New Encyclopedia of Neuroscience

Music

PJ Donnelly and CJ Limb,
The Johns Hopkins University, Baltimore, MD, USA

Charles J. Limb, M.D.
Assistant Professor
Department of Otolaryngology-Head and Neck Surgery
The Johns Hopkins Hospital
The Johns Hopkins University
601 N. Caroline St., 6th floor
Baltimore, MD 21287 USA

Patrick J. Donnelly
Department of Computer Music – Research Division
Peabody Conservatory of Music
The Johns Hopkins University
1 East Mount Vernon Place
Baltimore, MD 21201 USA

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Summary

Music is a complex human phenomenon, the perception of which involves a variety of neural processes. Data from neuroimaging, neurophysiologic, and lesion-based studies provide valuable evidence of the neural substrates that underlie the perception of musical aspects such as pitch, melody, rhythm, timbre, and musical syntax. Furthermore, these studies shed light on the relationship between music and language, music-induced emotion, and neural plasticity caused by musical training. Through the systematic examination of musical components, neuroscientists have begun to describe a compelling model of how the auditory brain processes and perceives the complex sounds of music.

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Introduction

Music is a phenomenon that appears to have been universally present throughout human history and across all human populations. The perception and performance of music is often delicately intertwined with a variety of perceptual (e.g., listening), sensorimotor (e.g., playing an instrument), visual (e.g., reading a musical score), mnemonic (e.g., playing a piece from memory), and affective (e.g., emotional interpretation) processes. For these reasons, music offers potentially powerful insights into complex brain organization and function. Additionally, musical aptitude and the unique effects of musical training are of specific interest to the study of the nature and effects of brain plasticity and reorganization.

Music is often compared to language, and indeed music does share many abstract similarities with language. In both language and music, perceptually distinct elements are combined into hierarchically organized sequences according to rules of syntax. While music and language are highly analogous in many respects, they are also quite different. Therefore the cognitive investigations of music perception provide the opportunity to reveal similarities and differences in the neural structures and functions involved in music and language perception. Furthermore, the search for the cognitive substrates of music perception complement the musicological investigations of the origins of music, its perceptual distinction from speech and other auditory input, and its evolutionary relationship to the development of language.

The last few decades have seen a major increase in the systematic study of the cognitive neuroscience of music. Recent advances in neuroscientific techniques, such as functional magnetic resonance imaging (fMRI), magnetoencephalography (MEG), and positron emission tomography (PET), enable new data to compare with neurophysiologic and lesion-based studies. Because of the breadth of processes and brain regions involved in musical perception, the cognitive investigations of music perception traditionally dissect music into its distinct fundamental elements.

Pitch and Melody

Pitch is the fundamental building block of music. For this reason the majority of research on the neurological correlates of music perception have focused on pitch, and to a lesser extent, melodic phrase. The perception of pitch relies on the acoustic properties of the spectra (the ratios of the fundamental frequency to the harmonics) and the envelope (the rise and decay time) of each harmonic constituent. Melody is a musical phrase created when a series of pitches are organized into sequential temporal patterns of varying musical contour and interval.

Numerous studies spanning nearly fifty years strongly indicate a “pitch center” in the posterior-superior temporal lobe, comprised of the auditory cortices and secondary auditory association areas. Early studies of patients with temporal lobe excisions note the prominence of the right hemisphere in pitch and melodic processing. Excisions that included the right-lateral Heschl's Gyrus significantly impaired the perception of changes in pitch, pitch direction, interval size, melodic contour, and complex tones. However, left-lateralized damage can also cause selective deficits in pitch and melodic processing. The results of a neuroimaging study using PET indicate a left-lateral specialization of the core auditory cortex for temporal processing of sound while the spectral processing of pitch correlated to activity in the right hemisphere belt cortical areas (Figure 1).

While considerable debate surrounds possible hemispheric specialization in pitch perception, recent studies have begun to investigate specialization of areas within the auditory cortices. Studies of primates have demonstrated the importance of the secondary auditory cortex in the tonotopic organization of pitch (Figure 2). Recent neuroimaging studies of human subjects have also implicated the importance of the secondary auditory association centers in complex pitch processing. When

subjects were examined listening to sequentially varied pitches—that is, a melody—increased activity was found beyond Heschl's Gyrus in the superior temporal gyrus and planum polare. Research in music perception implicates possible dissociation between the perception of pitch height (the octave of a pitch) and pitch chroma (the note within the octave). A recent fMRI study offers a potential neural correlate, indicating that regions anterior to the primary auditory cortex are important for pitch chroma while the posterior regions are important in the perception of pitch height.

Absolute Pitch

One particular area of pitch perception is of specific relevance to the discussion comparing the effects of musical training, musical exposure, and innate musical predisposition. Absolute pitch is the ability to identify a musical note by pitch without reference to any other sound. Genetic factors are implicated since absolute pitch is exceeding rare – even among musicians, has a sibling recurrence rate of 8-15%, and seems to be distributed differently across human populations. However environmental factors are clearly important, since absolute pitch requires musical training before the age of twelve in order to manifest itself.

