Music and language side by side in the brain: a PET study of the generation of melodies and sentences

Steven Brown,[1,*] Michael J. Martinez[1] and Lawrence M. Parsons[2]

[1]Research Imaging Center, University of Texas Health Science Center at San Antonio, USA
[2]Department of Psychology, University of Sheffield, Western Bank, Sheffield, S10 2TP, UK

Abstract

Parallel generational tasks for music and language were compared using positron emission tomography. Amateur musicians vocally improvised melodic or linguistic phrases in response to unfamiliar, auditorily presented melodies or phrases. Core areas for generating melodic phrases appeared to be in left Brodmann area (BA) 45, right BA 44, bilateral temporal planum polare, lateral BA 6, and pre-SMA. Core areas for generating sentences seemed to be in bilateral posterior superior and middle temporal cortex (BA 22, 21), left BA 39, bilateral superior frontal (BA 8, 9), left inferior frontal (BA 44, 45), anterior cingulate, and pre-SMA. Direct comparisons of the two tasks revealed activations in nearly identical functional brain areas, including the primary motor cortex, supplementary motor area, Broca's area, anterior insula, primary and secondary auditory cortices, temporal pole, basal ganglia, ventral thalamus, and posterior cerebellum. Most of the differences between melodic and sentential generation were seen in lateralization tendencies, with the language task favouring the left hemisphere. However, many of the activations for each modality were bilateral, and so there was significant overlap. While clarification of this overlapping activity awaits higher-resolution measurements and interventional assessments, plausible accounts for it include component sharing, interleaved representations, and adaptive coding. With these and related findings, we outline a comparative model of shared, parallel, and distinctive features of the neural systems supporting music and language. The model assumes that music and language show parallel combinatoric generativity for complex sound structures (phonology) but distinctly different informational content (semantics).

Introduction

Observations during the preceding two centuries by neurologists such as Broca, Wernicke, Penfield, Luria, and Geschwind established language as a paragon of specialization, localization, and lateralization of higher cognitive function in the human brain (Price, 2000). Less influential were the discoveries of early neurologists showing that brain lesions could have similarly specific effects on musical functioning (Johnson & Graziano, 2003), implying the existence of cognitive and neurobiological specificity for music, similar to that for language (Peretz, 2002; Peretz & Zatorre, 2005). However, the neurology of music, like that of language, has been plagued by ambiguities, as the underlying lesions are usually neither focal nor are they replicated across patients showing similar clinical symptoms. In addition, the picture of independent specializations for language and music is clouded by the fact that most amusias are accompanied by aphasias (Marin & Perry, 1999), although the reverse is not generally the case (but see Patel, 2003, 2005).

In terms of function, music and language appear to show strong divergences at the level of the meaning (or semantics) but significant parallels with respect to grammar (or syntax) and intonation (Swain, 1997; Besson & Schön, 2003; Patel, 2003). Language conveys semantic meaning in a manner that appears to have few parallels in music (but see Koelsch *et al.*, 2004), yet both music and speech are generative phrasing systems, in which phrases have larger meanings than the sum of their elements, unlike most animal vocal communication systems (Hauser, Chomsky, & Fitch, 2002). Both music and speech are combinatorial systems in which larger structures are generated hierarchically from a pool of smaller, more unitary components. Moreover, musical and linguistic phrases can undergo changes in conveyed emotion through variation in pitch, amplitude, tempo, rhythm, etc. To the extent that music and speech share the use of structured pitch and rhythmic patterns to express their meanings, they may be expected to have common or similar brain mechanisms (Patel *et al.*, 1998).

In the last decade, a view has emerged that music and language have reciprocal cerebral hemispheric dominance, with music and language localized predominantly to homologous regions of opposite hemispheres (reviewed in e.g. Price, 2000; Peretz & Zatorre, 2005). For instance, functional neuroimaging studies of nonmusicians often show activity in right hemispheric areas homologous to classical language areas; i.e. the auditory association cortex of the posterior superior temporal gyrus and regions of the inferior frontal gyrus (Zatorre *et al.*, 1994; Halpern & Zatorre, 1999; Zatorre & Binder, 2000; Jeffries *et al.*, 2003; Brown *et al.*, 2004a; Koelsch, 2005; reviewed in Peretz & Zatorre, 2005). Interestingly, two prior functional neuroimaging studies using within-subject comparisons of music and language processes in nonmusicians observed that speech and singing tasks elicited similar activity patterns but with tendencies

Correspondence: Dr Lawrence M. Parsons, as above.
E-mail: L.parsons@sheffield.ac.uk

*Present address: Department of Psychology, Simon Fraser University, Burnaby, B.C., Canada.

for speech and singing to be localized to homologous regions of the left and right hemispheres, respectively (Riecker *et al.*, 2000; Jeffries *et al.*, 2003).

Although a framework of reciprocal cerebral specialization based on parallel functional homology can appear to account for general patterns of neurological and functional neuroimaging data, a closer inspection of the published data shows bilateral activity for various language and musical tasks. For example, two recent fMRI studies of semantic ambiguity of words in sentences implicate bilateral inferior frontal gyri in computing word meaning (Rodd *et al.*, 2005). Likewise, a positron emission tomography (PET) study of bilingual native users of both American Sign Language and English, revealed strong bilateral activity in postrolandic areas common to the two auditory and visual languages when participants generated autobiographical narratives (Braun *et al.*, 2001).

The bilaterality of the language system only becomes problematic when examining music and language side by side in the brain, because in the absence of this comparison the bilaterality of language (or music) is readily justified in terms of well-worn dichotomies of hemispheric asymmetries in cognitive processing (Hellige, 1993, 2002; Ivry & Robertson, 1998), such as verbal/nonverbal, local/global, or analytic/synthetic. The right-hemisphere regions homologous to left-hemisphere areas for lexical and syntactic functions are thought to be specialized for global meta-linguistic functions such as affective prosody (Ross & Mesulam, 1979; Buchanan *et al.*, 2000), discourse processing (St. George *et al.*, 1999), and the disambiguation of alternative meanings in sentences or discourse (Bottini *et al.*, 1994; Rapp *et al.*, 2004; Stowe *et al.*, 2005). Moreover, there is some evidence that the right hemisphere can assume certain language functions when the left is incapacitated by stroke or developmental damage (Fernandez *et al.*, 2004; Price & Crinion, 2005). Similar tendencies are seen in subjects with other causes of language insufficiency, including second language users (Ding *et al.*, 2003), stutterers (Fox *et al.*, 1996; Braun *et al.*, 1997), autistic individuals (Muller *et al.*, 1999), and healthy elderly individuals with good comprehension (Grossman *et al.*, 2002). Moreover, corresponding structural tendencies for right hemispheric language functions are seen in the brains of individuals with outstanding language competence (Amunts *et al.*, 2004). These strategic compensations are viewed as confirming the ability of homologous regions of the right hemisphere to serve language functioning. Bilaterality of the language system, thus, seems to affirm a principle of 'functional equivalence of homologous regions' in which homologous cortical regions are seen to represent related features of a single function rather than divergent features or completely unrelated functions. In general, hemispheric asymmetry as used in research on brain and cognition has implicitly assumed that homologous cortical regions process complementary facets of single functions.

The complication for this view of the functional brain organization for language is that not only do music tasks activate right hemispheric areas homotopic to classic left hemispheric language areas (Peretz & Zatorre, 2005) but many music tasks elicit bilateral activations that appear to border on or coincide with left-hemispheric – presumably language-specific – areas (e.g. Koelsch *et al.*, 2002; Hickok *et al.*, 2003; Levitin & Menon, 2003; Brown *et al.*, 2004a). The bilaterality of the music system is equally compatible with traditional dichotomies of cerebral asymmetry. For example, musical expertise can moderate the laterality of music processing. Functional neuroimaging studies have observed greater bilaterality in musicians than nonmusicians (Ohnishi *et al.*, 2001; Parsons, 2003; also see related functional and anatomical evidence in Bever & Chiarello, 1974; Gaser & Schlaug, 2003; Parsons *et al.*, 2005). These laterality differences appear

consistent with the view that the music system is represented bilaterally in the brain, that it abides by a principle of functional equivalence of homologous areas, and that segregation of function may follow dichotomies of cerebral asymmetry (e.g. expert-based categorization vs. naive uncategorized perception).

