Dissociable systems of working memory for rhythm and melody

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ABSTRACT

Specialized neural systems are engaged by the rhythmic and melodic components of music. Here, we used PET to measure regional cerebral blood flow (rCBF) in a working memory task for sequences of rhythms and melodies, which were presented in separate blocks. Healthy subjects, without musical training, judged whether a target rhythm or melody was identical to a series of subsequently presented rhythms or melodies. When contrasted with passive listening to rhythms, working memory for rhythm activated the cerebellar hemispheres and vermis, right anterior insular cortex, and left anterior cingulate gyrus. These areas were not activated in a contrast between passive listening to rhythms and a non-auditory control, indicating their role in the temporal processing that was specific to working memory for rhythm. The contrast between working memory for melody and passive listening to melodies activated mainly a right-hemisphere network of frontal, parietal, and temporal cortices: areas involved in pitch processing and auditory working memory. Overall, these results demonstrate that rhythm and melody have unique neural signatures not only in the early stages of auditory processing, but also at the higher cognitive level of working memory.

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Introduction

Rhythm and melody are fundamental elements of music. Rhythm refers to the temporal organization of music, such as the duration of notes and the onset time between successive notes; melody refers to the patterns of pitch over time (Seashore, 1938). Neuropsychological studies of brain-damaged patients have demonstrated that rhythm discrimination can be disturbed while sparing melody discrimination (Brust, 1980; Mavlov, 1980; Peretz, 1990; Di Pietro et al., 2004). Likewise, melody discrimination can be impaired while sparing rhythm discrimination (Brust, 1980; Peretz, 1990, 1993; Peretz and Kolinsky, 1993; Peretz et al., 1994; Piccirilli et al., 2000). The relative independence of rhythm and melody has also been established in behavioral studies, which have shown that sounds are grouped into the dimensions of rhythm or melody (Palmer and Krumhansl, 1987; Jones, 1993). These results, and those from neuroimaging studies of auditory tasks (discussed below), indicate that rhythm and melody are processed independently in the brain.

There is a strong association between the rhythmic auditory and rhythmic motor systems (Zatorre et al., 2007), which is likely based on their inherent temporal structure (Thaut, 2005). The connection between music and movement manifests itself in tapping and dancing

to the rhythm of a song. Indeed, direct auditory-motor pathways may bypass the higher-level cortical influences on movement (Paltsev and Elner, 1967; Rossignol and Jones, 1976). Studies of rhythm perception commonly report activation in motor regions, such as the premotor cortex (Sakai et al., 1999), supplementary motor area (Chen et al., 2008), and basal ganglia (Grahn, 2009), even in tasks without appreciable movement (Schubotz et al., 2000; Chen et al., 2008). Activation in one key motor area, the cerebellum, has been reported in numerous auditory rhythm tasks (Sakai et al., 1999; Schubotz et al., 2000; Parsons, 2001; Chen et al., 2008; Bengtsson et al., 2009). This finding is in accord with the proposed role of the cerebellum in timing (Ivry and Keele, 1989) and with the role of rhythm as the primary organizer of musical time (Benjamin, 1984; Jones, 1987; Thaut, 2005).

Brain damage of the right hemisphere, especially temporal (Milner, 1962; Zatorre, 1985; Samson and Zatorre, 1988; Liegeois-Chauvel et al., 1998) and frontal cortices (Shapiro et al., 1981; Zatorre et al., 1994), impairs pitch processing and melody discrimination. Neuroimaging studies have demonstrated a right-hemisphere dominance for pitch in temporal (Griffiths et al., 1999; Patterson et al., 2002; Jamison et al., 2006) and frontal cortices (Zatorre et al., 1992; Zatorre et al., 1994). The involvement of temporal and frontal cortices in pitch processing is consistent with the anatomical connectivity between these areas (Petrides and Pandya, 1988; Romanski et al., 1999). Moreover, congenital amusia, a disorder of music processing that is linked to deficits in melodic pitch processing, is associated with structural and functional abnormalities in temporal and inferior frontal cortices (Foxton et al., 2004; Hyde and Peretz, 2004; Hyde et al., 2011). Interestingly, individuals with congenital amusia have

pitch-specific deficits in working memory, and thus the disorder is not merely one of pitch discrimination (Foxton et al., 2004; Tillmann et al., 2009; Williamson and Stewart, 2010). When pitch and melody are held in working memory, activation is also commonly observed in posterior parietal cortex (Zatorre et al., 1994; Janata et al., 2002; Gaab et al., 2003).

