

Separate cortical networks involved in music perception: preliminary functional MRI evidence for modularity of music processing

Vincent J. Schmithorst*

Imaging Research Center, Children's Hospital Medical Center, 3333 Burnet Avenue, ML 5031, Cincinnati, OH 45229, USA

Received 4 May 2004; revised 24 November 2004; accepted 7 December 2004

Music perception is a quite complex cognitive task, involving the perception and integration of various elements including melody, harmony, pitch, rhythm, and timbre. A preliminary functional MRI investigation of music perception was performed, using a simplified passive listening task. Group independent component analysis (ICA) was used to separate out various components involved in music processing, as the hemodynamic responses are not known a priori. Various components consistent with auditory processing, expressive language, syntactic processing, and visual association were found. The results are discussed in light of various hypotheses regarding modularity of music processing and its overlap with language processing. The results suggest that, while some networks overlap with ones used for language processing, music processing may involve its own domain-specific processing subsystems.

© 2004 Elsevier Inc. All rights reserved.

Keywords: Music perception; fMRI; Independent component analysis

Introduction

The neuropsychological bases and neural substrates of music processing continue to be a topic of much investigation. A modular functional architecture for music processing has recently been proposed (Peretz and Coltheart, 2003) involving components such as tonal encoding of pitch and contour analysis. This architecture was hypothesized based on the results of various lesion studies (e.g., Griffiths et al., 1997; Mendez, 2001; Metz-Lutz and Dahl, 1984; Peretz et al., 1994) showing selective impairment and selective sparing in the auditory recognition of words, tunes, and other sounds. On the other hand, an alternative framework (Patel, 2003) posits significant overlap between modules used for language processing and music processing and points to the overlap in neural structures used for language

and music processing (Koelsch et al., 2002; Maess et al., 2001; Tillmann et al., 2003) as evidence for such domain non-specificity. For instance, BA 47 has been found to be associated with the processing of both linguistic and musical structure (Levitin and Menon, 2003), while BA 44 (Broca's area) and its right hemisphere homologue have been associated with the processing of musical syntax (Maess et al., 2001).

However, to investigate any hypothesized framework for music processing with regard to the particular task of music perception is problematic using conventional neuroimaging techniques. While specific paradigms may be designed to test specific elements, (e.g., Platel et al., 1997), the tasks cannot be said to really be "music perception" due to the specific attentional demands (e.g., if the subjects are told to judge if two melodies are the same or different). Using a passive music listening task, however, is also problematic since the various modules will have a high degree of temporal interrelatedness, and the hemodynamic responses are not known a priori. Moreover, there are additional confounds such as attention. A simplified music perception task was designed and group independent component analysis (ICA) was used as a technique for disassociating the neural substrates involved with the various elements of music processing. The task involved the presentation of random tones, unharmonized melodies, and harmonized melodies using pure tones; hence, no element of timbre was present. Group ICA was selected as a technique for analysis of the data since the hemodynamic response functions (HRFs) of the various cognitive components are not known precisely a priori and may in fact have considerable variance across subjects.

ICA is a data-driven approach for analysis of fMRI data and operates by linearly unmixing the fMRI data into spatially independent component maps (details given in McKeown et al., 1998). The method has been extended for multisubject analyses (Calhoun et al., 2001b) and the generation of across-subjects random-effects statistical inferences. ICA offers the advantage of not requiring accurate modeling of the HRF for each subject and cognitive component. The group ICA technique has been shown to provide similar results to standard model-based approaches (Calhoun et al., 2001a) and has been used recently in studies investigating simulated driving (Calhoun et al., 2002), visual

* Fax: +1 513 636 3754.

E-mail address: Vince.Schmithorst@cchmc.org.

Available online on ScienceDirect (www.sciencedirect.com).

perception (Calhoun et al., 2001a), and language processing (Schmithorst and Holland, 2003). In a recent study involving a complex math processing task (Schmithorst and Brown, 2004), group ICA was able to separate out the neural correlates corresponding to the hypothesized triple-code model (Dehaene and Cohen, 1995) for math processing consisting of the three numerical representations of analog magnitude, auditory verbal, and visual Arabic.