In sum, there are two conflicting viewpoints on the functional organization of language and music; that homologous hemispheric regions process different facets of a single function; and that a given cortical region (and its homologue) can be specialized for processing different functions (e.g. music and language). A primary goal of the present study was to explore the foregoing issues.

A second aim of our study was to examine for the first time the neural basis of the improvization of music and language, specifically within the context of melodic cadences and propositional sentences. We used positron emission tomography (PET) to examine amateur musicians spontaneously generating and vocalizing melodic or sentential phrases in response to unfamiliar auditorily presented melody or sentence fragments. Each task required the on-line improvization of phrases based on processing of the stimulus material in order to complete or resolve the overall structure of the musical or linguistic phrase.

Music generation and improvization has been studied with various methods (Nettl & Russell, 1998; Sloboda, 1998), including phenomenology (Sudnow, 1978), cognitive science (Johnson-Laird, 1988, 1991; Pressing, 1988; Kenny & Gellirch, 2002), and computational modelling (Laske *et al.*, 1992; Honing, 2006; Sadakata *et al.*, 2006). Likewise, language generation and speech production have been examined in some detail with cognitive science and computational methods, as well as functional neuroimaging (e.g. Crocker *et al.*, 2000; Price, 2000; Braun *et al.*, 2001; Kirchner *et al.*, 2001; Munhall, 2001; Blank *et al.*, 2002; Vigliocco & Hartsuiker, 2002; Kempen, 2003; Indefrey & Levelt, 2004; Cutler, 2005; Stowe *et al.*, 2005; Wallentin *et al.*, 2005; Sahin *et al.*, 2006). A componental analysis of our two tasks on the basis of this prior research suggests that there should be commonalities at the level of input (basic auditory processing) and output (vocalization) but significant differences with regard to domain-specific processing. For the melody generation task, this would include the short-term processing of absolute pitch, melodic contour, intervals, rhythm, tempo, and motivic structure, as well as long-term representations of scale structure (e.g. pitch sets and their internal hierarchies) and tonal relations (e.g. cadences). From a cognitive standpoint, melody generations would be expected to preserve features such as pitch set, rhythm, tempo and motivic structure but to perhaps show inversions in melodic contour, progressing ultimately to the tonic pitch; in Western music, 'answer' phrases typically have descending contours compared to 'question' phrases, which generally have ascending contours. Finally, the intended pitch sequence would be mapped onto motor-planning areas for phonation. For the sentence generation task, component processes would include the processing of segmental and suprasegmental phonology, including prosody, as well as analysis of the corresponding semantic and syntactic structures. From a cognitive standpoint, the sentence generation process should involve conceptual/narrative processing (long-term memory for categories of objects and events) stimulated by associations to the stimulus fragment, leading to the formation of syntactically appropriate phrases. This would be followed by mapping of the intended phrase onto motor representations for segmental and suprasegmental phonology.

We analysed cerebral blood flow changes using PET as subjects performed the domain-specific tasks of melody generation and sentence generation. We attempted to channel the results into a synthetic model of sound structure, information content, and

sequencing for music and language in the brain, a model that examines the possible shared, parallel, or distinctive features to each domain.

Materials and methods

Subjects

Five male and five female neurologically healthy amateur musicians, with a mean age of 25 years (range 19–46 years), participated in the study after giving their informed consent (Institutional Review Board of the University of Texas Health Science Center). Each individual was strongly right-handed, as confirmed by a modified version of the Edinburgh Handedness Inventory (Oldfield, 1971). None was taking medication or had a history of neurological or psychiatric illness. All subjects were university students, most in their first or second years as music education majors, with a mean of 5.3 years of formal music instruction in voice or instrument. Subjects began music instruction at a mean age of 12.4 years, having had an involvement in musical production (e.g. school bands, church choirs) for an average of 12.6 years prior to the study. None of them had absolute pitch, as based on self-report. Their musical specializations included voice, flute, clarinet, trumpet, trombone, guitar, bass, piano, drums, and percussion. All subjects also participated in a study of imitative singing, whose results are described elsewhere (Brown *et al.*, 2004a). Subjects underwent a detailed behavioural screening procedure in order to determine their suitability for participation. Each potential subject was presented with 35 samples of monophonic melodies, which they had to sing back as precisely as possible, as well as 26 samples of chordal melodies whose melody lines they had to create harmonizations with, generally by singing a major third above the melody line. Criteria for inclusion in the study included the following: (i) a proficiency at singing in key; (ii) an ability to sing at least 50% of the repetition samples with perfect accuracy, and (iii) an ability to sing at least 50% of the harmonization samples in such a manner that the melodic contour of the original melody was shadowed perfectly, in accordance with the rules of tonal harmony. The ten subjects who were used in this study were taken from a pool of 36 amateur musicians who underwent the screening procedure.

Tasks

Subjects performed two vocal tasks and rest with the eyes closed, as follows (see Fig. 1). (i) Melody generation – subjects listened to a series of incomplete novel melodies and had to spontaneously generate an appropriate phrase that completed each one directly after it was played. Each melody was 6 s in duration, followed by a 6-s period for response generation. The intertrial interval was 1 s. Consecutive samples were never in the same key. Subjects were instructed to use the carrier syllable /da/ when singing; this was carried out to avoid humming, to minimize head and mouth movement, and to permit adequate respiration during performance of the task. (ii) Sentence generation – subjects listened to a series of novel sentence fragments and had to spontaneously generate semantically and syntactically appropriate phrases to complete the fragment directly after each one was presented. Each sentence was 4 s in duration, followed by a 4-s period for response generation. The intertrial interval was 1 s. For both of the generation tasks, subjects were instructed to start their responses immediately after the stimulus material was finished. (iii) Rest with eyes closed – stimulus fragments in the two vocal tasks were designed to terminate at a distinct, obvious point of continuation (i.e. at a musical cadence or an adverbial phrase). With training, subjects learned to initiate their improvizations shortly after the stimulus fragment stopped. In addition, subjects practised the vocal tasks to ensure that their generated output was of comparable duration to the stimulus material. Finally, subjects were instructed to create completions, rather than simply continuations, of the fragments. Therefore, a sense of finality (e.g. a return to a pitch from the tonic chord in the melody task) was sought in the generated output. Subjects performed each of the vocal tasks twice and the rest task once in pseudo-random order, for a total of five scans.

Stimuli

Stimuli for the melody generation task were sequences of digitized piano tones presented to both ears, as generated using Finale 2001 (Coda Music Technology) and presented in the scanner using CoolEdit (Syntrillium) from a laptop computer. The source material consisted of folk-music samples from around the world (from the Silver Burdett 'Making Music' collections; http://www.sbgmusic.com), modified to fit the time and musical constraints of the stimulus set. Pilot testing ($n = 7$) using a matched group of subjects not participating in the imaging study confirmed that all stimulus material was novel for our subject population. A hypothetical standard for the stimulus set consisted of a sample with ten quarter-notes at a tempo of 100 beats per minute. The stimuli, then, were generated so as to vary with regard to tempo (slower and faster than the standard), number of notes (fewer or more notes than the standard), tonality (major and minor), rhythm [duple (2/4, 6/8), triple, and quadruple time], motivic pattern (e.g. dotted vs. nondotted rhythms), and melodic contour (ascending and
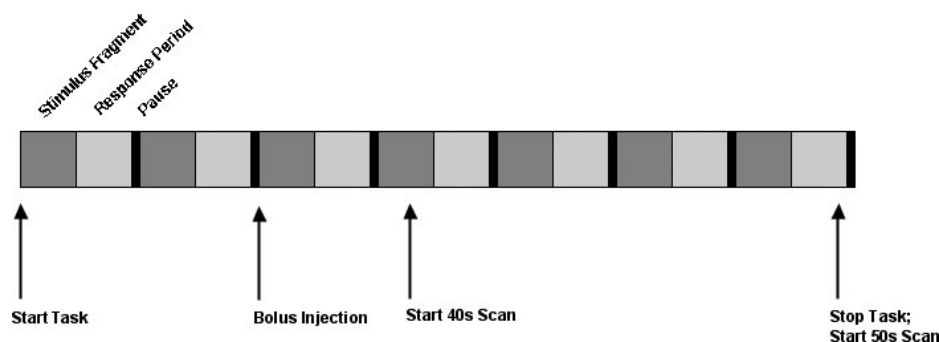