Through neuroimaging studies, the functional and structural correlates of absolute pitch are beginning to be identified. Investigations of the structural correlates of absolute pitch show that musicians with absolute pitch show a greater leftward asymmetry of the planum temporale than non-musicians or musicians without absolute pitch. A follow-up study indicated that this asymmetry results not from an enhancement of the left superior temporal cortex but rather from a structural reduction of the right planum temporale in those with absolute pitch. While these results suggest that a developmental "pruning effect" may be needed for acquisition of absolute pitch, the possible relationship between innate brain structure and predisposition for absolute pitch need be further explored.

A functional neuroimaging study using PET demonstrated that musicians without absolute pitch show greater activity in the right inferior frontal cortex, a region important for working memory for pitch, when making judgments of musical intervals compared to those with absolute pitch. Additionally, absolute pitch possessors show greater activation in the left posterior dorsolateral frontal cortex, a region associated with conditional associations in memory. This region was active in all subjects in tasks requiring the identification of musical intervals but uniquely active in those with absolute pitch when listening to single tones, possibly correlating mnemonic association with the ability to identify pitch without relative reference.

Timbre

Another fundamental aspect of music is timbre, or tone color, the psychoacoustic property of sound that permits us to differentiate between two different musical instruments playing at the same pitch. The perception of timbre relies on the acoustic properties of the spectra (harmonics) and timing (envelope) and therefore the cognition of timbre relies upon the neural regions important in the processing of pitch.

Imaging studies focusing on the alteration of spectrally dissimilar sounds demonstrate activity in the superior temporal lobes, especially Heschl's gyrus and the superior temporal sulcus, with a degree of right-lateralization. These findings are reinforced by data from patients who have undergone temporal lobectomy. Patients with right temporal lobe excisions show deficits in the discrimination of changes in timbre compared to left temporal lobe excision and normal control groups. Since the perception of timbre relies upon the fine spectral and temporal aspects of sound, deficits in timbral

perception are usually described in conjunction with deficits in pitch perception. However, in one particularly unique case, a patient, following a right temporal stroke, lost the ability to discriminate between the timbre of previously familiar musical instruments while retaining normal perception of melody, rhythm and other musical aspects.

Rhythm

The term *rhythm* is often used to describe broad macroscopic temporal patterns in music that encompass the structural musical elements of pulse, meter, and rhythmic grouping. Pulse or beat is the periodic repetition of acoustic stimuli in time, such as the unaccented "ticks" of the metronome. The speed of the underlying pulse of music defines the tempo of a piece of music, often measured in "beats-per-minute". Meter is defined by regularly recurring patterns of stressed ("strong") and unstressed ("weak") beats, and in some notated music is regulated by the presence of a time-signature. A more precise definition of rhythm is the subjective perception of groupings of accented and unaccented beats, which vary in length and relationship over time.

Because rhythm develops over time, the perception of rhythmic patterns involves brain regions important in temporal processing. In music, meter and rhythm are often intimately linked with movement, such as in dance or the urge to tap your foot to beat. The production of a timed motor response from an external stimulus involves a network including the sensorimotor cortices, superior temporal gyrus, cerebellum, and basal ganglia. Less well understood are the correlates of temporal perception without motoric reproduction, such as in tasks of passive rhythmic perception.

Early and contradicting lesion studies implicated both the left and right temporal cortices in the process of rhythmic sequences. More recent studies implicate a possible divergence in the perception of metric and rhythmic groupings . Damage to the temporal lobe in the right hemisphere impairs perception of meter whereas left-lateralized damage impairs the discrimination of rhythmic patterns, however such differences may only reflect the subtle differences in task and stimuli.

The specialization and complex interactions of the left and right hemispheres in the perception of temporal structures is not well understood. One fMRI study indicates separate processes in the cognition of metric (musical) rhythms and non-metric (non-musical) rhythms. Musical rhythms caused activation in the left premotor and left parietal areas and the right anterior cerebellar lobe, while non-musical rhythms led to activity in the right prefrontal, right premotor, right parietal areas as well as in the bilateral cerebellar posterior lobe (Figure 3).

Further evidence of a leftward dominance for temporal processing implicates the recruitment of the "language areas" in the perception of rhythmic patterns. Imaging studies of passive rhythmic perception show increased activation in the left inferior frontal gyrus, including Broca's area (BA 44/5) and BA 47. A case study of a subject with Wernicke's aphasia demonstrated a severe deficit in the perception of rhythm compared to pitch and melodic perception, indicating the importance of Wernicke's area (BA22) in rhythmic perception. Additionally, musicians show increased activity in the left-hemisphere in the passive perception of rhythm compared to non-musician, suggesting that hemispheric specialization for rhythm perception can be enhanced by musical training.

Musical Structure

Music, much like language, is governed by rules and syntax (grammar). In Western tonal music, these rules are governed by a metric structure, a hierarchy of musical keys, the order of chord progressions (tonality), and rules of harmony (counterpoint). Only very recently have researchers begun to investigate the neurological correlates of the perception of musical structure and syntax.

The majority of studies have focused on identifying the effects of presenting syntactically irregular chords within a structured harmonic sequence. Converging data from neuroimaging and electroencephalographic studies indicate that violations of tonality activate the inferior frontal regions including Broca's area (BA 44/5) and its homologue in the right hemisphere and BA 47, as well as the posterior temporal regions including Wernicke's area. Since both Broca's and Wernicke's areas are crucial in the processing of language this evidence indicates a significant overlap of these "language areas" in the syntactic processing of both language and music.