Materials and methods

Fifteen college-educated adults (4 F, 11 M, mean age = 37.8 ± 15.2 years) participated in the study. The subjects were roughly evenly divided between those who had received prior formal musical training (7 out of the 15 total) and those who had not (8 out of the 15). The criterion for “formal musical training” used was that the subject had studied either a musical instrument or voice, receiving formal instruction, continuously from early childhood (8 years old) throughout adolescence. Institutional review board approval and written informed consent were obtained for all subjects. Each subject was also prescreened for any history of neurological or psychiatric abnormalities, head trauma, or any other conditions that would prevent an MRI scan from being performed.

A three-phase block-periodic fMRI paradigm was used. The subjects were presented with 30 s of an unharmonized popular melody, followed by 30 s of tones of random frequency and duration, followed by 30 s of the previous melody, harmonized using triads an octave below. The melodies used were as follows: “America the Beautiful,” “O Little Town of Bethlehem,” “Star-Spangled Banner,” “Chariots of Fire,” and “O Holy Night.” These specific songs were chosen as stimuli due to their popularity and familiarity to non-musically-trained subjects and relatively simple form and harmonic progressions. The frequency range of the random tones was matched to the frequency range of the harmonized melodies. Pure sine tones were used throughout in order to negate any effects related to timbre. An audio interchange file format (AIFF) sound file was generated in interactive data language (IDL; Research Systems Inc., Boulder, CO) and played on an SGI O2 (Silicon Graphics Inc., Silicon Valley, CA) computer system through an MRI-compatible audio/video system (Magnetic Resonance Technologies, Van Nuys, CA). The volume was adjusted to ensure that the subjects could hear the stimuli clearly over the MRI scanner noise. The subjects were instructed to passively listen to the sounds and not actively generate any output such as lyrics to the melodies. The use of melodies with associated lyrics provides a method for verification of the ICA methodology; some subjects would likely generate, covertly or subconsciously, the lyrics to the melodies while listening to them. This provides a useful reliability check for the ICA decomposition since a transiently task-related component involving cortical regions recruited for expressive language tasks should be detected. A separate group of college-educated adults (6 F, 4 M, mean age = 31.5 ± 7.9 years) was used to rate the unharmonized and harmonized melodies for emotional affect and intensity. A five-point scale was used, with 5 being positive for affect and high for intensity.

A 3 T Bruker Medspec system (Bruker Medical Instruments, Karlsruhe, Germany) was used for imaging. For the functional scans, a 24-slice blipped echo-planar imaging (EPI) sequence was

used with the following parameters: matrix = 64×64 , BW = 125 kHz, FOV = 25.6×25.6 cm, TE = 38 ms, TR = 3 s, slice thickness = 5 mm. In addition, a whole-brain T1-weighted scan was acquired for anatomical coregistration.

fMRI post-processing was performed with routines written in IDL (Research Systems Inc., Boulder, CO). During reconstruction, the EPI data were corrected for geometric distortion and Nyquist ghost artifacts via the multiecho reference method (Schmithorst et al., 2001). The images were corrected for motion via a pyramid iterative algorithm (Thevenaz and Unser, 1998) and linearly transformed into stereotaxic coordinates (Talairach and Tournoux, 1988) using landmarks found from the whole-brain anatomical images. The fMRI data were then smoothed with a Gaussian filter of width 4 mm.

A previously published method for generating group random-effects statistical inferences using ICA (Calhoun et al., 2001b), demonstrated to provide superior performance to other proposed methods (Schmithorst and Holland, 2004), was used. Each data set was pre-processed by variance normalizing the voxel time courses, and the dimensionality was reduced via principal component analysis (PCA) to 40 points in the time dimension. This reduction resulted in 94% of the variance being maintained on average. After concatenation across subjects in the time dimension, a second PCA reduction was performed, reducing the dimensionality to 50 points in the time dimension. An empirically based choice of dimensionality in the second data reduction stage was used since an attempted Bayesian information criterion (BIC) estimation, similar to that suggested by (Calhoun et al., 2001b), resulted in a very large number of components. A greater number of components was kept after the second data reduction stage since not all components are expected to be present in all subjects (each subject is expected to have unique artifactual components stemming from motion and cardiac and respiratory effects), and these artifactual components might possibly mix into the task-related ones. After the PCA reduction, the infomax (Bell and Sejnowski, 1995) ICA algorithm was used to find independent components. The method of Calhoun et al. (2001b) was then used to find individual subject IC maps and associated time courses, and a random-effects analysis (one-sample *t* test) was used to test the composite IC maps for significance on a voxelwise basis. As a reliability check for the ICA decomposition, the epochs of the data corresponding to the presentation of harmonized melodies and unharmonized melodies were separated out and examined using additional group ICA analyses.