FIG. 1. The timeline of the PET trial. The dark grey and light grey boxes illustrate, respectively, the stimulus fragment and the period of response generation, followed by a 1-s pause. The subjects began each task 30 s prior to injection of the bolus. Bolus uptake required approximately 20 s to reach the brain, at which time a 40-s scan was initiated. At the end of the 40-s scan, the task was stopped and a 50-s scan was performed.

descending patterns). The samples covered a wide range of keys, more specifically eight major and three minor keys. The melody fragments presented to subjects consisted of typical 'question' phrases, generally ending on a pitch from the dominant chord. This was carried out to provide a tonal cue that aided the subjects in generating phrases to complete the fragment. The sentence generation task, in like manner, consisted of typical adverbial phrases that straightforwardly elicited the generation of phrases to finish the sentence (see example in Fig. 2). All the fragments were novel, were spoken by an unfamiliar, male, native English speaker, and were presented in the scanner using CoolEdit. The stimuli covered a wide variety of everyday themes. The auditory loudness was kept approximately constant both within and between stimulus sets for the two tasks.

Procedure

During the PET session, subjects lay supine in the scanning instrument with the head immobilized by a closely fitted thermal-plastic facial mask with openings for the eyes, ears, nose, and mouth. Auditory stimuli were presented through the earpieces of headphones taped over the subjects' ears. During scanning, subjects were told to close their eyes, lie motionless, and to clench their teeth lightly so as to make the syllable ⁄ da ⁄ when singing or to have minimal mouth movement while speaking. Pre-scan training enabled the subjects to perform the vocalization tasks with minimal head movement. Each subject had two PET scans for each of the vocal tasks and one of rest. Task order was counterbalanced pseudo-randomly across subjects. The timeline of a PET trial is shown in Fig. 1. The subjects began each task 30 s prior to injection of the bolus. Bolus uptake required approximately 20 s to reach the brain, at which time a 40-s scan was triggered by a sufficient rate of coincidence-counts, as measured by the PET camera. At the end of the 40-s scan, the auditory stimulus was terminated and the subject was asked to lie quietly without moving during a second scan of 50 s. From the initiation of the task until the start of the second scan, each subject had responded to six to seven stimuli.

Behavioural performance

The left side of Fig. 2 presents typical stimuli used for the melody and sentence tasks; the right side shows representative subject responses during scanning. Vocal responses were recorded on audiotape. We confirmed that all subjects performed with the same qualitative proficiency as during the screening session. The use of a stringent screening procedure for subject inclusion produced a homogeneous subject sample with minimally variable task performance across individuals. Therefore, by design, we were unable to employ covariance analysis for examining the relationship between brain activation and task performance.

Imaging procedures and analyses

PET scans were performed on a GE 4096 camera, with a pixel spacing of 2.0 mm, an interplane, centre-to-centre distance of 6.5 mm, 15 scan planes, and a z-axis field of view of 10 cm. Images were reconstructed using a Hann filter, resulting in images with a spatial resolution of approximately 7 mm (full-width at half-maximum). The data were smoothed with an isotropic 10 mm Gaussian kernal to yield a final image resolution of approximately 12 mm. Anatomical MRI scans were acquired on an Elscint 1.9 T Prestige system with an in-plane resolution of 1 mm^2 and 1.5 mm slice thickness.

Analyses of acquired PET data were performed exactly as described in Parsons & Osherson (2001), according to the methods of Raichle *et al.* (1983), Fox *et al.* (1988), and Mintun *et al.* (1989). Briefly, local extrema were identified within each image with a 3-D search algorithm (Mintun *et al.*, 1989) using a 125 voxel search cube (2 mm^3 voxel). A beta-2 statistic measuring kurtosis and a beta-1 statistic measuring skewness of the extrema histogram (Fox & Mintun, 1989) were used as omnibus tests to assess overall significance (D'Agostino *et al.*, 1990). Critical values for beta statistics were chosen at $P < 0.01$. If the null hypothesis of omnibus significance was rejected, then a *posthoc* (regional) test was performed (Fox *et al.*, 1988; Fox & Mintun, 1989). In this algorithm, the pooled variance of all brain voxels is used as the reference for computing significance. This method is distinct from methods that compute the variance at each voxel but is more sensitive (Strother *et al.*, 1997), particularly for small samples, than the voxel-wise variance methods of Friston *et al.* (1991) and others. The critical-value threshold for regional effects ($Z > 2.58$, $P < 0.005$, one-tailed) is not raised to correct for multiple comparisons as omnibus statistics are established before *posthoc* analysis.

FIG. 2. Representative stimuli (left side) and responses (right side) for melody generation (top) and sentence generation (bottom). Responses were of approximately equal duration to the initial heard stimuli.

Group mean whole-brain blood flow images for the rest conditions were subtracted from those for each of the two experimental tasks. The resulting contrasts were directly compared to reveal the significantly activated areas specific to melody generation, specific to sentence generation, and common to both.

Results

Melody generation (minus rest, Fig. 3A, Table 1) activated the supplementary motor area (SMA, medial BA 6), pre-SMA, primary motor cortex (BA 41), lateral premotor cortex (BA 6), frontal operculum (BA 44/45), anterior insula, primary auditory cortex (BA 1), secondary auditory cortex (BA 22), and superior temporal pole (anterior BA 22/38, or planum polare). Activations in SMA, primary motor cortex, and frontal operculum tended to be bilateral, whereas activations in the auditory cortex tended to have more intense foci in the right hemisphere and more diffuse ones in the left. Subcortical activations were observed in the thalamus, putamen, globus pallidus, caudate nucleus, midbrain, pons, and in bilateral posterior cerebellum in lobules VI, VIIIB, Crus I, and emboliform nucleus.

Sentence generation (minus rest, Fig. 3B, Table 2) activated pre-SMA, sensorimotor cortex (BA 4 and 3), premotor cortex (BA 6), frontal operculum (BA 44/45), superior frontal gyrus (BA 8, 9), cingulate motor area (BA 24/32), cingulate gyrus, anterior insula, inferior parietal cortex (BA 39), primary and secondary auditory cortex, middle temporal gyrus (BA 21), hippocampus, and ventral temporal pole (BA 38). Subcortical activations were observed in the thalamus, putamen, globus pallidus, caudate nucleus, midbrain, posterior cerebellum in lobules IV (vermis), V, VI, Crus I, and Crus II.

In terms of cytoarchitectonic brain areas, there was striking overlap in the activations between the music and speech conditions (Fig. 4). The functional regions that were activated by both tasks included bilateral SMA, left primary motor cortex (BA 4), bilateral premotor cortex (BA 6), left pars triangularis (BA 45), left primary auditory cortex (BA 41), bilateral secondary auditory cortex (BA 22), anterior insula, and left anterior cingulate cortex. Likewise, the subcortical activations were nearly identical between the two tasks. In addition, there was a dramatic overlap in the areas of deactivation – principally in parieto-occipital areas – across all brain slices for both tasks (data not shown; see Parsons et al., 2005; for a discussion of deactivations during musical tasks).

