BRAIN ORGANIZATION FOR MUSIC PROCESSING

Isabelle Peretz

Department of Psychology, University of Montreal, Montreal,
Quebec H3C 3J7; email: Isabelle.Peretz@Umontreal.ca

Robert J. Zatorre

Montreal Neurological Institute, McGill University, Montreal,
Quebec H3A 2B4; email: Robert.Zatorre@McGill.ca

Key Words auditory cognitive neuroscience, neural correlates, musical disorders, neuroimaging

■ **Abstract** Research on how the brain processes music is emerging as a rich and stimulating area of investigation of perception, memory, emotion, and performance. Results emanating from both lesion studies and neuroimaging techniques are reviewed and integrated for each of these musical functions. We focus our attention on the common core of musical abilities shared by musicians and nonmusicians alike. Hence, the effect of musical training on brain plasticity is examined in a separate section, after a review of the available data regarding music playing and reading skills that are typically cultivated by musicians. Finally, we address a currently debated issue regarding the putative existence of music-specific neural networks. Unfortunately, due to scarcity of research on the macrostructure of music organization and on cultural differences, the musical material under focus is at the level of the musical phrase, as typically used in Western popular music.

CONTENTS

INTRODUCTION

Music processing has fascinated neuroscientists for more than a century (Critchley & Henson 1977). Yet it is only over the last decade that music processing has become an area of intense and systematic study, as illustrated by three special issues recently published on the cognitive neuroscience of music (*Annals of the New York Academy of Sciences* issues 930 in 2001 and 999 in 2003, and *Nature Neuroscience* issue 6, 2003). Two forces have driven this scientific effort. First, music offers a unique opportunity to better understand the organization of the human brain. For example, only a minority of individuals become proficient musicians through explicit tutoring. This particularity in the distribution of acquired skills confers to music a privileged role in the exploration of the nature and extent of brain plasticity. The other major motivation is that the study of brain organization provides a unique tool to reveal the inner working of music processing. For instance, brain anomalies may reveal to what extent and at what level music processing recruits neural networks that are distinct from those involved in other auditory-vocal functions, such as language. Although these two major approaches for exploring the brain principles that underlie music processing may not always converge, it is hoped that the combined effort gives rise to a better understanding of the neurobiological roots of one of the most characteristic traits of humans, namely music.

MUSIC PERCEPTION AND RECOGNITION

A sound reaching the eardrum sets into motion a complex cascade of mechanical, chemical, and neural events in the cochlea, brain stem, midbrain nuclei, and cortex that eventually—but rapidly—results in a percept. The task of auditory cognitive neuroscience is to figure out how this happens. Musical sounds and all other sounds share most of the processing stages throughout the auditory neuraxis. However, as we discuss below, evidence points to a degree of functional segregation in the processing of music, which may in part be related to the important role played by pitch processing within music. In a broader context, the functional system that handles music processing must solve a similar computational problem to that faced by any perceptual system: It must generate internal representations of any given input, permitting the stimulus to be segregated from its background, analyzed along several dimensions, recognized, and possibly acted upon. Importantly, the nature of the representations eventually generated by this system need to be relatively abstract, in the sense that they must be insensitive to superficial variations in stimulus features (loudness, reverberation, spectral filtering, etc.). In other words, perceptual constancy must be maintained. Indeed, music is an excellent medium to study this process, as the Gestaltists realized long ago, because music relies on relations between elements, rather than on absolute values of elements (the most obvious example being a tune, which is defined not by the pitches of its constituent tones, but by the arrangement of the intervals between the pitches).

Pitch and Time Relations

Musical pitch-based (melodic) and time-based (temporal) relations traditionally are treated separately, both empirically and theoretically (Justus & Bharucha 2002, Krumhansl 2000). Their processing independence has been questioned, however. For example, Jones & Boltz (1989) have argued that perception, attention, and memory for pitch relations are inherently rhythmical. By this view, listeners treat melody and rhythm as a unified dimension. Nevertheless, the neuropsychological literature is more consistent with the traditional view, by which melodic and temporal structures are processed independently. Brain damage can interfere with the discrimination of pitch relations while sparing the accurate interpretation of time relations (Ayotte et al. 2000, Liégeois-Chauvel et al. 1998, Peretz 1990, Peretz & Kolinsky 1993, Piccirilli et al. 2000, Vignolo 2003). Conversely, rhythmic discrimination of musical events can be impaired while extraction of pitch content is spared (Di Pietro et al. 2004, Peretz 1990). This double dissociation between melodic and temporal processing has also been observed in singing and sight-reading (see below). Hence, the evidence suggests that these two dimensions involve the operation of separable neural subsystems. To our knowledge, neuroimaging techniques have not yet corroborated this dissociation. On the contrary, Griffiths et al. (1999) obtained similar activation patterns for pitch and time discrimination tasks. However, similarity of activation does not entail that the underlying operations are similar, or that the recruited brain areas are critical to performing a given task. This general point always must be taken into account in integrating lesion and neuroimaging findings.

Pitch Relations

The right temporal neocortex plays a particularly important role in the computation of pitch relations. The initial evidence came from studies of patients with focal brain excisions (Milner 1962), which showed that (a) right temporal damage entailed a greater deficit than left, and (b) such impairment could not be explained by a deficit in simple pitch discrimination. Subsequent studies have generally supported these findings (Liégeois-Chauvel et al. 1998, Zatorre 1985). In addition, however, deficits in certain aspects of pitch processing have been noted specifically after damage to the right anterolateral part of Heschl's gyrus. Patients with such damage have difficulty perceiving the pitch of the missing fundamental (Zatorre 1988) and have an increased threshold for determining the direction of pitch change (Johnsrude et al. 2000). Thus, this area of right auditory cortex seems to play a particular role in the analysis of pitch information (Tramo et al. 2002).

Converging evidence is now beginning to accumulate from neuroimaging studies to support the view that analysis of pitch changes may involve areas of posterior secondary cortex. Several investigators have found activation in this location when comparing complex tones containing frequency or amplitude modulation, or spectral changes, to static tones (Hall et al. 2002, Hart et al. 2003, Thivard et al. 2000). In many cases, manipulations of fine-grained pitch lead to greater response from right

auditory regions (Zatorre & Belin 2001, Zatorre et al. 2002). Using isochronous melodies made with iterated noise bursts, Patterson et al. (2002) observed similar results, but activity increases in anterior areas were also found (Griffiths et al. 1998). Warren et al. (2003) additionally report that posterior regions are involved in processing pitch height whereas anterior regions are important for pitch chroma. In summary, the data are quite consistent in implicating the right secondary auditory cortex region in operations related to processing relationships between pitch elements as they change over time, especially if the pitch changes are small.

One plausible interpretation of these findings is that they represent an early stage of melodic analysis, beyond simple pitch extraction, where interval and/or contour information is processed. This interpretation is consistent with data from electroencephalography and magnetoencephalography (MEG) recordings indicating that the auditory cortex responds to such pitch relations even in the absence of attention (Tervaniemi 2003). The contribution of contour (defined by pitch directions) and intervals (defined by frequency ratios between successive notes) to melodic perception and recognition also can be distinguished in brain-damaged patients (Peretz 2001). Taken together, the results converge to show that when listeners rely on contour representation to discriminate melodies, the right superior temporal gyrus plays a critical role. When contour cues are not available and interval information is required, both the right and left temporal structures appear to be involved (Ayotte et al. 2000, Liégeois-Chauvel et al. 1998, Peretz 1990, Vignolo 2003). This cooperation of the hemispheres in the integration of contour with interval information in melodies is echoed by the pattern of coherence observed dynamically with MEG while neurologically intact people listen to melody-like sequences (Patel & Balaban 2000). Such integration may occur very early in development. Balaban et al. (1998) have shown that the same left-right brain asymmetry in the processing of interval and contour cues in melodies is already present in infancy. In the adult, extraction of both contour and intervals does not require attention either, as electrical brain responses suggest (Tervaniemi 2003, Trainor et al. 2002).

Pitch relations do not define only direction and interval sizes in tonal music; they also evoke a particular scale. A musical scale refers to the use of a small subset of pitches (typically between five and seven) in a given piece. The scale tones are not equivalent and are organized around a central tone, called the tonic. A hierarchy of importance or stability exists among the other scale tones, with the fifth and the third scale tones more closely related to the tonic than to the other scale tones. Substantial empirical evidence demonstrates that listeners use scale structure in melodies for perception and memory, albeit in an implicit manner (Tillmann et al. 2000).

Despite the central importance of this tonal knowledge to the encoding of pitch relations in a melodic context, it has been little explored with neuropsychological methods. Yet, this processing component appears isolable both functionally and neuroanatomically. Brain damage can disrupt the normal intervention of tonal knowledge in melodic processing (Françès et al. 1973), while sparing perception

of intervals and contour (Peretz 1993). In such cases, the patient is no longer able to distinguish tonal from atonal music nor to judge melodic closure properly and suffers from a severe reduction in pitch memory. The use of scale structure in melody processing can also be indexed by electrical brain responses such as event-related potentials time-locked to tones that deviate from the expected scale degree (Besson & Faïta 1995, Besson et al. 1998) and, more surprisingly, by model-fitting of the haemodynamic responses obtained with functional magnetic resonance imaging (fMRI; Janata et al. 2002). Hence, the evidence points to the existence of neural networks that are specialized for the processing of scale structure in melodies. Their localization, however, remains to be determined.