Memory is critical in music because sounds are perceived in relation to each other in time (Peretz and Zatorre, 2005; Snyder, 2001). Indeed, many music tasks require subjects to compare musical notes, or compare a musical sequence to a template sequence. Implicit within such tasks is working memory, which is the temporary, online storage of information that is used to execute a task (Baddeley, 1986). Working memory is domain specific for tones in relation to pitch (Semal and Demany, 1991), timbre (Starr and Pitt, 1997), and verbal material (Deutsch, 1970); furthermore, accurate and specific representations of musical tempo and pitch are preserved in long-term memory (Levitin, 1994; Levitin and Cook, 1996). These results suggest that rhythm and melody are stored independently in the memory systems of the brain. Although some studies of brain-damaged patients (Zatorre, 1985; Zatorre and Samson, 1991; Penhune et al., 1999) and healthy humans (Zatorre et al., 1994; Sakai et al., 1999; Schubotz et al., 2000; Gaab et al., 2003; Koelsch et al., 2009) have examined rhythm and melody in memory tasks, most research has focused on them within the context of music perception or performance. Of those studies that examined rhythm and melody in memory tasks, most examined working memory over a short duration. Working memory for music, however, can last longer in time, as when segments of a song are played "in our head."

We here use positron emission tomography (PET) and a challenging task in which sequences of rhythms and melodies are held in working memory for an extended period of time (e.g., 90 s). PET is a good method for our relatively long task, since image acquisition is not noisy and the presentation of auditory stimuli is not mixed with scanner noise, as it is during routine functional magnetic resonance imaging (fMRI) (Amaro et al., 2002). Additionally, probing working memory with but a few targets, which would not produce in themselves significant activation during scan acquisition, isolates working memory of the target from regions related to stimulus recognition, identification, and selection. In essence, the scan shows neural regions involved in working memory for a single rhythmic or melodic sequence.

Materials and methods

Human subjects

Ten healthy male volunteers (average age 31 years, $SD \pm 18$) with no musical training were studied after providing written informed consent approved by the VAMC Human Subjects Committee and Radioactive Drug Research Committee. All subjects were screened for medical or psychiatric conditions. Data from three subjects were excluded due to movement artifacts. All but one subject were right-handed.

PET imaging and analysis

rCBF was estimated from integrated tissue radioactivity using a Siemens ECAT 953B camera (Siemens, Knoxville, TN) with septa retracted. A slow-bolus injection of $H_2^{15}O$ (initial dose of 814 Mbq or 22 mCi infused at a constant rate over 30 s (Silbersweig et al., 1993) was followed by a 90 s scan acquisition beginning upon radiotracer arrival into the brain (~10 min inter-scan intervals). Images were reconstructed with a 3D reconstruction algorithm using a 0.5 cycles-per-pixel Hanning filter (Kinahan and Rogers, 1989) and corrected for attenuation with a measured two-dimensional transmission scan. Measured coincidences were corrected for random detections and

electronic dead time, but no corrections were made for decay or scatter. Normalization for global activity (1000 counts), co-registration within each study session, placement of the inter-commissural line from image fiducials, nonlinear warping of each subject's scans to a reference stereotactic atlas (Talairach and Tournoux, 1988), and statistical analyses were accomplished with software developed and provided by Minoshima and coworkers (Minoshima et al., 1992; Minoshima et al., 1993; Minoshima et al., 1994). Images were blurred with a 4-pixel 3D Gaussian filter. Final image resolution was approximately 12 mm FWHM, yielding a mapping resolution of <2 mm (Fox et al., 1986). A significance threshold of P<0.001 was adopted as typically used in PET studies at this resolution. Effect sizes are reported as Z-scores (rCBF change at the peak pixel/global SD of all intracerebral pixels) (Worsley et al., 1992), and a Z-score of 3.5 was selected for the contrasts between the experimental conditions. This threshold, which is more conservative than that used typically (Z score>3.1), reflects an adjustment given the sample size available in this study.

Stimuli and experimental conditions

Two types of stimuli, rhythmic and melodic, were prepared with a DAT recorder and electronic keyboard using the piano timbre. Subjects participated in three conditions: (1) working memory for rhythm (WM-R) or melody (WM-M), in which sequences of rhythms and melodies were presented in separate blocks; (2) passive listening to rhythms (RC) or melodies (MC), also presented in separate blocks; and (3) a non-auditory condition of eyes closed rest (ECR). By contrasting working memory conditions with passive listening, working memory for the target sequence (either rhythmic or melodic) was isolated effectively during radioactive uptake over approximately one minute. Condition order (rhythm or melody) was counter-balanced across subjects, as was the hand used to make button presses. Subjects closed their eyes throughout the scanning period. Details of the conditions are given below.