A similar picture emerges from inspection of the peak activations within distinct functional regions (Tables 1 and 2). In inferior frontal cortex, for example, melody and sentence generation peaked within BA 44 at homologous right and left locations (44, 10, 10 and −48, 8, 8). The two tasks peaked approximately 7 mm apart within left BA 45 (−38, 22, 4 and −42, 26, 0). In temporal cortex, there were overlapping or adjacent activations bilaterally in BA 22 (with peaks at 58, −28, 4 and −60, −22, 4 for melody, as compared to 58, −30, 6 and −60, −20, 4 for sentences).

The activation profile for sentence generation was much more left-lateralized in both motor and sensory areas, in agreement with the results of Riecker et al. (2000) and Jeffries et al. (2003). Moreover, there were several activations for sentence generation that tended to be absent or weaker than those for music in the left hemisphere, including the superior frontal gyrus, cingulate motor area, dorsal part of Broca's area (BA 44), and the ventral part of the temporal pole (BA 38) bilaterally. Activated areas specific to melody generation were detected in the dorsal part of the right temporal pole (anterior BA 22) and right frontal operculum (BA 44).

Discussion

The capacity to improvise spontaneous adaptive behaviours is a high and valuable accomplishment for an organism. The present study explored the improvization of melodies and sentential phrases, comparing their underlying neural substrates. In what follows, we first consider key component processes and associated activations specific to melody and sentence generation, and then discuss a broader framework of possible shared, parallel, and distinctive neural mechanisms for music and language.

Several features of the observed activation patterns appear to provide core and support processes for spontaneous improvization of melodies. A network of areas is likely involved in (i) accessing rules of harmony and musical structure, and (ii) re-ordering, rhythmically altering, re-harmonizing, or concatenating the stimulus or recalled musical associations to generate musically appropriate phrases (also see later discussion of motivic forms). Use of implicit knowledge for harmonic and melodic rules may be reflected in activity in frontal operculum (BA 44, 45) and planum polare (Maess et al., 2001; Koelsch et al., 2002; Tillmann et al., 2003; Brown et al., 2004a). Representation of rhythmic musical features (i.e. pattern, meter) is likely reflected in activity in specific regions of lateral BA 6, basal ganglia, and posterior cerebellum (Sakai et al., 1999; Parsons, 2003). Kinaesthetically based musical expressivity may be supported in the activity detected in bilateral insula. All the foregoing areas, with support of pre-SMA, anterior cingulate, dorsolateral frontal areas (BA 6), and basal ganglia, are likely to be involved in the improvised manipulation of musical structures recalled or perceived in the stimulus. The foregoing areas are also likely to support deciding amongst generated possibilities to determine the next note in a phrase. Pre-SMA, which is associated with planning, specifically in the context of response selection (Picard & Strick, 1996), has connectivity with inferior frontal regions (Johansen-Berg et al., 2004), and the observed bilateral activation in regions of pre-SMA and inferior frontal cortex is consistent with a distributed network.

Aspects of the observed activation patterns are implicated in core and support processes for improvization of sentential phrases. Generating prelexical narratives from the stimuli was likely supported by activity in posterior middle and superior temporo-parietal cortex (BA 21, 22, 39, 40) (Price, 2000; Braun et al., 2001; Indefrey & Levelt, 2004; Stowe et al., 2005). Such right hemispheric areas are active when generating the final word for a sentence (Kirchner et al., 2001). The anterior temporal activity observed bilaterally (BA 38, 20) may maintain an online conjunction of the stimulus fragment and improvised phrases because the greater the requirement for processing semantic information and coherence across phrases, the more likely is activity in anterior temporal regions (Maguire et al., 1999). Selecting amongst generated phrases may depend upon evaluations of semantic plausibility that are associated with activity in superior frontal cortex (BA 9, 8; Gallagher et al., 2000; Blank et al., 2002; Stowe et al., 2005). Improvization likely induces activity in pre-SMA, which is associated with response selection planning (Picard & Strick, 1996). Pre-SMA has connectivity with prefrontal regions (Johansen-Berg et al., 2004) that are active here (bilateral BA 9 and left BA 8), consistent with distributed processing. The activity present in bilateral anterior cingulate may reflect error detection and conflict monitoring (Bush et al., 2002; Wang et al., 2005) related to choice amongst improvised narrative and word response options. Mapping selected narratives onto lexical items via morphosyntactical rules is likely performed in bilateral temporal and inferior

TABLE 1. Stereotaxic coordinates and *Z*-score values for activations in the melody generation task contrasted to rest

Region	x	y	z	Z-score
Frontal cortex				
Right				
Pre-Supplementary Motor Area (6)	10	4	64	5.40
Supplementary Motor Area (6)	4	−4	58	5.40
Frontal Operculum (44)	44	10	10	4.54
Premotor Cortex (6)	46	−8	40	4.46
Premotor Cortex (6)	54	−8	40	4.26
Pre-Supplementary Motor Area (6)	4	11	54	4.19
Left				
Primary Motor Cortex (4)	−48	−10	44	5.01
Supplementary Motor Area (6)	−14	−6	58	3.63
Inferior Frontal Gyrus (45)	−38	22	4	3.52
Cingulate Motor Area (24)	−4	0	47	3.48
Cingulate Motor Area (24/32)	−2	18	32	3.40
Temporal cortex				
Right				
Superior Temporal Gyrus (22)	58	−28	4	5.75
Planum Polare (22)	56	0	−2	5.32
Planum Polare (22)	48	8	0	4.46
Middle Temporal Gyrus (21)	66	−14	−4	4.15
Secondary Auditory Cortex (42)	46	−18	8	3.40
Left				
Planum Polare (22)	−50	2	−4	5.47
Superior Temporal Gyrus (22)	−50	−12	0	3.95
Superior Temporal Gyrus (22)	−58	−36	8	3.83
Primary Auditory Cortex (41)	−32	−36	14	3.83
Superior Temporal Gyrus (22)	−60	−22	4	3.56
Other regions				
Right				
Anterior Insula	38	20	6	4.73
Globus Pallidus	14	−4	−6	3.95
Anterior Insula	18	20	−8	3.83
Putamen	20	0	6	3.63
Putamen	24	8	0	3.40
Left				
Anterior Insula	−48	6	4	5.55
Anterior Insula	−42	10	0	5.16
Putamen	−22	6	6	5.16
Pons	−2	−34	−28	3.59
Pulvinar	−8	−24	6	3.48
Putamen	−24	−12	10	3.40
Cerebellum				
Right				
Lobule VI	28	−58	−24	5.67
Crus I	50	−56	−30	3.83
Lobule III (Vermis)	0	−46	−16	3.48
Left				
Lobule VI (Vermis)	−2	−68	−20	4.89
Lobule VIIIB (Vermis)	−10	−74	−34	3.79
Dentate	−6	−56	−28	3.79
Lobule VI	−34	−52	−30	3.67
Lobule VI	−20	−56	−26	3.63

Brain atlas coordinates in are in millimeters along the left-right (*x*), anterior-posterior (*y*), and superior-inferior (*z*) axes. In parentheses after each brain region is the Brodmann area, except in the case of the cerebellum, in which the anatomical labels of Schmahmann *et al.* (2000) are used. The intensity threshold is *Z* > 3.40.

TABLE 2. Stereotaxic coordinates and *Z*-score values for activations in the sentence generation task contrasted to rest.