However musical syntax involves a complex set of rules and harmonic relationships that extend beyond simple expectation of correct or incorrect chords. Isolating brain regions involved in this syntactic processing is rather difficult, especially since the correlates of the basic elements of music perception, such as pitch and rhythm, are not fully understood. For instance, a specific musical key (e.g., C-major or G-minor) determines both the pitch content (musical scale) and chords (harmony) permitted in a tonal musical phrase. In Western tonality, the various 24 different major and minor keys are cyclically inter-related based on a hierarchy prescribed in the musical "circle of fifths", and this hierarchy regulates the perceptual distance of musical keys and chords. An fMRI study designed to investigate the perception of melodic contour as a function of tonality (modulated through all 24 musical keys) implicates the rostromedial prefrontal cortex as a unique region that maintains a relative topographic map of tonality. These findings suggest a possible neural substrate for the perceptive ability to maintain the integrity of a melody despite musical transposition.

Musical Semantics

Although the issue of whether non-vocal music carriers any inherent semantics is highly controversial, music certainly has the power to convey culturally relevant interpretations and associations. One study measured the N400 component of the event-related brain potential during the presentation of "semantically" related words and musical excerpts, such as the word *staircase* and an ascending musical scale. The findings argue that words with descriptive, qualitative, structural, or abstract similarities to a particular musical excerpt activate a response pattern similar to semantically related word and sentence pairs, indicating that superficial semantic interpretations of certain musical aspects might be shared. These finding, while provocative, underscore the need for further investigation of the effects of environment factors such as culture, language, and training on music perception and interpretation.

Musical Memory and Imagery

Memory is crucial to the perception of music since the macroscopic structures of melody, rhythm and harmony unfold over periods of time. Working memory for pitch requires the interaction of the right temporal and right frontal cortices, indicated by imaging and lesion studies. Measurements of cerebral blood flow using positron emission tomography during tasks of recognition and identification of music as "familiar" show a broad network of activation including the bilateral superior temporal cortices; bilateral orbital, medial, and inferior frontal regions; precuneus; angular gyrus; and parahippocampal gyrus.

Musical imagery is the subjective task of imaging music in the absence of auditory input. When subjects were asked to imagine the continuation of a truncated musical stimuli, activation was observed in the inferior frontal and superior temporal regions and well as the supplementary motor areas. In addition, measurements of the topography of event-related potentials (ERP) found that activity in the imagination of the continuation of a melody is similar to the pattern activity when auditory stimuli is not withheld, further indicating that musical imagination employs auditory regions even in the absence of acoustic stimuli.

Emotion

Since music is ultimately abstract, the interpretation and understanding of music is highly subjective depending on culture, degree of musical training, and personal preference. Nevertheless, the power of music to elicit particularly strong emotive responses is well-recognized. At first glance this association seems quite unusual; however, neurophysiological investigations indicate that these emotive responses to music are associated with primitive neural systems associated with basic survival mechanisms, perhaps explaining why music has persisted through history despite the absence of any obvious evolutionary benefits. These associations between limbic structures and musical perception provide a potentially contradictory viewpoint to theories that postulate music to be the evolutionary side effect of an auditory system that has become specialized for language.

A seminal study used PET imaging to monitor neural responses to subject-selected music that elicited "chills" down the spine. Increases in the subjective intensity of the emotive experience correlated to changes of cerebral blood flow in the ventral striatum, dorsal midbrain, amygdala, orbitofrontal cortex, and ventral medial prefrontal cortex—regions associated with processing of reward and pleasure, such as hunger and sexual drive. Similar imaging studies have also shown correlation between pleasant responses to music and activity in the subcallosal cingulate gyrus, prefrontal anterior cingulate, retrosplenial cortex, hippocampus; the nucleus accumbens, ventral tegmental area, hypothalamus, and insula, the inferior frontal gyrus, Heschl's gyrus, and the Rolandic operculum. Increasingly dissonant music correlated with increased activity in the right parahippocampal gyrus and right precuneus (Figure 4).

Lesion based studies indicate both functional and structural dissociations between music perception and emotional responses to music. The recognition of emotional tone can be spared even when basic perception and recognition of music is impaired. Conversely, deficits in response to emotion in music are described even when basic music perception is unimpaired. A single case study found that following an infarction involving left amygdala and insula the patient lost the "shiver down the spine" phenomenon he had previously experienced when listening to Rachmaninoff, but retained both pitch and speech perception.

Furthermore, the neurological correlates of the emotional responses to music seem to vary based on the subjective perception of emotional tone. Patients with either left or right medial temporal lobe resections, including the amygdala but sparing the superior temporal gyrus, were found to be impaired in the recognition of "scary" music, but unimpaired in the recognition of "happy" or "sad" music. Another patient with complete bilateral damage relatively restricted to the amygdala was selectively impaired in the recognition of "scary" music, but was able to identify "happy" music as well as the control group. In a similar study, patients with significant loss of the parahippocampal cortex were unable to identify "unpleasant" music but able to identify consonant music as pleasing. Another subject with significant impairment in tasks of music perception caused by bilateral lesions to the auditory cortex was found to be indifferent to musical dissonance but able to identify music as either "happy" or "sad" as well as the normal controls. When taken together, these results imply that the emotive interpretation of consonance and dissonance relies initially on the perceptional organization of sound in the superior temporal gyri and other neocortical regions that is subsequently relayed to limbic and paralimbic regions responsible for affective responses.