Up to this point, we have considered pitch relations between sequentially presented tones, but pitch relations also exist in simultaneously presented tones, as in chords. The pitch relations in chord sequences are governed by harmonic principles that are similar to those described earlier for the tonal hierarchy of scale tones. That is, different chords are differently related to one another, with one chord acting as the reference: the triadic chord that builds on the first degree of the scale (the tonic). Listeners have assimilated these principles via passive exposure to samples of Western music (Bigand 2003). These harmonic principles influence chord processing automatically even when more veridical information about the chord progression has been made explicitly available (Justus & Bharucha 2001). Hence, perception of pitch relations in chords seems to operate like the perception of the tonal hierarchy among successive tones, although the acquisition of harmonic hierarchy appears to emerge later in development (Trainor & Trehub 1992). By the age of five, the degree of harmonic appropriateness of chord progression appears assimilated, as electric brain responses indicate (Koelsch et al. 2003).

Processing of harmonic relations rarely has been studied in brain-damaged populations. The only study, to our knowledge, in which chord processing has been examined showed sparing of the ability to generate expectancies from chord processing after bilateral lesion of the auditory cortex (Tramo et al. 1990). However, the patient suffered from a deficit in pitch processing, with a bias to judge well-tuned chords as out of tune (Tramo et al. 2003). In contrast, detection of harmonic violations has been studied with diverse neuroimaging techniques. Deviations from harmonic expectancies elicit robust event-related potentials (Regnault et al. 2001). Their neural generators appear to be located in the inferior frontal areas (the frontal operculum) on both sides of the brain (which corresponds to Broca's area on the left side; Maess et al. 2001). Involvement of the same areas has also been found in two recent fMRI studies of harmonic expectancies (Koelsch et al. 2002, Tillmann et al. 2003). Thus, the data point to bilateral involvement of the inferior frontal regions in detecting deviations from harmonic expectancies.

Finally, it should be pointed out that both harmonic relations between chords and tonal relations between tones might be rooted in pitch consonance (or dissonance). Consonant intervals typically are expressed in terms of simple frequency ratios, such as the octave (2:1) and the perfect fifth (3:2), whereas dissonant intervals are related by complex ratios, such as the minor second (16:15). Despite the

saliency of dissonance and its initial account in terms of the poor spatial resolution of the basilar membrane (Plomp & Levelt 1965), its functional origins and neural consequences are still open questions (Tramo et al. 2003). Current evidence suggests that dissonance might be further computed bilaterally in the superior temporal gyri by specialized mechanisms. Assemblies of auditory neuron populations in Heschl's gyrus exhibit phase-locked activity for dissonant chords but not for consonant chords, as measured with implanted electrodes in both humans and monkeys (Fishman et al. 2001). Such cortical responses to dissonance can be disrupted by bilateral lesion of the auditory cortex, resulting in a loss of sensitivity to dissonance (Peretz et al. 2001). A remaining question for the future is to determine at what stage in auditory processing (e.g., at the level of acoustical analysis and/or of tonal encoding of pitch) the computation of the perceptual attribute of dissonance is critical to the perceptual organization of music. This question often is framed in terms of a distinction between sensory and musical dissonance that would reflect built-in auditory constrains and learned associations, respectively (Krumhansl 2000, Schellenberg & Trehub 1994).

Time Relations

Two types of time relations are fundamental to the temporal organization, or "rhythm," of musical sequences: the segmentation of an ongoing sequence into temporal groups of events based on their durational values, and the extraction of an underlying temporal regularity or beat (Fraisse 1982). Beat perception leads to the perception of a metrical organization corresponding to periodic alternation between strong and weak beats (the strong beats generally correspond to the spontaneous tapping of the foot). Grouping and regularity are conceived as hierarchically organized by certain researchers (Povel & Essens 1985), while others (Drake 1998, Lerdahl & Jackendoff 1983) conceive these relations as the result of distinct processing components. The available neuropsychological evidence supports the latter view, in showing functional dissociations between grouping and regularity.

Ibbotson & Morton (1981) provided initial support by showing that subjects more easily tapped a rhythmic pattern with their right hand and the beat with their left hand than the other way around. These findings suggest that the right hemisphere better handles meter, whereas grouping would rely essentially on the left. Further support for the separation of the two types of organization mediating temporal pattern processing has been provided by the study of two brain-damaged patients who, after lesions of the right temporal auditory cortex, could no longer tap the beat or generate a steady pulse (Fries & Swihart 1990, Wilson et al. 2002). In contrast, both patients were able to discriminate or reproduce irregular temporal sequences. Neuroimaging data also suggest that metrical rhythms may be processed differently than nonmetrical rhythms, engaging different frontal and cerebellar mechanisms (Sakai et al. 1999). All of these studies have used tapping tasks. In studies that assessed more perceptual aspects of temporal processing, convergent

evidence for dissociating meter from grouping was also found (Liégeois-Chauvel et al. 1998, Peretz 1990). Patients who have sustained an excision in either their left or right temporal lobe have been found to discriminate rhythmic patterns normally, but fail on meter evaluation after a right-sided lesion of the anterior part of the superior temporal gyrus (Liégeois-Chauvel et al. 1998). Conversely, impairments in rhythmic discrimination that spare meter evaluation can also be observed in brain-damaged patients after a left-sided lesion (Di Pietro et al. 2004). Hence, the data are generally consistent with the manual asymmetries observed in normal tapping (Ibbotson & Morton 1981) in pointing to the left hemisphere for temporal grouping (Di Pietro et al. 2004, Vignolo 2003) and to the right temporal auditory cortex for meter (Liégeois-Chauvel et al. 1998, Penhune et al. 1999, Wilson et al. 2002). The fact that essentially all the results coming from production tasks have parallels in perceptual tasks suggests a strong motor component to the mental representation of musical rhythm.

Indeed, data from both lesion and neuroimaging studies have shown the participation of the cerebellum and/or basal ganglia as a possible central mechanism controlling motor and perceptual timing (Janata & Grafton 2003). Patients with cerebellar damage have increased variability in motor timing, as well as decrements in discrimination of auditory intervals (Ivry & Keele 1989). Further, patients with damage to the lateral cerebellar hemispheres showed increased variability in the timing component of the tapping task, in contrast to patients with damage to medial cerebellar regions who showed increased variability on the motor implementation component of the task (Ivry et al. 1988). The contribution of the lateral cerebellar hemispheres to timing has been corroborated by recent neuroimaging studies examining reproduction of rhythmic sequences (Penhune & Doyon 2002, Penhune et al. 1998) and perceptual monitoring of auditory and visual rhythmic sequences (Schubotz et al. 2000). These studies converge on the conclusion that a supramodal cerebellar timing system is involved in processing temporally organized events. Other fMRI studies have produced evidence for the possible involvement of the basal ganglia in both motor and perceptual timing (Harrington et al. 1998; Rao et al. 1997, 2001). Finally, several studies have pointed to the involvement of motor cortical areas in rhythm perception and production, including the supplementary motor area, premotor cortex, and parietal cortex (Halsband et al. 1993).

Memory

Adding to the complexity—and interest—of studying the neural correlates of musical processing is the fact that music, like all sounds, unfolds over time. Thus, the auditory cognitive system must depend to a large degree on mechanisms that allow a stimulus to be maintained on-line to be able to relate one element in a sequence to another that occurs later. These working memory mechanisms apply broadly to many types of processes. As applied to pitch processing, cognitive studies of working memory suggest that there may be dissociable systems for maintenance of pitch information over short periods as compared to speech information (Deutsch 1970, Semal et al. 1996). Similarly, lesion studies focusing on working memory

for pitch materials have implicated the right auditory cortex (Zatorre & Samson 1991), which is not surprising because a disruption in perceptual processing would likely lead to difficulty in maintaining a perceptual trace over a length of time. In addition to the participation of auditory cortex to working memory, both lesion and neuroimaging studies have found a role for frontal cortical areas (Gaab et al. 2003, Holcomb et al. 1998, Zatorre et al. 1994). In particular, dorsolateral and inferior frontal areas are most often recruited when working memory load is high (Griffiths et al. 1999, Zatorre et al. 1994). These studies largely converge on the idea that working memory for tones engages interactions between frontal cortical and posterior temporal areas, as is true for other domains. In general, auditory cortical regions are more strongly recruited during high-load conditions that require active rehearsal (Gaab et al. 2003, Zatorre et al. 1994), such as retaining a pitch in memory while other tones are presented, and may also be related to auditory-motor interactions (Hickok et al. 2003). These findings fit within a broader context in which working memory for pitch may be seen as a specialized subsystem within the framework of general working memory (Marin & Perry 1999).

The contribution of memory to music processing is crucial not only because music unfolds over long periods of time but also because music is highly structured along multiple principles that require the contribution of different sources of knowledge. In the present review, however, we limit our attention to the memory component that enables recognition and mental representation (imagery) of a familiar tune.

To enable recognition of a given tune, melodic and time relations must be mapped onto a stored long-term representation that contains invariant properties of the musical selection. As for words in language, the process of music recognition requires access and selection of potential candidates in a perceptual memory system (Dalla Bella et al. 2003). This musical memory is a perceptual representation system that is conceived as representing information about the form and structure of events, and not the meaning or other associative properties. Music is by essence perceptually driven. Unlike speech, music is not associated with a fixed semantic system, although it may convey meaning through other systems, such as emotional analysis (reviewed below) and associative memories (to retrieve contextual information, such as the title of a piece, the name of the singer, or its genre). Associative memories are probably the locus of the semantic priming effects recently observed between music and words with event-related brain potentials (Koelsch et al. 2004).