Several post hoc comparisons on the associated time courses were used to test the components for various elements of “task relatedness.” While it is possible to analyze the group-averaged time courses (e.g., Moritz et al., 2003), a different approach was chosen due to the expected large intersubject temporal variability for each particular aspect of music perception and processing. Each time course (for each component and each subject) was quadratically detrended. The time courses for each component were pooled across stimulus types (unharmonized melody, random tones, harmonized melody) and subjects, and statistical tests were performed using paired *t* tests. To test for relatedness to the switching between types, the second frame after the beginning of the stimulus was tested for greater signal intensity than the first frame. To test for melodic processing, the signal intensity during the presentation of melodies was tested for greater intensity than the intensity during random tones. To test for harmonic processing, the intensity during harmonized melodies was tested

for greater intensity than that found during unharmonized melodies. All tests were deemed significant at nominal $P < 0.05/150 = 3.3e-4$ (single-tailed, $P < 0.05$ Bonferroni corrected for the 50 components and 3 tests). For this preliminary study, components were also selected for display where the test was significant at a trend level ($P < 0.10$, Bonferroni corrected; nominal $P < 6.6e-4$). As an additional test, for the melodic processing and harmonic processing tests, the group-averaged time courses were correlated with the appropriate on-off task reference function.

Results

The Kruskal–Wallis H test was used to test for any effect on emotional affect or intensity due to the specific melody. The harmonized and unharmonized presentations of the melodies were tested separately. For the unharmonized presentations, neither emotional affect ($H = 1.37$, $P > 0.8$) nor emotional intensity ($H = 0.075$, $P > 0.9$) displayed any significant effect due to the specific melody. For the harmonized presentations, neither emotional affect ($H = 6.7$, $P > 0.15$) nor emotional intensity ($H = 1.74$, $P > 0.75$) displayed any significant effect. However, there was a significant effect due to the type of presentation (unharmonized or harmonized) both for intensity ($P < 0.05$; Mann–Whitney U test) and affect ($P < 0.01$; Mann–Whitney U test), with the harmonized presentations producing significantly greater affect and intensity.

Results for the post hoc comparisons on the associated time courses described above in the Materials and methods section and the cross-correlation coefficients for the melodic and harmonic processing tasks are shown in Table 1. Four components were found to be significant with regard to task switching, one component significant with regard to melodic processing and three components significant with regard to harmonic processing. In addition, three additional components were melodic processing and two additional components for harmonic processing were significant at a trend level. With the exception of one component only significant at the level of a trend for melodic processing, all of the group-averaged time courses had $R > 0.3$ for melodic or harmonic processing. Using the subject-wise random-effects approach

Table 1

Significance (X denotes $P < 0.05$, paired t test, Bonferroni corrected for 50 components and three tests; Y denotes $P < 0.10$, paired t test, Bonferroni corrected for 50 components and three tests) of three post hoc tests performed (S = switching between stimuli; M = unharmonized melodies > random tones; H = harmonized melodies > unharmonized melodies) on the associated time courses for the components displayed in Fig. 1

	S	M	H	S	M	H
a	X			g		X; 0.45
b	X			h		Y; 0.32
c	X	X; 0.35		i		Y; 0.34
d	X	Y; 0.20		j		X; 0.46
e		Y; 0.33		k		X; 0.32
f		Y; 0.36				

For components with unharmonized melodies > random tones or harmonized melodies > unharmonized melodies, the cross-correlation coefficient of the group-averaged time course with the appropriate on-off task reference function is also given.