Region	x	y	z	Z-score
Frontal cortex				
Right				
Sensorimotor Cortex (3/4)	46	−14	30	3.70
Premotor Cortex (6)	44	−12	36	3.61
Cingulate Motor Area (24/32)	10	16	34	3.61
Cingulate Motor Area (24/32)	8	10	38	3.57
Anterior Cingulate (24/32)	1	24	−6	3.53
Primary Motor Cortex (4)	54	−10	40	3.40
Dorsolateral Prefrontal Cortex (9)	42	0	40	3.40
Premotor Cortex (6)	52	−2	42	3.40
Left				
Pre-Supplementary Motor Area (6)	−4	6	56	7.26
Frontal Operculum (45)	−42	26	0	6.29
Primary Motor Cortex (4)	−44	−10	48	5.82
Frontal Operculum (44)	−48	8	8	5.74
Dorsal Broca's Area (44)	−42	12	18	5.61
Primary Motor Cortex (4)	−46	−18	36	5.48
Cingulate Motor Area (24/32)	−6	16	34	5.06
Prefrontal Cortex (9)	−21	44	18	4.72
Premotor Cortex (6)	−36	0	46	4.30
Primary Motor Cortex (4)	−50	−10	22	4.13
Superior Frontal Gyrus (8)	−14	40	40	3.70
Pre-Supplementary Motor Area (6)	−20	6	62	3.57
Medial Prefrontal Cortex (10/32)	−20	42	−4	3.44
Temporal cortex				
Right				
Superior Temporal Gyrus (22)	58	−30	6	5.44
Superior Temporal Sulcus	60	−10	−2	5.02
Planum Polare (38)	48	16	−20	4.89
Middle Temporal Gyrus (21)	62	0	−10	4.51
Superior Temporal Gyrus (22)	48	8	0	4.13
Left				
Superior Temporal Sulcus	−54	−12	0	6.29
Superior Temporal Gyrus (22)	−60	−20	4	6.12
Superior Temporal Sulcus	−54	−4	−6	5.69
Superior Temporal Gyrus (22)	−58	−38	6	5.44
Superior Temporal Sulcus	−50	−24	2	5.14
Superior Temporal Gyrus (22)	−54	−54	20	4.97
Primary Auditory Cortex (41)	−32	−34	16	3.96
Inferior Temporal Gyrus (20)	−38	−5	−29	3.96
Other regions				
Right				
Globus Pallidus	14	−4	−6	5.40
Putamen	26	18	6	4.30
Anterior Insula	38	20	6	3.79
Left				
Anterior Insula	−42	12	0	5.74
Anterior Insula	−34	22	6	5.57
Putamen	−24	4	2	4.93
Anterior Insula	−30	15	−6	4.59
Thalamus	−12	−22	18	4.30
Anterior Insula	−30	8	16	4.21
Hippocampus	−28	−30	−4	4.08
Thalamus	−6	−26	6	3.83
Caudate Nucleus	−12	12	18	3.40
Cerebellum				
Right				
Crus I	34	−62	−28	6.33
Crus II	12	−80	−32	4.25
Lobule V	10	−58	−22	3.91
Lobule VI	10	−68	−28	3.70
Left				
Lobule IV (vermis)	−4	−56	−30	5.19
Crus I	−50	−66	−20	3.65
Lobule IV (vermis)	−2	−50	−12	3.48
Lobule VI	−36	−50	−28	3.44
Lobule VI	−42	−52	−28	3.44

Brain atlas coordinates in are in millimeters along the left-right (*x*), anterior-posterior (*y*), and superior-inferior (*z*) axes. In parentheses after each brain region is the Brodmann area, except in the case of the cerebellum, in which the anatomical labels of Schmahmann *et al.* (2000) are used. The intensity threshold in is *Z* > 3.40.

frontal cortex (Price, 2000; Blank *et al.*, 2002; Indefrey & Levelt, 2004; Stowe *et al.*, 2005; Tyler *et al.*, 2005; Sahin *et al.*, 2006). Ordering lexical items according to syntactic rules (e.g. linearizing hierarchical structures) may occur with coactivity in Broca's area, and posterior superior and middle temporal areas (Blank *et al.*, 2002; Stowe *et al.*, 2005). Mapping lexical items to constituent phonemes via morphophonological rules may be supported by coactivity in posterior sections of the left middle and superior
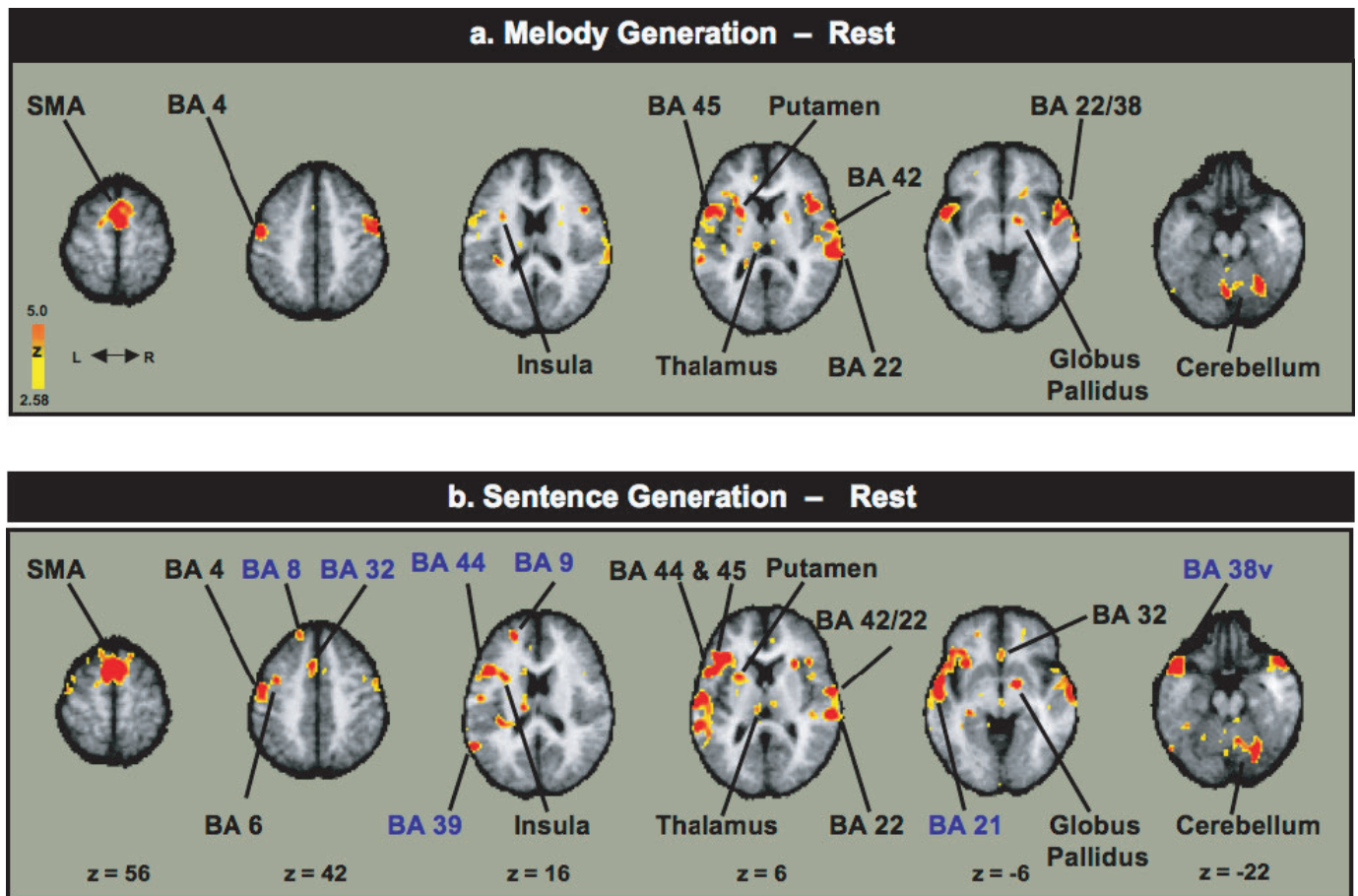
FIG. 3. Grand mean PET-rCBF changes for each task minus rest (see Tables 1 and 2). Activations are overlayed onto an averaged brain in all figures. Bilateral activations are labelled unilaterally. Labels for activations unique to sentence generation are in blue print in panel B. BA 38v refers to the ventral temporal pole. The intensity threshold in Figs 2 and 4 is $Z > 2.58$, $P < 0.005$ (one-tailed). The left BA 39 activation in panel B was below this threshold; its peak is located at $-46, -74, 29$.
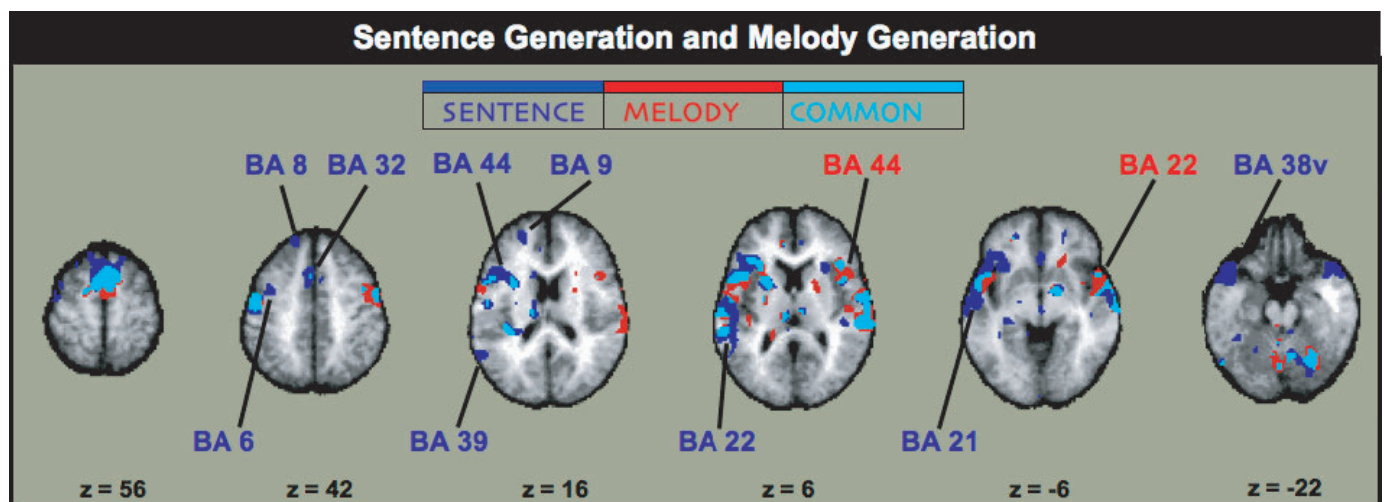