Perceptual memories of familiar tunes must be relatively abstract in order to allow recognition despite transposition to a different register (Dowling & Fujitani 1971), change in instrumentation (Radvansky et al. 1995), and change in tempo (Warren et al. 1991). The stored representations can nonetheless preserve some surface features, such as absolute pitch and precise tempo (Halpern 1988, 1989; Levitin 1994; Levitin & Cook 1996). This duality between abstract and surface representations is congruent with our intuitions as to the role of memory in music listening. On the one hand, most listeners will not remember every detail of a musical segment but instead will follow the piece by a process of abstraction

and organization, remembering its "gist" (Dowling & Harwood 1986, Large et al. 1995). On the other hand, appreciation of interpretation requires the consideration of surface characteristics that are unique to a particular rendition (Raffman 1993). Thus, both surface and structural features may be contained in the stored representations and fit with the role and definition of the perceptual representation systems that are posited in other perceptual domains.

Neuropsychological support for a perceptually based memory system for music derives mainly from lesion studies. In effect, persistent loss of recognition abilities for music can occur despite normal or near-normal perceptual processing of musical input (Eustache et al. 1990, Peretz 1996). Above all, such memory loss can be limited to music. For instance, an amusic patient with bilateral damage to the auditory cortex was normal at recognizing and memorizing spoken lyrics, whereas she performed at chance when required to recognize or to relearn the corresponding melody (played without lyrics). The deficit was selective because the patient had no difficulties with other nonmusical auditory materials, such as voices and animal cries, and had no memory impairment for visual stimuli (Peretz 1996). Hence, the memory failures were not only modality-specific but also music-specific. A milder dissociation between melodies and speech sounds has also been reported in patients with focal lesions of the medial temporal lobe (Samson & Zatorre 1992). A lesion to either medial temporal region led to initial difficulties in learning the melodies; after right-sided lesions, retention of melodies was affected more severely and selectively over time.

The right temporal structures appear less critically involved when recognition of highly familiar tunes is considered. Difficulties in recognizing familiar melodies tend to occur after a surgery to either superior temporal region (Ayotte et al. 2000). Moreover, the participation of left inferior temporal and frontal areas for recognizing familiar music has been pointed out in neuroimaging studies (Platel et al. 1997, 2003). These findings do not imply that familiar tunes are processed differently from novel melodies. Familiar melodies are associated to a series of extramusical and extraexperimental events that may contribute to recognition. For instance, song melodies (played without lyrics) automatically trigger the lyrics with which they are typically paired (Peretz et al. 2004b). The presence of these associate memories may even confer an advantage in the case of lesion. As uncovered by Steinke et al. (2001), brain damage can impair recognition of instrumental music but spare recognition of song melodies. The principles along which the stored representations of music can be impaired, when partially damaged, are potentially instructive with respect to the structure of their internal organization. Such degradation remains, however, to be observed and systematically studied.

One way to probe the nature of the representations that are stored in memory is to study musical imagery. Imagery refers here to the subjective experience of being able to imagine music or musical attributes in the absence of real sound input. By applying behavioral methods developed by Halpern (1988) to patients with focal auditory cortex lesions, it was possible to demonstrate that perceptual deficits and imagery deficits are found in common, following damage to right auditory

cortical areas (Zatorre & Halpern 1993), suggesting that imagery requires access to perceptual mechanisms that are involved in processing melodies. This general conclusion has been supported in subsequent work using functional neuroimaging, which consistently indicates that secondary auditory cortices are recruited during a variety of tasks that require imagery or rehearsal of melodies (Halpern & Zatorre 1999, Zatorre et al. 1996), including sequences of tones (Penhune et al. 1998, Rao et al. 1997, Yoo et al. 2001) and isolated tones (Halpern et al. 2004). Further evidence comes from electrophysiological measures showing that the scalp topography elicited by imagining the continuation of a melody is similar to the electrical activity elicited by a real tone (Janata 2001). These demonstrations of auditory cortex activity in the absence of an acoustical stimulus, or at least not driven solely by external input, support the contention that perceptual mechanisms within auditory areas are responsible for the subjective experience of imagery. Retrieval processes from long-term representations, such as might occur when generating a familiar tune, tend to engage inferior frontal regions (Halpern & Zatorre 1999, Zatorre et al. 1996) in accord with many studies showing the importance of these mechanisms for memory retrieval in general (Nyberg & Tulving 1996). Additional neural mechanisms related to motor processes may also be involved in musical imagery. In particular, the supplementary motor area has often been identified in musical imagery studies (Halpern & Zatorre 1999, Halpern et al. 2004, Zatorre et al. 1996), which may relate to subvocalization and motor imagery (Lotze et al. 1999).

Emotion

Music experience is not limited to perception and memory. Music experience is intimately related to its emotional appeal (Juslin & Sloboda 2001). Although the study of music as a means to express and induce emotions is a recent endeavor in neurosciences, a few studies (Blood et al. 1999, Peretz et al. 1998, Schmidt & Trainor 2001) have already highlighted important facts about music, emotions, and the brain. More specifically, these studies have suggested that the system for the analysis of emotional expression is neurally isolable (Peretz & Gagnon 1999, Peretz et al. 1998). Recognition of the emotional tone in music can be spared by brain damage while recognition of music identity is impaired (Peretz & Gagnon 1999), indicating that emotion recognition may rely on perceptual determinants that play little role in identity recognition. For example, the mode (major or minor) in which the music is written and the tempo (fast or slow) at which it is played can convey the happy-sad distinction (e.g., Peretz et al. 1998). In contrast, mode and tempo are not perceptually relevant for recognition; a piece of music can be easily recognized despite changes in mode and tempo (Halpern et al. 1998). Thus, the analysis of emotion expression may take as input emotion-specific musical features, as derived from pitch and time relation computations. In other words, emotional analysis could be mediated by a common (perceptual) cortical relay, suggesting no direct access to subcortical, limbic structures (Peretz et al. 2001).

It would make sense for affective responses elicited by music to be cortically mediated, since there is a large cultural learning component to musically induced

emotion. Yet it is possible to elicit consistent affective responses, albeit not necessarily to the same stimuli across people. One such response that has been studied with neuroimaging techniques is the "chills" effect, which many people report as a particularly pleasant or even euphoric musical experience. This effect has been documented behaviorally (Panksepp 1995) and can be elicited relatively reliably. Moreover, this and other emotions are associated with objective physiological markers (Goldstein 1980, Krumhansl 1997). Blood & Zatorre (2001) reported that while people experienced musical chills, cerebral blood flow changes occurred in several brain areas, including the dorsal midbrain, ventral striatum (which contains the nucleus accumbens), insula, and orbitofrontal cortex. Some of these regions have previously been implicated in response to highly rewarding or motivationally important stimuli, including food (Small 2001) and drugs of abuse (Breiter et al. 1997). Thus, under certain circumstances, music can access neural substrates that are primarily associated with biologically significant stimuli. Whether music is unique in this respect remains to be seen; it may be one of a class of human constructs that elicit pleasure by co-opting ancient neural systems via inputs from neocortex. In this respect, music may serve as an excellent paradigm to explore the interactions between neocortically mediated cognitive processes and subcortically mediated affective responses.

MUSIC PERFORMANCE

Music performance includes a variety of tasks, such as playing or singing well-learned pieces from memory, sight-reading, and improvisation. They all combine rapid motor skills and relatively elaborate cognitive operations in addition to the perceptual, memory, and emotion components described above. In order to account for production, one can add to this core system a visual-to-musical conversion subsystem for sight-reading (Cappelletti et al. 2000) and a motor planning component for singing and for playing (Peretz & Coltheart 2003). Such a tight coupling between input and output processes is reflected in the involuntary motor activity observed in pianists as they listen to well-trained music (Haueisen 2001), which may reflect a so-called mirror system important for imitation and learning (Rizzolatti & Arbib 1998). However, there is very little neuropsychological research bearing on this issue. Part of this situation is due to the limited number of proficient musicians who have sustained focal brain damage and to methodological difficulties in studying motor behavior with neuroimaging techniques. Yet, singing is not the privilege of musicians. Singing is the most widespread mode of musical expression; hence, it has the potential to shed light on how the brain orchestrates music production in general.

Singing

Infants spontaneously sing around the age of one. By the age of five, children have a large repertoire of songs of their own culture, and they display singing

abilities that will remain qualitatively unchanged in adulthood (Dowling 1999). Thus, even without much practice, the ordinary adult seems to be endowed with the basic abilities that are necessary to sing simple songs. This conclusion has a long history in clinical neurology because researchers frequently observe nonfluent aphasics who can hardly speak intelligibly but who can produce recognizable songs (Yamadori et al. 1977). Similarly, transcranial magnetic stimulation to the left frontal cortex can temporarily produce speech arrest without interfering with singing in normal subjects (Stewart et al. 2001). These observations point to a neural dissociation between speech and music performance that is supported by the detailed analysis of aphasics' production errors. Hébert and colleagues (Hébert et al. 2003, Peretz et al. 2004a) have shown that patients produce as few intelligible words in speaking as in singing, when tested in comparable conditions. Hence, the results indicate that verbal production, be it sung or spoken, is mediated by the same (impaired) language output system and that this speech route is distinct from the (spared) melodic output system. Conversely, amusic individuals can be normal at speaking while being unable to sing (Ayotte et al. 2002, Peretz et al. 1994). This distinction between singing and speaking is consistent with recent PET studies (Jeffries et al. 2003, Perry et al. 1999) that observed relative increases in activity during singing (versus speaking or listening) in bilateral motor structures, with predominance in the right hemisphere, particularly for premotor, insular, and auditory regions. Thus, in the vocal mode of expression, music can be dissociated from speech, as is also true in perception (see Music Specificity below).