described in Calhoun et al. (2001b), the voxels in the found “task-related” component maps were thresholded to a nominal $t > 6$ (nominal $P < 1.65e-5$) and are displayed in Fig. 1. (A Monte Carlo simulation, using the exogenous spatial filtering applied as an estimate of intrinsic smoothness, showed that the nominal threshold, coupled with a spatial extent threshold of 7 voxels, corresponds to a corrected $P < 0.01$.) The group-averaged time courses associated with the displayed component maps are displayed in Fig. 2. Wide intersubject variability is evident for the components involved in melodic and harmonic processing (Figs. 2e–k), as is expected from the likely variation across subjects in the temporal characteristics in the use of each hypothesized music processing module. Less variability is present in those components consistent with task switching (Figs. 2a–d).

Music perception, even in the simplified version used here, is a very complex task and thus it is not surprising that many separate cognitive components were found using ICA (detailed listing given in Table 2). Several networks were found to be involved in switching between stimulus types (Figs. 1a–d) including the superior temporal gyrus (Fig. 1a), the medial temporal gyrus (Fig. 1b), Broca’s and Wernicke’s areas and their right hemisphere homologues (Fig. 1c), and superior prefrontal cortex (Fig. 1d). The networks shown in Figs. 1c–d were also found to be involved in melodic processing, as well as a left-hemispheric perisylvian language network (Fig. 1e) and the hippocampus bilaterally (Fig. 1f). For harmonic processing, the networks found (Figs. 1g–k) involve the inferior parietal lobules (Fig. 1g), the inferior occipital gyrus (Fig. 1h), the fusiform and lingual gyri (Fig. 1i), the precuneus (Fig. 1j), and the medial frontal gyrus (Fig. 1k). Via visual inspection, the sources shown in Fig. 1 corresponding to harmonic and melodic processing were verified to be present in the sources found from the separate analyses (data not shown) performed on the subsets of data from the epochs of harmonized melodies and unharmonized melodies, respectively.

The cortical network in Fig. 1e (including Broca’s area and the left angular gyrus), consistent with expressive language, is in agreement with our expectation of subjects’ generation of lyrics to the melodies. The activation increase in the unharmonized melodies relative to the random tones is only significant at the level of a trend. However, one of the melodies presented, “Chariots of Fire,” does not have any associated lyrics. Thus, a separate analysis was performed on the associated time course (Fig. 2e) with the data corresponding to the presentation of “Chariots of Fire” removed. Including only melodies with associated lyrics, the component in Fig. 1e was found to be significant for melodic processing (nominal $P = 1.2e-5$; Bonferroni-corrected $P < 0.01$). Neither the unharmonized nor the harmonized presentation of “Chariots of Fire” resulted in a significant difference in signal intensity when compared with the presentation of random tones ($P > 0.5$, double-tailed t test).

Since there was a significant effect in emotional affect and intensity shown due to the addition of harmony to the melodies, the comparisons for harmonic processing were repeated for the five significant components (Figs. 1g–k), with effects due to emotional affect and intensity removed via stepwise regression for each subject prior to testing the combined time courses for a significant effect due to harmony. The component in Fig. 1k (medial frontal gyrus) was significant ($P < 0.05$, Bonferroni corrected for the five comparisons) while the component in Fig. 1j (precuneus and medial frontal gyrus bilaterally) was significant