FIG. 4. Activation specific to melody generation (in red), specific to sentence generation (in blue), and common to the two tasks (in cyan). Brodmann labels are colour-coded to highlight activations unique to the sentence generation (blue) or melody generation (red) tasks.

temporal gyrus (Indefrey & Levelt, 2004) and inferior frontal cortex (Sahin *et al.* in press). Building phonemes into syllables likely is supported by activity in Broca's area (Indefrey & Levelt, 2004).

Syntactic prosody, which includes metrical or stress features of word articulation, appears to be supported by bilateral temporal and frontal cortical, and subcortical structures, which are active here

(Van Lancker & Sidtis, 1992; Baum & Pell, 1999; Riecker *et al.*, 2000; Schirmer, 2004).

Apart from the foregoing core and support areas implicated in melodic and sentential improvization, respectively, each task was supported by activity in other neural structures, such as those for auditory perception and vocalization (see later).

Localization of possible shared, parallel, and distinctive features for music and language

We now discuss processing components of our tasks in a comparative, cross-modal manner in light of a provisional synthetic model of the localization of music and language in the brain. The model aims to reconcile differing brain functional accounts of music and language; one in which homologous hemispheric regions process different facets of a single function and one in which a given cortical region (and its homologue) can be specialized for processing multiple functions. The model (Fig. 5) assumes that music and language are generative systems, relying on combinatorial operations to generate novel, complex and meaningful sound structures by concatenating simpler, memorized acoustic units. We will describe the features of music and language as being either 'shared', 'parallel', or 'distinctive' (Brown, 2000; Brown, 2001). Within this framework, we will discuss shared resources and overlapping activations for primary auditory processing and vocal motor-somatosensory processing for music and language. Then, we describe parallel and partially overlapping representations for combinatoric generativity for sound sequences (phonology) in homologous brain regions. Finally, we outline domain-specific and nonoverlapping representations for distinctive, information bearing (semantic) functions of music and language. We apply the idea of an 'interface area', a region where more than one facet of language (or music) comes together. Interface areas are discussed with respect to phonology/semantics, semantics/syntax, and syntax/phonology.

Although the model is presented with implied processing sequences, these are illustrative, as we are aware that considerable continuous parallel processing occurs (e.g. Spivey *et al.*, 2005), and
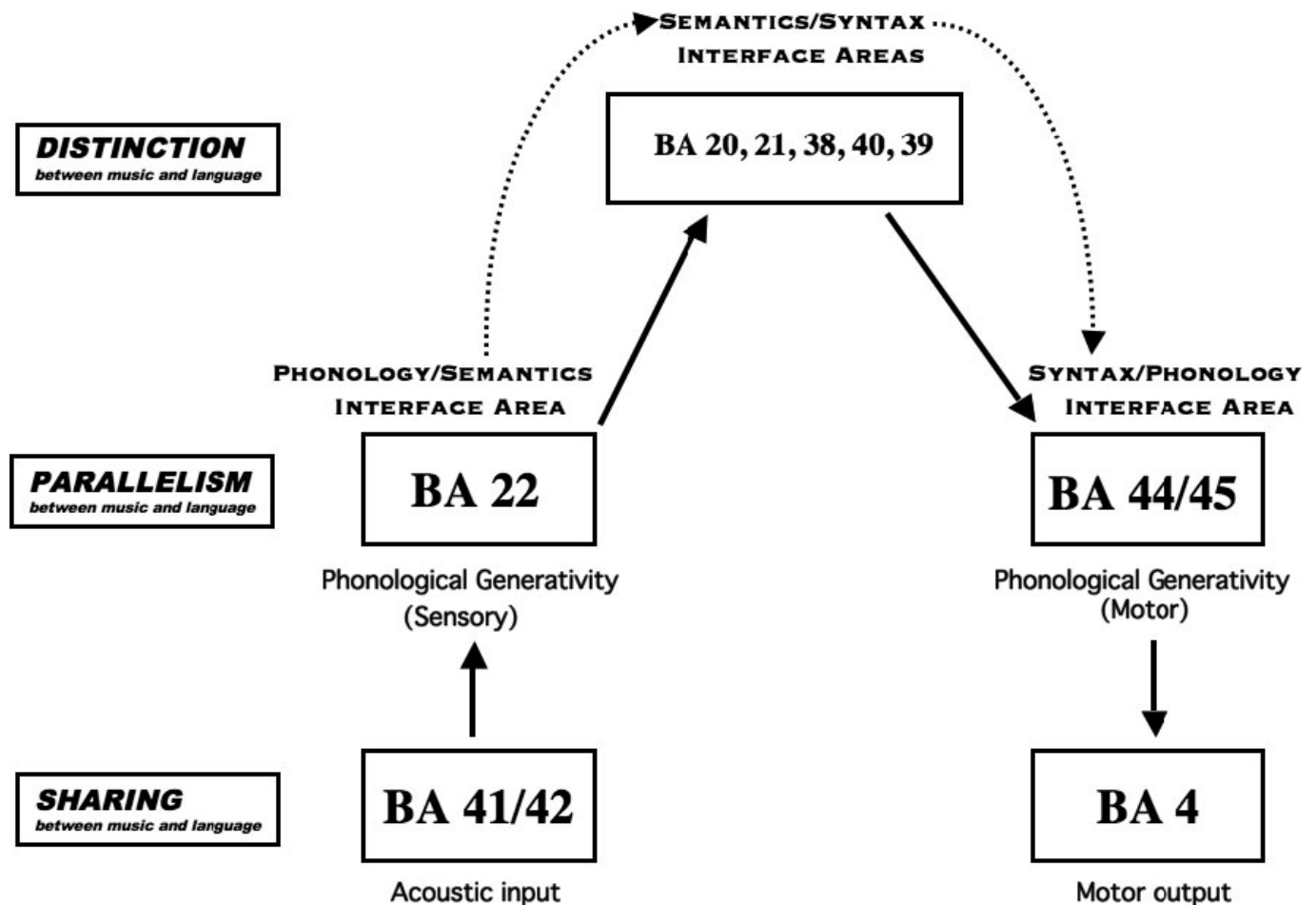