Musical Training

Professional musicians achieve expertise through years of rigorous training, usually starting at an early age. Studies comparing skilled musicians and non-musicians demonstrate both morphological and functional differences in the musical brain. Such differences provide the opportunity to investigate the effects of musical training on brain plasticity and reorganization. Imaging studies comparing musicians and non-musicians have shown structural differences in the motor cortex, the somatosensory and superior-parietal areas; the auditory cortex, the corpus callosum, and cerebellum (Figure 5).

In addition to the anatomical differences of musicians and non-musicians, functional differences in brain organization have also been observed. Neuroimaging studies comparing musicians and non-musicians have demonstrated differences of activity in the auditory cortex; motor cortices; and cerebellum. These studies reveal both enhancements and reductions of activity, suggesting the complex effects of musical training on brain reorganization. One such MEG study demonstrated an enhanced cortical representation of the four fingers of the left hand used in string playing compared to the non-musicians and the right hand of the string players themselves. Furthermore, increases in the cortical representation of the somatosensory and auditory areas in skilled musicians has been shown to correlate with age at which musical training was begun.

Some of the plastic effects of musical training can relate to the musician's specific area of training. Orchestra conductors show a superior spatial processing in the auditory periphery, reflecting the skill of localizing the sounds of various musical instruments in space. Instrumental performers show a preference to their own musical instrument in both functional and morphological enhancements of the auditory cortex, further indicating long-term training-induced plasticity. But even short periods of intense musical training can cause functional brain reorganization. While differences certainly exist in the musical brain, the precise nature and complex interaction of these structural and function brain changes caused by musical training are little understood. Furthermore, the relationship between brain structure and function and innate musical predisposition prior to training has not yet been fully explored.

Music and Culture

While music is universally present across cultures, the subjective interpretation of music depends on a host of factors including culture, musical exposure, and musical training. Culturally specific definitions of music vary to such a degree that what is deemed highly musical in one culture may be perceived as completely unmusical in another. The majority of studies of the neural correlates of music perception have focused on subjects and stimuli from Western musical traditions. Yet, the functional and structural differences found between musician and non-musicians invite investigation into possible effects of cultural exposure on music perception.

Subjects culturally exposed to Western music react to violations of musical syntax at a very young age, when musically untrained, when distracted, and even when explicitly primed for the violation. Furthermore, acquisition of implicit musical expectation seems to occur early in development, possibly within the first year of development.

Only a few studies have explicitly investigated the correlates between music perception and cultural exposure. Subjects show a behavioral preference in the ability to synchronize with culturally specific music and electroencephalography (EEG) data indicate cultural-specific differences in listening strategies of musical phrase, musical instrument, and musical scale. However, while the processing of a familiar language may use distinct brain regions, one functional imaging study found no differences in the processing of culturally familiar and unfamiliar music – only differences correlating to the degree of musical training that were culturally independent.

Conclusion

The various ways music is perceived, performed, learned, identified, and interpreted indicate a broad system of complex neurological interactions involving a wide array of brain regions and structures. Historically, investigations of the cognitive neuroscience of music strive to isolate regions and processes associated with the individual aspects of music. Emerging neuroimaging literature continues to isolate substrates responsible for the perception of individual elements of music. While many argue this dissection of musical stimuli threatens the "ecological validity" of music, this improving understanding of basic musical elements undoubtedly provides a foundation for future macroscopic comparisons and investigations. Ideally, an eventual convergence of musicologic, psychologic and neuroimaging data will extend our knowledge to advanced concepts of musical learning, performance, and composition, as well as the complex questions surrounding the innate musical ability and musical creativity.