Rhythm tasks

Rhythmic sequences lasted four seconds, spanning two measures of 4/4 time in musical notation (i.e., at a tempo of 120 beats per minute). The rhythms consisted of quarter notes, eighth notes, eighth note triplets, and sixteenth notes, which were presented in one pitch. Examples of a rhythmic target and probe are shown in Fig. 1a. In the WM-R condition, a target rhythm was played three times immediately before scanning, followed by ten probes (i.e., non-target rhythmic sequences) and three presentations of the target rhythm, which were intermixed during the scan period. Scan acquisition began after the third presentation of the target (Fig. 1c). A two-second delay followed each rhythmic sequence to allow for a button press. Subjects pressed a button to indicate whether the rhythm was the same or different as the target rhythm. In the RC condition, subjects were instructed to passively listen to different rhythms and press a button at random during the two-second period after each sequence. Sets of novel rhythms were used in each RC condition. Four RC conditions and four WM-R conditions were pseudo-randomly presented to subjects.

Melody tasks

Each melody spanned two measures in 4/4 time, and consisted of quarter notes, eighth notes, and half notes in a consonant arrangement centered around middle C and drawn from the C major scale. The melodies were rhythmically identical and covered a pitch range of 3–5 notes. Examples of a melodic target and probe are shown in Fig. 1b. During the WM-M condition, a target melody was presented three times immediately before scanning, after which ten probes and three target melodies were played in a pseudo-random order. Scan acquisition began after the third presentation of the target (Fig. 1c). Subjects then pressed a button during a two-second delay after each
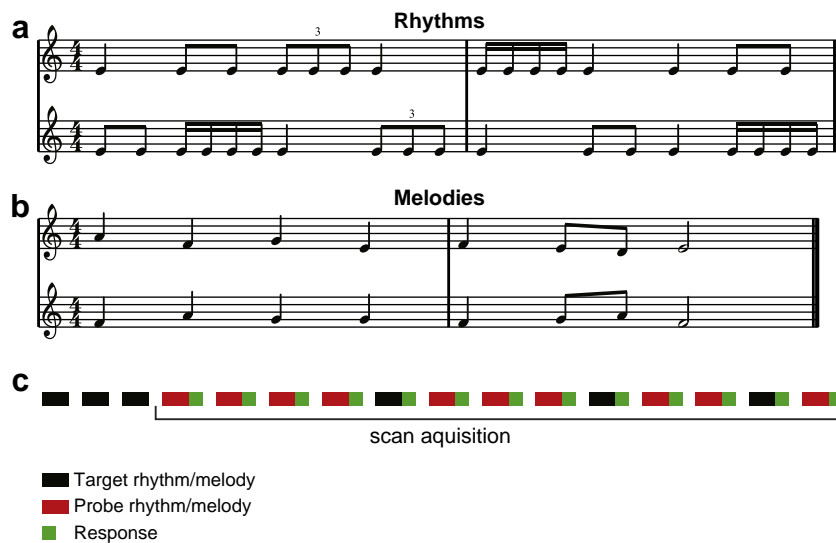
Fig. 1. Examples of (a) rhythmic and (b) melodic sequences that could serve as the target or probes during working memory conditions, or be presented by themselves during the passive listening conditions. (c) An example of the order of presentation of the target and probe sequences during an experiment. A target sequence (rhythm or melody, depending on the condition) was played three times before scanning, followed by ten probes (i.e., non-target sequences) and three presentations of the target, which were intermixed during the scan period. Subjects pressed a button after each probe sequence to indicate whether it was the same or different as the target.

sequence to indicate whether it was the same or different as the target melody. In the MC condition, subjects were instructed to passively listen to melodies and press a button at random during the two-second period after each sequence. Each MC condition consisted of different melodies. Four MC conditions and four WM-M conditions were presented to subjects in a pseudo-random order.

Results

Task performance

Subjects scored 90% correct on the WM-R task and 91% correct on the WM-M task, indicating that rhythm and melody taxed general cognitive functions equally.

Rhythm control (RC) minus eyes closed rest (ECR)

The contrast between RC and ECR revealed brain regions activated during passive listening to rhythms (Fig. 2a and Table 1). Significant increases in rCBF were observed in the right superior temporal gyrus (two foci in BA 22), left middle temporal gyrus (BA 22/21), and inferior temporal gyrus bilaterally (BA 20). Two regions in the left superior temporal gyrus would have reached significance (BA 42, Z-score = 3.2; BA 22, Z-score = 3.0) had we not used a conservative significance threshold. Activation in temporal areas was expected given their role in audition and the lack of auditory stimulation during the ECR condition. This contrast also activated the right postcentral gyrus (BA 3), right paracentral lobule (BA 7), and frontal regions: right superior frontal gyrus (BA 6), bilateral medial frontal gyrus (BA 6), and left orbital gyrus (BA 11).

