

**ATTENTIONAL AND AFFECTIVE RESPONSES TO
COMPLEX MUSICAL RHYTHMS**

by

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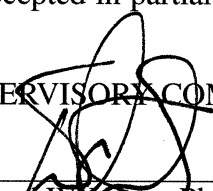
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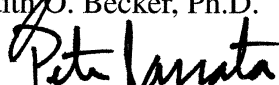
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This dissertation was prepared under the direction of the candidate's dissertation advisor, Dr. Edward W. Large, Program in Complex Systems and Brain Sciences, and has been approved by the members of her supervisory committee. It was submitted to the faculty of the Charles E. Schmidt College of Science and was accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

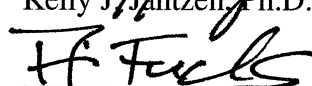
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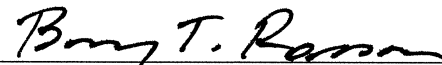

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ABSTRACT

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I investigated how two types of rhythmic complexity, syncopation and tempo fluctuation, affect the neural and behavioral responses of listeners. The aim of Experiment 1 was to explore the role of attention in pulse and meter perception using complex rhythms. A selective attention paradigm was used in which participants attended either to a complex auditory rhythm or a visually presented list of words. Performance on a reproduction task was used to gauge whether participants were attending to the appropriate stimulus. Selective attention to rhythms led to increased BOLD (Blood Oxygen Level-Dependent) responses in basal ganglia, and basal ganglia activity was observed only after the rhythms had cycled enough times for a stable pulse percept to develop. These observations show that attention is needed to recruit motor activations associated with the perception of pulse in complex rhythms. Moreover, attention to the auditory stimulus enhanced activity in an attentional sensory network including primary auditory, insula, anterior cingulate, and prefrontal cortex, and suppressed activity in sensory areas associated with attending to the visual stimulus. In Experiment 2, the effect of tempo fluctuation in expressive music on emotional responding in musically experienced and inexperienced listeners was

investigated. Participants listened to a skilled music performance, including natural fluctuations in timing and sound intensity that musicians use to evoke emotional responses, and a mechanical performance of the same piece, that served as a control. Participants reported emotional responses on a 2-dimensional rating scale (arousal and valence), before and after fMRI scanning. During fMRI scanning, participants listened without reporting emotional responses. Tempo fluctuations predicted emotional arousal ratings for all listeners. Expressive performance was associated with BOLD increases in limbic areas for all listeners and in limbic and reward related areas for those with musical experience. Activity in the dorsal anterior cingulate, which may reflect temporal expectancy, was also dependent on the musical experience of the listener. Changes in tempo correlated with activity in a mirror neuron network in all listeners, and mirror neuron activity was associated with emotional arousal in experienced listeners. These results suggest that emotional responding to music occurs through an empathic motor resonance.

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CHAPTER 1

INTRODUCTION

The transformation of an auditory stimulus into a coherent musical percept is a complex high-level cognitive capacity that necessarily involves an extensive network of brain areas involved in perception, attention, learning, memory, and emotion. Music, like language, uses sound, organized into a complex temporally structured sequence of events, for communication. Music is universal, occurring in all known human cultures, however, the form music takes is culture specific and requires learning. Also like language, some aspects of music seem to rely on innate human capacities, for example, the ability to perceive a pulse is present at birth (Winkler et al., 2009). However, in contrast to language, music does not refer to the external world. Rather, music connects with the inner world of emotion, affect, and, subjective experience. The universality of music, its power to communicate subjective feeling, and the presence of some musical qualities at birth, suggest that music may be a useful tool for probing the fundamental dynamics of the brain. In this dissertation, music, and, more specifically, musical rhythm, is used to further understand two important aspects of cognition: attention and emotion. In Experiment 1, the role of attention in the perception of rhythmic complexity is investigated, and in Experiment 2, the effect of rhythmic complexity on emotional responses is explored.

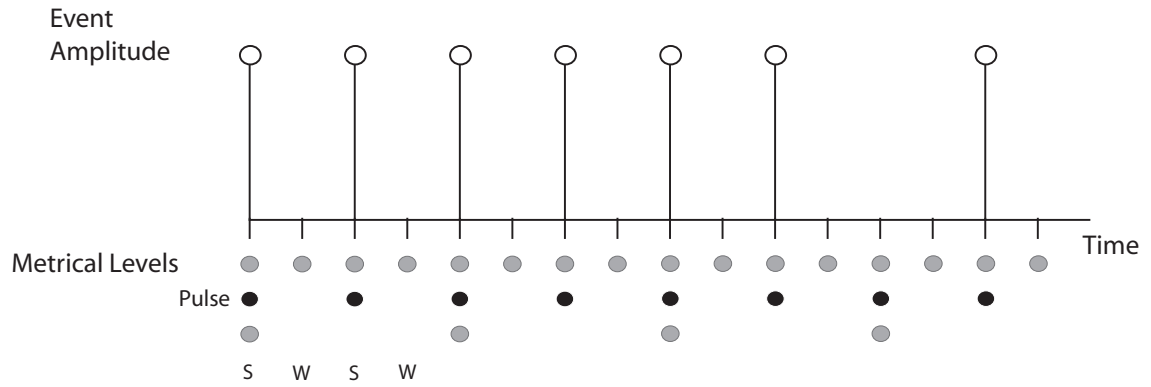
1.1 Pulse, Meter, and Attention

1.1.1 Rhythmic Complexity

Rhythms in music are complex sequences of acoustic events made up of repeating patterns of alternating sounds and silences that flow in time. *Pulse*, or beat, is the perceived periodicity of a rhythm, while *metrical accent*, or *meter*, refers to the perception of alternating stronger and weaker pulses. Figure 1.1a illustrates these concepts using the notation of Lerdahl and Jackendoff (1983). Pulse and meter are thought to correspond to temporal expectations, which are expectations for when rhythmic events should occur (e.g., Large & Jones, 1999; London, 2004). Pulse and meter develop over time through a process called *induction*, and rhythms that give rise to pulse and meter perception are called *metrical rhythms*. Metrical rhythms are easier to remember and reproduce than rhythms that are less likely to give rise to metrical percepts (See also Essens & Povel, 1985; Grahn & Brett, 2007). The degree of metricality affects the precision of the temporal encoding of rhythmic sequences (Grube & Griffiths, 2009), and pulse and meter are thought to enable synchronistic entrainment of body movements to complex musical rhythms (Large, 2000).

This dissertation considers two types of rhythmic complexity in music: syncopation and tempo fluctuation. Syncopated rhythms contain event onsets that violate the expectancy for acoustic events to occur on strong beats (Figure 1.1b). With tempo fluctuation, the tempo of the rhythmic pattern changes while the underlying metrical structure remains constant. In both cases, pulse tends towards generalized synchrony with musical rhythm, whether or not the rhythmic pattern itself is periodic or more complex (Large, 2008). For example, a periodic pulse is commonly perceived in syncopated rhythms even when no corresponding (objective) periodicity exists among the acoustic events that com-

a. Metrical structure and accent



b. Syncopation

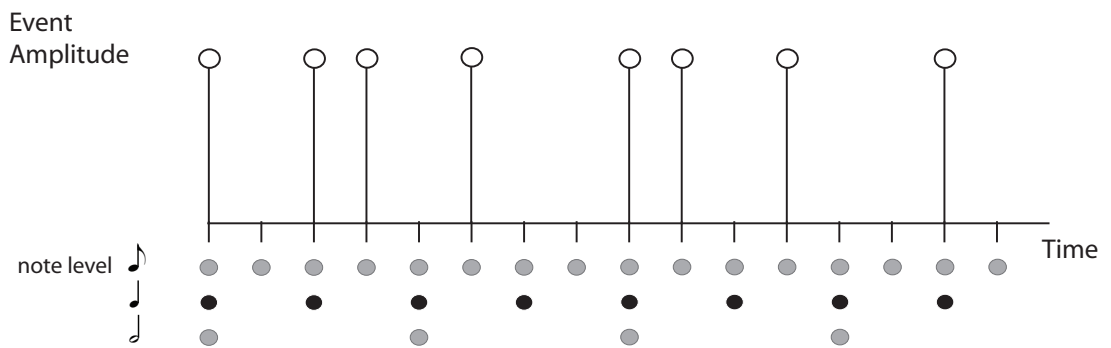


Figure 1.1: An illustration of the concepts of rhythm, beat, pulse, meter, and syncopation. S = Strong beat, W = Weak beat. Note that the syncopation example shows violation of expectation based on metrical structure of strong/weak beats, with the absence of events on some strong beats and the presence of events on weak beats.

prise the rhythm (Patel et al., 2005). Nevertheless, for highly syncopated sequences, pulse and meter induction often take longer (Snyder & Krumhansl, 2001), and may sometimes be unsuccessful (Patel et al., 2005). Similarly, it has been shown that listeners are able to perceive and tap the pulse of naturalistic music containing large tempo fluctuations, although there may be increased tap variability and synchronization may sometimes be unsuccessful (Rankin, Large, & Fink, 2009). This thesis addresses 1) the role of attention to syncopated rhythms in pulse perception, and 2) the relationship of tempo fluctuation in performed music to the emotional and neural responses of listeners.

1.1.2 Neuroimaging Rhythm, Pulse, and Meter

Investigations of the neural circuitry underlying rhythm and meter perception reveal overlap between brain regions sensitive to the production of rhythmic sequences and those related to movement (Chen, Penhune, & Zatorre, 2008b; Chen, Zatorre, & Penhune, 2006; Dhamala et al., 2003; Karabanov et al., 2009; Thaut et al., 2009). Rhythm perception recruits motor related areas even in the absence of overt movement, showing activity in pre-motor cortex (PMC) (Bengtsson et al., 2009; Chen, Penhune, & Zatorre, 2008a; Grahn & Brett, 2007; Schubotz, Friederici, & Cramon, 2000), cerebellum (Bengtsson et al., 2009; Chen et al., 2008a; Grahn & Brett, 2007; Schubotz et al., 2000), pre-supplementary motor area (pre-SMA) (Bengtsson et al., 2009; Grahn & Brett, 2007; Schubotz et al., 2000), supplementary motor area (SMA) (Bengtsson et al., 2009; Chen et al., 2008a; Grahn & Brett, 2007; Schubotz et al., 2000), and basal ganglia (Grahn & Brett, 2007; Schubotz et al., 2000). Moreover, basal ganglia and SMA have been implicated specifically in pulse and meter perception and have been shown to be more active while listening to metrical rhythms than in listening to rhythms not likely to induce a pulse percept (Grahn & Brett, 2007). The role of basal ganglia in mediating pulse perception is further supported by the finding that Parkinsons patients do not show the same benefit for beat-based rhythms as

normal controls in a rhythm discrimination task (Grahn & Brett, 2009).

The foregoing results stress that the perception of pulse and meter involves integration across widespread auditory and motor related brain regions (Stewart et al., 2006; Todd, O'Boyle, & Lee, 1999; Warren, Wise, & Warren, 2005; Zatorre, Chen, & Penhune, 2007). It has been proposed that the interaction between auditory and motor networks is mediated through the dorsal auditory pathway that leads from posterior superior temporal gyrus (planum temporale, PT) to prefrontal, premotor (PMC), and motor cortices (Warren et al., 2005; Zatorre et al., 2007). The dorsal auditory pathway is activated in the production of rhythmic sequences regardless of whether the rhythm was learned through auditory or visual modalities, suggesting that all rhythms learned for the purposes of production, at least with short-term training, are maintained through an auditory-motor representation (Karabanov et al., 2009). Both the PT and PMC have been shown to be recruited when tapping to increasingly metrical rhythms (Chen et al., 2006), to be functionally correlated when tapping to increasingly complex rhythms (Chen et al., 2008b), and to be active during passive listening to rhythms (Chen et al., 2008a).

What is the nature of the interaction between auditory and motor areas? Recent studies have found that the time course of high frequency neural activity in certain brain areas provides a good temporal correlate of pulse and meter perception. For example, using electroencephalography (EEG), Snyder and Large (2005) reported anticipatory beta and gamma (20-60 Hz) activity when passively listening to an isochronous loud/soft pattern and when single tones were occasionally omitted. Subsequent work employing similar stimuli with magnetoencephalography (MEG) found that beta band activity (~ 20 Hz) localized to auditory cortex followed the same periodic pattern as the stimulus, whereas gamma oscillations (~ 40 Hz) in auditory cortex appeared to play an anticipatory role in beat perception (Fujioka et al., 2009). The foregoing results suggest that activity in the beta/gamma range synchronizes with and predicts events in rhythmic stimuli and could

be related to the experience of pulse and rhythmic expectancy. Using MEG, Iversen, Repp, and Patel (2009) showed a link between activity in the beta band (20-30 Hz) and subjective metrical interpretation of an ambiguous three-beat phrase. Because of the role that beta band activity plays in motor processes (McFarland et al., 2000; Stanck Jr & Pfurtscheller, 1996) and in long-range coordination of brain areas (Brovelli et al., 2004; Kopell et al., 2000), the authors suggested that the modulation of beta band activity might indicate internal modulation of auditory responses by the motor system.

The EEG and MEG results are consistent with the postulate that neural oscillation underlies the experience of pulse and meter (Large, 2000; Large & Kolen, 1994). Entrainment of neural oscillations explains how the perception of pulse and meter could arise from listening to complex sequences and how rhythmic expectancies develop over time (Large, 2008; Large & Palmer, 2002). Dynamic attending theory (DAT) conceptualizes neural oscillations as attending rhythms that target attentional energy toward expected points in time (Large & Jones, 1999), and perceptual facilitation of temporally expected events has been observed in a number of studies (Barnes & Jones, 2000; Jones & McAuley, 2005; Jones et al., 2002; Jones & Yee, 1997; Large & Jones, 1999; McAuley & Kidd, 1995; Quene & Port, 2005). Conceiving of attentional rhythms as rhythmic bursts of high-frequency oscillations may also provide an explanation for how attention coordinates the interaction between auditory and motor areas (Large & Snyder, 2009). Bursts of beta and gamma band activity (Izhikevich, 2007) could provide a mechanism for rhythmic communication between distant brain regions.

If attentional high-frequency bursting mediates temporal coordination between brain areas, then attention may be required for the integration of auditory sensory and motor areas in the perception of complex rhythmic structures. Neural responses to metrical changes (Geiser et al., 2009) and behavioral responses to tempo changes have been shown to be attention dependent (Repp & Keller, 2004). Thus, it is possible that pulse and meter

perception in complex rhythms is also attention dependent. If so, activation differences should be seen in auditory and motor areas depending on whether attention is directed toward or away from a rhythmic stimulus. To test this hypothesis, Experiment 1 required participants to selectively attend to either a complex rhythmic sequence or a visually presented list of words so that activation related specifically to auditory attention to complex rhythms could be observed.

1.2 Emotion in Music

1.2.1 Measuring Responses to Music

Rhythmic complexity and temporal expectancy have also been linked to the communication of emotion through music, and to the emotional experience evoked by music listening. Although we know a great deal about peoples' ability to detect and recognize emotional stimuli, we know less about affective responses that people experience in natural settings. Precise quantification of emotional reactions and their associated brain responses is challenging because emotional responses are often dynamic experiences that unfold on several timescales. Emotional responses to identical stimuli vary among people, adding to the difficulty of linking specific stimulus parameters to individual responses. Moreover, measuring and imaging emotional responses simultaneously is problematic because explicit instructions to monitor and report emotional reactions can interfere with the affective responses one is attempting to measure (Neale & Liebert, 1986). Music has a number of key properties that make it an excellent model system for the study of emotion, addressing some of these issues. It is an ecologically valid stimulus that is used every day across cultures to communicate and modulate emotion. It is a dynamic stimulus whose parameters evolve over timescales ranging from fractions of a second to minutes. Furthermore, the existence of populations with and without music performance experience

allows for the opportunity to explore the role of learning and experience in modifying the relationship between a stimulus and its associated emotional response. In Experiment 2, the dynamics of emotional responding to a natural music performance was investigated, focusing on the role of changing stimulus parameters and listener experience.

Previous neuroimaging work has revealed the involvement of several brain areas in emotional responses to music, focusing on contrasting musical attributes such as consonant/dissonant, pleasant/unpleasant, and happy/sad. Not surprisingly, areas associated with emotion processing and reward in general are also involved in emotional responding to music. Parahippocampus and precuneus activity were found to increase in response to increasing dissonance of short chord sequences (for review see Blood et al., 1999), whereas increasing consonance was associated with activation of orbitofrontal and frontopolar cortices and subcallosal cingulate, a region implicated in emotion processing (Phan et al., 2002; Royet et al., 2000). Similarly, Koelsch, Fritz et al. (2006) found unpleasant, compared to pleasant, excerpts activated parahippocampal gyrus as well as amygdala, and the temporal poles. Listening to pleasant, relative to unpleasant, music was associated with activation of insula, inferior frontal gyrus (IFG, including Brodmann Area (BA) 44), and the ventral striatum, a key structure in reward and addiction circuits (Berridge & Robinson, 2003; Knutson et al., 2001; Koob & Moal, 1997). In another study, listening to pleasant, unfamiliar instrumental music (compared to silence) led to increased regional cerebral blood flow (rCBF) in prefrontal cortex, insula, subcallosal cingulate, nucleus accumbens (part of the ventral striatum) and anterior cingulate (Brown, Martinez, & Parsons, 2004). Levitin and Menon (2003) found blood oxygen level dependent (BOLD) response increases in non-musicians for normal versus temporally scrambled musical excerpts in IFG (BA 47), anterior cingulate, nucleus accumbens, brainstem, and posterior cerebellar vermis. These participants also showed increased BOLD responses in reward related brain areas for the normal excerpts and another group of non-musicians rated

the normal versions as more pleasant than the scrambled versions (Menon & Levitin, 2005). Similar emotion and reward related networks were found to be associated with increasing pleasurable chill ratings in response to listening to self-selected musical excerpts (Blood & Zatorre, 2001) and while listening to music rated as happy (versus sad; Mitterschiffthaler et al., 2007). Thus current research has identified the broad neural circuitry associated with positive and negative affect in music. However, these approaches did not tackle the issue of how specific stimulus parameters may give rise to emotional responses.

Behavioral studies of emotion in music have focused on the role of specific musical parameters in communication accuracy (Juslin, 2001). In this approach, performers are asked to record short musical excerpts in a way that will convey basic emotions, such as anger, fear or joy. Listeners then attempt to name the basic emotion that the performance was intended to convey. Regardless of musical training or cultural background, people are generally able to name the intended emotion providing evidence that the expression of basic emotions (happiness, sadness, and fear) in music can be recognized universally (e.g., Balkwill & Thompson, 1999; Fritz et al., 2009). Listener judgments of intended emotion have been linked to specific musical features, including tempo, articulation, intensity, and timbre (Gabrielsson & Juslin, 1996; Juslin, 2000; Juslin & Laukka, 2003; Juslin & Sloboda, 2001 for review). These studies have mostly used short excerpts and required participants to express their responses using single word labels. Thus, while listeners recognize intended emotions, it is possible that they do not actually experience emotional responses to music in such tasks (cf., Schubert, 2001). Furthermore, short excerpts and discrete categories employed in many behavioral and neuroimaging studies do not capture the dynamic aspect of musical emotion (Meyer, 1956; Schubert, 2001; Sloboda & Juslin, 2001).