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Figures

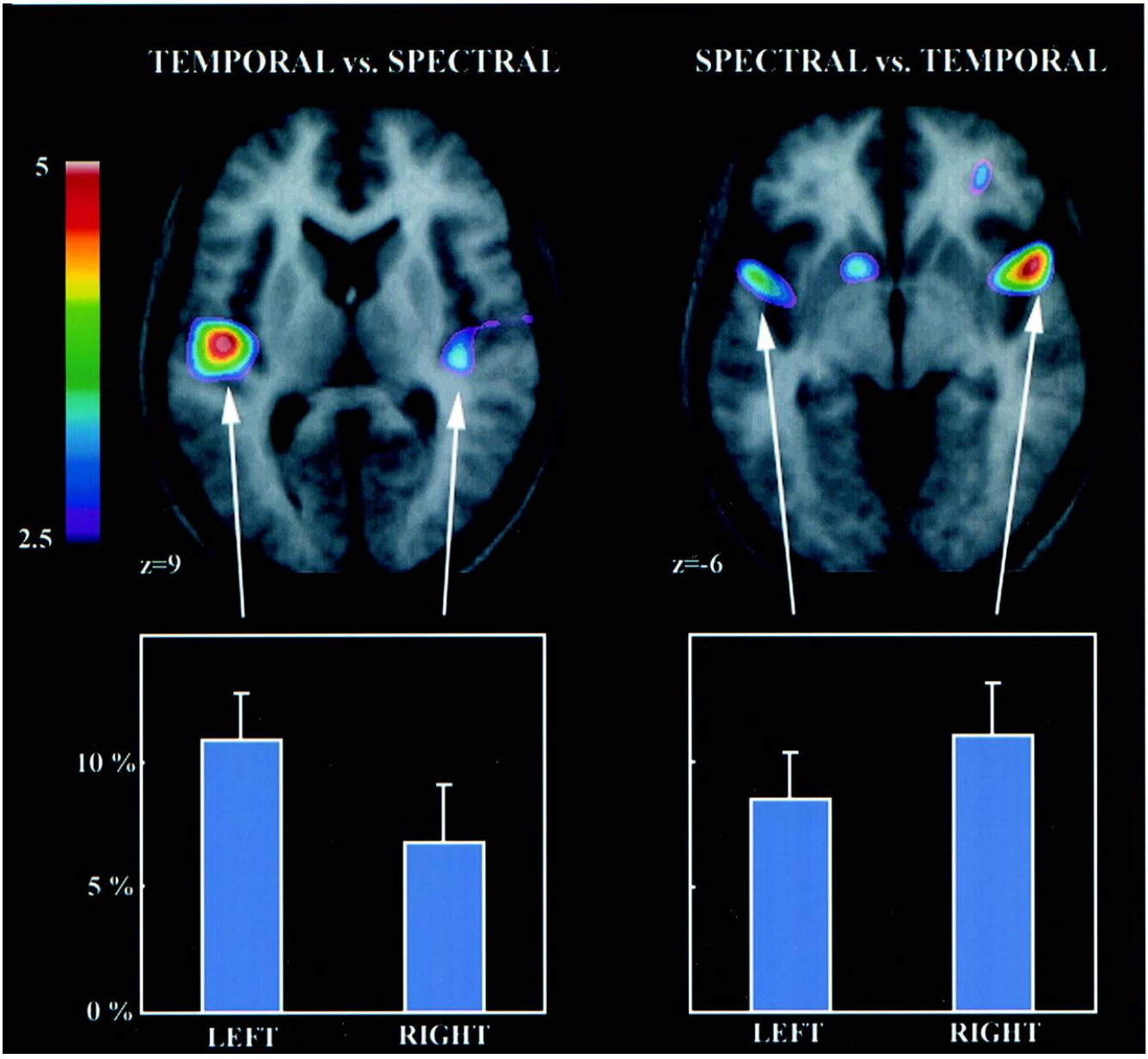


Figure 1. Merged PET and MRI volumes corresponding to the direct comparison of temporal and spectral conditions to one another. The image on the left shows a horizontal section taken through the region of Heschl's gyri, which showed significantly greater activity in the combined temporal conditions than in the combined spectral conditions. The section on the right is taken through the maxima corresponding to the anterior superior temporal region which showed a greater response to the spectral conditions than to the temporal conditions. The bar graphs illustrate the percent difference between condition in regions of interest taken from corresponding locations. Reprinted by permission from Oxford University Press: Cerebral Cortex, Zatorre RJ and Belin P. "Spectral and temporal processing in human auditory cortex." 11:949 (2001).