Working memory for rhythm (WM-R) minus rhythm control (RC)

The contrast between WM-R and RC yielded activation due to working memory for rhythmic tones above and beyond the activation observed in passive listening to acoustically matched stimuli (Table 2). Robust activation was found in the right cerebellar hemi-

sphere (Z-score = 5.5), left cerebellar hemisphere (Z-score = 4.2), and vermis (Z-score = 3.6); the atlas of Schmahmann et al. (2000) was used to localize activation within cerebellar regions (Table 2). A robust focus was also observed in the right anterior insular cortex (BA 13). Fig. 2c illustrates activation in these regions. Other areas of activation included the left anterior cingulate gyrus (BA 32), right inferior frontal gyrus (BA 10), right inferior parietal lobule (BA 39), and left precuneus (BA 7).

### Melody control (MC) minus eyes closed rest (ECR)

The contrast of MC and ECR revealed regions activated during passive listening to tonal melodies (Fig. 2b and Table 3). The most robust rCBF increases occurred in the superior temporal gyrus, including Brodmann area 22 bilaterally and BA 42 in the left hemisphere. A significant activation was also observed in the left transverse temporal lobe, within Heschl's gyrus (BA 41). Three foci of activation were observed in the cerebellum (Z-scores 4.3, 4.3, and 3.8).

Working memory for melody (WM-M) minus melody control (MC)

Subtracting MC from WM-M yielded activation for melodic working memory above and beyond the activation observed in passive listening to acoustically matched stimuli (Table 4). rCBF increases were observed bilaterally in the inferior parietal lobule (BA 40), middle frontal gyrus (BA 6, BA 9, and BA 10), and medial frontal gyrus (BA 6 and BA 8). Right hemisphere activation was observed in the superior parietal lobule (BA 7), superior frontal gyrus (BA 6/8), precentral gyrus (BA 6), and middle temporal gyrus (BA 21). Fig. 2 e,f shows the location of rCBF increases in these regions. Left hemisphere activation was observed in the anterior cingulate gyrus (BA 32/8).