In order to explore dynamic affective responses of listeners to entire pieces of music, Schubert (1999, 2001, 2004) developed a continuous response paradigm in which

listeners report perceived emotion in real-time in a 2-dimensional emotion space (Schubert, 1999), with emotional valence and arousal as the orthogonal dimensions (Russell & Pratt, 1980). In one such study, Schubert (2004) used four compositions to capture a wide range of music feature variations. Schubert explicitly instructed participants to report “the emotion the music (is) trying to express,” not their own emotional experiences. Musical variables such as melodic contour, tempo, loudness, texture, and timbral sharpness, were shown to predict emotion ratings. Interestingly, tempo and loudness accounted for over 60% of the variance along the emotional arousal dimension. Experiment 2 differs from Schubert’s approach in two important ways. First, the relationship between musical feature variations and emotional responses is measured *within* performances rather than *across* performances. Second, listeners were asked to report the emotion that they experienced, rather than the emotion they believed the music was trying to express.

1.2.2 Emotion and Temporal Expectancy

Experiment 2 focuses on the dynamic fluctuations in performance parameters that musicians use to be expressive. The notion that fluctuations in performance parameters may be a fundamental emotive cue is supported by the fact that pianists express structural and emotional interpretation dynamically by varying tempo and sound intensity. Fluctuating tempo in music performance is one way of violating temporal expectancy. Sloboda and Lehmann (2001) showed that in music performance, changes in tempo and sound intensity are correlated with one another, and with real-time ratings of emotional arousal. They also showed a systematic relationship between emotionality ratings, timing, and loudness when listeners rated their moment-to-moment level of perceived emotionality while listening to music performances. Bhatara et al. (2009) created versions of music performances in which changes in timing and intensity were parametrically manipulated, and asked participants to rate the emotional expressivity. Emotional judgments mono-

tonically decreased with performance variability, and timing changes were found to explain more variance in reported emotional expressivity than sound intensity. Furthermore, musically experienced listeners were more sensitive to performance expression than less experienced listeners. Additionally, Koelsch et al. (2008) showed that emotion-related physiological and neural responses to unexpected chords were greater when the chords were played in an expressive context.

Why—and how—would dynamic changes in tempo and sound intensity shape the emotional experiences of listeners? One widely held view is that expectancy violations cause dynamic affective responses to music (Meyer, 1956). Musical expectancy and expectancy violations have been shown to give rise to characteristic behavioral and neural responses (Koelsch et al., 2008; Sloboda, 1991; Sloboda & Lehmann, 2001; Steinbeis, Koelsch, & Sloboda, 2006), and the theory of expectancy has been extended to the temporal domain (Jones, 1976; Large & Jones, 1999; McAuley, 1995). The latter approach suggests that oscillations in the sensory cortices entrain to events in an attended auditory stream (Large & Jones, 1999). Empirical support for the temporal expectancy hypothesis has been found in humans (Snyder & Large, 2005) and monkeys (Lakatos et al., 2008). Temporal expectancy violations are responded to behaviorally, for example, by adaptation of the period and phase of taps in response to changes in tempo (Large, Fink, & Kelso, 2002; Repp & Keller, 2004). It has been shown that temporal expectancies are not purely periodic. Both musicians' and non-musicians' temporal expectations deviate from periodicity in ways that are related to musical structure and correlate with tempo fluctuations typical of expressive performance (for review see Repp, 2005), and these fluctuations enable prediction of some aspects of tempo fluctuation in performed music (Rankin et al., 2009; Repp, 2002). However, measured fluctuations of temporal expectancies are of a far smaller magnitude than tempo fluctuations present in performed music (Repp, 1998) and prediction of tempo fluctuations explains only a portion of the variance in entrain-

ment tasks (Rankin et al., 2009; Repp, 2002). The proportion of variance left unexplained after the prediction response has been accounted for (Rankin et al., 2009) and is what we consider to be 'deviation from temporal expectancy'. The hypothesis of Experiment 2 is that temporal expectancy violations might also evoke emotional responses. Neural responses to temporal expectancy violations have been demonstrated in beta and gamma band oscillations (Fujioka et al., 2008; Snyder & Large, 2005; Zanto et al., 2005). Moreover, it has recently been shown that temporal unpredictability in the auditory domain is sufficient to produce amygdala activation in mice and humans (Herry et al., 2007). The expressive performance used in Experiment 2 contained large tempo fluctuations and long-range temporal correlations, and, in a previous experiment, the relative phase of participants' taps indexed violations of temporal expectancies (Rankin et al., 2009). Thus, tempo fluctuations in this performance were predicted to evoke emotional responses in listeners.

CHAPTER 2

NEURAL RESPONSES TO COMPLEX AUDITORY RHYTHMS: THE ROLE OF ATTENDING

Experiment 1 was designed to uncover neural activation associated with attending to complex rhythms. Syncopated stimuli were constructed such that observed neural correlates of pulse perception would necessarily reflect endogenous processes, not merely responses to acoustic events in the rhythmic stimulus. For these stimuli, it was hypothesized that activations in auditory and motor areas associated with pulse and meter perception would depend on whether attention was directed toward or away from the rhythm. Specifically, activity in motor areas thought to support pulse perception, such as basal ganglia and SMA, was expected to be seen when participants selectively attended to the rhythms but not when participants attended to the visual stimuli. Selective attention to the auditory rhythms was also expected to reveal modality related differences in areas known to be involved in attention, such as anterior cingulate, which, given its role in error detection (Bush, Luu, & Posner, 2000), could be implicated in temporal expectancy as well. Selectively attending to rhythms was further expected to modulate activity in cortex specific to the modality (e.g., greater primary auditory activity seen when attending to the rhythms, Johnson & Zatorre, 2006; Lakatos et al., 2008; Woodruff et al., 1996). Because these stimuli were complex rhythms with no intensity cues, pulse induction depended in part

upon repetition of the rhythmic pattern and was expected to unfold over two or more pattern repetitions. Therefore, it was hypothesized that activations in pulse-related areas, such as basal ganglia and SMA, would be observed only after a sufficient number of pattern repetitions.

2.1 Methods

2.1.1 Participants

Thirteen participants, five female and seven male (aged 20–46 years, M 28.83= years), gave informed consent before participating in the study. Musical experience ranged from 0-24 years (1 had 24 years experience playing music, 3 had 20 years experience, 1 had 7 years playing experience, 1 had 2 years experience and 7 had no experience playing music.)

2.1.2 Stimuli and Task

Auditory and visual stimuli were presented simultaneously in the fMRI scanner in two conditions 1) *auditory* and 2) *visual*. Participants were instructed to either 1) attend to rhythmic patterns while ignoring visual stimuli or 2) attend to visual stimuli while ignoring the rhythms. Performance on auditory and visual reproduction tasks was used to gauge whether participants were attending to the appropriate stimulus. This allowed us to directly compare activity associated with actively attending to complex rhythms with activity related to passive exposure to rhythmic stimuli. Two stages of rhythm perception were investigated, an early phase during which pulse and meter are first induced and a later phase in which the listener has developed a stable pulse and meter percept.

Auditory Stimulus. Ten complex rhythms were based on a metrical grid with sixteen beats at the eighth-note metrical level, and eight (strong) beats at the quarter-note level (the pulse). Each of the eighth-note level beats was the possible temporal location of an acoustic event. Acoustic events were 440 Hz pure tones with a duration of 80 ms and 10 ms rise and fall times. The inter-beat-interval (IBI) at the eighth-note level was 250 ms and each pattern was 4 sec long. Syncopated patterns were constructed as follows. Each pattern contained eight tones. The first tone always occurred on the first beat (which was a strong beat) and the final beat (a weak beat) always contained a rest (i.e., a tone never occurred on the last beat). The remaining seven tones were distributed such that half of the tones of the pattern occurred on strong beats and half occurred on weak beats. Thus, each pattern was expected to give rise to a basic pulse at 500 ms (i.e., the quarter-note level of the metrical grid) but would be highly syncopated (half of the pulse times would not be marked by a tone onset; see Figure 2.2). Fourier analysis of the rhythms verified that none of the patterns contained significant energy at the pulse frequency (i.e., $1/0.500 \text{ sec} = 2 \text{ Hz}$). A higher pitched 880 Hz tone began and ended the interval in which participants were asked to reproduce the rhythm. The auditory stimulus was adjusted to a comfortable listening level.

Visual Stimulus. Participants looked at a fixation-cross surrounded by 3 letter words (see Figure 2.1) while they listened to the rhythmic patterns. Words were randomly selected from a list of 300 three-letter English words. The visual stimulus was arranged in such a way that the participant could see the entire word list even though s/he was fixating on the cross. The same word list/auditory pattern pairing was used in both auditory and visual conditions.

elm row bib
yen X ear
dab pew ace

Figure 2.1: Visual stimuli consisted of eight words surrounding a central fixation point.

Auditory Task. In the auditory condition, the participant was instructed to attend to the rhythmic pattern, which repeated for six cycles (*attend* = 24 sec), mentally rehearse the rhythm for the duration of three cycles (*rehearsal* = 12 sec), and reproduce the rhythm for three cycles (*reproduction* = 12 sec). The rhythm reproductions corresponded to the events illustrated in Figure 2.2. The stimulus presentation portion of the experiment was divided into two parts, termed *attend 1* (first 3 repetitions–12 seconds) and *attend 2* (second 3 repetitions–12 seconds). Stimulus presentation was continuous through both Attend 1 and Attend 2.

Visual Task. In the visual condition, the participant was instructed to attend to the words surrounding the fixation cross (*attend* = 24 sec), rehearse them in memory once the words disappeared (*rehearsal* = 12 sec), and then report the remembered words (*reproduction* = 12 sec).

Pulse perception and synchronization. Prior to participating in the fMRI experiment, participants were tested to determine whether they could perceive the pulse of the complex rhythmic stimuli using a pulse perception and synchronization paradigm (cf. Patel et al., 2005). Participants were seated in an IAC sound-attenuated experimental chamber wearing Sennheiser HD250 linear II headphones. The rhythms were presented by a custom Max/MSP program running on a Macintosh G3 computer. Participants tapped on a Roland Handsonic HPD-15 drumpad that sent the time and velocity of the taps via MIDI¹

¹Musical Instrument Digital Interface

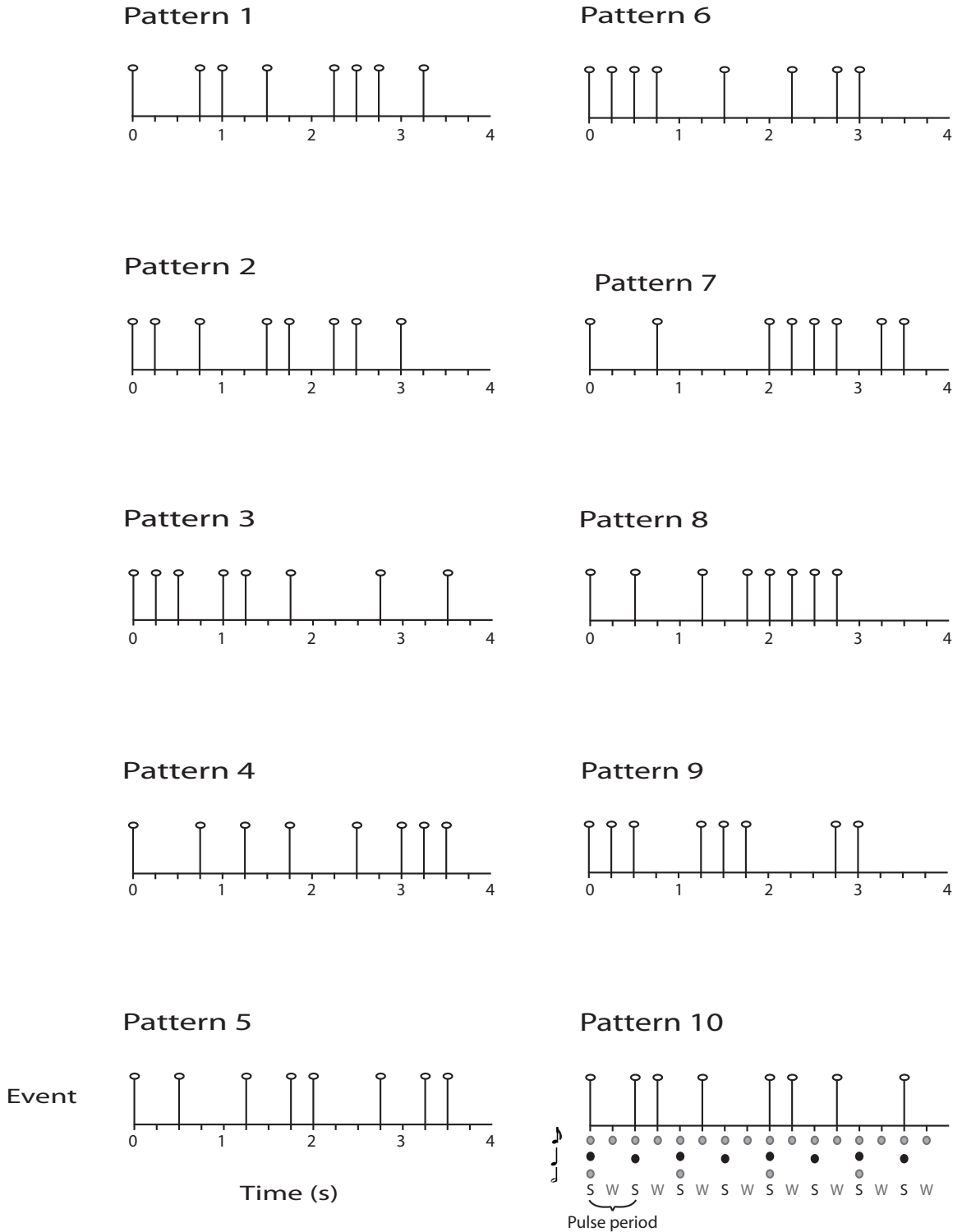


Figure 2.2: Auditory stimuli consisted of ten syncopated rhythms each with sixteen event positions (placed at an IBI of 250 ms) and eight acoustic events. This figure also illustrates the pulse rate at which participants were asked to tap to during the pulse perception and synchronization task (corresponding to the strong beats (S), pulse rate = 500 ms).

to the Max/MSP program. The experimenter instructed participants to listen to the pattern and begin tapping the pulse when they could “feel the beat” at a rate equal to that at which they would “normally tap (their) foot to a song.” The experimenter demonstrated tapping the pulse for two practice patterns (not used in the study) at a rate corresponding to the pulse (strong beats) illustrated in Figure 2.2. Participants were encouraged to practice pulse synchronization while listening to the practice patterns. Once they felt comfortable synchronizing with the practice patterns, participants began the experiment.

2.1.3 Magnetic Resonance Imaging

As a correlate for neural activity, changes in blood oxygenation (BOLD response) were measured using echo planar imaging on a 3.0 T Signa Scanner equipped with real time fMRI capabilities (General Electric Medical Systems, Milwaukee, WI). Echo-planar images were collected using a single shot, gradient-echo, echo planar pulse sequence (field of view (FOV) = 24 cm, echo time (TE) = 35 ms, flip angle (FA) = 90°, in plane matrix = 64 x 64). All images were collected using a sparse sampling technique with an effective repetition time (TR) of 12 seconds. Adequate coverage of the brain was achieved by collecting thirty interleaved 5 mm thick axial slices with no spacing between (voxel size = 3.75 x 3.75 x 5 mm). Immediately following the functional imaging, high resolution anatomical spoiled gradient-recalled at steady state (SPGR) images (5 mm thick, no spacing, number of excitations = 2, TE = in phase, TR = 325 ms, FA = 90°, in plane resolution 256 x 256, bandwidth = 31.25) were collected at the same slice locations as the functional images. Using an 8-channel head coil another set of high resolution FSPGR images (1 mm thick, no spacing, 180 locs per slab, TE = min full, TR = prep time 400 ms, FA = 12°, in plane resolution 256 x 256, bandwidth = 31.25) were collected.

Acquisition. A sparse sampling technique was used in the scanner to increase the signal response from baseline (which was silence) and to avoid nonlinear interaction of the scanner sound and the auditory stimulus (Figure 2.3). Participants were presented six 10-minute blocks (3 auditory attend, 3 visual attend conditions), with 10 trials in each block. A custom Visual Basic 5 program running on a Dell Optiplex GX260 was used to generate both sound and visual stimuli. Sound stimuli were presented using custom noise-attenuating headphones (Avotec Inc., Stuart, FL). Visual stimuli were presented through a set of fiber optic goggles (Avotec Inc., Stuart, FL) mounted to the head-coil. Participants were instructed to tap with their right index finger on an MR compatible button box.

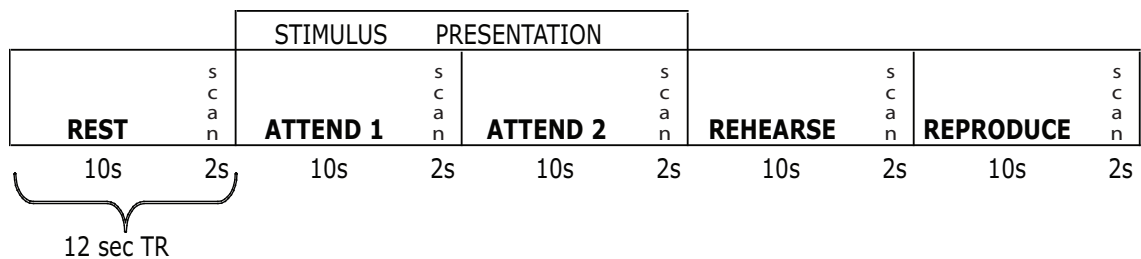


Figure 2.3: A schematic representation of the fMRI scanning session for both auditory and visual conditions. A sparse sampling approach was adopted by clustering image acquisition into a 2 second interval preceded by 10 seconds of scanner silence. This approach gave an effective TR of 12 seconds.

2.1.4 Data Analysis

Behavioral measures. Performance on the pulse perception and synchronization task was measured by calculating the synchronization coefficient, also called vector strength (Batschelet, 1980; Pikovsky, 2000), which quantified how well taps were time-locked to the perceived pulse of the rhythms. Synchronization coefficients ranged from 0 (no synchronization) to 1 (perfect synchronization). Performance on the rhythm reproduction task was measured by correlating the participants inter-tap-intervals (ITI) with the inter-onset-intervals (IOI) of the rhythms.

fMRI. Successful reproduction of the rhythmic patterns indicated attention to the auditory task. In the *attend auditory* condition, trials in which the participant correctly reproduced the pattern were used in the fMRI analysis. Exclusion criteria for rhythm reproduction trials were based in part on the correlation between the participants ITIs and the IOIs of the rhythms. In addition, two judges listened to each reproduction and agreed on whether or not participants had tapped the qualitatively correct pattern. The judgment allowed us to retain four trials in which the participant tapped the correct pattern but did not have a high ITI/IOI correlation (e.g., because they started tapping in the middle of the pattern). Similarly, *attend visual* trials in which participants remembered 3 or more words were included in the fMRI analysis. There were not a sufficient number of unsuccessful rhythm reproductions to compare trials in which reproduction was successful to trials in which participants were not able to reproduce the rhythms accurately (103/390 trials were unsuccessful).