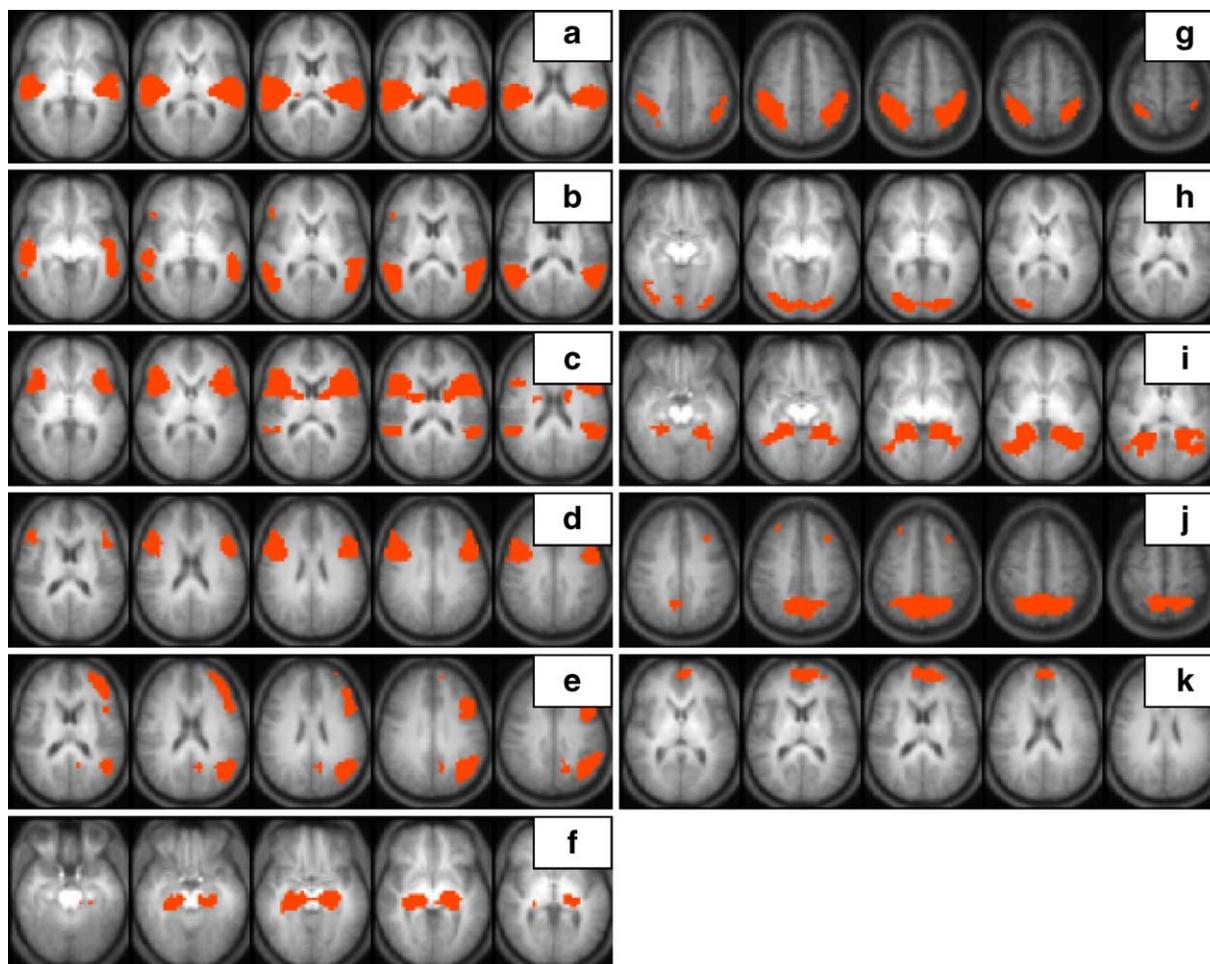


Fig. 1. Eleven IC maps found from group ICA analysis of fMRI data obtained from 15 subjects performing a simplified music perception task of passive listening to random tones, unharmonized melodies, and harmonized melodies. Five representative axial slices selected for display (radiologic orientation). Active voxels have $P < 0.01$ (corrected for multiple voxel comparisons).

at the level of a trend ($P < 0.1$, Bonferroni corrected). None of the other components (Figs. 1g–i) were significant at even a nominal $P < 0.05$ (uncorrected for multiple comparisons).

Discussion

While a potential drawback of using group ICA for post-processing of fMRI data is that it is impossible to definitively ascertain the exact cognitive roles of the found components, the methodology is capable of providing supporting evidence in favor of or against differing neuropsychological models of various cognitive tasks, as has been done previously for the triple-code model of math processing (Schmithorst and Brown, 2004). In the current study, many of the found components agree well with previous neuroimaging findings and hypotheses about the specific functions of cognitive regions for music processing.