Discussion

The present study examined brain activity in healthy subjects, without musical training, in a working memory task for sequences of rhythms and melodies. We observed strikingly different patterns of activation, which we discuss below.
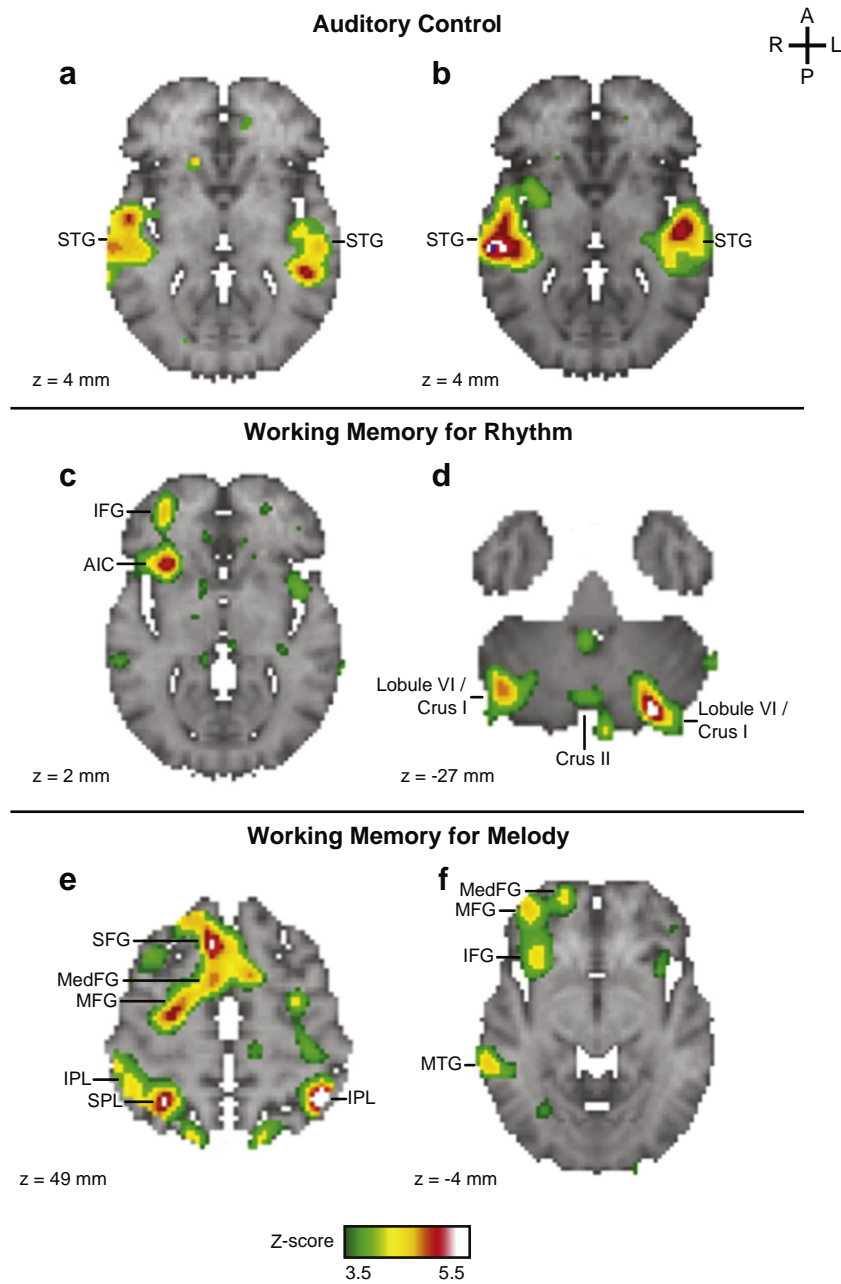
Fig. 2. Axial slices display activation evoked by the contrast of passive listening to (a) rhythms and (b) melodies vs. a non-auditory condition of resting with eyes closed; see Tables 1 and 3 for details. (c and d) Illustration of activation from the contrast of working memory for rhythm vs. passive listening to rhythms; see Table 2 for details. (e and f) Illustration of activation from the contrast of working memory for melody vs. passive listening to melodies; see Table 4 for details. R = right, L = left, A = anterior, P = posterior. STG = superior temporal gyrus; IFG = inferior frontal gyrus; AIC = anterior insular cortex; SFG: superior frontal gyrus; Med-FG: medial frontal gyrus; MFG: middle frontal gyrus; MTG: middle temporal gyrus; IPL: inferior parietal lobule; SPL: superior parietal lobule.

Working memory for rhythm (WM-R) minus rhythm control (RC)

The most robust activation occurred in the cerebellum, followed by activation of the right anterior insular cortex (AIC) and left anterior cingulate cortex (ACC). The activation of the cerebellum is consistent with studies of rhythmic auditory processing that required movements (Penhune et al., 1998; Thaut et al., 2009), simple responses such as button presses (Griffiths et al., 1999; Sakai et al., 1999; Schubotz et al., 2000), or no movements at all (Bengtsson et al., 2009). In a meta-analysis, Petacchi et al. (2005) reported that five of the eleven neural regions that are consistently activated by auditory tasks are in the cerebellum, with the extent of cerebellar activation

exceeded only by that of primary and secondary auditory cortices. Furthermore, damage of the cerebellum has been reported to cause deficits in working memory (Ravizza et al., 2006; Ziemus et al., 2007). In the present study, activation of the cerebellar hemispheres and vermis (Fig. 2d) occurred during working memory for rhythm, but not during working memory for melody or passive listening to rhythms. This result highlights the involvement of the cerebellum in auditory rhythmic processing during working memory. In the cerebellar hemispheres, bilateral activation was observed in lobule VI and Crus I, consistent with the meta-analysis of Petacchi et al. (2005). Whether this activation reflects the rehearsal or error correction components of working memory (Desmond et al., 1997; Durisko and Fiez, 2010;

Table 1
rCBF local maxima arising from the contrast between passive listening to rhythms (RC) and eyes closed rest (ECR).

Region	Hemi	BA	x	y	z	Z-score
Postcentral gyrus	R	3	39	−24	54	4.5
Superior frontal gyrus	R	6	8	14	54	4.1
Medial frontal gyrus	L	6	−19	−6	54	4.1
Paracentral lobule	R	7	8	−28	54	4.0
Superior temporal gyrus	R	22	53	−8	0	4.0
Middle temporal gyrus	L	21/22	−46	−40	4	3.9
Medial frontal gyrus	R	6	1	−6	54	3.8
Inferior temporal gyrus	R	20	44	−8	−32	3.7
Inferior temporal gyrus	L	20	−48	−8	−27	3.7
Orbital gyrus	L	11	−3	50	−22	3.7
Superior temporal gyrus	R	22	62	−26	4	3.5

Stereotactic coordinates (mm) identify the location of the rCBF maxima according to the atlas of Talairach and Tournoux (1988). Hemi = hemisphere. R = right; L = left. BA = Brodmann area. x = medial–lateral position relative to the midline (right hemisphere, positive); y = anterior–posterior position relative to the anterior commissure (anterior positive); z = inferior–superior position relative to the intercommissural plane (superior positive).