Except where noted, data analysis was performed using AFNI (Cox, 1996; Cox & Hyde, 1997) running on an Apple G5. Functional data sets were corrected for motion and smoothed spatially by convolution with a Gaussian kernel (FWHM 4mm). Data was high-pass filtered at 1/90 seconds ($\sim .0111\text{Hz}$) to correct for low frequency drift. A hemodynamic response function (HRF) was convolved with a binary vector representing the off/on timing of each condition to create a model time series. Multiple regression was used to determine the contribution of the model to the data at each voxel. Functional images were registered to a template brain in the coordinate system of Talairach and Tournoux (1988) using SPM2 (Wellcome Department of Imaging Neuroscience, London) using a two step process. First the high resolution SPGR image of each participant was registered to the template brain. Second, the same transformation matrix was applied to each of the low-resolution functional images. Group analysis was conducted by submitting individual beta weights to one sample *t*-tests. To correct for multiple comparisons,

a Monte Carlo simulation was conducted to determine the random distribution of voxel cluster sizes for a given threshold (for similar approaches see, Ledberg, Åekerman, & Roland, 1998). A corrected alpha of $p < 0.002$ was achieved by the combination of a per voxel threshold of $p < 0.01$ and a cluster size of 8 contiguous voxels (512mm^3).

2.2 Results

2.2.1 Behavioral measures

The mean time to begin pulse synchronization was 1.37 pattern repetitions (equal to 5.48 sec, $SD = .93\text{sec}$). Therefore, participants perceived and attempted to synchronize with the pulse about halfway through the second repetition of the pattern. A wide range of synchronization coefficients was observed in the pulse perception and synchronization task ($r_{sync} = .28$ to $r_{sync} = .93$, mean $r_{sync} = .60$). Performance on the rhythm reproduction task varied as well ($r_{corr} = .32$ to $r_{corr} = .88$, mean $r_{corr} = .62$). Thus, some participants had an easier time perceiving and synchronizing to the pulse and some participants had an easier time reproducing the rhythmic patterns. Correlation analysis revealed a significant relationship between performance on the pulse perception and synchronization task and rhythm reproduction task ($r = .58, p < .04$). Thus, the ability to perceive the pulse of a complex rhythm predicted the ability to accurately reproduce the rhythm, as has been previously observed (Essens & Povel, 1985).

2.2.2 fMRI

In evaluating the imaging results the auditory conditions were first compared to rest. BOLD signal increases during *auditory attend 1* (Figure 2.4, Table 2.1) were restricted to bilateral superior temporal gyrus (STG, BA 22,41) in areas compatible with primary auditory cortex. Similar activity in primary and secondary auditory areas (BA 41, 22)

was associated with *auditory attend 2* (Figure 2.4, Table 2.1). Additionally, for *auditory attend 2* An increase in the BOLD response was observed in motor areas including left SMA, right basal ganglia (caudate, globus pallidus, extending into nucleus accumbens), and left postcentral gyrus (BA 3).

Table 2.1: Auditory Condition Activations (compared to Rest)

REGION (cluster peak)	BA	Cluster includes	X	Y	Z	Volume (mm ³)	Activation
<u>Attend 1</u>							
L STG	41	22	-58	-25	8	6016	positive
R STG	22	41, 42	58	-17	4	3200	positive
R SFG	9	medial FG (9,10), cingulate, vACC (24)	2	51	32	19776	negative
L posterior cingulate	29	bilateral 30, 23, cingulate (31), precuneus (7)	-2	-41	20	18560	negative
L MTG	39	19, angular gyrus, SOG, MOG, supramarginal gyrus, IPL	-46	-69	24	6464	negative
R MOG		MTG (39), angular gyrus, supramarginal gyrus, IPL	42	-73	16	5184	negative
L IFG	47		-30	15	-12	1856	negative
R IFG	47		34	15	-12	1536	negative
L precuneus	7		-10	-57	56	1216	negative
R IFG	46		42	43	0	960	negative
L SFG	10		-26	55	0	896	negative
L cuneus	18		-2	-77	28	896	negative
L near cerebellum		R thalamus	-2	-25	-8	768	negative
R SFG	10		22	59	16	768	negative
R MTG	21		46	-5	-12	704	negative
L MTG			-46	-21	-12	640	negative
L ITG	37		-54	-57	-8	640	negative
L cerebellar declive		fusiform gyrus (37), parahippocampal gyrus (36)	-22	-53	-12	576	negative
R culmen		parahippocampal gyrus (36)	18	-41	-8	576	negative
R thalamus			10	-17	16	576	negative
<u>Attend 2</u>							
L STG	41,22		-54	-29	8	13504	positive
R STG	41,22		54	-17	4	13120	positive
L medial frontal gyrus, SMA	6		-2	-9	56	2176	positive
L postcentral gyrus/S1	3		-38	-29	52	1856	positive
R occipital lingual gyrus	17,18		6	-85	0	1344	positive
L occipital lingual gyrus	17		-14	-89	-4	896	positive
R thalamus/ basal ganglia		caudate and GP, nucleus accumbens	6	-1	4	768	positive
R middle occipital gyrus			42	-73	16	768	negative

REGION (cluster peak)	BA	Cluster includes	X	Y	Z	Volume (mm ³)	Activation
Rehearse							
L medial frontal gyrus, SMA	6	extends bilateral SMA and cingulate 24,32, R MFG (9, 10)	-2	-9	56	25280	positive
L SFG	11	extends to 9	-30	51	16	13568	positive
L postcentral gyrus/S1	3	2, precentral gyrus (4),	-38	-29	56	5248	positive
R basal ganglia		caudate, nucleus accumbens, lentiform nucleus, putamen	6	-1	4	1472	positive
L basal ganglia		lentiform nucleus, putamen, lateral globus pallidus	-18	-1	4	1280	positive
R precentral gyrus, PMC	6		50	-5	40	1280	positive
R cerebellar uvula		culmen	30	-65	-24	768	positive
L STG	22	MTG (22)	-54	-37	8	576	positive
R cerebellar culmen		parahippocampal gyrus, bilateral lingual gyrus, cuneus	2	-45	4	16832	negative
R cuneus	19		6	-81	32	3904	negative
R MOG	19		30	-77	8	2688	negative
L precuneus	7		-2	-49	56	2368	negative
L parahippocampal gyrus	27		-18	-29	-4	1728	negative
R medial FG	10	bilateral	2	63	12	1024	negative
L cerebellar uvula		pyramis	-14	-77	-32	640	negative
L cerebellar culmen			-34	-49	-20	640	negative
L posterior cingulate			-10	-49	24	640	negative
R postcentral gyrus	7		22	-49	64	576	negative
Reproduce							
L postcentral gyrus/S1	3	precentral gyrus (4), postcentral gyrus (2), IPL (40), STG (41, 22), insula (13), vPMC, bilateral SMA, cingulate	-34	-33	60	51456	positive
R cerebellum dentate		declive, culmen	18	-57	-20	6720	positive
R STG	22	MTG (21), STG (41), insula, IPL (40)	54	-25	0	4224	positive
R insula	13	precentral gyrus, STG (22), IFG (44)	50	11	4	4160	positive
R MFG	9	10	34	43	28	2816	positive
R cerebellum		uvula	22	-65	-48	2240	positive
R IPL		postcentral gyrus (2), supramarginal gyrus	50	-33	32	1664	positive
L basal ganglia		lentiform nucleus, putamen, lateral globus pallidus	-26	-13	0	1408	positive
R cuneus	19	bilateral 18, MOG (19), cuneus (17), lingual gyrus	14	-81	32	34560	negative
L parahippocampal gyrus	35	culmen, declive, fusiform gyrus	-22	-29	-12	8128	negative
L precuneus	7	bilateral	-2	-61	48	3968	negative
L IFG	47		-30	31	-8	1024	negative
R paracentral lobule		postcentral gyrus (3)	10	-37	64	768	negative
L SFG	9		-14	39	40	704	negative
L SFG/pre-SMA	6		-14	15	56	576	negative

Auditory rehearse (Figure 2.5, Table 2.1) was associated with BOLD increases in motor areas including bilateral SMA, bilateral basal ganglia (right side caudate lentiform nucleus, and putamen, extending into nucleus accumbens; left side lentiform nucleus, putamen, lateral globus pallidus), right precentral gyrus (6), left postcentral gyrus (3,2), cerebellum (uvula, culmen), left prefrontal cortex, and secondary auditory cortices.

During *auditory reproduce* (Figure 2.6, Table 2.1), increased activation was observed in left postcentral gyrus (BA 3,2, extending into precentral gyrus (BA 4), ventral PMC,

SMA, inferior parietal lobe (IPL, BA 40), left basal ganglia (lentiform nucleus, putamen, lateral globus pallidus), right cerebellum (declive culmen, uvula), bilateral inferior frontal gyrus (IFG, BA 44), as well as in primary and secondary auditory areas (mainly left lateralized).

Activations associated with attending to complex auditory rhythms were revealed by comparing *auditory attend 2* with *visual attend 2* (Figure 2.7, Table 2.2). Increased BOLD responses associated with auditory attention were seen in right basal ganglia (caudate), left primary auditory, left superior frontal gyrus (BA 8, extending into pre-SMA), and right medial prefrontal cortex (extending to bilateral anterior cingulate (ACC) and cingulate).

Activity associated with attending to a rhythm once a pulse percept had sufficient time to fully develop was uncovered by comparing *auditory attend 2* with *auditory attend 1* (Figure 2.8, Table 2.2). Increased BOLD responses were seen in left IFG (BA 47, extending into bilateral basal ganglia (caudate), nucleus accumbens), left STG (BA 22, 41, extending to insula, basal ganglia (lentiform nucleus, putamen)), left postcentral gyrus (BA 3, extending into primary and secondary auditory cortex), left medial frontal gyrus (extending to ventral ACC, cingulate (BA 24, 32)), and left dorsal ACC (BA 24).

Rehearsing rhythms compared to rehearsing words (Figure 2.9, Table 2.2) revealed greater activity in bilateral basal ganglia (lentiform nucleus, putamen, caudate), left medial frontal gyrus (BA 9, extends to bilateral cingulate, ACC (BA 24, 32), extending into anterior cingulate and pre-SMA), left postcentral gyrus (BA 3), and left primary auditory cortex.

Table 2.2: Between Condition Comparisons

REGION (cluster peak)	BA	Cluster includes	X	Y	Z	Volume (mm ³)	Activation
Auditory Attend 2 vs Visual Attend 2							
R medial frontal gyrus	9	10 and bilateral anterior cingulate 32, 24	2	47	24	7808	positive
L cingulate	31	paracentral lobule	-2	-21	40	2304	positive
L insula	13		-38	-13	0	1664	positive
L postcentral gyrus	40		-38	-33	56	896	positive
L SFG	8	pre-SMA	-2	23	48	640	positive
R basal ganglia		caudate	2	3	8	576	positive
L STG	41		-50	-29	12	576	positive
L precuneus	7	19, 18, cuneus, MOG, IOG, lingual gyrus, fusiform gyrus, declive	-18	-69	48	31104	negative
R precuneus	7	19, 18, cuneus, MOG, IOG, lingual gyrus, fusiform gyrus, declive	2	-69	44	23040	negative
R cerebellar declive		fusiform gyrus, lingual gyrus, parahippocampal gyrus, hippocampus	22	-73	-12	7808	negative
R MFG	6		26	-9	44	3712	negative
L precentral gyrus	6	vPMC	-46	3	28	2816	negative
L medial FG, SMA	6	bilateral	-6	-5	56	2816	negative
L cerebellar declive			-6	-77	-20	896	negative
L hippocampus			-30	-29	-8	896	negative
R cerebellar declive			6	-73	-20	576	negative
R cuneus	23		6	-73	8	576	negative
Auditory Attend 2 vs Auditory Attend 1							
L medial FG	9	vACC, cingulate (24, 32)	-2	51	32	13312	positive
L IFG	47	bilateral basal ganglia (caudate), nucleus accumbens	-30	15	-16	6464	positive
L STG	22	41, insula, basal ganglia (lentiform nucleus, putamen)	-50	-29	4	6080	positive
L transverse, STG	41	STG (22), insula (13)	50	-25	12	5312	positive
L postcentral gyrus, S1	3	IPL (40)	-34	-29	52	2944	positive
L MTG	39	STG (39), angular gyrus, supramarginal gyrus	-46	-61	28	2240	positive
L MTG	20		-46	-21	-12	1792	positive
L red nucleus		extends bilaterally, R substantia nigra	-2	-21	-4	896	positive
L dACC	24		6	35	8	896	positive
R MFG	9		30	31	28	896	positive
R ITG	37		-50	-69	0	768	positive
L paracentral lobule	31		-6	-21	44	704	positive
L STG		posterior insula (13)	-50	-37	16	640	positive
Auditory Rehearse vs Visual Rehearse							
L MFG	9	bilateral cingulate, ACC (24, 32), pre-SMA	2	47	24	16960	positive
R subcallosal gyrus		bilateral basal ganglia (lentiform nucleus, putamen, caudate)	22	11	-12	14784	positive
L cingulate		bilateral 24, 31, paracentral lobule	-2	-21	40	4800	positive
R lingual gyrus		MOG, IOG (18), cuneus	2	-69	0	4096	positive
L MOG	18	MOG, IOG (18), lingual gyrus	-26	-85	4	2944	positive
L postcentral gyrus, S1	3		-38	-29	56	2176	positive
L STG	41		-50	-33	12	704	positive
R hippocampus			30	-37	0	1216	negative
L precuneus	7	MTG (39)	-26	-61	36	768	negative
L fusiform gyrus			-38	-53	-4	640	negative

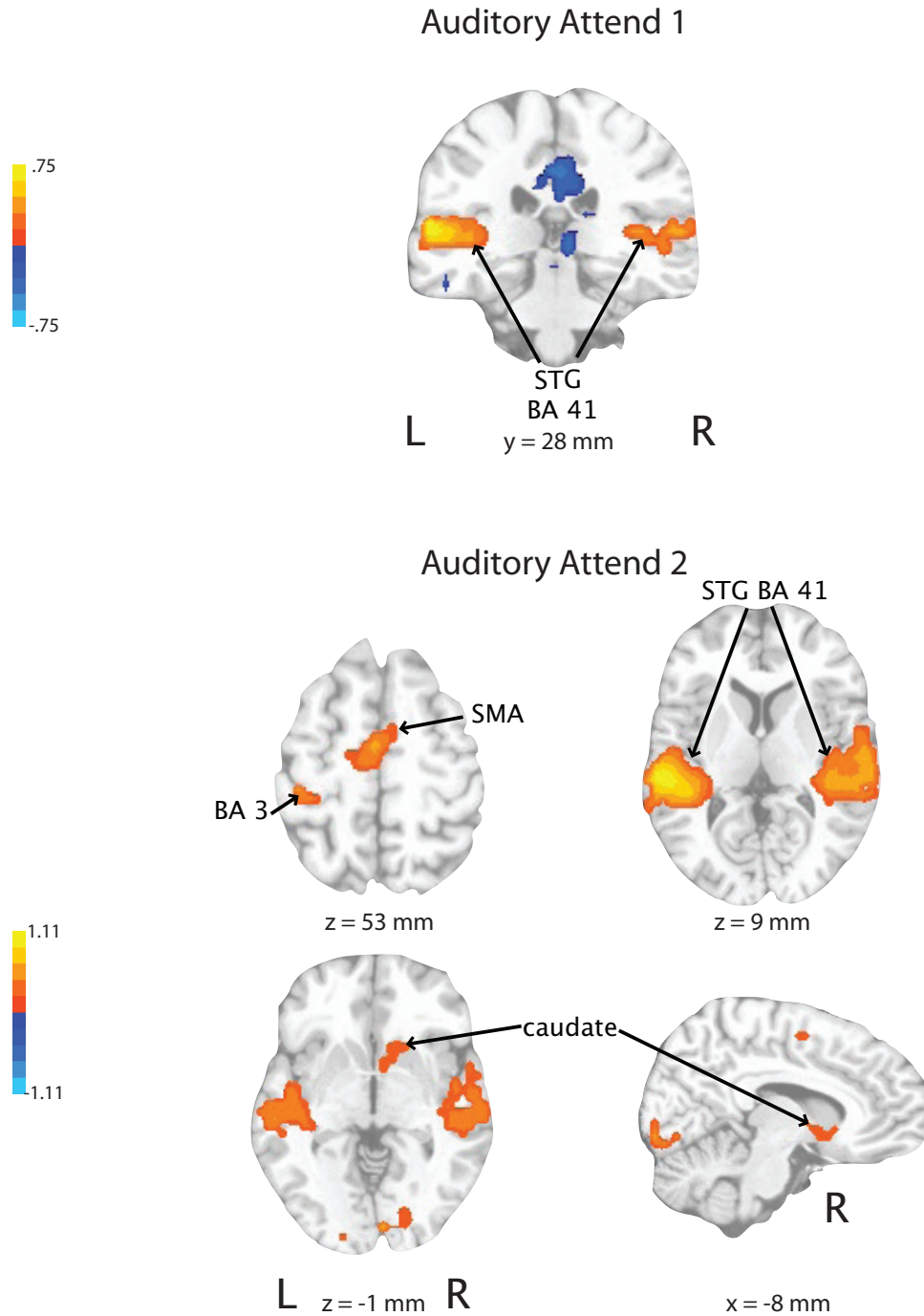


Figure 2.4: Brain regions where BOLD signal was significantly different during the *auditory attend 1* condition compared to rest ($p < 0.002$ corrected) and *auditory attend 2* compared to rest. Red to yellow colored voxels represent brain areas where *auditory attend 1* > rest and *attend 2* > rest. Blue areas show where *auditory attend 1* < rest and *auditory attend 2* < rest. The coronal slice is shown with the left (L) on the left side of the figure. The colorbar reflects t -values. STG = superior temporal gyrus, SMA = supplementary motor area.