Similarly, as in perception studies, it has been found that singing pitch relations can be maintained while temporal relations are lost and vice versa; the melody can be impaired while the rhythm is intact (Alcock et al. 2000). Loss of melody, in both perception and production, is associated with a right-hemisphere lesion, whereas the loss of rhythm, in both perception and production, is related to a lesion of left-hemispheric structures. These findings are consistent with the notion that the melodic and temporal processing subsystems can function relatively independently of one another in music processing and that these support both perception and production.

Music Playing

The study of musical playing can also yield insights into the mental representations used to plan the execution of music. Generally, a planned sequence is segmented in small units such as phrases. With practice, these units become larger, future events are more strongly anticipated, and expressive features of the performance are enhanced. The performer's task is to highlight the structure of the musical piece and its emotional content through the complex programming of finely coordinated motor movements (Gabrielson 1999, Palmer 1997). Unfortunately, the contribution of cognitive neuroscience to the understanding of musical playing skills lags behind its cognitive study. Lesion studies are either anecdotal or sketchy regarding the nature of the expressive disorder (McFarland & Fortin 1982). Several neuroimaging

studies (Kristeva et al. 2003, Lotze et al. 2003) have attempted to identify the neural correlates of musical performance but this has proven to be a difficult task due to its complex nature. Some of these findings highlight brain activity in certain areas (such as bilateral frontal opercular regions) when both executing and imagining music, which is consistent with the perceptual imagery research reviewed above.

Sight-Reading

The cognitive neuroscience of sight-reading is more informative. It has been known for some time that sight-reading of musical notation is a distinct ability because it is neurally and functionally separable from reading words and Arabic numerals. Brain damage can selectively impair reading of musical notation while sparing reading of other kinds of symbols (Brust 1980, Cappelletti et al. 2000, Horikoshi et al. 1997). Moreover, the musical reading disorder can be observed in relative isolation because playing, singing, and musical memory can be well preserved (e.g., Cappelletti et al. 2000). The reverse situation has also been described. Brain damage can impair the ability to read letters and words while sparing music reading (Signoret et al. 1987). The lesions responsible for music alexia are located in the left hemispheric structures (Midorikawa et al. 2003, Schön et al. 2001). However, results of a recent fMRI study indicate the right occipital-temporal region is critically involved in deciphering pitch notation on a keyboard (Schön et al. 2002).

The fact that sight-reading of musical notation has been examined as a unitary function might explain in part this conflicting information regarding the neural correlates of music reading. Music sight-reading calls for the simultaneous and sequential processing of a vast amount of information in a very brief time for immediate use. This task requires, at the very least, interpretation of the pitch and duration of the notes (written on the two staves of a piano score) in the context of the prespecified key signature and meter, detection of familiar patterns, anticipation of what the music should sound like, and generation of a performance plan suited for motor translation. This sketchy componential task analysis illustrates the number of operations that are involved in music sight-reading and that in principle can be distinguished neuropsychologically.

The need for further fractionation of sight-reading skills finds support in the recurrent observation that after brain damage pitch and time relations are dissociable in reading musical notation, as seen in both perception and singing. Some patients are still able to convert printed information into a rhythmical pattern but are no longer able to decipher pitch-related information (see, e.g., Brust 1980, Fasanaro et al. 1990) and vice versa: Pitch reading can be preserved while rhythm reading is impaired (Midorikawa et al. 2003). This dissociation needs to be studied in more detail because it may arise as a result of damage at different levels in the decoding of musical notation. It can occur as early as when the music score is visually inspected because pitch and duration are represented differently in print (duration is determined by the shape of the note itself, whereas pitch is indicated by the spatial position on the stave). This dissociation may also result from a difficulty occurring

at a later stage, when the reader imagines what the written code sounds like (Schön & Besson 2002). Moreover, there are different routes to achieve a proper interpretation of the pitch code. One route involves naming, which is learned by association between a spatial location on the stave and a name (Do, ré, mi or A, B, C; see below). Another involves some form of procedural memory, which is the consequence of learning to associate a notated pitch to a motor gesture (key press). However, most musicians are able to sight-read the same score in different modalities by singing and playing different musical instruments, and hence are likely to use a more abstract, modality-independent representation system of written scores. In sum, there are different ways to read musical notation. Moreover, this is a skill that is highly automated and specialized compared to what novices may learn (Stewart et al. 2003), an issue we discuss next.

Training

Even if everyone engages in some sort of musical activity in everyday life, it is generally limited in time and effort. In contrast, a few individuals become proficient musicians through extensive practice from an early age and often with the help of explicit tutoring. The fact that musical training is not uniformly and systematically imposed in current educational curricula makes this natural variety of musically acquired skills a formidable laboratory in which to study the effects of training on brain functioning. Musicians represent a unique model in which to study plastic changes in the human brain (Münte et al. 2002).

As suggested by animal research, experience can shape the size of cortical networks either by expansion or by reduction, depending on stimuli and on the structural levels examined (i.e., synaptic or macroscopic; see Münte et al. 2002 for a review). Hence, one would expect to find evidence of size differences in certain regions of the musician's brain compared to the brain of an untrained person. The prime areas to look for differences are the motor areas. Indeed, there is clear evidence that the motor cortex of musicians is enhanced structurally (Gaser & Schlaug 2003) and functionally (Krings et al. 2000). Anatomical changes also have been seen in other motor-related structures, including cerebellum and corpus callosum (Schlaug 2003). In a seminal study, Elbert et al. (1995) investigated somatosensory-evoked magnetic fields in string players. Source analysis revealed that the cortical representation of the digits of the left hand (the fingering hand, especially for its fifth digit) was larger in musicians than in nonmusicians. In the case of the right hand, in which no independent movements of the fingers are required in string players, no differences were found between musicians and nonmusicians. Moreover, the cortical reorganization of the representation of the fingers was more pronounced in musicians who had begun their musical training at an early age.

However, an investigation of sequential finger movements with fMRI found a reduction rather than an increase in activity in motor areas when comparing professional pianists to nonmusicians (Hund-Georgiadis & von Cramon 1999).

In general, there is no doubt that a complex interplay exists between structural changes that may accompany prolonged behavioral performance and neural responses that underlie that performance. A greater volume of tissue may reflect a reorganization, which in turn may manifest itself as recruitment of fewer neurons, or differently synchronized firing patterns, or different effective connectivity with other regions under different circumstances. Each of these possibilities would have quite different consequences for functional measures; different functional measures are sensitive to different parameters of neuronal function. Thus, we are far from understanding in detail the nature of the reorganization associated with musical training. Yet, the study of musical training effects is a unique paradigm to achieve this understanding.

A few fascinating training effects are worth reporting in some detail. One of these is the fact that functional and morphological brain changes as a function of musical training are not limited to motor control. Researchers have identified several auditory brain areas that differ between musicians and nonmusicians. For example, Pantev and colleagues (Pantev et al. 1989), using MEG, have shown that brain responses to piano tones were 25% larger in musicians than in nonmusicians. This effect appears to be more pronounced for tones from each musician's own type of instrument (Pantev et al. 2003, Tervaniemi 2003), strongly implying a use-dependent plasticity phenomenon. However, using a similar MEG technique, Schneider and collaborators (Schneider et al. 2002) found that both the early activity evoked by pure tones and the gray matter volume of the anteromedial portion of Heschl's gyrus were more than 100% larger in professional musicians than in nonmusicians. Pure tones do not exist in the environment and hence may not account for the observed plasticity effects. In fact, the functional and the morphological differences were related to musical aptitude, suggesting influence of innate determinants. These findings reopen the debate about whether the observed brain differences between musicians and nonmusicians arise from genetic or other predispositions (or talent) as well as from practice and experience.

Absolute pitch (AP) is another domain in which the issues of training or exposure, development, and innate predispositions arise (Takeuchi & Hulse 1993, Ward 1999, Zatorre 2003). The principal feature that distinguishes an AP possessor from anyone else is that he or she can identify any pitch by its musical note name without reference to any other sound. In other words, with AP, one has a fixed associative memory for a large number of pitch categories (as many as 70, according to Ward 1999); nonpossessors of AP—nonmusicians and most musicians—also have fixed categories available (Levitin 1994), but the precision is an order of magnitude lower. Because AP is not a universally expressed trait, other predispositions must be at play. One possibility is that genetic factors may be involved. The evidence for this idea is growing (Baharloo et al. 2000, Gregersen et al. 2000). The sibling recurrence rate, for example, is quite high (on the order of 8% to 15%). Thus, AP likely depends on some innate neural substrate (genetically determined or not) in interaction with a certain environmental input at a certain time during neural development.