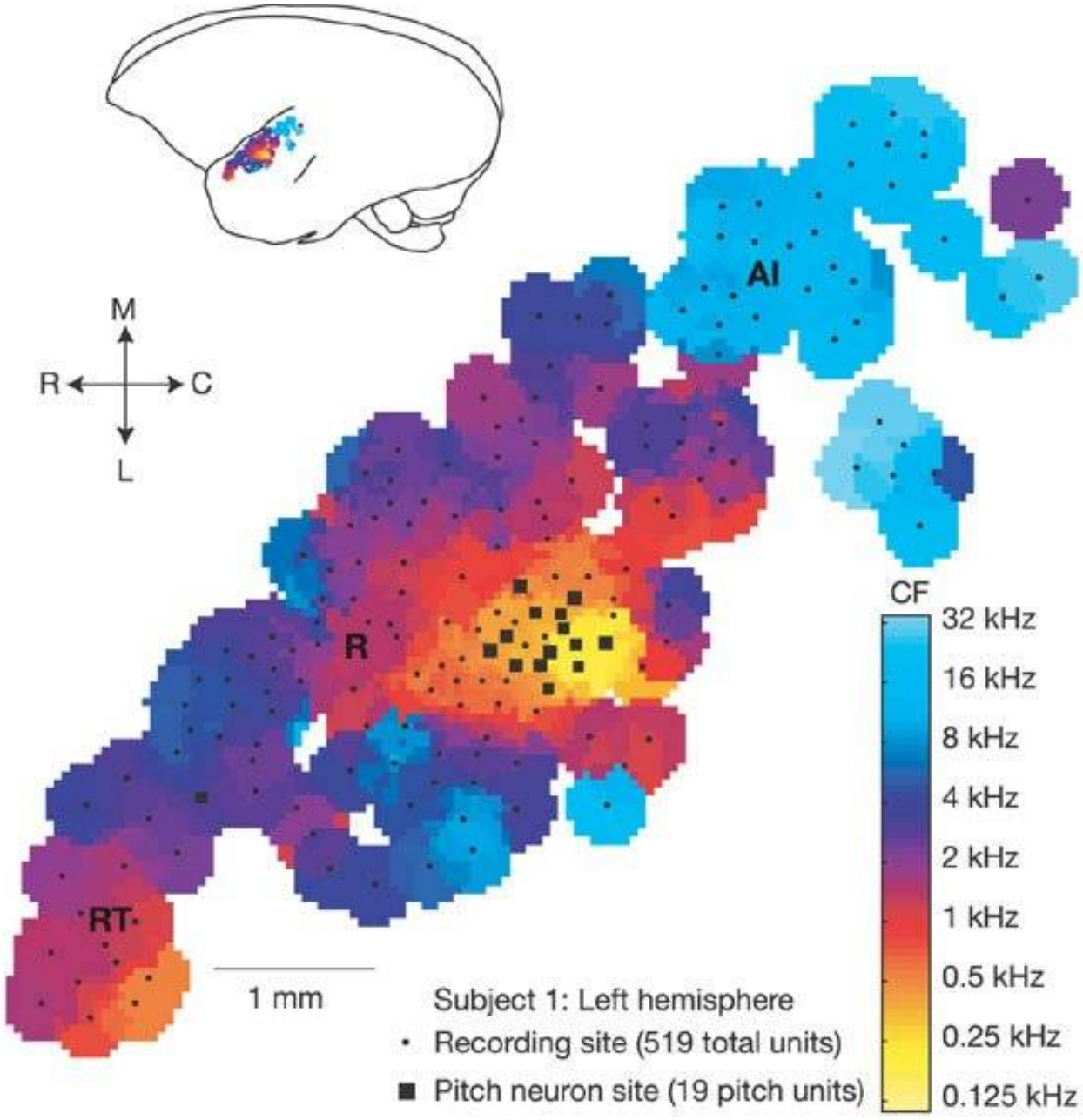


Figure 2. Characteristic frequency topographical map from the left hemisphere of one marmoset. Pitch-selective neurons (black squares) were found clustered near the anterolateral border of primary auditory cortex (AI). Frequency reversals indicate the borders between AI/R and R/RT (rostral temporal field). Adapted by permission from Macmillan Publishers Ltd: Nature, Bendor, D. and Wang, X. "The neuronal representation of pitch in primate auditory cortex." 436:1163 (2005).