Auditory Rehearse

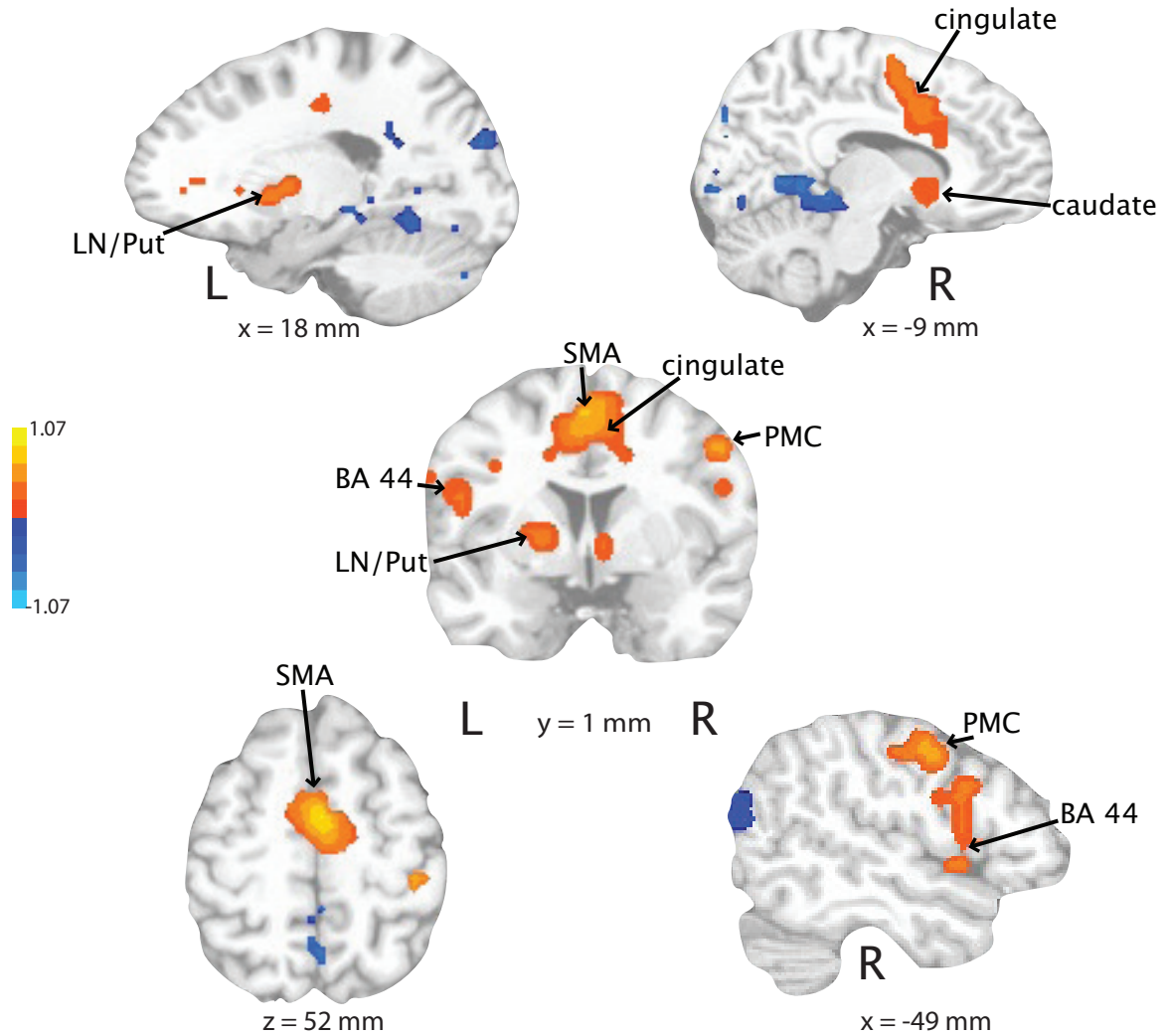


Figure 2.5: Brain regions where BOLD signal was significantly different during the *auditory rehearse* condition compared to rest ($p < 0.002$ corrected). Red to yellow colored voxels represent brain areas where *auditory rehearse* $>$ rest. Blue areas show where *auditory rehearse* $<$ rest. The coronal slice is shown with the left (L) on the left side of the figure. The colorbar reflects t -values. SMA = supplementary motor area, PMC = premotor cortex, LN = lentiform nucleus, Put = putamen.

Auditory Reproduce

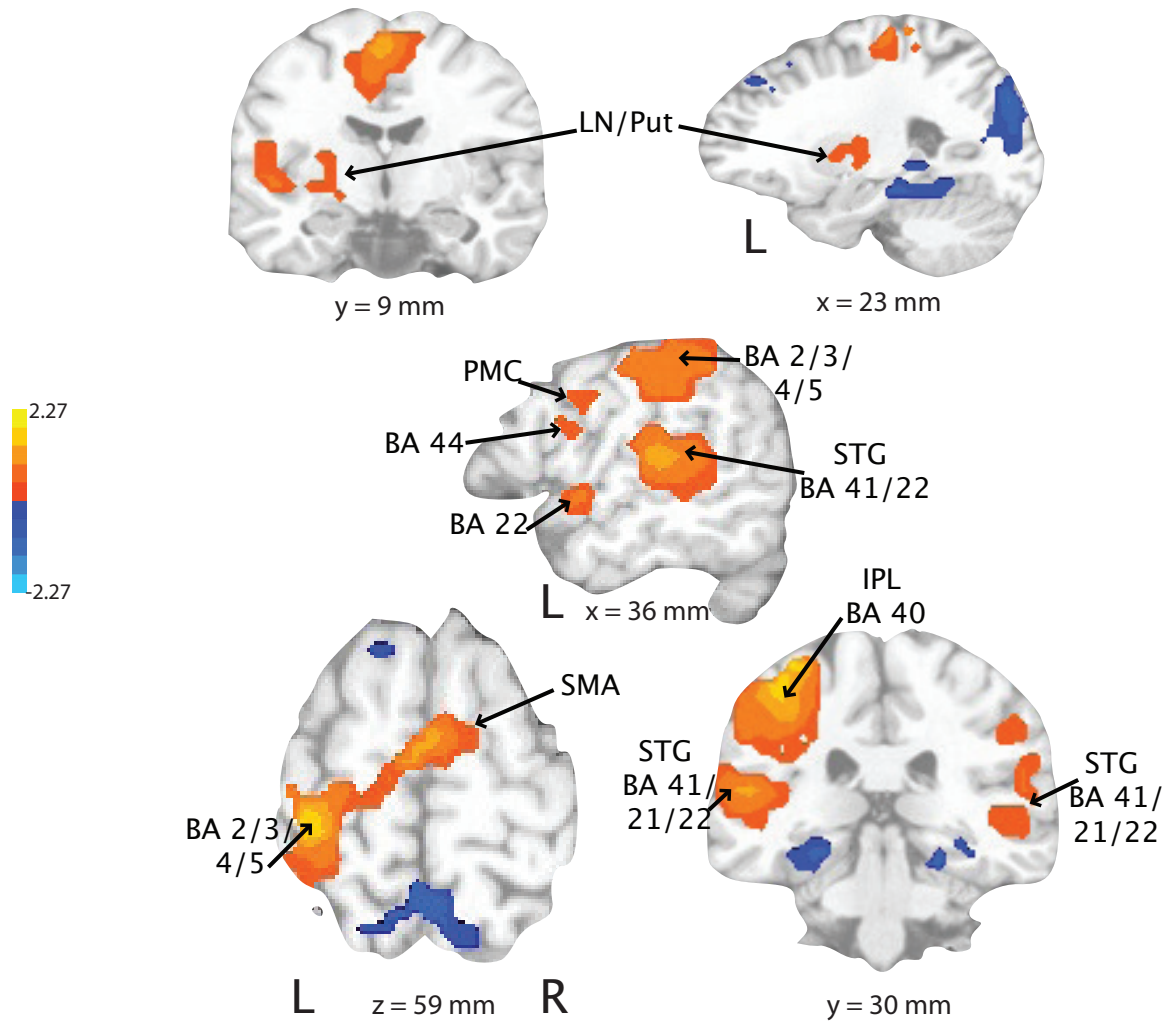


Figure 2.6: Brain regions where BOLD signal was significantly different during the *auditory reproduce* condition compared to rest ($p < 0.002$ corrected). Red to yellow colored voxels represent brain areas where *auditory reproduce* $>$ rest. Blue areas show where *auditory reproduce* $<$ rest. The axial slice is shown with the left (L) on the left side of the figure. The colorbar reflects t -values. SMA = supplementary motor area, STG = superior temporal gyrus, IPL = inferior parietal lobe, PMc = premotor cortex, LN = lentiform nucleus, Put = putamen.

Auditory Attend 2 > Visual Attend 2

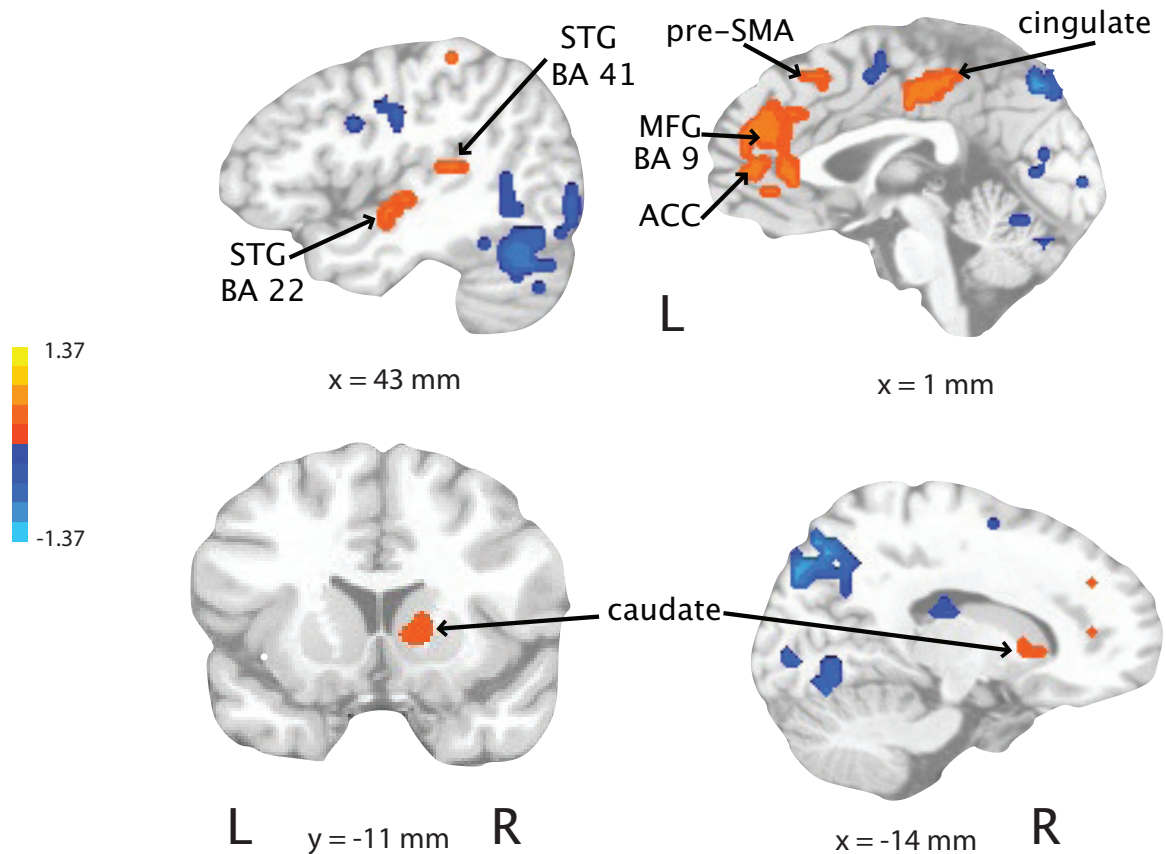


Figure 2.7: Brain regions where BOLD signal was greater during the *auditory attend 2* compared to *visual attend 2* condition ($p < 0.002$ corrected). Red to yellow colored voxels represent brain areas where *auditory attend 2* > *visual attend 2* condition. The coronal slice is shown with the left (L) on the left side of the figure. The colorbar reflects t -values. STG = superior temporal gyrus, pre-SMA = pre-supplementary motor area, MFG = medial frontal gyrus, ACC = anterior cingulate cortex.

Auditory Attend 2 > Attend 1

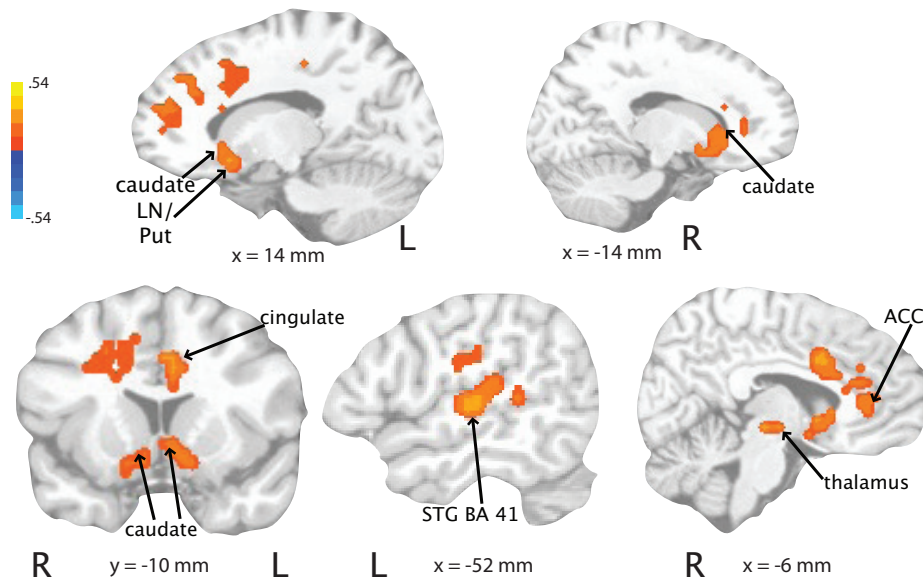


Figure 2.8: Brain regions where BOLD signal was greater during the *auditory attend 2* compared to *auditory attend 1* condition ($p < 0.002$ corrected). Red to yellow colored voxels represent brain areas where *auditory attend 2* > *auditory attend 1* condition. The coronal slice is shown with the left (L) on the left side of the figure. The colorbar reflects t -values. STG = superior temporal gyrus, LN = lentiform nucleus, Put = putamen, ACC = anterior cingulate cortex.

Auditory Rehearse > Visual Rehearse

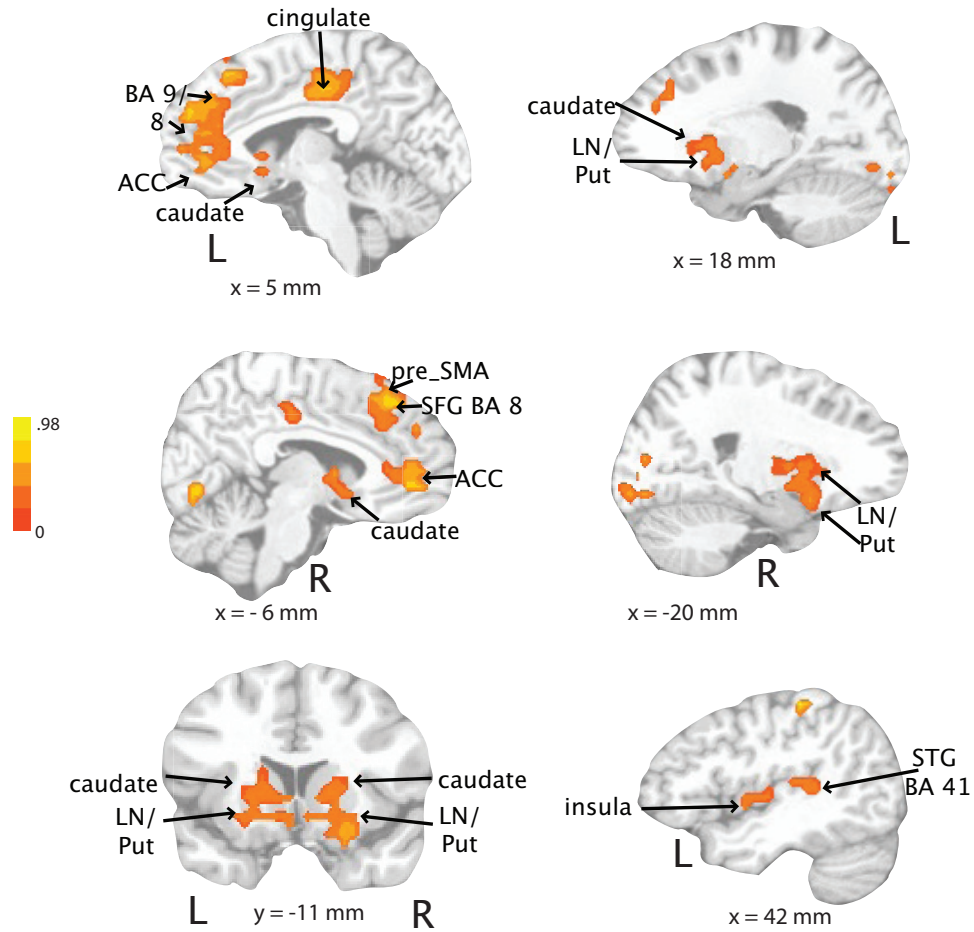


Figure 2.9: Brain regions where BOLD signal was greater during the *auditory rehearse* compared to *visual rehearse* condition ($p < 0.002$ corrected). Red to yellow colored voxels represent brain areas where *auditory rehearse* > *visual rehearse* condition. The coronal slice is shown with the left (L) on the left side of the figure. The colorbar reflects t -values. STG = superior temporal gyrus, pre-SMA = pre-supplementary motor area, SFG = superior frontal gyrus, LN = lentiform nucleus, Put = putamen, ACC = anterior cingulate cortex.

2.3 Discussion

Attending to the first three repetitions of a complex rhythmic pattern activated primary sensory areas. During the next three repetitions of the pattern, the activation became more complex. Areas related to pulse and meter perception, such as basal ganglia and SMA, were recruited as the participant attended to additional repetitions of the pattern. After the external stimulus stopped, the pattern was maintained by these same structures with the added support of the dorsal auditory pathway (PT, PMC, prefrontal cortex) and insula. Reproduction of the rhythmic pattern recruited primary auditory sensory areas (mainly lateralized to the left), insula, and the dorsal auditory pathway, in addition to motor areas, which may be indicative of the utilization of an auditory sensory memory.

Basal ganglia activity was observed when attention was directed to the rhythms but not while attention was directed to the visual stimulus. This finding confirms the hypothesis that attention is necessary to recruit basal ganglia when listening to complex rhythms. Because there is evidence linking pulse perception to basal ganglia activation (Grahn & Brett, 2007, 2009), the presence of basal ganglia activity only while selectively attending to the auditory stimulus could mean that attention to the complex rhythms was needed to form a pulse percept. Further supporting this interpretation, basal ganglia activity was observed only after the rhythms had been presented a sufficient number of times for the listener to perceive a pulse. Basal ganglia have also been discussed as playing a role in training more frontal areas during learning of musical sequences (Leaver et al., 2009). In agreement with this notion, basal ganglia were found to remain active during rhythm rehearsal (and more so than during word rehearsal), when frontal areas were also recruited to maintain and learn the rhythm in preparation for reproduction.

