument, gamma band activity specific to the timbre, or sound quality, of that instrument is elicited (Shahin et al. 2008). The response also occurs for piano timbre in children after only one year of piano lessons.

Musical practice also enhances phase-locking in the brain stem to the fundamental frequencies of both musical and linguistic stimuli (Musacchia et al. 2007). When participants were presented with both audio and audiovisual stimuli in the domains of music and speech, musicians had an earlier onset and larger amplitude evoked brainstem response than nonmusicians. Because this response is a function of the amount of training as opposed to musical aptitude or basic pitch discrimination tasks, this finding gives empirical support for the saying, "practice makes perfect." A number of studies show regional changes in brain volume and in gray-to-white matter density as a function of musical practice (see Münte et al. 2002 for a review).

Musicians show additional activation in motor areas compared to nonmusicians during rhythm perception (Grahn & Brett 2007). Rhythm production in musicians produces greater activation in the dorsolateral right prefrontal cortex (dLPFC) as well as right inferior

frontal gyrus, regions shown to subserve working memory for music (Chen et al. 2008). This difference is thought to represent a more advantageous cognitive strategy for reproducing rhythm, which relies on top-down as opposed to bottom-up processing.

A compelling recent finding in the area of transfer effects is the relatively high performance on a three-dimensional mental rotation task by orchestral musicians, compared to others who were highly practiced at that task (Sluming et al. 2007). Behaviorally, the musicians attempted more trials, achieved more correct answers (at par with individuals who have had extensive practice), and displayed a response time profile uncharacteristic of the typical profile for the task. Neurofunctionally, the orchestral musicians displayed greater activation in Broca's area (BA 44/45) compared to the control group during task performance, an area known to subserve music sight reading.

Summary

The study of music cognition, and more recently of music and the brain, has a rich and old intellectual history. We now know that musical operations involve disparate regions of the brain, including all lobes of the brain, and both cortical and subcortical structures. In particular, the roles of the cerebellum and amygdala are becoming increasingly appreciated. The components of music, including pitch, rhythm, contour, and timbre, are subserved by distinct and separable neural processing units. Music processing shares some circuitry with spoken language processing yet also involves distinct neural circuits. The study of the neuroanatomical underpinnings of musical emotion is an area of particularly recent focus, as are the putative evolutionary origins of the music faculty.

Conflicts of Interest

The authors declare no conflicts of interest.

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Whilst music therapy is benefiting from neuroscience collaborations, neuroscience is becoming more enriched by learning about the neural effects of â€œreal worldâ€ clinical applications in music therapy. Not only do neuroscientific imaging methods provide biomarking evidence for the efficacy of music therapy interventions, they also offer important tools to describe time-locked interactive therapy processes, feeding into the emerging field of social neuroscience. Music therapy is bound to the process of creating and experiencing music together in improvisation, listening and reflection.Â Current advances in the cognitive neuroscience of music. Ann. N. Y. Acad.