The bilateral activation (Fig. 1a) found in the superior temporal gyrus (BA 22) was found to be associated with the switching between the types of auditory stimuli, but not with melodic or harmonic processing. A subsequent exploratory analysis on the associated time courses, however, revealed that the signal was elevated during the random tones portion ($P < 0.001$, unpaired t test) relative to the harmonized and unharmonized melodies (Fig.

2a). A PET study investigating music perception (Platel et al., 1997) found activation in BA 22 when the subjects attempted to recognize a given melody. This was interpreted as being related to the processing of non-verbal semantic information; our results, however, also agree with those of a more recent fMRI study (Griffiths, 2003) relating this area to pitch perception of individual notes, as opposed to melodies, as the random tones portion of the auditory stimuli contained significantly more pitch movement than the portions containing melodies.

The bilateral activation (Fig. 1b) in the middle temporal gyrus (BA 21) was also found to be consistent with the switching between stimulus types. In a previous PET study (Platel et al., 2003), the middle temporal gyrus was associated with musical semantic memory associated with recognition of melodies as familiar or unfamiliar. Our results mesh with that study quite nicely, if consideration is taken into account as to when the familiar vs. unfamiliar judgment occurs. In the PET study, the presented melodies were only 5 s long, and thus it is likely that the subjects' judgment of "familiar" vs. "unfamiliar" is made quite rapidly, within the first few seconds of hearing the melody. Our stimuli, however, are 30 s long, and subjects are likely not continuing to make the judgment of familiar or not throughout the entire duration. Further, while in the current study, the subjects were not asked specifically to make a judgment of familiar or not, the