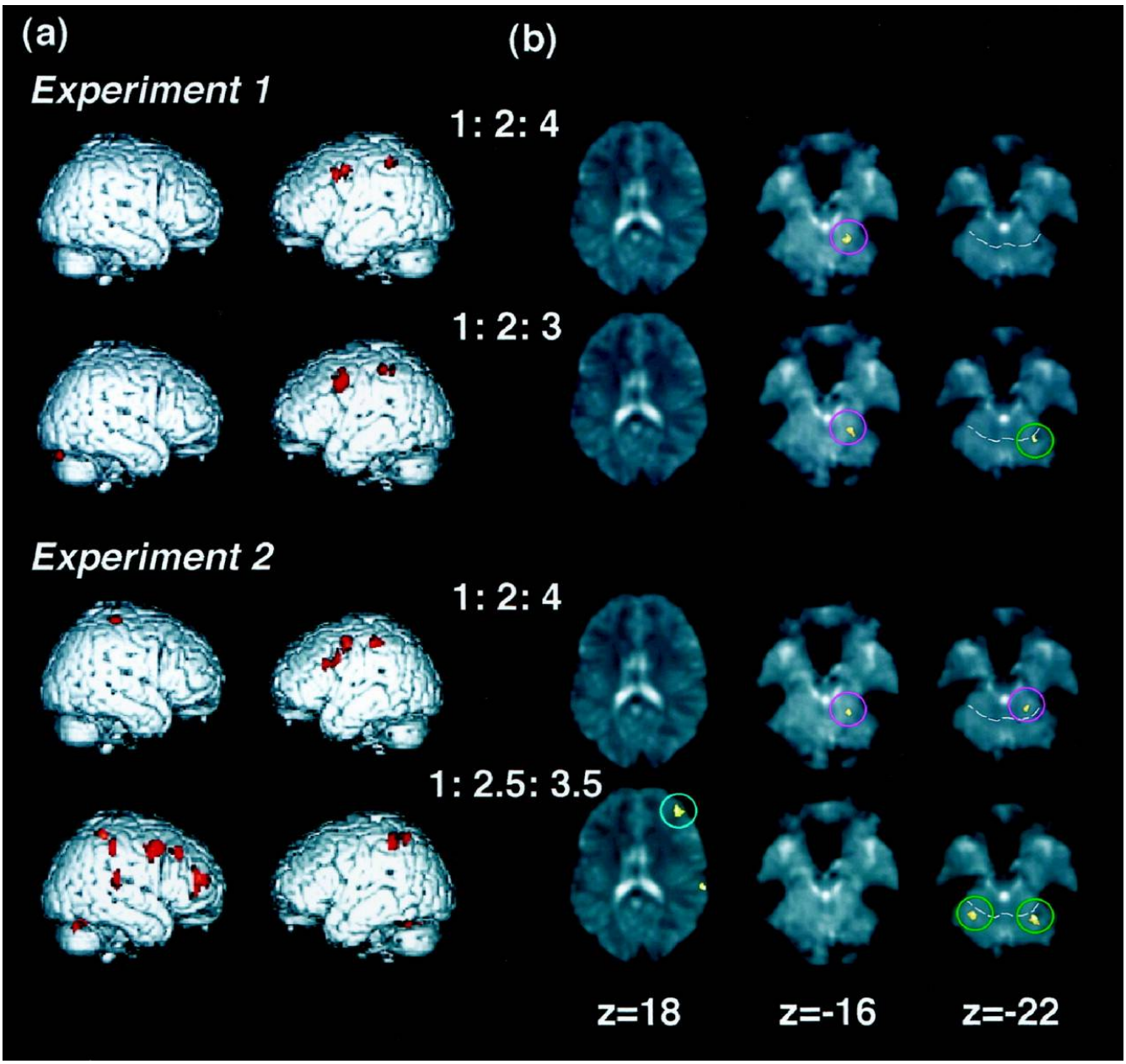


Figure 3. (A) Statistical parametric activation maps of the six subjects when 1:2:4, 1:2:3, and 1:2.5:3.5 rhythms were respectively compared with controls (activations are shown in *red)*. (B) Activation foci in *a* are shown in three axial slices though the prefrontal cortex (*blue circle*), cerebellar anterior lobe (*pink circle*), and cerebellar posterior lobe (*green circle*). *White dotted lines* in the cerebellum indicate the primary fissure that separates the anterior and posterior lobes of the cerebellum. Reprinted by permission: Journal of Neuroscience, Sakai K *et al.* "Neural representation of a rhythm depends on its interval ratio." 19:1078 (1999).