SMA and PMC activations were found when attention was directed toward auditory rhythms. However, increased activation in these areas was not found in comparison with

the visual attend condition, possibly because SMA and PMC activations were also observed during the attend visual conditions (compared to rest). Activation of these areas during visual attend conditions could either reflect their involvement in the visual word task or indicate automatic engagement of the motor system in response to rhythm presentation regardless of the modality to which attention is directed. SMA and PMC have been implicated in the semantic processing of words (Chee, Edsel, & Thorsten, 1999), and maintenance of working memory (Smith & Jonides, 1998). Furthermore, in the current study, rehearsal of the words was also associated with SMA and PMC activation when there was no stimulus presentation. Thus, while automatic engagement of these areas during rhythm presentation cannot be ruled out, these results suggest that the activations seen in SMA and PMC during the attend visual condition were due to the role of the motor system in perception and memory of verbal information. Thus, the activity of the SMA and PMC during both visual and auditory conditions may reflect the inherent role of the motor system in verbal and rhythm perception respectively.

Actively attending to the auditory rhythms additionally resulted in greater activity in an attentional sensory network including primary auditory cortex, insula, anterior cingulate, and prefrontal cortex, indicating the role of attention in modulating activity in primary sensory areas through higher-level cognitive areas involved in learning complex sequences. Similar areas, such as STG, insula, and prefrontal cortex, have also been correlated with selective attention to different streams in polyphonic music (Janata, Tillmann, & Bharucha, 2002). Dorsal anterior cingulate activity was seen when comparing the auditory to visual attend and rehearse conditions and when comparing the later and earlier phases of the auditory attend condition. Consistent with its involvement in on-line monitoring of expectancies (Bush et al., 2000), the dorsal portion of the anterior cingulate may be related to temporal expectancy in the complex rhythms presented in this study. Anterior cingulate has also been associated with tracking dynamic changes in tonality

in autobiographically salient musical excerpts (Janata, 2009). In addition, in line with previous work, selective attention to the auditory stimulus enhanced activity in auditory sensory areas (Johnson & Zatorre, 2006; Woodruff et al., 1996) and suppressed activity in sensory areas associated with attending to the visual stimulus (Johnson & Zatorre, 2006; Lakatos et al., 2008).

As predicted, activity in pulse associated areas (basal ganglia and SMA) was seen during the second half of stimulus presentation in the auditory attend condition. Activation in these areas was not seen during the first three repetitions of the rhythms. This activity was also seen to continue during rehearsal and reproduction of the rhythms, when no stimulus was present. These observations suggest that the basal ganglia and SMA circuit is important for the perception and representation of pulse and rhythm. The role of the frontal motor circuit in rhythm generation is not surprising given the established role of these motor areas in human timing (Meck, Penney, & Pouthas, 2008), selective attention to time (Coull et al., 2004) and sequencing (reviewed in Nachev, Kennard, & Husain, 2008). The current findings further support the growing understanding that pre-motor regions such as the SMA (Chen et al., 2008a) and basal ganglia are important for the representation of pulse and rhythm even in the absence of movement (Grahn & Brett, 2007; Zatorre et al., 2007). Here this finding has been extended to demonstrate that the proposed auditory to motor mapping thought to underlie pulse perception is not automatic, but requires attention to the rhythmic stimulus. Although it cannot be ruled out that activation of motor areas is possibly related to imagination and preparation of the subsequent rehearsal/reproduction stage, the finding that similar circuits are associated with perception during passive listening in the absence of any motor demands (Bengtsson et al., 2009; Chen et al., 2008a; Grahn & Brett, 2007; Schubotz et al., 2000) supports the hypothesis that SMA and basal ganglia are involved in pulse and rhythm perception in addition to motor function.

In general, the current results confirm previous findings and illustrate the fundamental importance of an extended motor network in pulse and meter perception (Chen et al., 2008a; Grahn & Brett, 2007). Integrated auditory-motor activity corresponding to meter may help explain the universal subjective experience of the spontaneous urge to move to rhythmic music. This interaction may also explain why the most common tempo for popular dance music (van Noorden & Moelants, 1999), preferred and spontaneous tapping rates (Fraisse, 1982), and preferred gait frequency are all well matched (averaging around 2 Hz) (for review see Todd et al., 1999), as well as the benefit that rhythmic stimuli have on those with movement disorders (McIntosh et al., 1997; Thaut, Rathbun, & Miller, 1997; Whittall et al., 2000). Moreover, auditory-motor interactions are reciprocal such that movement can influence meter perception in infants (Phillips-Silver & Trainor, 2005) and adults (Phillips-Silver & Trainor, 2007). Rhythm perception can even be influenced without any overt motion by the illusory sensation of movement induced through vestibular stimulation (Trainor et al., 2009).

It was shown that attention modulates brain networks responsible for the perception of complex, syncopated rhythms. The current observations suggest that attention may be necessary for the induction of a pulse percept when listening to complex rhythms that do not contain energy at the pulse frequency. Whether attention is similarly necessary when such a frequency component is exogenously present is not yet clear, but previous work suggests that the answer to this question may be no (Chen et al., 2008a; Grahn & Brett, 2007). There was also evidence that participants had developed an internal pulse percept during the last three rhythm repetitions and that they maintained this percept during rehearsal and reproduction of the complex rhythmic patterns. How can these observations be incorporated with our current knowledge of pulse, meter, and attention? Previous theorizing has suggested that pulse and meter are essentially a form of attentional allocation, serving to direct processing resources toward expected points in time; and performance

on change detection tasks confirms that perception is facilitated for metrically regular sequences in both adults (Jones et al., 2002; Jones & Yee, 1997) and infants (Bergeson & Trehub, 2006; Trehub & Hannon, 2009). Moreover, multiunit recordings in macaques have shown that, when attending selectively to visual stimuli, low frequency oscillations entrain to rhythmic stimuli and modulate power in the gamma band, resulting in increased response gain for task-relevant events and decreased reaction times (Lakatos et al., 2008). Further, electrophysiological recordings in humans have revealed that bursts of beta and gamma oscillations entrain to and predict events in rhythmic stimuli (Fujioka et al., 2009; Iversen et al., 2009; Snyder & Large, 2005; Zanto et al., 2005). Within this context, the current results suggest attention may be responsible not only for the temporal coordination of neural activity with external events, but also for the integration of brain regions necessary for task performance. This raises the possibility that both aspects of attention may be manifest in beta and gamma activity that coordinates brain areas in the perception of meter and rhythm. Future work is needed to understand the oscillations mediating dynamic attending and the relationship between rhythmic entrainment and network coordination.

CHAPTER 3

DYNAMIC EMOTIONAL AND NEURAL RESPONSES TO MUSIC DEPEND ON PERFORMANCE EXPRESSION AND LISTENER EXPERIENCE

Experiment 2 focused on how temporal complexity, in the form of tempo fluctuation, influenced the dynamic emotional responses to a musical stimulus that unfolded over a period of minutes. An expressive music performance, recorded by a skilled pianist, with natural variations in timing and sound intensity, was used to evoke emotion, and a *mechanical* performance was used to control for compositional aspects of the stimulus (Nair et al., 2002; Rankin et al., 2009). To study emotional experience, “deep listeners” (Becker, 2004) were recruited and asked to report their emotional responses to the music in real-time. Emotional responses were imaged separately to prevent self-report from interfering with *experienced* affect. Although this does not guarantee that participants reported felt (rather than perceived) emotion, this procedure was intended to increase the likelihood that participants would attend to and report their own emotional reactions to the music. Listeners reported listening to and enjoying classical music, but were not professional musicians and were not familiar with the piece used in the experiment. These non-expert listeners had varying degrees of musical experience, however, allowing us to

address the role of moderate levels of musical experience (such as singing in a choir) in modulating emotional responses.

3.1 Methods

3.1.1 Participants

One hundred and twenty-five undergraduate psychology students completed a music response questionnaire (85 female and 40 male, aged 18–29 years, mean = 18.76 years) to determine eligibility for participation in the fMRI experiment. The questionnaire assessed musical background and personal responses to music. “Deep listeners” (Becker, 2004) were first identified as those who believed that their response to music and/or the role that music played in their lives was greater than that of the average person. Those who reported being moved by or having a strong emotional response to classical music were also identified. Twenty-seven participants qualified as deep listeners, and two additional participants were included who, while not deep listeners according to the criteria, reported having strong emotional responses evoked by classical music. Of these twenty-nine potential participants, twenty-one completed the fMRI study (14 female and 7 male, aged 18–21 years, mean = 18.76) ¹. Ten *experienced* participants were identified who had at least five years of music lessons or musical experience, such as playing in a band or singing in a choir. Two were undergraduate music majors. Of the remaining eleven *inexperienced* participants, eight reported no musical training or music-making experience whatsoever, two reported four years of playing experience, and one reported one year of music lessons. One musically *inexperienced* male participant was not included in the fMRI analysis because of equipment failure. One *experienced* and one *inexperienced*

¹The mean age for the 125 questionnaire participants coincidentally equaled the mean age of the 21 experimental participants to the second decimal (stranger things have happened.)

participant (both female) were eliminated from the fMRI analysis because of excessive movement while in the scanner. Four additional participants were eliminated due to inconsistent behavioral report, or because their behavioral scores did not correlate with an *expressive* performance measure, as described in detail below. As a result, complete fMRI analysis was available for seven *experienced* (range of experience 6.5 to 18 years, 5 female) and seven *inexperienced* participants (range of experience 0 to 4 years, 4 female). Five of the seven *experienced* participants played piano (range of experience with piano 2–10 yrs), but none reported being familiar with the composition used in this experiment.

3.1.2 Stimuli and Task

Sound Stimulus. Frédéric Chopin’s Etude in E major, Op. 10, No. 3, was performed by an undergraduate piano major (female, 22 years old) on a Kawai CA 950 digital piano and recorded in Cubase on a Macintosh G3 450MHz computer (Rankin et al., 2009). The performer was asked to rehearse and play the piece as she would in a performance (*expressive* performance). A *mechanical* performance was synthesized on the computer by changing the onset time and duration of each note to precisely match that of the musical notation. The MIDI² onset velocity (key pressure) of each note (correlating with sound level) was set to 64 (range 0-128), and pedal information was eliminated. Mean tempo of the *mechanical* performance was adjusted to equal the mean tempo of the *expressive* performance, making the duration of the *mechanical* performance equal to the *expressive* (3 minutes and 36 seconds). Finally, the MIDI files were played on the digital piano to create audio files, and the root mean square (RMS) amplitude of the *mechanical* performance was adjusted to equal the mean RMS amplitude of the *expressive* performance. Therefore, whereas the *mechanical* performance did not include *expressive* changes in tempo (rubato) or sound level (dynamics), the *expressive* performance varied in both tempo and

²Musical Instrument Digital Interface

sound intensity about a mean common to both performances.

Behavioral Task. Sound stimuli were presented using MaxMSP 4.2.1 software running on a PowerBook G4. A 2-dimensional emotion response space, adapted from Schubert (1996), was presented visually so that participants could report emotional responses to the performances in real time (Figure 3.1). The two dimensions were emotional arousal (vertical dimension on a scale from 0 to 10) and emotional valence (horizontal dimension on a scale from -10 to 10). Participants were instructed to move the mouse cursor to the position in the emotion response space that best matched their emotional responses to the music being played. They were specifically instructed to “tell us about (their) own emotional experience” rather than the emotion they thought the piece was trying to express. They were told that higher arousal values corresponded to feeling an emotion more intensely, positive valence values corresponded to positive emotions (like happiness or excitement), and negative valence values corresponded to negative emotions (like sadness or anger). The position of the cursor for all participants started at zero arousal, zero valence (bottom middle point in the response space). The software recorded cursor position automatically during music playback at unequal intervals, with an average sampling period of 135ms. Participants performed this task immediately before and after fMRI acquisition.

fMRI Recording A custom Visual Basic 5 program running on a Dell Optiplex GX260 was used to play sound stimuli which were presented to participants using custom noise-attenuating headphones (Avotec, Inc). They were instructed to lie motionless in the scanner with eyes closed and listen attentively to the music without actively monitoring or reporting their emotional response. During the rest period, participants were instructed to rest quietly with eyes closed and wait for the music to begin again.

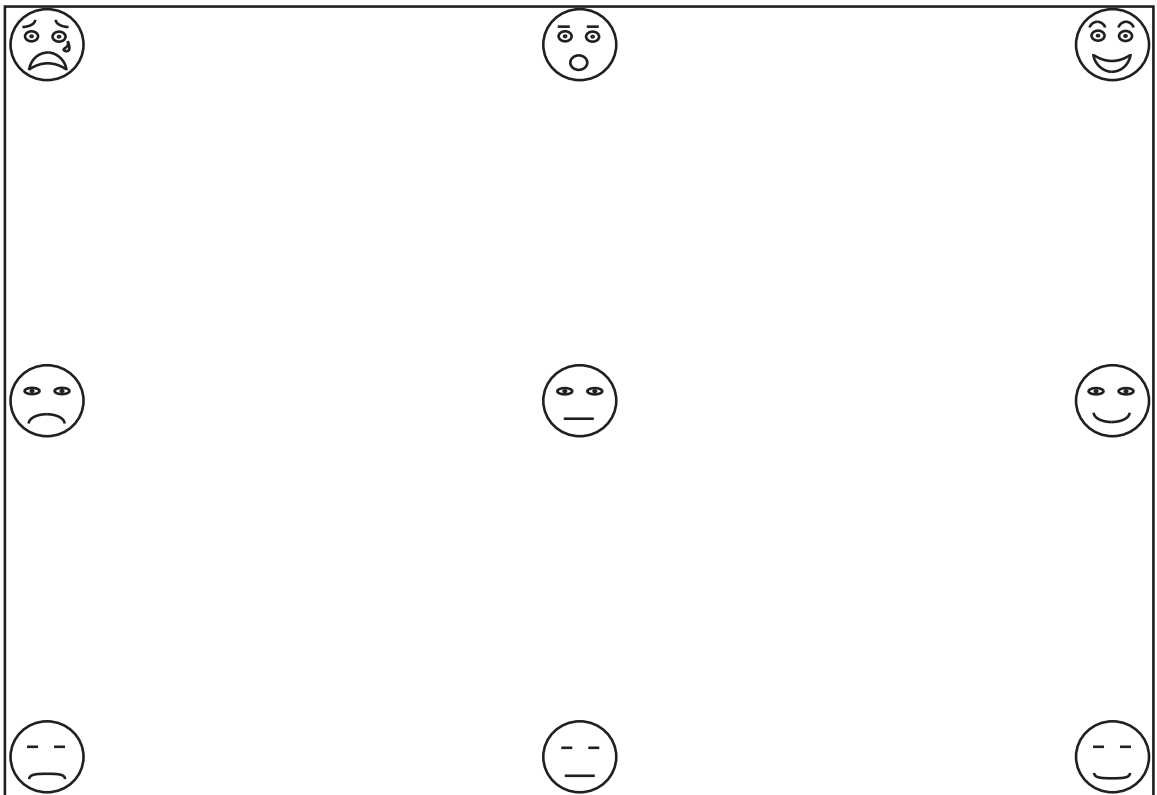


Figure 3.1: The 2-Dimensional emotion response space with valence on the horizontal dimension and arousal on the vertical dimension.

3.1.3 Magnetic Resonance Imaging

Changes in blood oxygenation (BOLD response) were measured using echo planar imaging on a 3.0 T Signa Scanner equipped with real time fMRI capabilities (General Electric Medical Systems, Milwaukee, WI). Echo-planar images were collected using a single shot, gradient-echo, echo planar pulse sequence (field of view (FOV) = 24 cm, echo time (TE) = 35 ms, flip angle (FA) = 90°, in plane resolution = 64 x 64). All images were collected using a sparse sampling technique with a repetition time (TR) of 12 seconds. Adequate coverage of the brain was achieved by collecting thirty interleaved 4 mm axial slices with no spacing between (voxel size = 3.75 x 3.75 x 4 mm). Immediately following the functional imaging, high resolution anatomical spoiled gradient-recalled at steady state (SPGR) images (4 mm thick, no spacing, number of excitations = 2, TE = in phase, TR = 325 ms, FA = 90°, in plane resolution 256 x 256, bandwidth = 31.25) were collected at the same slice locations as the functional images.

Acquisition. A sparse sampling technique was used in the scanner to increase the signal response from baseline (which was silence) and to avoid nonlinear interaction of the scanner sound with the auditory stimulus (Hall et al., 1999). There were a total of two trials. Within each trial, there was one minute of rest between each stimulus and after the last stimulus presentation. One trial started with twelve seconds of rest, followed by the *expressive* performance and then the *mechanical* performance. The other trial started with six seconds of rest, followed by the *mechanical* and *expressive* performances. The variable amount of time in the first rest period allowed scans over the two trials, when combined, to have an effective TR of 6 seconds (Figure 3.2). The total number of scans acquired for each participant over both trials was 96 (36 scans per performance). Trial order was randomized across participants.

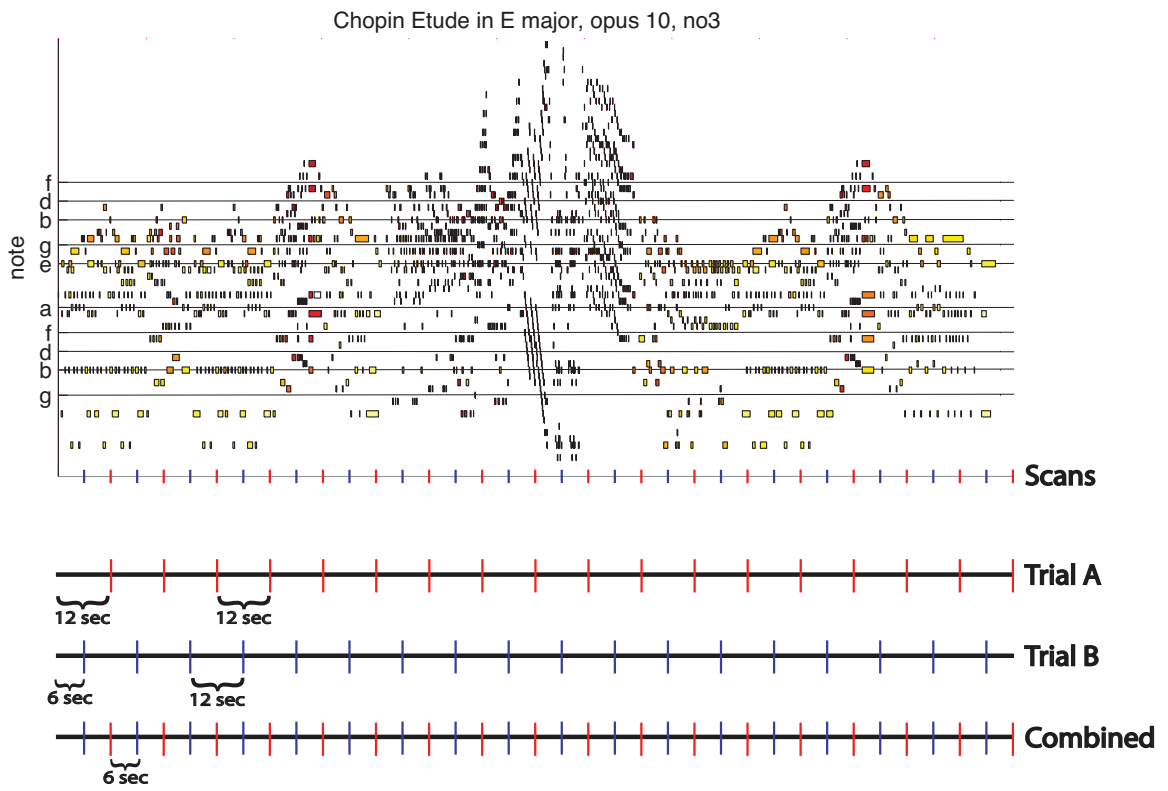


Figure 3.2: Piano roll notation and fMRI scan times.