Kirschen et al., 2010), timing (Schubotz et al., 2000), sensory auditory processing (Bower, 1997), the interval ratio of the rhythms (Sakai et al., 1999), or a combination of these factors remains to be investigated.

The insula is activated in auditory rhythm tasks (Platel et al., 1997; Grahn and Brett, 2007; Thaut et al., 2008; Bengtsson et al., 2009) and has extensive anatomical connections with auditory cortex (Mesulam and Mufson, 1982). The right AIC in particular is one of the main neural regions activated across auditory studies (Petacchi et al., 2005), and damage to it can disturb auditory function (Spreen et al., 1965; Fifer, 1993; Griffiths et al., 1997). We observed robust activation of the right AIC (Fig. 2c). Why was the AIC activated during working memory for rhythm but not for melody? One possibility is that the AIC was engaged by the body's inherent urge to move when processing rhythms (Thaut, 2003; Thaut et al., 2009). Craig (2003, 2009b) has proposed that the insula plays a role in interoception, which is the sense of the physiological condition of the body. According to this view, the highly expanded AIC in humans integrates homeostatic conditions in response to significant features of the sensory environment (Craig, 2009a). The right AIC activation in our experiment may thus reflect a bodily response to the rhythms. A second possibility is that the AIC was engaged by the awareness of temporal intervals during rhythms (Coull, 2004; Livesey et al., 2007). Unlike the proposed role of the cerebellum in timing, which usually emphasizes its role in perception (Ivry and Keele, 1989), the insula has been proposed to create the awareness of time or time intervals (Craig, 2009a; Sterzer and Kleinschmidt, 2010). In our rhythmic working memory condition, an internal representation of temporal patterns could be formed by the temporal pattern of tonal sequences (Povel and Essens, 1985). The AIC activation may thus have resulted from

Table 2
rCBF local maxima arising from the contrast between working memory for rhythm (WM-R) and the control condition of passively listening to rhythms (RC).

Region	Hemi	BA	x	y	z	Z-score
Cerebellum, lobule VI/Crus I	L		−26	−69	−29	5.5
Insula	R	13	30	19	2	4.8
Cingulate gyrus	L	32	−1	14	38	4.4
Cerebellum, lobule VI/Crus I	R		42	−62	−27	4.2
Precuneus	L	7	−10	−58	47	3.9
Inferior frontal gyrus	R	10	33	48	2	3.8
Inferior parietal lobule	R	39	30	−62	38	3.7
Cerebellum, Crus II	L		−6	−80	−29	3.6

Cerebellar regions are based on the atlas of Schmahmann et al. (2000).

Table 3
rCBF local maxima arising from the contrast between the control condition of passive listening to melodies (MC) and eyes closed rest (ECR).

Region	Hemi	BA	x	y	z	Z-score
Superior temporal gyrus	R	22	55	−26	4	4.9
Superior temporal gyrus	L	42	−46	−19	7	4.7
Superior temporal gyrus	R	21/22	48	−13	0	4.4
Cerebellum, lobule VI	L		−24	−64	−25	4.3
Cerebellum, lobule VI/Crus I	R		37	−62	−32	4.3
Superior temporal gyrus	L	22	−48	−10	0	4.2
Transversal temporal gyrus	L	41	−39	−33	11	4.0
Superior temporal gyrus	R	38	26	12	−32	3.8
Cerebellum, Crus I	L		−10	−78	−29	3.8

Cerebellar regions are based on the atlas of Schmahmann et al. (2000).

interoception and/or the awareness of the temporal nature of the rhythmic musical sequences.