Several studies have probed the differences in patterns of brain activity in AP possessors and musicians who do not have AP. One of the earliest demonstrations reported that AP listeners showed an absent or reduced electrical-evoked potential component thought to index updating of working memory (Klein et al. 1984, Wayman et al. 1992). Thus, a typical listener will show an electrophysiological response to a pitch change, indicating that some type of "on-line" memory system has been refreshed, but AP possessors do not show this effect. A related phenomenon is that an area of the right frontal cortex believed to be important for monitoring pitch information in working memory is more active in musicians lacking AP than in those who have AP (Zatorre et al. 1998). Thus, instead of requiring continuous maintenance of a sensory trace, AP possessors appear to use their categorical representation of tones in such tasks. The posterior dorsolateral frontal cortex also responds differentially in AP possessors as compared to control musicians (Zatorre et al. 1998). This area, concerned with establishing and maintaining conditional associations in memory (Petrides 1995), is a logical candidate area for the link between a pitch and its label in AP subjects. These findings help to demystify AP somewhat, by demonstrating that working memory and associative learning aspects of AP draw on well-understood neural resources. However, this still does not explain why some people are able to form the pitch categories in the first place and others are not. Part of the answer to this issue has been proposed to lie in the function of subcortical nuclei that are important for periodicity coding, such as the inferior colliculus (Langner et al. 2002)

The presence of functional differences between AP and non-AP people leads to the question of whether brain anatomy might not also differ. Several studies have now shown that there are indeed significant differences in the degree of lateral asymmetry of auditory cortical areas (Schlaug et al. 1995, Zatorre et al. 1998). However, it remains uncertain how to interpret this effect: Whereas initial indications were that AP subjects showed relative enhancement of left-hemisphere structures, the latest evidence suggests that instead it may be a relative reduction in volume of right-hemisphere structures that accounts for the difference (Keenan et al. 2001). A simple explanation based on size may not be sufficient because there are likely complex interactions between gross morphological features and the underlying cortical function.

One way to study the neural correlates of musical training while controlling for complex interactions between innate and environmental factors is to train novices to learn to play music. For example, training on the piano for two hours a day over five days leads to increased excitability of the cortical motor areas that control the contralateral finger muscles of the hand, as measured by applying transcranial magnetic stimulation. Interestingly, mental practice of the motor tasks leads to similar but less-pronounced effects (Pascual-Leone 2001). This type of research allows control for the short- and long-term effects of training on the nature of the plastic changes in the brain. However, this sort of study should be undertaken longitudinally to explore the interaction between plasticity and brain development.

All of these studies demonstrate quantitative neural changes associated with musical training. Musicians appear to recruit more neural tissue or to use it more efficiently than do nonmusicians. An important question is to what extent training also modifies the way music is processed and organized in the brain. For instance, it has been widely argued that musicians might be more prone to adopt an analytical mode of processing music (Bever & Chiarello 1974). However, the use of such a strategy is not exclusive to musicians. As seen earlier, nonmusicians are able to consider local interval sizes when required by the task (Peretz & Morais 1987), and they do so automatically (Trainor et al. 2002). Moreover, musicians' approach of musical material is not confined to an analytic mode; they can flexibly use either contour or interval information, depending on the structure of the stimuli (Peretz & Babai 1992). More generally, when musical abilities are assessed indirectly, more similarities than differences are noted between musicians and nonmusicians (Bigand 2003).

MUSIC SPECIFICITY

As we have seen, a vast network of regions located in both the left and right hemispheres of the brain, with an overall right-sided asymmetry for pitch-based processing, is recruited by musical activities. This should not come as a surprise since musical activities are numerous, complex, and diverse (Tramo 2001). However, finding such a wide distributed network of brain regions raises the issue of which of these brain areas is dedicated to music processing. Some of these regions might not only overlap but might also share processing components with other functions, such as those involved in language.

This issue of music and language specificity has a long history in neurology (Henschen 1924) and has been recently reopened by the observation that the detection of harmonic deviations activates Broca's area (Koelsch et al. 2002). This research suggests that the mechanisms underlying syntactic processing are shared between music and language (Levitin & Menon 2003, Patel 2003). However, there are problems with this conclusion that we address in the present review, because the question of domain-specificity is important from both an evolutionary (Hauser et al. 2002) and an empirical perspective. First, we should keep in mind that Broca's area is a vast brain region that can easily accommodate more than one distinct processing network (Marcus et al. 2003). Second, the degree of anatomical proximity of activation maxima that should count as reactivation of the same region in another task is not straightforward, particularly when activation is not limited to Broca's area but involves the right hemisphere homologous region (Maess et al. 2001) and when the cognitive domains (music and language) are studied separately in different laboratories. Clearly, further comparison is needed between music and language in the same experimental setting, using similar tasks that are matched (or manipulated) for attentional resources (Shallice 2003).

Indeed, comparisons across domains have generally been more consistent with the idea that musical abilities are subserved, at least in part, by neural networks that are dedicated to their respective processing. As seen previously, singing, memory, and sight-reading are all musical activities that are functionally and neuroanatomically dissociable from analogous activities that involve speech. The evidence rests on both lesion and neuroimaging studies. The strongest support for the existence of processing components whose operation is specific to the processing of music comes from the study of auditory disorders. Selective impairments and sparing of music recognition abilities can occur after brain damage. As recently reviewed in Peretz & Coltheart (2003), patients may suffer from recognition failures that affect the musical domain exclusively. Such patients can no longer recognize melodies (presented without words) that were highly familiar to them prior to the onset of their brain damage. In contrast, they are normal at recognizing spoken lyrics (and spoken words, in general), familiar voices, and other environmental sounds (such as animal cries). Similarly, there are individuals who suffer from lifelong difficulties with music but can recognize the lyrics of familiar songs even though they are unable to recognize the accompanying tune. Conversely, one can find people in whom brain damage has impaired the ability to recognize spoken words while sparing the ability to recognize music. Hence, the evidence points to the existence of distinct processing modules for music and speech.

Music specificity may concern different processing components. Some components might be perceptual prerequisites for music processing (Peretz & Hyde 2003), while some processing components appear to be genuinely specialized for music (Peretz & Morais 1989). Still other components conceivably could be involved in the processing not only of music but also of speech (Patel et al. 1998). One important question for the future is to determine which other processing components are uniquely involved in music and which components are not. This would provide clues as to the roots of brain specialization for music processing and hence the roots of musicality in general.

CONCLUSIONS

The work presented in this review constitutes a selection of what currently is known (and is not known) about how musical functions are organized in the brain. As pointed out, a number of musical processes have not yet been considered in neuropsychology. Yet, we trust that the accumulated knowledge on how and where short musical phrases are perceived, recognized, imagined, appreciated, and sung will provide the building blocks of a broader and more complete neurofunctional account of music processing.

One such fundamental principle concerns the distinction between pitch-based and time-based mechanisms. As seen in both perception and performance, the musical processing of pitch and rhythm appears to result from the operation of largely distinct neural mechanisms. Extraction of musical pitch relations seems to depend on a series of operations that predominantly involve the right auditory

cortex, whereas extraction of musical time relations recruits more widespread and bilateral neural networks. Obviously, music processing cannot be ascribed wholly to one cerebral hemisphere. However, as we have argued elsewhere (Peretz & Hyde 2003, Zatorre et al. 2002), it might be the case that right-sided neural mechanisms play a determinant role. Pitch-based mechanisms might be rooted in the specialization of the right auditory cortex for spectral resolution (Zatorre et al. 2002) and be instrumental in the normal development of musical competence (Peretz et al. 2002).

These conclusions also assume that music processing is mapped onto the human brain with a certain consistency. If there were no consistency, understanding the relations between music and its neural correlates would be impossible. However, as discussed above, people differ in their musical training or experience, and perhaps also in aptitude or talent; these differences manifest themselves at various levels, and understanding the interplay between brain processes, environmental inputs, innate factors, and development will be one of the major challenges for our field.

It should also be considered that the mapping between processing components and neural networks might not be one-to-one. The fact that the processing framework can account for the musical disorders exhibited by brain-damaged patients suggests that this mapping is feasible. Indeed, it is conceivable that some music processing components lack neuroanatomical separability. In that case, the neural substrates of the components would be intermingled with the neural systems devoted to the processing of other complex patterns. If so, brain damage could never affect just one processing component while sparing all other aspects. If the process under study possesses the property of neural separability, as we have described here for most processing components, then we expect to find corresponding isolable neural areas in the brain. Thus, we believe that the evidence is solid enough to envisage a proper mapping between processes and neural networks. Above all, we believe that convergence between lesion and neuroimaging data is the optimal strategy to build a sound model of how the brain processes music.