3.1.4 Data Analysis

Behavioral measures. Data analysis was performed using Matlab 7.2.0 (The MathWorks, Inc.) running on an Apple G5. First, the performance was matched to its score using a custom dynamic programming algorithm (Large, 1992; Large & Rankin, 2007). Chords were grouped by the same dynamic programming algorithm, and onset time of a chord was defined to be equal to the average of component note onset times. This procedure enabled the identification of timing fluctuations. Beat times were extracted as the times of performed events that matched events on the notated beat. Beat times were extracted at the sixteenth note level, and notated beats to which no event corresponded were interpolated using local tempo. Inter-beat intervals (IBIs, in seconds) were calculated by subtracting successive beat times, and a tempo curve in beats per minute (bpm) was constructed according to the formula ($\text{local tempo} = 60/\text{IBI}$). Each value in the tempo curve was divided by 4 because calculations had been made at the sixteenth note level (four sixteenth notes per quarter note; for details see Rankin et al., 2009). One measure provided by MIDI is the velocity at which the key is struck, which is related to sound intensity (Palmer & Brown, 1991). A velocity curve, showing how sound intensity changed over the piece, was created by averaging the velocities of each note in a chord. These procedures resulted in tempo and velocity curves sampled at event onset times, so each time-series was interpolated at equal intervals (10 ms; i.e. 100 Hz). Finally, frequency content of the tempo curve was measured using a Fast Fourier Transform and the Nyquist frequency was determined to be approximately 0.5 Hz. Therefore, time-series data were high-pass filtered and down-sampled at 2-second intervals (0.5 Hz) to prevent spuriously high correlations with emotion rating time-series, discussed next.

Two behavioral sessions were conducted to test reliability of reported emotional responses. It was assumed that if participants' reported emotional responses were reliable over time, similar emotional responses would be experienced in the scanner, allowing for

correlations between behavioral and physiological data. First, arousal and valence time-series were interpolated to an equal sample rate (10 ms), and decimated to 0.5 Hz. Then they were correlated across trials at an optimal time lag to test for reliability. For participants whose ratings were reliable, means of first and second trial rating curves were calculated for use in subsequent analyses. Next, optimal lag times (12-second maximum) were calculated for correlations between the behavioral data and the tempo curve. Finally, mean arousal and valence ratings, each advanced by the optimal lag time, were correlated with the tempo curve of the *expressive* performance.

fMRI. Data analysis and display were performed using AFNI (Cox, 1996; Cox & Hyde, 1997) and image registration was conducted using FSL (Analysis Group, FMRIB, Oxford, UK), both running on an Apple G5. Functional data sets were corrected for motion and globally normalized. To model the BOLD response to the presence of music, a hemodynamic response function (HRF) was convolved with a binary vector representing the off/on timing of each condition. Each participants head motion information was added to the baseline model to account for the variance due to head motion in all of the comparisons. A general linear approach, as implemented in AFNI, was used to determine the contribution of the model to the data from each voxel. Functional images were then coregistered and transformed into Talairach & Tournoux (1988) coordinates.

A separate second-level analysis was used to combine across participants. A mixed-design 2-way ANOVA with the factors performance type (*expressive vs. mechanical*) and musical experience (*experienced vs. inexperienced*) was conducted on the beta weights from each voxel. To correct for multiple comparisons, a Monte Carlo simulation was conducted to determine the random distribution of voxel cluster sizes for a given threshold (for similar approaches, see Ledberg, Åkerman, & Roland, 1998). A two-tailed alpha level of $p < .02$ was achieved through the combination of a per voxel threshold of $p < .05$ and a cluster size of 10 contiguous voxels (640 mm).

Additional analyses were performed to determine the contribution of dynamic fluctuations in stimulus tempo and reported emotional arousal to BOLD activity. The tempo curve and the time-advanced mean arousal ratings were filtered with a hemodynamic response function (HRF) and were resampled at six-second intervals to match the sampling rate of the fMRI data. HRF filtered emotion ratings were then normalized about 0 by dividing each time-series by its mean and subtracting 1. The HRF filtered tempo curve for the *expressive* performance and the HRF filtered arousal ratings of each participant were regressed against the BOLD time series. The *expressive* and *mechanical* performance models used in the first analysis were added to the baseline model to account for tonic changes in BOLD intensity associated with listening to the music. Head motion parameters were also included as part of the baseline model. Group analysis was conducted by submitting individual beta weights to between subject t-tests. Again, a Monte Carlo simulation was conducted to correct for multiple comparisons and an alpha level of $p < 0.02$ was achieved with a per voxel threshold of $p < 0.02$ and a cluster size of 12 contiguous voxels (768 mm).

3.2 Results

3.2.1 Behavioral measures

For the *expressive* performance, emotional arousal ratings were significantly positively correlated across trials for 19/21 participants (mean $r = .62$, $SD = .23$)³. Emotional valence ratings were less reliable across trials, but still significantly positively correlated in 18/21 participants (mean $r = .46$, $SD = .22$). Given the reliability of emotion ratings over time, mean arousal and valence ratings were calculated across the two trials for each participant for comparison with dynamic measures of the music performance. Mean

³All significant correlations in the behavioral measures are significant at value of $p < .05$

Table 3.1: Behavioral Correlations Based on Reported Emotional Responses

Subject	Arousal (Trial 1/ Trial 2)	Valence (Trial 1/ Trial 2)	Arousal - Valence (Mean of Trials)	Arousal - Tempo (Mean of Trials)
Exp1	0.77 *	0.30 *	-0.56 *	0.54 *
Exp2	0.70 *	0.50 *	0.04 *	0.51 *
Exp3	0.65 *	0.10	0.26	0.71 *
Exp4	0.62 *	0.41 *	-0.87 *	-0.10
Exp5	0.80 *	0.65 *	0.14 *	0.41 *
Exp6	0.53 *	0.48 *	-0.21	0.66 *
Exp7	0.64 *	0.64 *	-0.57 *	0.71 *
Exp8	0.04	0.51 *	-0.21	0.33 *
Exp9	0.63 *	0.47 *	0.64 *	0.59 *
Exp10	0.87 *	0.50 *	0.78 *	0.73 *
Inexp1	0.75 *	0.83 *	0.24 *	0.55 *
Inexp2	0.76 *	0.80 *	0.54	0.49 *
Inexp3	0.52 *	0.16	-0.16 *	0.43 *
Inexp4	0.75 *	0.59 *	-0.71 *	0.63 *
Inexp5	0.78 *	0.68 *	-0.80 *	0.75 *
Inexp6	0.57 *	0.01 *	-0.08 *	0.44 *
Inexp7	0.71 *	0.63 *	-0.67 *	0.18
Inexp8	0.74 *	0.52 *	-0.31	0.54 *
Inexp9	0.73 *	0.35 *	0.19	0.62 *
Inexp10	-0.07	0.20 *	0.07 *	0.47 *
Inexp11	0.46 *	0.35 *	-0.15 *	0.34 *
Mean	0.62	0.46	-0.11	0.50
St. Dev.	0.23	0.22	0.47	0.20

*p<.05

arousal and valence ratings were positively correlated in six participants, negatively correlated in nine participants, and uncorrelated in six participants. Therefore, arousal and valence ratings appear to be orthogonal measures of emotional response in this sample. See Table 3.1 for a summary of the behavioral results. Two participants whose ratings were not reliable across time were eliminated from further analysis because they may not have similar emotional responses while listening to the performances in the scanner as when they reported their responses.

Regression analysis revealed that BOLD filtered tempo and velocity curves for the *expressive* performance were highly correlated ($r = .87$). For this reason, and because

previous findings suggest that tempo fluctuation accounts for more variance in emotionality ratings than loudness changes in performed music (Bhatara et al., 2009), subsequent analyses focused on tempo changes. Figure 3.3 illustrates the relationship between one participants mean emotional arousal ratings and the tempo curve of the *expressive* performance. Arousal ratings were significantly positively correlated with the tempo curve in 19/21 participants at their optimal time lag (mean of significant correlations $r = .50, SD = .20$, mean lag 7.2 seconds). Therefore, tempo fluctuation in the *expressive* performance was a predictor of perceived emotional arousal in this population. Emotional valence ratings were significantly negatively correlated with the tempo curve of the *expressive* performance in 16/21 participants and significantly positively correlated in 4/21 participants (mean $r = -.25, SD = .32$). Because of the stronger and more reliable relationship between tempo and arousal, arousal was focused on in subsequent analyses. Only participants whose arousal ratings correlated significantly with tempo were included in further analyses (eliminating one *experienced* and one *inexperienced* participant). Emotional arousal correlations with the tempo curve of the *expressive* performance did not differ significantly between *experienced* and *inexperienced* participants (paired $t(6) = .97, p = .18$).

Tempo and Mean Arousal for the Expressive Performance in an Experienced Listener

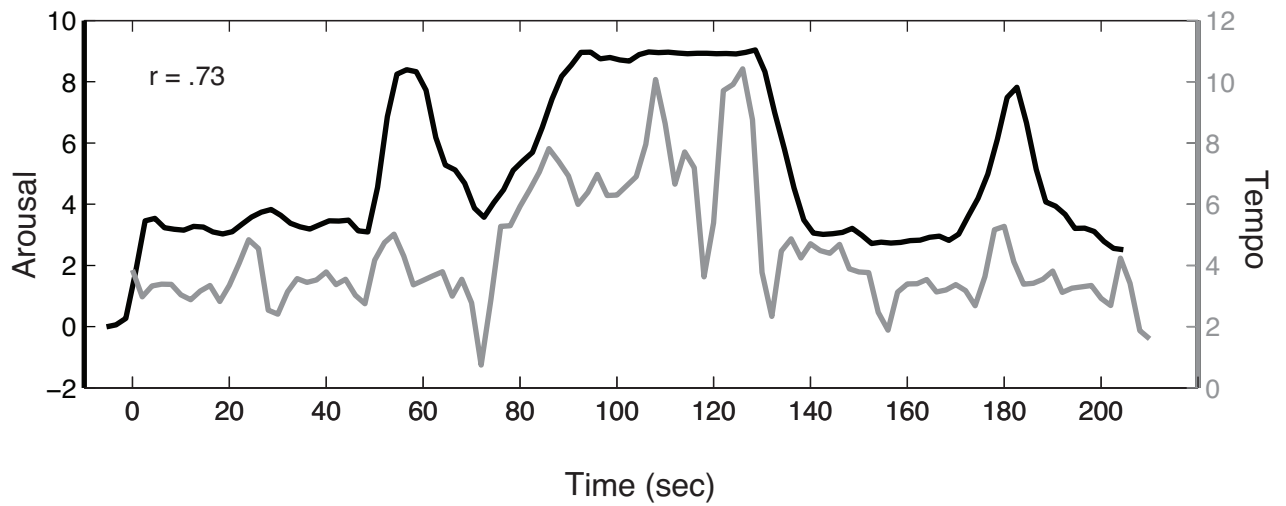


Figure 3.3: Correlation between tempo and mean arousal for the *expressive* performance for one participant. ($r = .73, p < .0001$) For this participant, the optimal lag time was -5.4 seconds and time shifted arousal ratings are shown.

3.2.2 fMRI

ANOVA. Table 3.2 and Figure 3.4 present summaries of the fMRI ANOVA results. A main effect of performance type (*expressive* versus *mechanical*) was the result of an increased BOLD signal for the *expressive* performance in right posterior parahippocampal gyrus (extending into amygdala and hippocampus), fusiform gyrus, inferior parietal lobule (BA 40), IFG (BA 47), anterior parahippocampal gyrus, bilateral ventral anterior cingulate (predominately right lateralized), left medial prefrontal cortex (BA 10, frontopolar area), right dorsal medial prefrontal cortex (BA 8) and precuneus (BA 7). An increased BOLD response for the *mechanical* performance was observed only in the supramarginal gyrus (BA 40).

A main effect of musical experience was found with greater BOLD activity for *experienced* compared to *inexperienced* listeners occurring in right ventral striatum (extending into lentiform nucleus, putamen, and subcallosal gyrus) and left ventral anterior cingulate. *Inexperienced* listeners had greater BOLD activity than *experienced* listeners in the left anterior parahippocampal/hippocampal gyrus (see Figure 3.4b).

Several brain regions showed a significant interaction of performance type with musical experience (see Figure 3.5). In the left cerebellum (culmen), left IFG (BA 47), right inferior parietal lobe (BA 40), and right dorsal cingulate (near pre-SMA), *experienced* participants showed a greater percent signal change for the *expressive* than the *mechanical* performance whereas *inexperienced* listeners showed the opposite response.

Contrast images revealed that the response of *experienced* participants to the *expressive* (versus *mechanical*) performance (Figure 3.4c) was similar in some respects to that of the larger group. Greater BOLD activity was observed in left cerebellum/lingual gyrus, right fusiform gyrus, inferior parietal lobe (BA 40), left temporal pole (BA 38), IFG (BA 47), right dorsal cingulate gyrus, anterior parahippocampal gyrus (extending into amygdala and hippocampus), cingulate (BA 31), and dorsal medial prefrontal gyrus (BA 8).

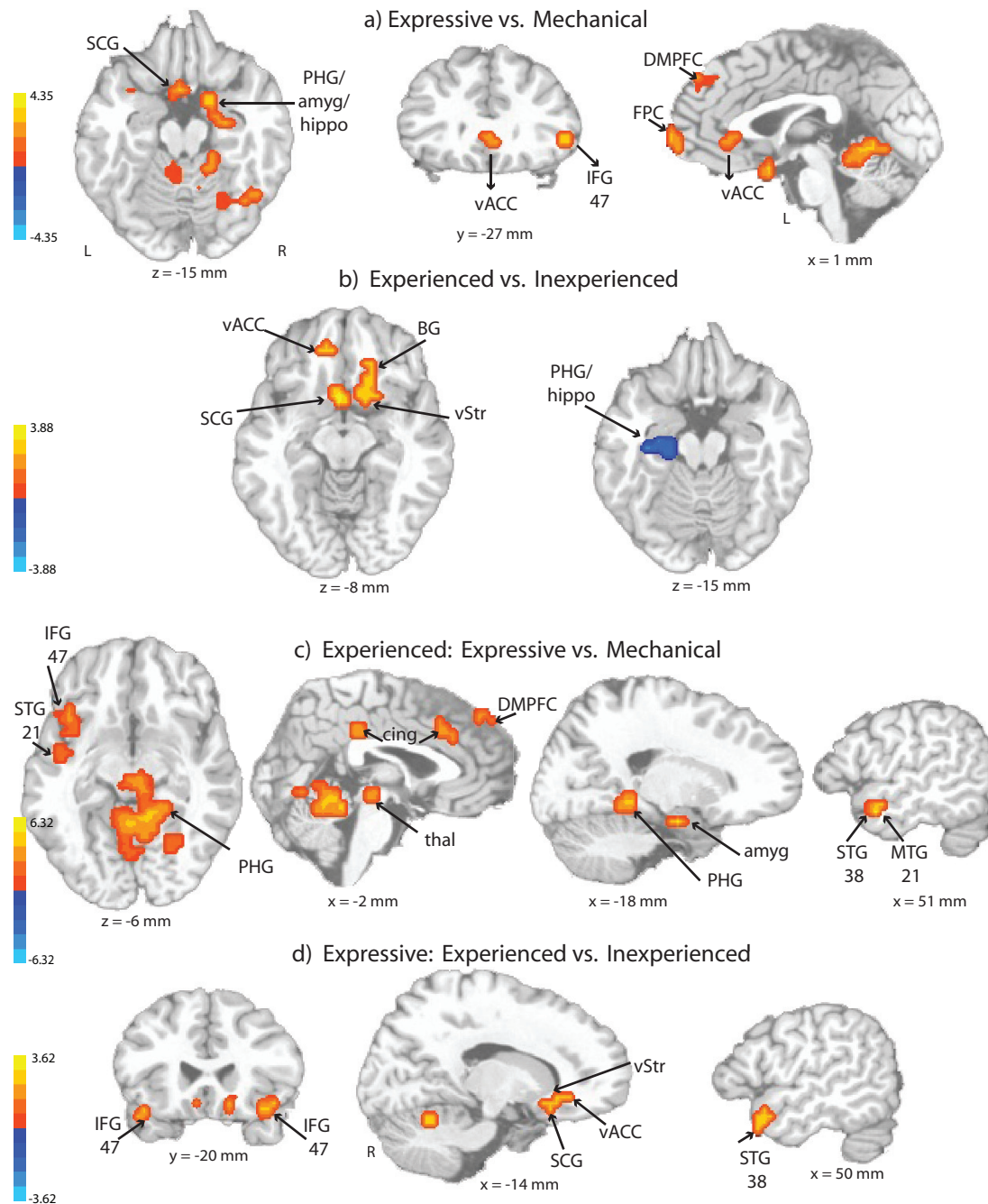


Figure 3.4: Brain activations as a function of a) main effect of performance type, SCG = subcallosal gyrus, PHG = parahippocampal gyrus, vACC = ventral anterior cingulate, FPC = frontopolar cortex, DMPFC = dorsal medial prefrontal cortex; b) main effect of musical experience, BG = basal ganglia, vStr = ventral striatum; c) *experienced* participants listening to *expressive* versus *mechanical* performance, MTG = middle temporal gyrus, thal = thalamus, STG = superior temporal gyrus; and d) *experienced* versus *inexperienced* participants listening to *expressive* performance.