Joint activation of the AIC and ACC is common (Craig, 2009b), e.g., in time perception (Coull, 2004) and goal-directed attention (Weissman et al., 2006): two functions used in working memory. The left ACC was activated in working memory for both rhythm and melody, although less prominently in the latter. This result suggests that the left ACC played a general role in the working memory conditions, irrespective of the rhythmic or melodic nature of the stimuli. One such role is attention, which would have been more engaged during working memory than for passive listening (Pardo et al., 1990). We note that a potential limitation of our study is that the working memory conditions may have recruited more cognitive resources than the passive listening conditions, potentially yielding activation due to general cognitive resources rather than to working memory for rhythm and melody. However, it seems unlikely that rhythmic and melodic working memory would have differed in this respect, given the nearly identical behavioral performance for each condition (see Results section). Moreover, the fact that we observed different patterns of activity in the working memory contrasts for rhythm and melody, rather than extensive overlap, indicates that our results reflect the unique activation patterns that are particular to rhythm and melody. With respect to the greater ACC activation during working memory for rhythm compared to melody, an intriguing possibility is that certain higher cognitive functions, such as attention, are inherently rhythmical, in that they are entrained by the temporal regularities of the environment (Bolton, 1894; Parncutt, 1987; Jones and Boltz, 1989). In support of this idea, it has been shown that subjects use temporal cues to strategically attend to auditory material (Klein and Jones, 1996). The ACC activation may thus reflect the temporal nature of attention that is engaged by the rhythmic and, to a lesser extent, melodic sequences (Jones, 1976; Jones and Boltz, 1989).

Table 4
rCBF local maxima arising from the contrast between working memory for melody (WM-M) and the control condition of passively listening to melodies (MC).

Region	Hemi	BA	x	y	z	Z-score
Inferior parietal lobule	L	40	−44	−51	50	5.9
Medial frontal gyrus	R	6	8	3	54	5.7
Medial frontal gyrus	R	8	8	21	47	5.3
Superior parietal lobule	R	7	30	−51	50	4.9
Precentral gyrus	R	6	30	−13	52	4.7
Superior frontal gyrus	R	6	1	19	54	4.4
Middle frontal gyrus	L	6	−33	−4	52	4.2
Medial frontal gyrus	L	6	−10	8	52	4.1
Middle frontal gyrus	R	46	37	28	20	3.9
Middle frontal gyrus	R	9	42	23	32	3.8
Inferior parietal lobule	R	40	44	−55	45	3.8
Inferior parietal lobule	R	40	57	−35	45	3.7
Middle frontal gyrus	R	10	37	48	−2	3.7
Inferior frontal gyrus	R	47	35	21	−9	3.6
Middle temporal gyrus	R	21	60	−37	−4	3.6
Cingulate gyrus	L	32	−1	26	38	3.5

Regarding the lack of activation of temporal gyri during working memory for rhythm, lesions of the superior temporal lobe impair melody perception but spare rhythm processing (Peretz et al., 1994); and neuroimaging studies have reported no activation or greatly reduced activation in temporal gyri during rhythm processing in relation to pitch or melody processing (Parsons, 2001). We note that our musical sequences were relatively brief in duration, and lacked the beat component of rhythm, not to mention the emotive qualities of music. These characteristics may explain the absence of activation in motor regions, such as the supplementary motor area, that may be engaged by more complex auditory stimuli (Grahn and Brett, 2007), and limbic/paralimbic regions such as the ventromedial prefrontal cortex and amygdala that respond to emotional aspects of music.

Working memory for melody (WM-M) minus melody control (MC)

This contrast revealed areas recruited by working memory for tonal melodies and subtracted regions associated with melodic perception, pitch extraction, and auditory sensory information. We observed activation in frontal, temporal, and parietal cortices, mainly of the right hemisphere, which we will discuss as a specialized network of working memory for pitch and melody.

The extensive activation of the superior, middle, and inferior frontal gyri demonstrates the crucial engagement of the frontal cortex in working memory for melody (Fig. 2 e,f and Table 4). The frontal activation is consistent with human lesion and functional imaging studies of melody processing and pitch retention (Zatorre and Samson, 1991; Zatorre et al., 1994; Griffiths et al., 1999; Gaab et al., 2003), and with the anatomical connectivity between frontal and auditory cortices (Hackett et al., 1999; Romanski et al., 1999). The frontal activation was strongly lateralized to the right hemisphere (Fig. 2 e,f), consistent with the right-hemisphere dominance for sustained attention (Pardo et al., 1991). The increase in rCBF in the right middle frontal gyrus occurred in regions that have been implicated in working memory (Stevens et al., 1998; Raye et al., 2002). The activation of the left middle frontal and medial frontal gyri is noteworthy and may reflect the relatively long and challenging task, which required the ongoing rehearsal of the target melody and its comparison with other melodies (Halpern and Zatorre, 1999). The right inferior frontal gyrus was activated in working memory for both melody and rhythm. Interestingly, amusic individuals have a reduction in white matter concentration in the right inferior frontal gyrus (Hyde et al., 2006). This area thus appears to play an important role in auditory working memory. One function of the inferior frontal gyrus may be the detection of unexpected sounds (Koelsch et al., 2002; Tillmann et al., 2003), which is a critical component of our working memory task, in that subjects had to judge whether musical sequences matched the target sequence or not.