ACKNOWLEDGMENTS

The *Annual Review of Psychology* is online at http://psych.annualreviews.org

LITERATURE CITED

Alcock KJ, Wade D, Anslow P, Passingham RE. 2000. Pitch and timing abilities in adult left-hemisphere-dysphasic and right-hemisphere subjects. *Brain Lang.* 75:47–65

Ayotte J, Peretz I, Rousseau I, Bard C, Bojanowski M. 2000. Patterns of music agnosia associated with middle cerebral artery infarcts. *Brain* 123:1926–38

Baharloo S, Service E, Risch N, Gitschier J, Freimer NB. 2000. Familial agregation of absolute pitch. *Am. J. Hum. Genet.* 67:755–58

Balaban MT, Anderson LM, Wisniewski AB. 1998. Lateral asymmetries in infant melody perception. *Dev. Psychol.* 34:39–48

Besson M, Faïta F. 1995. An event-related potential (ERP) study of musical expectancy: comparison of musicians with nonmusicians. *J. Exp. Psychol.: Hum. Percept. Perform.* 21:1278–96

Besson M, Faïta F, Peretz I, Bonnel A-M, Requin J. 1998. Singing in the brain: independence of lyrics and tunes. *Psychol. Sci.* 9:494–98

Bever TG, Chiarello RJ. 1974. Cerebral dominance in musicians and nonmusicians. *Science* 185:537–39

Bigand E. 2003. More about the musical expertise of musically untrained listeners. *Ann. NY Acad. Sci.* 999:304–12

Blood AJ, Zatorre RJ. 2001. Intensely pleasurable responses to music correlates with activity in brain regions implicated in reward and emotion. *Proc. Natl. Acad. Sci. USA* 98:11818–23

Blood AJ, Zatorre RJ, Bermudez P, Evans AC. 1999. Emotional responses to pleasant and unpleasant music correlate with activity in paralimbic brain regions. *Nat. Neurosci.* 2:382–87

Breiter HC, Gollub RL, Weisskoff RM, Kennedy D, Makris N, et al. 1997. Acute effects of cocaine on human brain activity. *Neuron* 19:591–611

Brust JC. 1980. Music and language: musical alexia and agraphia. *Brain* 103:367–92

Cappelletti M, Waley-Cohen H, Butterworth B, Kopelman M. 2000. A selective loss of the ability to read and write music. *Neurocase* 6:321–32

Critchley M, Henson R, eds. 1977. *Music and the Brain. Studies in the Neurology of Music.* London: Heinemann

Dalla Bella S, Peretz I, Aronoff N. 2003. Time course of melody recognition: a gating paradigm study. *Percept. Psychophys.* 65:1019–28

Deutsch D. 1970. Tones and numbers: specificity of interference in immediate memory. *Science* 168:1604–5

Deutsch D. 1999. *The Psychology of Music.* San Diego: Academic

Di Pietro M, Laganaro M, Lèeman B, Schnider A. 2004. Receptive amusia: temporal auditory deficit in a professional musician following a left temporo-parietal lesion. *Neuropsychologia* 42:868–977

Dowling WJ. 1999. The development of music perception and cognition. See Deutsch 1999, pp. 603–25

Dowling WJ, Fujitani DS. 1971. Contour, interval, and pitch recognition in memory for melodies. *J. Acoust. Soc. Am.* 49:524–31

Dowling WJ, Harwood D. 1986. *Music Cognition.* New York: Academic

Drake C. 1998. Psychological processes involved in the temporal organization of complex auditory sequences: universal and acquired processes. *Music Percept.* 16:11–26

Elbert T, Pantev C, Wienbruch C, Rockstroh B, Taub E. 1995. Increased cortical representation of the fingers of the left hand in string players. *Science* 270:305–7

Eustache F, Lechevalier B, Viader F, Lambert J. 1990. Identification and discrimination disorders in auditory perception: a report on two cases. *Neuropsychologia* 28:257–70

Fasanaro AM, Spitaleri DLA, Valiani R. 1990. Dissociation in musical reading: a musician affected by alexia without agraphia. *Music Percept.* 7:259–72

Fishman YI, Volkov IO, Noh MD, Garell PC, Bakken H, et al. 2001. Consonance and dissonance of musical chords: neural correlates in auditory cortex of monkeys and humans. *J. Neurophysiol.* 86:2761–88

Fraisse P. 1982. Rhythm and tempo. See Deutsch 1999, pp. 149–80

Francès R, Lhermitte F, Verdy M. 1973. Le déficit musical des aphasiques. *Rev. Int. Psychol. Appl.* 22:117–35

Fries W, Swihart AA. 1990. Disturbance of rhythm sense following right hemisphere damage. *Neuropsychologia* 28:1317–23

Gaab N, Gaser C, Zaehle T, Jäncke L, Schlaug G. 2003. Functional anatomy of pitch memory—an fMRI study with sparse temporal sampling. *NeuroImage* 19:1417–26

Gabrielson A. 1999. The performance of music. See Deutsch 1999, pp. 501–602

Gaser C, Schlaug G. 2003. Brain structures differ between musicians and non-musicians. *J. Neurosci.* 23:9240–45

Goldstein A. 1980. Thrills in response to music and other stimuli. *Physiol. Psychol.* 8:126–29

Gregersen PK, Kowalsky E, Kohn N, Marvin EW. 2000. Early childhood music education and predisposition to absolute pitch: teasing apart genes and environment. *Am. J. Hum. Genet.* 98:280–82

Griffiths TD, Beuchel C, Frackowiak RSJ, Patterson RD. 1998. Analysis of temporal structure in sound by the human brain. *Nat. Neurosci.* 1:422–27

Griffiths TD, Johnsrude I, Dean JL, Green GGR. 1999. A common neural substrate for the analysis of pitch and duration pattern in segmented sound? *NeuroReport* 10:3825–30

Hall DA, Johnsrude I, Haggard MP, Palmer AR, Akeroyd MA, Summerfield AQ. 2002. Spectral and temporal processing in human auditory cortex. *Cereb. Cortex* 12:140–49

Halpern AR. 1988. Mental scanning in auditory imagery for songs. *J. Exp. Psychol.: Learn. Mem. Cogn.* 14:434–43

Halpern AR. 1989. Memory for the absolute pitch of familiar songs. *Mem. Cogn.* 17:572–81

Halpern AR, Bartlett D, Dowling W. 1998. Perception of mode, rhythm, and contour in unfamiliar melodies: effects of age and experience. *Music Percept.* 15:335–56

Halpern AR, Zatorre R. 1999. When that tune runs through your head: a PET investigation of auditory imagery for familiar melodies. *Cereb. Cortex* 9:697–704

Halpern AR, Zatorre R, Bouffard M, Johnson JA. 2004. Behavioral and neural correlates of perceived and imagined musical timbre. *Neuropsychologia.* In press

Halsband U, Tanji J, Freund H-J. 1993. The role of premotor cortex and the supplementary motor area in the temporal control of movement in man. *Brain* 116:243–46

Harrington DL, Haaland K, Hermanowicz N. 1998. Temporal processing in the basal ganglia. *Neuropsychology* 12:3–12

Hart HC, Palmer AR, Hall DA. 2003. Amplitude and frequency-modulated stimuli activate common regions of human auditory cortex. *Cereb. Cortex* 13:773–81

Haueisen JK, Knösche T. 2001. Involuntary motor activity in pianists evoked by music perception. *J. Cogn. Neurosci.* 13:786–92

Hauser M, Chomsky N, Fitch WT. 2002. The faculty of language: What is it, who has it, and how did it evolve? *Science* 298:1569–79

Hébert S, Racette A, Gagnon L, Peretz I. 2003. Revisiting the dissociation between singing and speaking in expressive aphasia. *Brain* 126:1838–50

Henschen SE. 1924. On the function of the right hemisphere of the brain in relation to the left in speech, music and calculation. *Brain* 44:110–23

Hickok G, Buchsbaum B, Humphries C, Muftuler T. 2003. Auditory-motor interaction revealed by fMRI: speech, music, and working memory in area SPT. *J. Cogn. Neurosci.* 15:673–82

Holcomb H, Medoff D, Caudill P, Zhao Z, Lahti A, et al. 1998. Cerebral blood flow relationships associated with difficult tone recognition task in trained normal volunteers. *Cereb. Cortex* 8:534–42

Horikoshi T, Asari Y, Watanabe A, Nagaseki Y, Nukui H, et al. 1997. Music alexia in a patient with mild pure alexia: disturbed visual perception of nonverbal meaningful figures. *Cortex* 33:187–94

Hund-Georgiadis M, von Cramon DY. 1999. Motor-learning-related changes in piano players and non-musicians revealed by functional magnetic-resonance signals. *Exp. Brain Res.* 125:417–25

Ibbotson NR, Morton J. 1981. Rhythm and dominance. *Cognition* 9:125–38

Ivry RB, Keele S. 1989. Timing functions of the cerebellum. *J. Cogn. Neurosci.* 1:136–52

Ivry RB, Keele S, Diener H. 1988. Dissociation of the lateral and medial cerebellum in movement timing and movement execution. *Exp. Brain Res.* 73:167–80

Janata P. 2001. Brain electrical activity evoked by mental formation of auditory expectations and images. *Brain Topogr.* 13:169–93

Janata P, Birk J, Van Horn J, Leman M, Tillmann B, Bharucha J. 2002. The cortical topography of tonal structures underlying Western music. *Science* 298:2167–70

Janata P, Grafton S. 2003. Swinging in the brain: shared neural substrates for behaviors related to sequencing and music. *Nat. Neurosci.* 6:682–87

Jeffries KJ, Fritz JB, Braun AR. 2003. Words in melody: an H2 15O PET study of brain activation during singing and speaking. *NeuroReport* 14:749–54

Johnsrude I, Penhune V, Zatorre R. 2000. Functional specificity in the right auditory cortex for perceiving pitch direction. *Brain* 123:155–63

Jones MR, Boltz M. 1989. Dynamic attending and responses to time. *Psychol. Rev.* 96:459–91

Juslin P, Sloboda J, eds. 2001. *Music and Emotion: Theory and Research.* Oxford: Oxford Univ. Press

Justus T, Bharucha J. 2001. Modularity in musical processing: the automaticity of harmonic priming. *J. Exp. Psychol.: Hum. Percept. Perform.* 27:1000–11