FIG. 5. An illustrative model specifying three levels of interaction between music and language in the brain: sharing (in grey), parallelism (in blue), or distinction (in red), with 'interface areas' serving as links for semantic processing (in orange) or syntactic processing (in green). (i) Sharing. Shared processing elicits overlapping activations between music and language in primary auditory cortex (BA 41) and primary motor cortex (BA 4). (ii) Parallelism. Phonological generativity is seen as the major point of parallelism between music and speech. Regions of BA 22 and BA 44/45 are seen as sensory and motor centres, respectively, for phonological generativity. These areas of parallelism may be localized such that BA 22/44/45 of the left hemisphere is specialized for speech phonology and the corresponding right hemispheric areas are specialized for musical phonology. The processes for phonological generativity in BA 22 and BA 44/45 may interface differentially with other functions, with BA 22 being a phonology/semantic interface area and BA 44/45 being a phonology/syntax interface area. (iii) Distinction. Domain-specific areas for music or language, with nonoverlapping activation profiles for melody generation and sentence generation, are interposed between BA 22 and BA 44/45 in a series of semantics/syntax interface areas distributed throughout the extrasylvian temporal lobe (BA 21, 38, 39,40) as well as the inferior frontal gyrus (BA 47).

that different tasks (e.g. generation vs. detection) may elicit different processing sequences.

Sharing: primary audition (BA 41) and vocal production (BA 4)

Shared resources would be a plausible hypothesis to explain common activations in the primary auditory cortex and subcortical auditory system for the music and language tasks. For example, the two tasks showed common activity in left primary auditory cortex BA 41 (peaking at −32, −36, 14 for melody and −32, −34, 16 for sentences) and considerable overlap in the right auditory cortex (Fig. 4). Resources may be shared if such processing is limited to a frequency representation before features such as pitch and phonemes are extracted.

Sharing of resources would also be a sensible explanation for overlapping activations in motor and kinesthetic areas underlying vocalization. The main regions that fall into this category are the primary motor cortex, SMA, pre-SMA, anterior insula, somatosensory cortex, and the subcortical areas (putamen, globus pallidus, ventral thalamus), as well as the posterior cerebellum (Ivry, 1997; Dreher & Grafman, 2002; Bower & Parsons, 2003). All of these areas have been strongly implicated in the motor-sensory processes underlying human vocalization (Turkeltaub et al., 2002; Jürgens, 2002; Indefrey & Levelt, 2004; Schirmer, 2004; Brown et al., 2005), including singing (Perry et al., 1999; Jeffries et al., 2003; Brown et al., 2004a) and affective prosody (Baum & Pell, 1999; Schirmer, 2004). For the SMA, activity was strongly overlapping between tasks, with activity for sentence generation extending anteriorly and that for melody generation extending posteriorly to a common core. The activity observed in pre-SMA, which is associated with planning in the context of response selection (Picard & Strick, 1996), is consistent with the requirements of spontaneous improvization. In primary motor cortex (BA 4), activation for sentence generation tended to be left lateralized while that for melody generation tended to be bilateral (with a peak in left BA 4 at −48, −10, 44, near that for sentence generation at −44, −10, 48) and greatly overlapped the left-hemisphere sentence generation activity (Fig. 4). These areas likely represent a sharing of neural resources for the control of phonation and articulation during speaking and singing. (Subjects used the carrier syllable /da/ while singing.)

Parallelism: combinatorial generativity of complex sound structures (BA 22, BA 44/45)

That regions of BA 22 are involved in the perceptual processing of complex sound patterns, including communication sounds such as speech and music, is firmly established, especially with regard to the posterior region, or planum temporale (e.g. Griffiths & Warren, 2002). BA 22 is a form of unimodal auditory association area, homologous to the belt and parabelt areas of the monkey auditory cortex (Kaas & Hackett, 2000; Poremba et al., 2003). In monkey, these regions receive their major input from the core areas of primary auditory cortex, and send a principal projection to the frontal cortex and superior temporal gyrus and sulcus (Kaas & Hackett, 2000). Functional neuroimaging studies of humans typically report activity in BA 22 during tasks with complex auditory stimuli, including passive listening to sentences or music (reviewed in Binder et al., 2000; Ohnishi et al., 2001; Scott & Wise, 2004; also our unpublished observations).

The role of BA 22 in phonological processing for speech seems to be well founded in the literature (reviewed in Scott & Wise, 2004). We would argue that BA 22 serves a parallel function in phonological

decoding for music, as based on the extensive number of studies showing activations here during both passive and active listening to music (e.g. Binder et al., 2000; Ohnishi et al., 2001). Such a function could have important relevance in our melody generation task for processing pitch, interval, and perhaps even scale structure (Griffiths & Warren, 2002; Patterson et al., 2002; Peretz & Zatorre, 2005). It is unlikely that there is anything truly language-specific or music-specific about this brain region (Binder et al., 2000; Scott & Wise, 2004). This is not to argue that its role is nonspecific but instead that it may encode features of acoustic sequencing that are common to speech and music.

The role of BA 22, especially in left hemisphere, in semantic processing for language dates back to early neurological observations by Wernicke and others that damage to this region is associated with severe speech comprehension deficits, including sensory aphasia and pure word deafness (Price, 2000). Interestingly, Wernicke's area includes not only BA 22 but also adjacent parts of the inferior parietal lobe – mainly BA 39. Indeed, this area is recruited for (nonauditory) visual sign language comprehension in deaf native signers, although it is recruited for heard speech in hearing native signers (MacSweeney et al., 2002). In neurology and functional neuroimaging studies, posterior BA 22 is implicated in phonological decoding and language semantics, suggesting it is a phonology/semantic interface area. Moreover, certain speech-perception deficits associated with damage to BA 22, such as pure word deafness, may be secondary to problems with phonological decoding (Binder et al., 2000). Thus, this region of BA 22 may be an interface area for interpreting the phonology of combinatorially and recursively generated complex sounds and transmitting it to areas supporting the semantics of words and phrases.

Clarifying initial observations, recent research suggests that lesions associated with Broca's aphasia and similar speech–ataxic syndromes involve a broader part of the brain than just Broca's area, including the anterior insula and basal ganglia (Dronkers, 1996; also see Hillis et al., 2004). Broca's area (regions of left BA 44 and 45) in particular is now often viewed as a large functional region (Marcus et al., 2003), with evidence for subregions supporting syntactic, semantic, and phonological operations (see, e.g. meta-analysis by Chein et al., 2002). Here we focus on the involvement of BA 44/45, particularly the frontal operculum, in motor aspects of phonological generativity connected with vocal production (Poeppel, 1996; Janata & Grafton, 2003), as contrasted to BA 22's role in sensory aspects of phonological generativity. In this respect, BA 44/45 may be an interface between phonological generativity and syntactic functioning. A similar argument (Hagoort, 2005) has been made about a 'unification' between syntax and phonology in BA 44/45 (and semantics extending into BA 47).

That Broca's area is involved in phonological generativity is suggested by several functional neuroimaging studies reporting its activation during phoneme-processing tasks (e.g. Demonet et al., 1992, 1994; Zatorre et al., 1992, 1996). Indeed, in an fMRI study directly comparing tasks in which sequences of three syllables or three hummed notes were either remembered or manipulated for a match decision (i.e. delete the middle element, reverse sequence order), the hummed manipulation produced greater activity in inferior frontal BA 44 than the linguistic task (Gelfand & Bookheimer, 2003). Broca's area cannot be a purely motor structure, like the primary motor cortex, as many functional imaging studies detect its activation during tasks involving no vocal output. Hence, this area's role in phonology might be related more to sequencing (Gelfand & Bookheimer, 2003; Janata & Grafton, 2003), and thus generativity, than to vocalization per se.