Table 3.2: Brain Activations as a Function of Performance Type and Musical Experience

REGION (cluster peak)	BA	Cluster includes	X	Y	Z	Volume (mm ³)	Activation
<u>Main Effect: Expressive vs Mechanical</u>							
R parahippocampus	30	bilateral culmen and vermis	18	-41	-4	8256	positive
R fusiform gyrus		declive (19, 37)	42	-57	-12	2752	positive
R inferior parietal	40	superior parietal (7)	38	-37	48	2304	positive
R inferior frontal	47		46	27	0	1088	positive
R parahippocampus	34	amygdala, hippocampus, subcallosal (34)	14	-1	-16	1024	positive
L medial frontal (frontopolar)	10		-2	67	4	1024	positive
R ventral anterior cingulate	24,32	bilateral (24)	6	35	-4	1024	positive
L precuneus	7		-30	-49	48	1024	positive
L supramarginal (Decrease)		inferior parietal (40)	-58	-45	28	768	negative
R medial frontal	8		2	51	40	768	positive
L superior frontal	8		-14	43	48	640	positive
<u>Main Effect: Experienced vs Inexperienced</u>							
R ventral striatum		lentiform, putamen, subcallosal	14	11	-8	1664	positive
L parahippocampus (Decrease)	35	hippocampus	-22	-21	-16	1088	negative
L ventral anterior cingulate		(10)	-14	39	4	960	positive
L ventral anterior cingulate	25	subcallosal	-2	11	-8	704	positive
<u>Expressive Performance: Experienced vs Inexperienced</u>							
L superior temporal	38	inferior frontal (47)	-50	15	-20	1280	positive
R inferior frontal	47		34	23	-16	1088	positive
R cerebellum dentate		culmen into vermis, declive	14	-53	-20	960	positive
R ventral anterior cingulate		subcallosal and ventral striatum	18	27	-4	832	positive
L inferior parietal	40		-62	-29	31	832	positive
L ventral anterior cingulate	25	subcallosal, caudate head	-2	11	-8	704	positive
L cerebellum declive		uvula	-18	-69	-20	640	positive
<u>Experienced Listeners: Expressive vs Mechanical</u>							
L cerebellum/lingual gyrus		bilateral lingual, culmen and vermis, thalamus, R parahippocampus (30),	-2	-45	-16	10304	positive
R fusiform gyrus	19	(37), declive	26	-61	-8	1728	positive
R inferior parietal	40		46	-37	52	1664	positive
L middle temporal		(38, 21)	-50	3	-16	1600	positive
L inferior frontal	47		-38	15	-8	1344	positive
R cingulate	32		10	19	40	1280	positive
R parahippocampus	34	amygdala, hippocampus	18	-9	-16	704	positive
R cingulate	31		2	-33	36	704	positive
R superior frontal	8	middle frontal	2	43	44	640	positive

Significant Interaction Effects

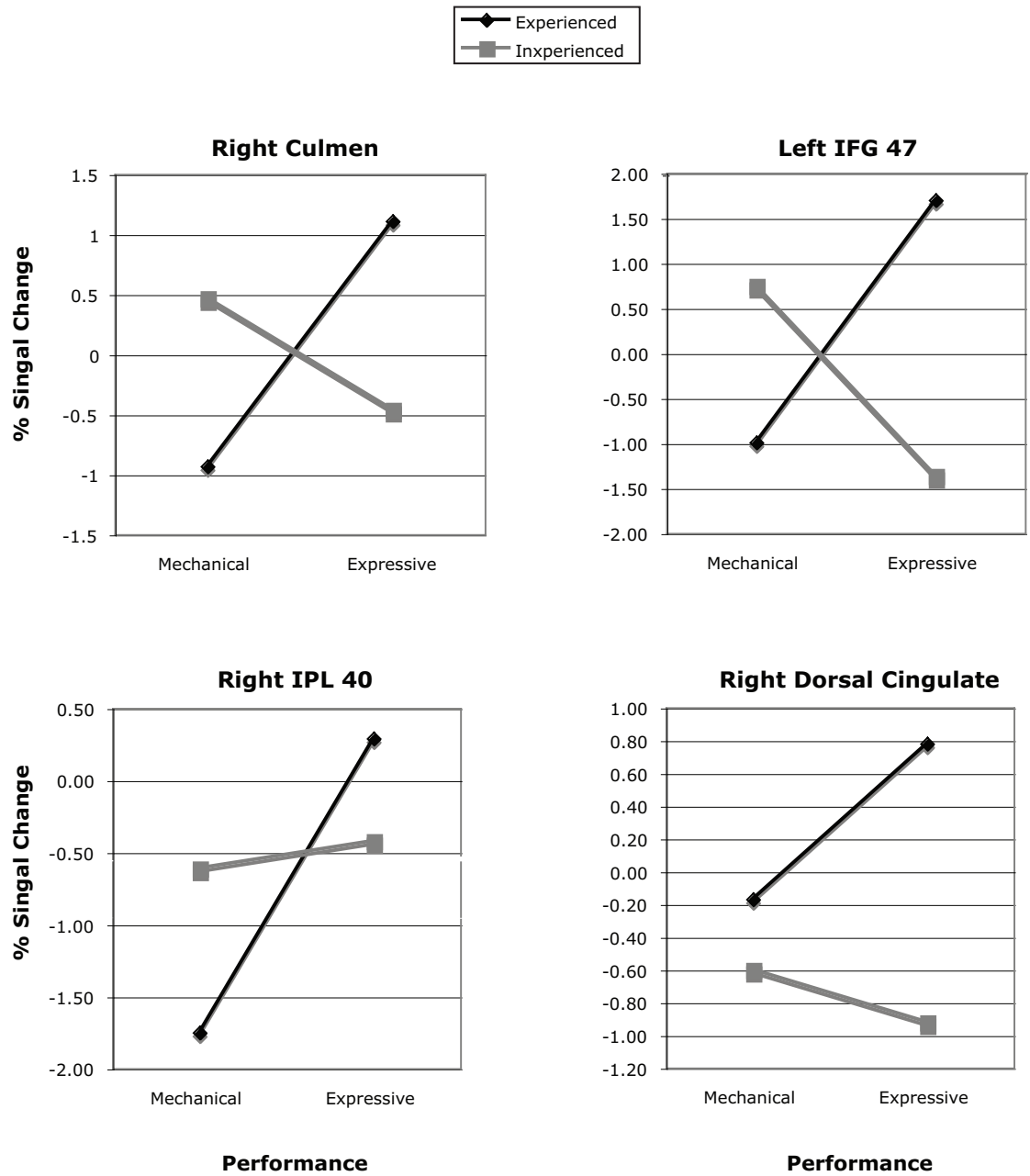


Figure 3.5: Peak voxels showing a significant interaction between performance type and experience, IPL = inferior parietal lobe.

Tempo

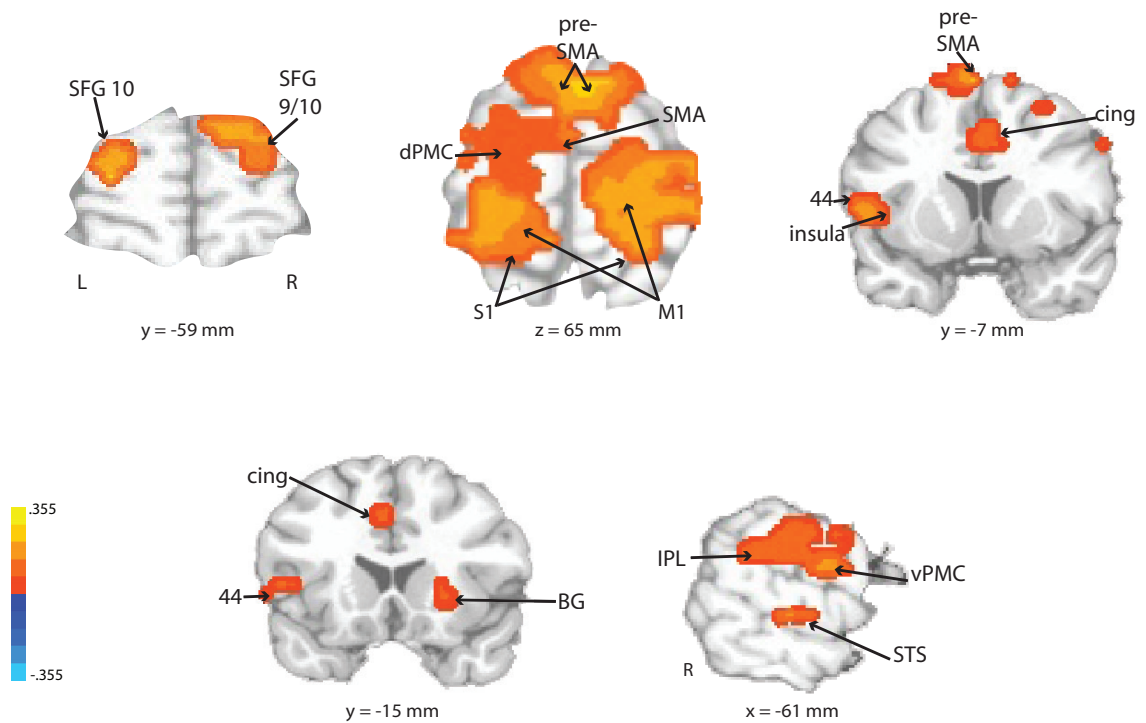


Figure 3.6: Brain activations as a function of the tempo of the *expressive* performance, SFG = superior frontal gyrus, dPMC = dorsal premotor cortex, SMA = supplementary motor area, S1 = primary somatosensory cortex, M1 = primary motor cortex, vPMC = ventral premotor cortex, STS = superior sulcus.

When listening to the *expressive* performance *experienced* compared to *inexperienced* participants (Figure 3.4d) showed greater BOLD responses in left temporal pole (BA 38), right IFG (BA 47), cerebellar dentate, anterior cingulate, left inferior parietal lobe (BA 40), cerebellar declive, and bilateral ventral anterior cingulate (extending into subcallosal gyrus, ventral striatum (right) and caudate head (left)).

Tempo. BOLD signal changes in a number of areas showed significant positive correlations with the tempo curve of the *expressive* performance (see Table 3.3 and Figure 3.6). They included right lingual gyrus, premotor cortex, left primary motor and somatosensory cortex (extending into inferior parietal lobe BA 40), right postcentral gyrus (BA 43, extending into primary motor, premotor cortex, and inferior parietal lobe BA 40), bilateral dorsal lateral prefrontal cortex (right BA 9/10 extending into ventral anterior cingulate, left BA 10), left insula, BA 44, and right secondary auditory cortex (BA 21 and 22).

Emotional Arousal. A positive correlation between BOLD signal changes and real-time reports of emotional arousal was found in left cuneus and right middle occipital gyrus. *Experienced* relative to *inexperienced* listeners showed positive correlations between BOLD signal changes and emotional arousal ratings in left premotor cortex (extending into IFG BA 44 and 45), right cingulate gyrus (including dorsal anterior cingulate), left inferior parietal lobe, insula, IFG (BA 47), right secondary auditory cortex, pre-SMA, inferior parietal lobe (BA 40) and lateral prefrontal gyrus. Similar results were found for correlations between the BOLD response and emotional arousal for just the *experienced* listeners (see Figure 3.7 and Table 3.3).

Table 3.3: Brain Activations as a Function of Expressive Tempo and Reported Emotional Arousal

REGION (cluster peak)	BA	Cluster includes	X	Y	Z	Volume (mm ³)	Activation
Tempo							
R lingual gyrus		cuneus (17, 18), bilateral cuneus (17), L culmen, vermis and declive, L posterior cingulate, L middle occipital, inferior occipital	6	-89	4	33088	positive
R medial frontal, SMA	6	SFG (6), precentral (6), bilateral precentral (4), postcentral (3, 5), bilateral cingulate	2	-13	68	28800	positive
R lingual gyrus	18	middle occipital (18, 19), inferior occipital, fusiform gyrus (19, 37), MTG (37)	18	-81	-4	13504	positive
L postcentral	3	precentral (4, 6), inferior parietal, insula (13)	-46	-17	48	11840	positive
R postcentral	43	precentral (4, 6), insula (13), inferior parietal	58	-9	16	10496	positive
R superior frontal	9	middle frontal (10), ventral anterior cingulate	10	59	32	6784	positive
L insula	13	pulvinar of thalamus	-30	-29	16	1920	positive
L precentral		insula (13), precentral (44)	-50	7	8	1536	positive
L superior frontal	10	middle frontal (10)	-22	59	16	1408	positive
R superior temporal	21	(22)	62	-21	0	1216	positive
R insula	13		38	-5	16	1024	positive
R lentiform nucleus, putamen			22	15	4	832	positive
L insula	13		-42	-13	4	768	positive
Emotional Arousal							
L cuneus	19	(18)	-14	-89	24	1280	positive
R middle occipital		(19)	30	-85	16	1088	positive
Emotional Arousal: Experienced							
R cingulate	32	R anterior cingulate (32, 24), medial frontal (9), SFG (9), L cingulate (32,24)	2	23	32	10624	positive
L precentral	4	postcentral (2), inferior parietal (40), supramarginal gyrus, posterior insula	-54	-17	36	4224	positive
L superior temporal	22	transverse temporal (41), precentral (43, 44) postcentral (43), insula (13)	-58	-9	8	3136	positive
L middle temporal	22		-58	-33	4	2112	positive
R superior frontal, pre-SMA	6		2	3	64	1024	positive
R inferior frontal	47		30	31	-4	768	positive
R middle frontal (DPMC)	6		30	3	60	768	positive
R paracentral lobule	4	postcentral (5)	10	-37	68	768	positive
Emotional Arousal: Experienced vs Inexperienced							
L middle frontal		precentral (6, 4), IFG (44, 45, 9)	-46	7	44	3840	positive
R cingulate	24	R anterior cingulate (32), bilateral to L (32, 24)	2	11	32	3840	positive
L inferior parietal		supramarginal, insula (13)	-46	-41	28	2880	positive
L insula	13	STG (22, 41), MTG (22)	-42	-25	16	2240	positive
L inferior frontal	47	(45), precentral (44)	-42	23	0	2176	positive
R middle temporal	21	STG (22, 39)	62	-49	8	1472	positive
R superior frontal/medial frontal	6	preSMA	2	3	64	1344	positive
R inferior parietal	40	insula	58	-29	36	1152	positive
R middle frontal	9	cingulate	54	19	28	1152	positive

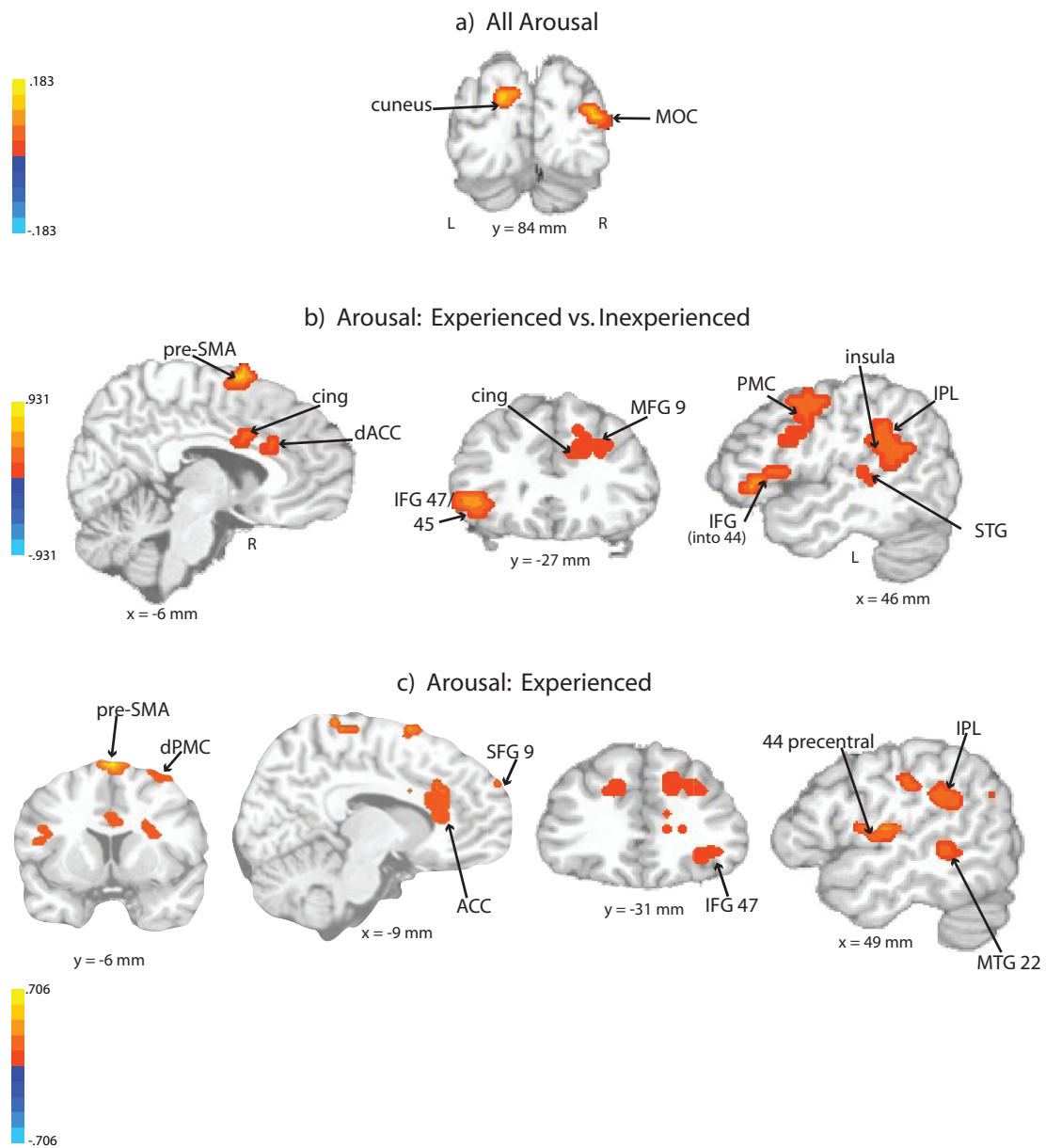


Figure 3.7: Brain activations as a function of a) emotional arousal ratings in response to the *expressive* performance for all participants, MOC = middle occipital gyrus, dACC = dorsal anterior cingulate, MFG = middle frontal gyrus, MedFG = medial frontal gyrus; b) emotional arousal ratings in response to the *expressive* performance for *experienced* versus *inexperienced* participants; and c) emotional arousal ratings in response to the *expressive* performance for *experienced* participants.

3.3 Discussion

The goals of Experiment 2 were to link time-varying stimulus parameters with dynamic emotional and neural responses and to investigate the role of experience in modulating these responses. It was found that emotional responding depends upon dynamic changes in stimulus parameters. Specifically, expressive dynamics in performed music were found to predict listener ratings of emotional arousal as they evolved over time. Moreover, fMRI scanning revealed activation of emotion-related structures, including parahippocampal gyrus, amygdala, ventral anterior cingulate, and dorsal medial prefrontal cortex, for the expressive performance. The presence of these activations and the self-report of the participants suggest that listeners did experience emotional responses while listening to the expressive performance. Because the design controlled for variables such as melody, harmony, and rhythm, it was concluded that changes in timing and sound intensity were responsible for these increased activations. In addition, for the expressive performance, musically experienced listeners were found to have increased activation (compared to inexperienced listeners) in IFG 47, temporal pole, ventral striatum, anterior cingulate, and the basal ganglia. For experienced participants, listening to the expressive (compared to the mechanical) performance showed activity in IFG 47, temporal pole, parahippocampal gyrus, amygdala, thalamus, and dorsal medial prefrontal cortex. These experienced listeners were not professional musicians; they had moderate levels of experience performing music. Nevertheless, they exhibited enhanced neural responses related to emotion and reward when compared to inexperienced participants.