Justus T, Bharucha J. 2002. Music perception and cognition. In *Stevens Handbook of Experimental Psychology, Volume I: Sensation and Perception,* ed. S Yantis, H Pasler, pp. 453–92. New York: Wiley

Keenan J, Thangaraj V, Halpern A, Schlaug G. 2001. Absolute pitch and planum temporale. *NeuroImage* 14:1402–8

Klein M, Coles MGH, Donchin E. 1984. People with absolute pitch process tones without producing a P300. *Science* 223:1306–9

Koelsch S, Grossmann T, Gunter T, Hahne A, Schröger E, Friederici AD. 2003. Children processing music: electric brain responses reveal musical competence and gender differences. *J. Cogn. Neurosci.* 15:683–93

Koelsch S, Gunter TC, van Cramon DY, Zysset S, Lohmann G, Friederici AD. 2002. Bach speaks: a cortical "language-network" serves the processing of music. *NeuroImage* 17:956–66

Koelsch S, Kasper E, Sammler D, Schulze K, Gunter T, Friederici AD. 2004. Music, language and meaning: brain signatures of semantic processing. *Nat. Neurosci.* 7:302–7

Krings T, Töpper R, Foltys H, Erbich S, Sparing R, et al. 2000. Cortical activation patterns during complex motor tasks in piano players and control subjects. A functional magnetic resonance imaging study. *Neurosci. Lett.* 278:189–93

Kristeva R, Chakarov V, Schulte-Mönting J, Spreer J. 2003. Activation of cortical areas in music execution and imagining: a high-resolution EEG study. *NeuroImage* 20:1872–83

Krumhansl CL. 1997. An exploratory study of musical emotions and psychophysiology. *Can. J. Exp. Psychol.* 51:336–52

Krumhansl CL. 2000. Rhythm and pitch in music cognition. *Psychol. Bull.* 126:159–79

Langner G, Albert M, Briede T. 2002. Temporal and spatial coding of periodicity information in the inferior colliculus of awake chinchilla (*Chinchilla laniger*). *Hear. Res.* 168:110–30

Large EW, Palmer C, Pollack JB. 1995. Reduced memory representations for music. *Cogn. Sci.* 19:53–96

Lerdahl F, Jackendoff R. 1983. *A Generative Theory of Tonal Music.* Cambridge, MA: MIT Press

Levitin DJ. 1994. Absolute memory for musical pitch: evidence from the production of learned melodies. *Percept. Psychophys.* 56:414–23

Levitin DJ, Cook PR. 1996. Memory for musical tempo: additional evidence that auditory memory is absolute. *Percept. Psychophys.* 58:927–35

Levitin DJ, Menon V. 2003. Musical structure is processed in "language" areas of the brain:

a possible role for Brodmann area 47 in temporal coherence. *Neuroimage* 20:2142–52

Liégeois-Chauvel C, Peretz I, Babai M, Laguitton V, Chauvel P. 1998. Contribution of different cortical areas in the temporal lobes to music processing. *Brain* 121:1853–67

Lotze M, Montoya P, Erb M, Hulsmann E, Flor H, et al. 1999. Activation of cortical and cerebellar motor areas during executed and imagined hand movements: an fMRI study. *J. Cogn. Neurosci.* 11:491–501

Lotze M, Scheler G, Tan H-R, Braun C, Birbaumer N. 2003. The musician's brain: functional imaging of amateurs and professionals during performance and imagery. *Neuroimage* 20:1817–29

Maess B, Koelsch S, Gunter TC, Friederici AD. 2001. Musical syntax is processed in Broca's area: an MEG study. *Nat. Neurosci.* 4:540–45

Marcus GF, Vouloumanos A, Sag IA. 2003. Does Broca's play by the rules? *Nat. Neurosci.* 6:651–52

Marin OSM, Perry DW. 1999. Neurological aspects of music perception and performance. See Deutsch 1999, pp. 653–724

McFarland HR, Fortin D. 1982. Amusia due to right temporoparietal infarct. *Arch. Neurol.* 39:725–27

Midorikawa A, Kawamura M, Kezuka M. 2003. Musical alexia for rhythm notation: a discrepancy between pitch and rhythm. *Neurocase* 9:232–38

Milner B. 1962. Laterality effects in audition. In *Interhemispheric Relations and Cerebral Dominance*, ed. VB Mountcastle, pp. 177–95. Baltimore, MD: Johns Hopkins Press

Münte TF, Altenmüller E, Jäncke L. 2002. The musician's brain as a model of neuroplasticity. *Nat. Rev.* 3:473–78

Nyberg L, Tulving E. 1996. Classifying human long-term memory: evidence from converging dissociations. *Eur. J. Cogn. Psychol.* 8:163–83

Palmer C. 1997. Music performance. *Annu. Rev. Psychol.* 48:115–38

Panksepp J. 1995. The emotional sources of "chills" induced by music. *Music Percept.* 13:171–207

Pantev C, Engelien A, Candia V, Elbert T. 2003. Representational cortex in musicians. See Peretz & Zatorre 2003, pp. 382–95

Pantev C, Hoke M, Lutkenhoner B, Lehnertz K. 1989. Tonotopic organization of the auditory cortex: pitch versus frequency representation. *Science* 246:486–88

Pascual-Leone A. 2001. The brain that plays music and is changed by it. See Peretz & Zatorre 2003, pp. 396–409

Patel A. 2003. Language, music, syntax and the brain. *Nat. Neurosci.* 6:674–81

Patel AD, Balaban E. 2000. Temporal patterns of human cortical activity reflect tone sequence structure. *Nature* 404:80–84

Patel AD, Peretz I, Tramo M, Labrecque R. 1998. Processing prosodic and musical patterns: a neuropsychological investigation. *Brain Lang.* 61:123–44

Patterson R, Uppenkamp S, Johnsrude I, Griffiths T. 2002. The processing of temporal pitch and melody information in auditory cortex. *Neuron* 36:767–76

Penhune V, Doyon J. 2002. Dynamic cortical and subcortical networks in learning and delayed recall of timed motor sequences. *J. Neurosci.* 22:1397–406

Penhune V, Zatorre R, Evans AC. 1998. Cerebellar contributions to motor timing: a PET study of auditory and visual rhythm reproduction. *J. Cogn. Neurosci.* 10:752–65

Penhune VB, Zatorre RJ, Feindel W. 1999. The role of auditory cortex in retention of rhythmic patterns in patients with temporal-lobe removals including Heschl's gyrus. *Neuropsychologia* 37:315–31

Peretz I. 1990. Processing of local and global musical information by unilateral brain-damaged patients. *Brain* 113(Pt. 4):1185–205

Peretz I. 1993. Auditory atonalia for melodies. *Cogn. Neuropsychol.* 10:21–56

Peretz I. 1996. Can we lose memories for music? The case of music agnosia in a nonmusician. *J. Cogn. Neurosci.* 8:481–96

Peretz I. 2001. Music perception and recognition. In *The Handbook of Cognitive Neuropsychology*, ed. B Rapp, pp. 519–40. Hove, UK: Psychology Press

Peretz I, Ayotte J, Zatorre RJ, Mehler J, Ahad P, et al. 2002. Congenital amusia: a disorder of fine-grained pitch discrimination. *Neuron* 33:185–91

Peretz I, Babai M. 1992. The role of contour and intervals in the recognition of melody parts: evidence from cerebral asymmetries in musicians. *Neuropsychologia* 30:277–92

Peretz I, Blood AJ, Penhune V, Zatorre R. 2001. Cortical deafness to dissonance. *Brain* 124:928–40

Peretz I, Coltheart M. 2003. Modularity of music processing. *Nat. Neurosci.* 6:688–91

Peretz I, Gagnon L. 1999. Dissociation between recognition and emotional judgment for melodies. *Neurocase* 5:21–30

Peretz I, Gagnon L, Bouchard B. 1998. Music and emotion: perceptual determinants, immediacy, and isolation after brain damage. *Cognition* 68:111–41

Peretz I, Gagnon L, Macoir J, Hébert S. 2004a. Singing in the brain: insights from cognitive neuropsychology. *Music Percept.* 21:373–90

Peretz I, Hyde K. 2003. What is specific to music processing? Insights from congenital amusia. *Trends Cogn. Sci.* 7:362–67

Peretz I, Kolinsky R. 1993. Boundaries of separability between melody and rhythm in music discrimination: a neuropsychological perspective. *Q. J. Exp. Psychol. A* 46:301–25

Peretz I, Kolinsky R, Tramo M, Labrecque R, Hublet C, et al. 1994. Functional dissociations following bilateral lesions of auditory cortex. *Brain* 117:1283–301

Peretz I, Morais J. 1987. Analytic processing in the classification of melodies as same or different. *Neuropsychologia* 25:645–52

Peretz I, Morais J. 1989. Music and modularity. *Contemp. Music Rev.* 4:277–91

Peretz I, Radeau M, Arguin M. 2004b. Two-way interactions between music and language: evidence from priming recognition of tune and lyrics in familiar songs. *Mem. Cogn.* 32:142–52

Peretz I, Zatorre R. 2003. *The Cognitive Neuroscience of Music*. Oxford: Oxford Univ. Press

Perry DW, Zatorre RJ, Petrides M, Alivisatos B, Meyer E, Evans AC. 1999. Localization of cerebral activity during simple singing. *Neuroreport* 10:3979–84