The observed focus in the right middle temporal cortex is consistent with studies of pitch and melody processing (Mazziotta et al., 1982; Parsons, 2001; Hyde et al., 2008; Watanabe et al., 2008). In a PET study of healthy subjects, Zatorre et al. (1994) reported activation of the right middle temporal gyrus during a high-memory load condition of single pitch retention. Their focus was in close proximity to the focus observed in the present study. Furthermore, patients with lesions in secondary auditory areas of the right hemisphere have detriments in pitch retention over short intervals (Zatorre and Samson, 1991). These studies from Zatorre's group examined the retention of a single pitch in working memory, whereas the present investigation required subjects to store a complex sequence of tones for a relatively long period of time. The similar activation foci indicate a role for the right middle temporal gyrus in melodic working memory beyond tonal sensory processing.

Recent work has shown that the posterior parietal cortex (PPC) is activated when auditory information is transformed (Zatorre et al., 2010; Foster and Zatorre, 2010). In terms of whether the PPC is specialized for the manipulation or monitoring of information in working memory (Champod and Petrides, 2010), our task would appear to emphasize the monitoring of auditory stimuli. Activation of the inferior parietal lobule bilaterally and the right superior parietal lobule is in agreement with studies of working memory for pitch (Zatorre et al., 1994; Platel et al., 1997; Janata et al., 2002; Gaab and Schlaug, 2003; Schulze et al., 2009; Schulze et al., 2011), musical sequences (Gaab et al., 2003), and sung material (Koelsch et al., 2009). The right inferior parietal lobule was activated in both the melodic and rhythmic working memory conditions, suggesting that it plays a general role in working memory, probably for both auditory and non-auditory stimuli. For example, the right inferior parietal lobule has been implicated in the recognition component of visual working memory (Berryhill and Olson, 2008) and in the maintenance of auditory information (Gaab et al., 2003; Vines et al., 2006). Given the involvement of the PPC in myriad sensori-motor transformations (Buneo and Andersen, 2006) and attentional functions (Gourtzelidis et al., 2005; Jerde et al., 2008), future studies are needed to elucidate its precise roles with respect to audition.

Passive listening conditions (RC and MC) minus ECR

These contrasts assessed activation evoked by the perception of rhythms and melodies, and allowed us to compare such activation to the contrasts involving working memory (Fig. 2a,b). In the contrast of RC and ECR, we observed temporal lobe activation in the right superior temporal gyrus, left middle temporal gyrus, and inferior temporal gyrus bilaterally (Table 1). Two foci in the left superior temporal gyrus nearly reached significance (see Results section).

In the contrast of MC and ECR, the unilateral focus in the left transverse temporal gyrus, corresponding to the primary auditory cortex, is consistent with a meta-analysis showing that this region is activated in a variety of auditory tasks (Petacchi et al., 2005). Zatorre and Samson (1991) noted that patients with right anterior temporal lobectomy performed poorly on a pitch retention task, whereas no additional impairment was observed if the lesion extended into Heschl's gyrus. Our results thus support the view that elementary sounds are largely processed in the left primary auditory cortex, and complex pitch extraction and melody processing are mainly functions of the right auditory cortex (Patterson et al., 2002; Hyde et al., 2008). The extensive bilateral activation of the superior temporal gyrus is consistent with the established role of this region in auditory processing. The activation of the cerebellum probably reflects the inherent rhythmic component of the melodies, since the melodic sequences unfolded in time and possessed a temporal structure. The cerebellar activation would thus have been subtracted away when contrasting WM-M and MC because the rhythmic component was present in both conditions.

Conclusions

The present study showed that working memory for rhythm and melody activated markedly different brain regions. Working memory for rhythm evoked prominent activation of bilateral cerebellar hemispheres and vermis, right anterior insular cortex, and left anterior cingulate gyrus. We propose that these areas contribute uniquely to the temporal processing of rhythmic auditory stimuli. Working memory for melody activated frontal, temporal, and parietal areas, mainly of the right hemisphere, indicating that these areas form a network for pitch and melody processing. Overall, our results provide further evidence that the neural specialization for rhythm and melody occurs not just in the perception of music but also at higher cognitive levels such as working memory. These results suggest that clinical evaluations of a patient's auditory and musical capacities should be sensitive to the contributions of different brain regions to the elements of music, such as rhythm and melody. It would be useful

for future studies to examine more precisely how the elements of music are dissociated along the perceptual-cognitive continuum and ultimately combined into the subjective experience of music.

Acknowledgments

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