In addition to the role of Broca's area in motor phonology is its suggested role in syntax processing for language (also a process of sequence generation), hence supporting the notion that Broca's area is a true interface area. Beyond the well-recognized fact that Broca's aphasics suffer from agrammaticism are the findings of a large number of neuroimaging studies with healthy individuals that Broca's area is activated during syntax tasks (e.g. Dapretto & Bookheimer, 1999; Price, 2000; Indefrey *et al.*, 2001; Heim *et al.*, 2003; Indefrey & Levelt, 2004; Stowe *et al.*, 2005) and during morphological processing (Sahin *et al.* in press). Indeed, sentences with scrambled noun phrases activate this area more strongly when they contain real words than pseudowords, implicating the area in both syntactic processing and semantic integration (Roder *et al.*, 2002). Ordering lexical items according to syntactic rules may be supported by coactivity in Broca's area and posterior superior and middle temporal areas (Stowe *et al.*, 2005; Tyler *et al.*, 2005). The pars triangularis (BA 45), but not pars operucularis (BA 44), has been shown to be responsive to sentence constructions that are permissible by Universal Grammar (Chomsky, 1980), but not to impermissible ones (Musso *et al.*, 2003). With regard to music, recent functional neuroimaging and electrophysiological studies suggest that detecting violations in the harmonic rules of music (i.e. its syntax) activates Broca's area, typically the pars opercularis (BA 44) rather than the pars triangularis (BA 45) (Maess *et al.*, 2001; Koelsch *et al.*, 2002; see also, Janata & Grafton, 2003; Patel, 2003; Koelsch, 2005). These results suggest that sequential ordering of music may be processed in a homologous manner to language syntax. It is significant to note that the other major brain areas aside from Broca's area that are shown to be activated during syntax tasks are extrasylvian temporal lobe areas such as BA 21 and BA 38 (see meta-analyses in Kaan & Swaab, 2002). The latter observations are consistent with the existence of interface areas for syntax and semantics, as discussed below.

Overlapping representations

We have argued throughout this section that combinatorial generativity is a key point of cognitive parallelism between language and music, and that BA 22 and BA 44/45 might be pivotal points of neural parallelism between sensory and motor aspects, respectively, of such generativity for both language and music, as mediated in part by hemispheric differences in activation in homologous cortical areas. In the present study of melody and sentence generation, we observed overlapping or adjacent activations in both hemispheres in BA 22, but not in other areas of temporal cortex. In addition, while we saw homologous, domain-specific activations for sentence and melody, respectively, in left and right BA 44, we saw adjacent activations more anteriorly within the left frontal operculum, at the border of BA 45 and 47 (with peaks at −42, 10, 0 for music and −42, 26, 0 for speech). Activity in left BA 47 is intriguing as neuroimaging studies of both language and music have implicated this area in processing temporal coherence within and between phrases (Levitin & Menon, 2003). Thus, our findings, which show this effect for the first time with generative tasks, further reinforce the possibility that this area supports a function at the level of meaning and time-extended structure for music and language. In addition, activity in BA 47 for the music task may reflect an element of affective processing (Menon & Levitin, 2005).

Given our proposal of parallelism between music and language in these regions, we can imagine four plausible explanations for these coincident patterns. First, it is possible that some areas of activation during one or the other task are epiphenomenal – rather than essential –

to the underlying neural operations. Hence, common activations need to be evaluated with interventional methods such as transcranial magnetic stimulation or direct (subdural) brain stimulation in order to verify their necessity for the functions being studied. Second, there may be sharing in the systems involved in phonological decoding or encoding between music and language in these parts of the brain, most especially related to the operations of sequencing and concatenation. A third possibility is that these regions have an 'adaptive coding' capacity to process different types of information (music or language) by virtue of pluripotential neurons (as hypothesized in certain prefrontal areas; see Duncan, 2001). Finally, what appears as overlap at the 4 mm spatial resolution of PET may instead reflect the existence of interleaved functional domains. fMRI studies at higher spatial resolution have been able to demonstrate separability among apparently overlapping functional areas (cf. Schwarzlose *et al.*, 2005 for work on the fusiform gyrus; on the uncertainties of localization, see Brett *et al.*, 2002). Suggestions of potential separability in the present data are seen in the left frontal operculum (BA 45), where there were differences in peak activation for the two tasks, and in SMA and pre-SMA, where the music activation extended posteriorly to an area of overlap and the speech activation extended anterior to it.

Distinction: semantics (extrasylvian temporo-parietal areas)

The distinct, nonoverlapping, domain-specific activations in the extrasylvian temporal areas observed for the melody and sentence generation tasks may be due to operationalized task-related differences in their informational content (semantics). However, the distinct activations may also be due to inequalities in information processing (note the greater number of activated foci for the generation of sentences than melodies, Tables 1 and 2). Indeed, the informational content of music (i.e. its 'semantics') is still ill-defined operationally (but see Koelsch, 2005). Furthermore, cross-talk between the systems of information content for music and language may occur because in event-related potential (ERP) studies of priming, musical primes can influence the N400 component (a reflection of linguistic semantic processing) in a manner similar to linguistic primes (Koelsch *et al.*, 2004).

From a componential standpoint, semantics would be involved in the sentence generation task both during the presentation of the fragment and during conceptual/narrative processing to create a semantically appropriate completion to that fragment. Key semantic areas for language appear to be found in the left middle and inferior temporal gyrus (BA 21/20), bilateral ventral temporal pole (BA 38v), left inferior parietal cortex (BA 39/40), and inferior frontal gyrus (BA 47) (Price, 2000; Bookheimer, 2002; Thompson-Schill, 2003; Indefrey & Levelt, 2004).

The superior temporal pole (anterior BA 22 and dorsal BA 38) is a plausible candidate area for representing the semantics of music (see Brown *et al.*, 2004b). Activations here in the music generation task likely reflect this component of the task. A related study comparing speaking and singing (Jeffries *et al.*, 2003) highlighted nonhomologous activations between tasks in many brain regions, and, like the current study, detected music-specific activations in the dorsal part of the temporal pole.

From a componential perspective, a semantic function in music might relate to the processing of motives, which are coherent units of musical pattern or form. Motives serve as thematic elements in music, perhaps in an analogous fashion to conceptual themes in language. As our subjects generally showed a preservation of motives between the stimulus fragment and the improvised response (data not shown), it is

likely that the processing of motivic pattern was strongly active in our melody generation task. While there is neurological evidence that distinct neural systems underlie the representation of interval size and melodic contour, as dissociated from tonal scale structure, it is not yet known where these systems are localized (Peretz & Zatorre, 2005).

In sum, these areas (Fig. 5) may be semantics/syntax interface areas, with a principal input to these regions consisting of semantic information coming from the auditory association area in BA 22 and that, at least for language, there is evidence of syntactical processing in most of these areas (Kaan & Swaab, 2002). Such an interface area may be a reflection of the close intertwining of syntactic and semantic processing in language (Jackendoff, 2002).

Conclusion

Based on an analysis of parallel generative tasks for music and language, we have presented a synthetic model for the representation of these two functions in the brain. Whereas music and language may share resources for audition and vocalization, phonological generativity is seen as the major point of cognitive parallelism between them, in which parallel cognitive operations related to combinatorial phrase generation occur on divergent semantic units. We foresee a period of intense and fruitful research into the brain organization of music and language marked by the uses of higher spatial-resolution measurements, parametric processing variables, meta-analyses of functional neuroimaging and electrophysiology studies, articulately contrasted designs for studying music and language creativity in fuller structural complexity, and explicit tests for domain specificity. In the latter case, predictions about domain specificity follow from the model outlined here. For example, the model suggests that if BA 44 is indeed an interface area for motor phonology and syntax, then aphasic patients will have difficulties singing novel melodies (such as those used in Brown et al., 2004a) requiring on-line processing of musical structure (for evidence of impairments in harmonic priming in patients afflicted with Broca's aphasia, see Patel, 2005). Important insights about language processing will be gained by close examination of music and language side by side.

Acknowledgements

Abbreviations

BA, Brodmann area; PET, positron emission tomography; SMA, supplementary motor area.

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