Petrides M. 1995. Functional organization of the human frontal cortex for mnemonic processing: evidence from neuroimaging studies. *Ann. NY Acad. Sci.* 769:85–96

Piccirilli M, Sciarma T, Luzzi S. 2000. Modularity of music: evidence from a case of pure amusia. *J. Neurol. Neurosurg. Psychiatry* 69:541–45

Platel H, Baron JC, Desgranges B, Bernard F, Eustache F. 2003. Semantic and episodic memory for music are subserved by distinct neural networks. *Neuroimage* 20:244–56

Platel H, Price C, Baron JC, Wise R, Lambert J, et al. 1997. The structural components of music perception. A functional anatomical study. *Brain* 120:229–43

Plomp R, Levelt WJ. 1965. Tonal consonance and critical bandwidth. *J. Acoust. Soc. Am.* 38:548–60

Povel DJ, Essens P. 1985. Perception of temporal patterns. *Music Percept.* 2:411–40

Radvansky GA, Flemming KJ, Simmons JA. 1995. Timbre reliance in nonmusicians' memory for melodies. *Music Percept.* 13:127–40

Raffman D. 1993. *Language, Music and Mind*. Cambridge, MA: MIT Press

Rao SM, Harrington DL, Haaland K, Bobholz JA, Cox RW, Binder J. 1997. Distributed neural systems underlying the timing of movements. *J. Neurosci.* 17:5528–35

Rao SM, Mayer AR, Harrington DL. 2001. The evolution of brain activation during temporal processing. *Nat. Neurosci.* 4:317–23

Regnault P, Bigand E, Besson M. 2001. Event-related brain potentials show top-down and bottom-up modulations of musical expectations. *J. Cogn. Neurosci.* 13:241–55

Sakai K, Hikosaka O, Miyauchi S, Takino R, Tamada T, et al. 1999. Neural representation of a rhythm depends on its interval ratio. *J. Neurosci.* 19:10074–81

Samson S, Zatorre RJ. 1992. Learning and retention of melodic and verbal information after unilateral temporal lobectomy. *Neuropsychologia* 30:815–26

Schellenberg E, Trehub SE. 1994. Frequency ratios and the perception of tone patterns. *Psychon. Bull. Rev.* 1:191–201

Schlaug G. 2003. The brain of musicians. See Peretz & Zatorre 2003, pp. 366–81

Schlaug G, Jancke L, Huang Y, Steinmetz H. 1995. In vivo evidence of structural brain asymmetry in musicians. *Science* 267:699–701

Schmidt LA, Trainor LJ. 2001. Frontal brain electrical activity (EEG) distinguishes valence and intensity of musical emotions. *Cogn. Emot.* 15:487–500

Schneider P, Scherg M, Dosch G, Specht H, Gutschalk A. 2002. Morphology of Heschl's gyrus reflects enhanced activation in the auditory cortex of musicians. *Nat. Neurosci.* 5:688–94

Schön D, Anton J-L, Roth M, Besson M. 2002. An fMRI study of music sight-reading. *NeuroReport* 13:2285–89

Schön D, Besson M. 2002. Processing pitch and duration in music reading: a RT-ERP study. *Neuropsychologia* 40:868–78

Schön D, Semenza C, Denes G. 2001. Naming of musical notes: a selective deficit in one musical clef. *Cortex* 37:407–21

Schubotz RI, Friederici AD, von Cramon DY. 2000. Time perception and motor timing: a common cortical and subcortical basis revealed by fMRI. *Neuroimage* 11:1–12

Semal C, Demany L, Ueda K, Halle P-A. 1996. Speech versus nonspeech in pitch memory. *J. Acoust. Soc. Am.* 100:1132–40

Shallice T. 2003. Functional imaging and neuropsychology findings: How can they be linked? *NeuroImage* 20:S146–54

Signoret JL, van Eeckhout P, Poncet M, Castaigne P. 1987. Aphasia without amusia in a blind organist. Verbal alexia-agraphia without musical alexia-agraphia in braille. *Rev. Neurol. (Paris)* 143:172–81

Small DM, Zatorre R, Dagher A, Jones-Gotman M. 2001. Brain activity related to eating chocolate: from pleasure to aversion. *Brain* 124:1720–33

Steinke WR, Cuddy LL, Jakobson LS. 2001. Dissociations among functional subsystems governing melody recognition after right-hemisphere damage. *Cogn. Neuropsychol.* 18:411–37

Stewart L, Henson R, Kamp K, Walsh V, Turner R, Frith U. 2003. Brain changes after learning to read and play music. *Neuroimage* 20:71–83

Stewart L, Walsh V, Frith U, Rothwell J. 2001. Transcranial magnetic stimulation produces speech arrest but not song arrest. *Ann. NY Acad. Sci.* 930:433–35

Takeuchi AH, Hulse SH. 1993. Absolute pitch. *Psychol. Bull.* 113:345–61

Tervaniemi M. 2003. Musical sound processing: EEG and MEG evidence. See Peretz & Zatorre 2003, pp. 294–309

Thivard L, Belin P, Zibovicius M, Poline J, Samson Y. 2000. A cortical region sensitive to auditory spectral motion. *NeuroReport* 11:2969–72

Tillmann B, Bharucha JJ, Bigand E. 2000. Implicit learning of tonality: a self-organizing approach. *Psychol. Rev.* 107:885–913

Tillmann B, Janata P, Bharucha J. 2003. Activation of the inferior frontal cortex in musical priming. *Cogn. Brain Res.* 16:145–61

Trainor LJ, McDonald KL, Alain C. 2002. Automatic and controlled processing of melodic contour and interval information measured by electrical brain activity. *J. Cogn. Neurosci.* 14:430–42

Trainor LJ, Trehub SE. 1992. A comparison of infants' and adults' sensitivity to Western musical structure. *J. Exp. Psychol.: Hum. Percept. Perform.* 18:394–402

Tramo M, Cariani PA, Delgutte B, Braida LD. 2003. Neurobiology of harmony perception. See Peretz & Zatorre 2003, pp. 127–51

Tramo M, Shah GD, Braida LD. 2002. Functional role of auditory cortex in frequency processing and pitch perception. *J. Neurophysiol.* 87:122–39

Tramo MJ. 2001. Biology and music. Music of the hemispheres. *Science* 291:54–56

Tramo MJ, Bharucha JJ, Musiek FE. 1990. Music perception and cognition following bilateral lesions of auditory cortex. *J. Cogn. Neurosci.* 2:195–212

Vignolo LA. 2003. Music agnosia and auditory agnosia. Dissociations in stroke patients. *Ann. NY Acad. Sci.* 999:50–57

Ward WD. 1999. Absolute pitch. See Deutsch 1999, pp. 265–99

Warren J, Uppenkamp S, Patterson R, Griffiths T. 2003. Separating pitch chroma and pitch height in the human brain. *Proc. Natl. Acad. Sci. USA* 100:10038–42

Warren RM, Gardner DA, Brubaker BS, Bashford JA. 1991. Melodic and nonmelodic sequences of tones: effects of duration on perception. *Music Percept.* 8:277–90

Wayman JW, Frisina RD, Walton JP. 1992. Effects of musical training and absolute pitch ability on event-related activity in response to sine tones. *J. Acoust. Soc. Am.* 91:3527–31

Wilson SJ, Pressing J, Wales RJ. 2002. Modelling rhythmic function in a musician post-stroke. *Neuropsychologia* 40:1494–505

Yamadori A, Osumi Y, Masuhara S, Okubo M. 1977. Preservation of singing in Broca's aphasia. *J. Neurol. Neurosurg. Psychiatry* 40: 221–24

Yoo S-S, Lee CU, Choi BG. 2001. Human brain mapping of auditory imagery: event-related functional MRI study. *NeuroReport* 12:3045–49

Zatorre RJ. 1985. Discrimination and recognition of tonal melodies after unilateral cerebral excisions. *Neuropsychologia* 23:31–41

Zatorre RJ. 1988. Pitch perception of complex tones and human temporal-lobe function. *J. Acoust. Soc. Am.* 84:566–72

Zatorre RJ. 2003. Absolute pitch: a paradigm for understanding the influence of genes and development on cognitive function. *Nat. Neurosci.* 6:692–95

Zatorre RJ, Belin P. 2001. Spectral and temporal processing in human auditory cortex. *Cereb. Cortex* 11:946–53

Zatorre RJ, Belin P, Penhune VB. 2002. Structure and function of auditory cortex: music and speech. *Trends Cogn. Sci.* 6:37–46

Zatorre RJ, Evans AC, Meyer E. 1994. Neural mechanisms underlying melodic perception and memory for pitch. *J. Neurosci.* 14:1908–19

Zatorre RJ, Halpern AR. 1993. Effect of unilateral temporal-lobe excision on perception and imagery of songs. *Neuropsychologia* 31:221–32

Zatorre RJ, Halpern AR, Perry DW, Meyer E, Evans AC. 1996. Hearing in the mind's ear: a pet investigation of musical imagery and perception. *J. Cogn. Neurosci.* 8:29–46

Zatorre RJ, Perry DW, Beckett CA, Westbury CF, Evans AC. 1998. Functional anatomy of musical processing in listeners with absolute pitch and relative pitch. *Proc. Natl. Acad. Sci. USA* 95:3172–77

Zatorre RJ, Samson S. 1991. Role of the right temporal neocortex in retention of pitch in auditory short-term memory. *Brain* 114 (Pt. 6):2403–17