But how might such timing fluctuations communicate and evoke emotion in listeners? To address this question, performance fluctuations and real-time ratings of emotional arousal were compared with dynamic changes in BOLD activation. Evidence was found consistent with a temporal expectancy theory of emotional responding to music.

Dorsal anterior cingulate (dACC) activity correlated with emotional arousal in the experienced participants. Thus, consistent with its involvement in error detection and correction (Bush, Luu, & Posner, 2000), the dorsal portion of the anterior cingulate could also play a role in the detection of violations of temporal expectancy in music. Moreover, in accord with amygdala response to temporal unpredictability in the auditory domain (Herry et al., 2007), it was found that right amygdala was more active for all participants when listening to the expressive performance and this effect was more pronounced for experienced listeners. It should be noted, however, that the amygdala is also activated by rising sound intensity in humans (Bach et al., 2008) and that changes in tempo and sound intensity are highly correlated in performed music in general (Todd, 1992), and in this performance in particular. It seems likely that the interaction between tempo and sound intensity heightens the emotional response of listeners, but it remains to be demonstrated whether tempo or intensity changes in isolation could cause the effect demonstrated here.

In addition, a great deal of evidence was found in support of a mirror neuron theory of musically induced emotional responses (cf. Molnar-Szakacs & Overy, 2006). In all participants, the tempo fluctuations of the expressive performance correlated with dynamic activation changes in brain regions compatible with the mirror neuron system⁴, including bilateral BA 44/45, superior temporal sulcus, ventral premotor cortex, and inferior parietal cortex, along with other motor-related areas and with insula. One possible explanation for these results is that the communication of emotion during music listening is an empathic process in which a listener *feels* the emotion communicated by the performer. A mechanism for this action could involve engagement of the mirror neuron system and its interaction with the limbic system via the insula (Carr et al., 2003). Rizzolatti and Craighero (2004) theorized that the mirror neuron system provides a mechanism

⁴In humans, the neuroanatomy of the mirror neuron system is still being debated. Here the human mirror neuron system is considered to be comprised of the ventral premotor cortex, inferior parietal lobe (BA 40), superior temporal sulcus, and BA 44 as outlined in Rizzolatti and Craighero (2004).

for mapping the actions and intentions of others onto our own motor system as a means of action understanding. Importantly, mirror neuron activity has been reported when listening to common action sounds (Gazzola, Aziz-Zadeh, & Keysers, 2006) and to previously learned music (Lahav, Saltzman, & Schlaug, 2007). Molnar-Szakacs & Overy (2006) hypothesized that the mirror neuron system provides a mechanism by which listeners may experience music empathically rather than by cognitively interpreting an internal representation. However, they left open the question of what property of musical organization would engage this empathic process involving action representation in the mirror neuron system. Tempo and sound intensity, parameters that are manipulated through emotionally charged movement, are two properties of music that convey emotion from performer to listener through a process of empathic motor resonance. Perception of motion in music (Jones, 1981) may occur through activation of mirror neuron and motor systems and lead to emotional responses through interactions of the mirror neuron network and the limbic system taking place via the insula (cf. Carr et al., 2003). The current results suggest the possibility that listeners perceive goal-directed motion in the dynamic fluctuations of music performance, and this results in a form of empathic motor resonance leading to emotional responses (cf. Molnar-Szakacs & Overy, 2006).

It has been shown that those with musical training listen to music differently (Madsen & Geringer, 1990), exhibit different activation patterns during music perception (Besson, Fata, & Requin, 1994; Koelsch, Schroger, & Tervaniemi, 1999; Ohnishi et al., 2001; Pantev et al., 2001), show enhanced processing of affective vocal sounds (Strait et al., 2009), and even show differences in brain anatomy (Gaser & Schlaug, 2003; Schmithorst & Wilke, 2002). Also, expertise in a particular type of movement, such as dance, has been shown to alter the way mirror neurons respond during observation (Calvo-Merino et al., 2005), demonstrating that experience is an important factor in determining whether perceptions will resonate with one's own motor repertoire. In the current study, mirror

neuron regions were correlated with dynamic ratings of emotional arousal only in the experienced listeners, who also showed increased activation in emotion and reward-related areas. Thus, the pathways mediating emotional responses based on temporal fluctuations may differ with musical experience. It may be that all listeners perceive motion arising from changes in tempo through activation of mirror neuron and motor systems. However, it may be that mirror neuron activity only influences emotional responses in listeners with explicit experience conveying emotion through music performance. Therefore, network interactions between the mirror neuron system, insula, and limbic system may be more readily engaged in those with musical experience. Such individuals have the experience of conveying emotion through music performance and may have a more developed mapping between musical structure, motor experience, and emotion.

Activations in motor-related areas, such as preSMA, SMA, premotor, primary motor, basal ganglia (lentiform nucleus, putamen), cerebellum, and thalamus also correlated with the tempo of the expressive performance. Previous results showed that subjects are able to successfully track the changing tempo of the expressive performance used in the present study (Rankin et al., 2009), and Popescu et al. (2004) showed motor related areas (lateral premotor, SMA, somatosensory, and cerebellum) were associated with fine temporal structures of sound in a tempo tracking experiment. Activation of motor regions was also reported by Chen et al. during rhythm perception (2008b; 2006) and performance (2006). Basal ganglia activation has been linked to pulse perception (Grahn & Brett, 2007) and has also been shown to be involved in emotion processing in general (Phan et al., 2002). In the current study, basal ganglia activity was associated with changing tempo in all subjects and with music listening in experienced compared to inexperienced listeners. Listening to the expressive performance also increased activity in IFG (BA 47) overall, but more so for experienced participants. Previous work has linked IFG 47 (along with insula activity) to the perceptual organization of temporally patterned stimuli (Lev-

itin & Menon, 2003). Along with the previously mentioned experiment conducted by Bhatara et al. (2009), these results suggest that musically experienced listeners may be more aware of and respond more to tempo fluctuations in performed music. Based on their involvement in the perception of pulse and temporally patterned stimuli, it could be that motor areas (especially basal ganglia) and BA 47 contribute to the development of expectancy, and that their activity, combined with dACC, contributes to the experience of temporal expectancy violations. Emotional responses to these temporal violations may result from an empathic response of the mirror neuron system to the perception of motion in music (related to expectancy) and its interaction with the limbic system.

Increased sensitivity to expressive performance parameters may help explain why experienced participants showed enhanced responses in areas related to emotion, memory, and reward. Overall, listening to the expressive performance increased activity in parahippocampal gyrus, hippocampus, medial prefrontal cortex (mPFC), and ventral anterior cingulate (vACC) for all participants. Experienced participants showed a greater response than inexperienced listeners in the ventral striatum, hippocampus, and ventral anterior cingulate while listening to music in general, and in the ventral striatum and vACC while listening to the expressive performance. The ventral striatum (including nucleus accumbens) has been associated with the rewarding property of music (Blood & Zatorre, 2001; Brown et al., 2004; Koelsch et al., 2006; Menon & Levitin, 2005; Mitterschiffthaler et al., 2007). The vACC has been shown to be related to emotional processing in general (for review see Bush et al., 2000; Phan et al., 2002) and more specifically in music (Blood & Zatorre, 2001; Brown et al., 2004; Mitterschiffthaler et al., 2007). The mPFC, specifically BA 10, has been implicated in emotion processing and attending to one's own emotional state (for review see Gilbert et al., 2006). Parahippocampal gyrus activity has been shown in previous studies investigating emotional responses to music (Blood et al., 1999; Koelsch et al., 2006; Mitterschiffthaler et al., 2007) and has been linked to un-

derstanding social contextual cues (Hurley, 2008). These results suggest that expressive music performance activates emotion related structures in listeners and that even a moderate level of musical experience enhances this emotion associated activation and increases the rewarding aspect of music listening, perhaps through the engagement of the mirror neuron system and its interactions with the limbic system via the insula. Familiarity with a specific musical piece does not seem to be necessary to evoke this response.

CHAPTER 4

SUMMARY AND CONCLUSIONS

This dissertation used two kinds of rhythmic complexity, syncopation and tempo fluctuation, to study two aspects of cognition: attention and emotion. These types of complexity violate temporal expectancies in two qualitatively different ways. Syncopated rhythms, such as those used in Experiment 1, can violate expectancy for events to occur on the perceived pulse. Tempo fluctuation, present in the expressive performance of Experiment 2, violates the expectancy for events to occur approximately periodically. It was shown in Experiment 1 that attention might be an important part of how pulse is perceived when no energy is present in the stimulus at the pulse frequency. Auditory-motor integration was attention dependent and occurred only after the rhythms had been repeated a sufficient number of times for pulse induction. It was also shown that there was a relationship between peoples ability to tap the pulse and reproduce the rhythmic pattern. These results, combined with what is known from the literature about motor areas underlying pulse perception (Grahn & Brett, 2007, 2009) and attention being needed to perceive and respond to fluctuating tempo (Repp & Keller, 2004a), suggest that attention may be needed to perceive a pulse in complex rhythms.

Experiment 2 explored whether tempo fluctuation would elicit emotional responses in listeners. Ratings of emotional arousal correlated in real time with tempo changes. Limbic and emotion related areas responded to the expressive dynamics of music performance

containing tempo fluctuations and activity in areas related to emotion processing and reward were dependent upon the musical experience of listeners. Emotional arousal in response to an expressive performance correlated with dorsal anterior cingulate activity, which could indicate the role of temporal expectancy violation in emotional responding to music. Also, changes in activation levels of the mirror neuron system and insula were found to correlate with expressive timing fluctuations in performed music. These findings are consistent with the hypothesis that music evokes an empathic emotional response (Molnar-Szakacs & Overy, 2006), perhaps related to temporal expectancy, and show that music's affective impact on the brains of listeners is altered by musical experience.

The underlying commonalities between Experiments 1 and 2 are rhythmic complexity and consequent temporal expectancy violations. In Experiment 1, syncopated rhythms were designed to violate temporal expectancy, with some events being absent on strong beats and some events occurring on weak beats. In Experiment 2, violations of temporal expectancy came in the form of tempo fluctuation, where events sometimes occurred just before or after when they would be expected based on the expectancy for approximate periodicity. The development of temporal expectancy would likely be mediated by areas underlying the perception of pulse, such as basal ganglia. Basal ganglia (putamen) have also been implicated in violations of temporal expectancy in the visual domain (Coull et al., 2000). Attention dependent basal ganglia activation was seen in Experiment 1, and, in Experiment 2, basal ganglia tracked tempo fluctuations for all listeners. Dorsal ACC was discussed as playing a possible role in the detection of temporal expectancy violations. In Experiment 1, dACC activity was seen in association with attention to the complex rhythms, and in Experiment 2 dACC activity was correlated with emotional arousal in experienced participants. To explore how the degree of expectancy violation correlates with dACC activity and modifies its functional connections to pulse-related and emotion-related areas, it would be informative to investigate the functional connectivity

of the dACC with auditory, motor, and limbic areas during attention to varying degrees of rhythmic complexity (be it syncopation or tempo fluctuation).

In Experiment 1, the main experimental question was the role of attention in auditory-motor integration during the *perception* of complex rhythms. However, to test directly whether attention is needed to form a pulse percept for syncopated rhythms, one could perform a simple behavioral experiment by having subjects attend to, for example, a word list, while trying to tap the pulse of a syncopated rhythm. To better understand the attention dependent interaction between auditory and motor areas during the development of a pulse percept, it would be informative to perform an experiment similar to Experiment 1 using complex rhythms and a participant population that varies widely in their pulse perception and synchronization ability. In this case, it would be useful to have participants who are *not* able to successfully perceive or synchronize to a pulse when attending to the rhythms. Comparisons of the brain activation patterns of those who cannot perceive a pulse to those who are able to form a pulse percept that they can synchronize to should reveal activity underlying the formation and experience of pulse. Once the brain areas subserving pulse perception are identified from this comparison, correlations could be made between levels of activations in those areas and how well participants are able to perceive and synchronize to the pulse of the complex rhythms. For example, it may be that the strength and/or spread of activations in basal ganglia (striatum) and SMA are positively correlated with ability to accurately perceive a pulse percept (as measured by a synchronization task). It would also be interesting to perform a functional connectivity analysis during the auditory attend relative to visual attend conditions to see how attention modulates the functional connectivity between auditory and motor areas underlying pulse perception. In addition, with the use of Granger causality, one may be able to determine the direction of influence between auditory and motor areas during selective attention to complex rhythms, and if and how this influence changes over time. It could be that au-

ditory areas exert more influence over motor areas during the first few repetitions of a complex rhythm, but the direction reverses to motor areas having greater influence over auditory areas as the pulse percept is formed.

MEG could be an appropriate methodology to tackle the question of how high-frequency bursting relates to attention dependent rhythmic entrainment of auditory and motor areas to an external stimulus and to one another. Using the same complex rhythms along with an attentional manipulation similar to Experiment 1, one may observe bursts of high-frequency activity localized to auditory and motor areas (e.g., basal ganglia and SMA) bursting at the pulse frequency of the complex rhythmic stimuli. It could be that this bursting is present only during attention to the complex rhythms, or that attention increases coherence between these areas at the bursting frequency.

Future work is needed to further explore the role of the mirror neuron system in mediating emotional responses and to understand how this network relates to violations of temporal expectancy. The finding in Experiment 2, that mirror neuron activity correlated with emotional arousal in experienced participants, raises the question: does the mirror neuron system influence emotional responding only in listeners with performance experience? It would be of interest to test, for example, pianists and non-musicians listening to self-selected piano compositions that they report elicit strong emotional reactions (without the presence of any specific associated emotional memories). These compositions would be subject to the same experimental manipulation as in Experiment 1, except that all musical parameters (including loudness) but tempo would be held constant between two versions of the same composition. If mirror neuron activity were associated with the tempo variations only in pianists, then this would suggest mirror neuron involvement in emotional responding only occurs in those who have experience manipulating tempo in their own performances to convey emotion. If non-musicians show similar mirror neuron responses as the performers in response to tempo fluctuations, then mirror neuron involve-

ment may play a more general role in musical communication. Comparing responses to compositions that musicians had experience playing with pieces they had not performed, or using musicians who had only played instruments other than piano, would also help to answer the question of how mirror neuron activity relates to experience and emotional responses to music.

In Experiment 1, a link was found between attention and the perception of pulse for syncopated rhythms. In Experiment 2, tempo fluctuations were linked to emotion. An important follow-up question to these two experiments would be: Is there a link between attention and emotional responses in music? The current work showed that attention might be needed for the development of temporal expectancy when listening to syncopated rhythms. Attention has been shown to be needed to follow tempo fluctuations (Repp & Keller, 2004). Attention, therefore, may be a key component in the development of expectancy and consequently in the detection of expectancy violations that influence emotional responses. Insight into the development of expectancy and how violations of expectancy result in emotional responding may be obtained by investigating the functional connectivity of the dACC with primary and secondary auditory areas, basal ganglia (striatum), SMA, mirror neuron, and limbic areas (including nucleus accumbens). To explore this connectivity, one could perform an experiment that both incorporates an attentional manipulation and measures emotional responses to expressive music or syncopated rhythms. In this experiment, neural activity and emotional responses (including psychophysiological data) could be measured while participants selectively attend to musical stimuli containing events that violate temporal expectancy. This manipulation would also reveal whether attention is needed for emotional responses to occur in association with temporal expectancy violations.

The journey from listening to feeling involves a dynamic interplay between several neural systems (Juslin & Västfjäll, 2008). Auditory and attentional systems (which are

both modulated by previous experience, expectancy, and initial emotional conditions) must attend to and integrate sensory information into temporally and harmonically coherent structures. The development of expectancy, which may arise from an attention dependent process of pulse and meter perception, forms the backdrop against which musical events will be experienced. The dynamic integration of incoming musical stimuli with ongoing neural processes—which perhaps reflect previously developed expectancy—will result in the formation, strengthening, and maintenance of expectancies if the stimulus properties match the expected temporal and tonal structures. When the stimulus properties conflict with internal expectancy, violations may register in deep primal structures, such as the amygdala and ventral striatum, that mediate emotion, arousal, motivation, and reward. The interpretive analysis of higher-order cognitive structures, including those involved in memory, on this integrative process and its consequent effects on limbic function could give rise to musical meaning. It is from this complex interaction of auditory, attentional, motor, emotion, and cognitive networks that feeling takes form and sound becomes music.

APPENDIX A

VISUAL ATTEND CONDITIONS (COMPARED TO REST)

Table A.1: Visual Attend Conditions (Compared to Rest)

REGION (cluster peak)	BA	Cluster includes	X	Y	Z	Volume (mm ³)	Activation
Attend 2							
R cerebellar declive		bilateral lingual gyrus, precuneus (31, 7), cuneus, MOG, left IOG, bilateral STG (41, 22), SMA, mid-PMC, cingulate, hippocampus, parahippocampus	22	-73	-12	113472	positive
L MFG	10		-30	51	12	1216	positive
R SFG	9		30	47	28	960	positive
L posterior cingulate	30	bilateral cingulate (31, 23, 24)	-2	-49	20	11648	negative
R MFG	9	bilateral medial SFG 9, ACC (32)	2	51	24	11072	negative
R precuneus	39	angular gyrus	38	-69	36	2304	negative
L MTG	39	precuneus, angular gyrus	-46	-69	28	1280	negative
R IFG	47		22	3	-12	576	negative
Rehearse							
L IFG	9	IFG (44), vPMC	-46	7	24	11136	positive
L SMA		bilateral, cingulate (32)	-2	-5	52	6912	positive
R posterior cingulate		hippocampus, parahippocampus, precuneus	22	-49	12	6656	positive
L angular gyrus	39	precuneus, MTG (39)	-30	-57	32	3904	positive
L MFG	9	SFG (9, 10)	-30	47	20	2688	positive
R insula	13	MFG (10)	30	19	8	1024	positive
R MFG	10		38	47	12	832	positive
L posterior cingulate	29	bilateral cingulate (31), cuneus, precuneus (7), MTG (39), angular gyrus, lingual gyrus, MOG, IOG, cerebellar, fusiform gyrus, left declive, bilateral SMA, right dPMC, pre- and postcentral gyrus (3,4)	-2	-49	12	102976	negative
R SFG	8	bilateral pre-SMA, ACC (32, 24), medial FG (8, 9, 10)	2	27	52	31872	negative
R parahippocampal gyrus	35	subcallosal gyrus, IFG (47), BG (lentiform nucleus, putamen (not the same BG areas as in A vs. V rehearse))	18	-21	-12	7168	negative
L parahippocampal gyrus		amygdala, BG (lentiform nucleus, putamen (also not same BG areas as in A vs V rehearse))	-26	-1	-12	3584	negative
R IFG	47		42	31	-8	2112	negative
R MTG		20, 21	46	-1	-28	1536	negative
L IFG	47		-30	31	-8	896	negative
R subcallosal gyrus	25	bilateral vACC (25)	2	-1	-12	832	negative

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