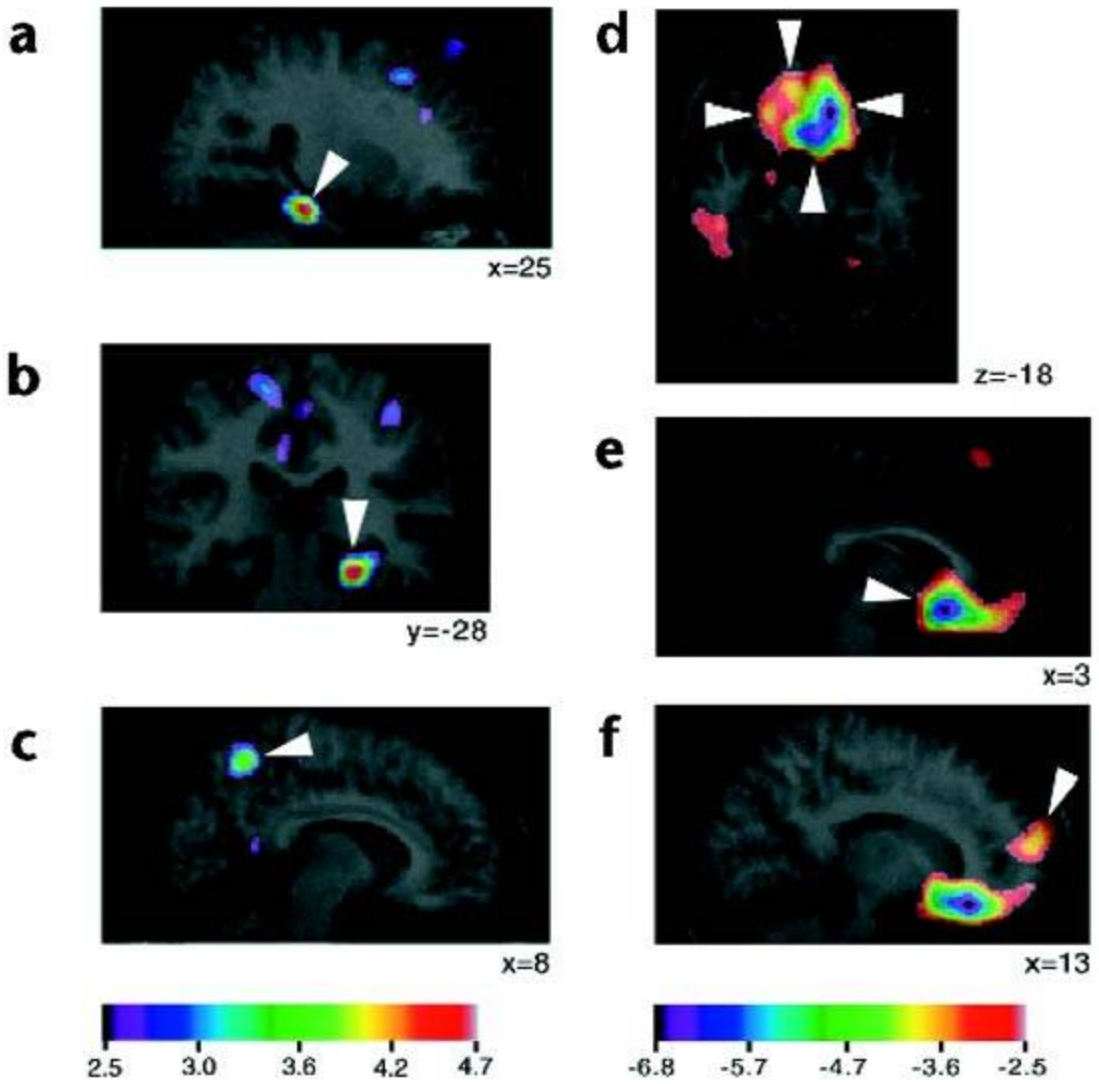


Figure 4. Cortical regions demonstrating significant regional cerebral blood flow correlations with dissonance level. Correlations are shown as *t*-statistic images superimposed on corresponding averaged MRI scans. The *t*-statistic ranges for each set of images are coded by color scales below each column, corresponding to images **(a-c)** and **(d-f)**. **(a-c)** Positive correlations with increasing dissonance demonstrated rCBF activity in right parahippocampal gyrus and right precuneus. **(d−f)** Negative correlations with increasing dissonance (equivalent to positive correlations with increasing consonance) demonstrated rCBF activity in bilateral orbitofrontal cortex, medial subcallosal cingulate and right frontal polar regions. Reprinted by permission from Macmillan Publishers Ltd: Nature Neuroscience, Blood AJ, Zatorre RJ, Bermudez P, *et al*. "Emotional responses to pleasant and unpleasant music correlate with activity in paralimbic brain regions." 2:384 (1999).

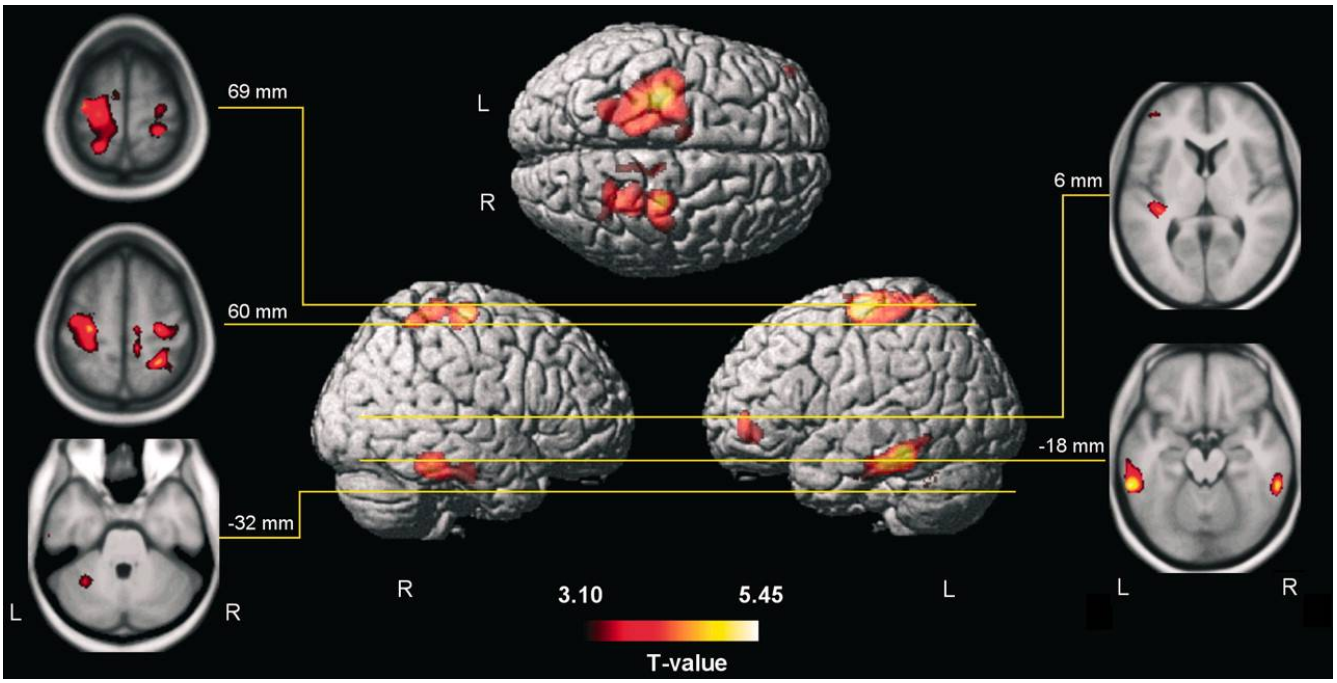


Figure 5. Brain regions with gray matter differences between professional musicians, amateur musicians, and non-musicians. The musician status was modeled as a three-level gradation in which professional musicians were ranked highest, amateur musicians were ranked intermediate, and non-musicians were ranked lowest. Only those voxels with a significant positive correlation between musician status and increase in gray matter volume are shown ($p < 0.05$; corrected for multiple comparisons). These clusters were overlaid on the rendered cortex surface of a selected single subject. Yellow lines indicate selected cuts through this brain, and the corresponding axial slices are shown in the left and right panels. These axial slices show the overlay of the results onto the average of all single anatomical images. Reprinted by permission: Journal of Neuroscience, Gaser C and Schlaug G. "Brain structures differ between musicians and non-musicians." 23:9242 (2003).