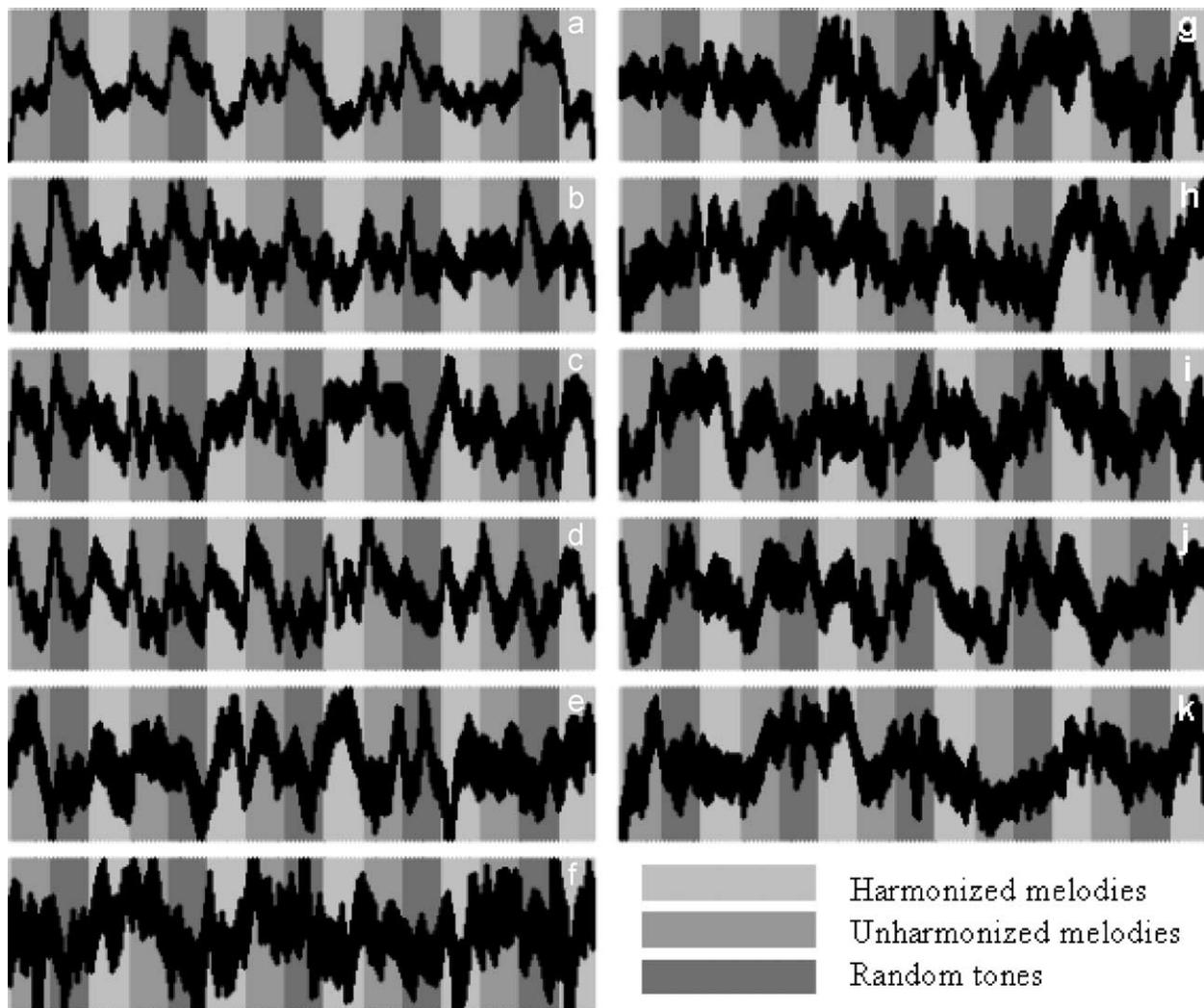


Fig. 2. Associated time courses (bands $\pm 1\sigma$), smoothed with a boxcar filter of width 3, for the IC maps shown in Fig. 1. Grayscale bands are overlaid corresponding to the epochs of the fMRI auditory stimulus paradigm (harmonized melodies, unharmonized melodies, or random tones), shifted by 3 s to account for the hemodynamic delay.

subjects would definitely recognize the auditory stimuli at the times of switching between auditory stimuli as unfamiliar, thus leading to signal increases in brain regions related to musical semantic memory at those times.

The components in Figs. 1c–d display activation in Broca’s area (BA 44/45), its right hemisphere homologue, and an additional area of the inferior frontal gyrus (BA 47) bilaterally. These components are not only consistent with switching between stimulus types but also display signal increases during the presentation of the unharmonized melodies relative to the random tones. These results are in concordance with previous studies investigating musical syntax (Maess et al., 2001) and musical structure (Levitin and Menon, 2003). The left-hemisphere expressive language component (Fig. 1e) also found for melodic processing is consistent with the interpretation that the subjects were producing, perhaps involuntarily, the words associated with the melodies (which were popular tunes for which many subjects would know the lyrics, although such knowledge was not tested post hoc). This interpretation is strongly supported by the fact that, for the one melody which did not have associated lyrics (“Chariots of Fire”), the associated time course did not display an increase

either for the harmonized or the unharmonized presentation of the melody relative to random tones, and removing this melody from the analysis resulted in a much greater significance for the comparison of melodies vs. random tones. The language areas also agree with those found in a PET study (Jeffries et al., 2003) contrasting the speaking and the singing of words associated with melodies.

The components with signal increases during the presentation of harmonized melodies compared to unharmonized melodies (Figs. 1g–k) also show activation in regions previously hypothesized to be involved with harmonic processing. The parietal lobes (Fig. 1g) were found to be implicated in a previous study investigating harmonic processing in a musically trained population (Beisteiner et al., 1999), although our results do not help to elucidate the precise role of the parietal lobes in music processing, whether auditory working memory (Platel et al., 1997), visuoauditory integration (Sergent, 1993), or other factors. The occipital lobes and precuneus (Figs. 1h–j) have also been previously hypothesized to be related to harmonic processing. Activation was found in the occipital lobe during a previous study when subjects were instructed to listen specifically to the

Table 2
Activation foci (Talairach coordinates) for each of the components displayed in Fig. 1

Component	BA	Region	x,y,z
1a	42, 22	L. Superior temporal gyrus	-38, -17, 10
	42, 22	R. Superior temporal gyrus	46, -13, 10
1b	21, 39	R. Medial temporal gyrus	54, -49, 10
	21, 39	L. Medial temporal gyrus	-58, -49, 15
1c	46	R. Inferior frontal gyrus	46, 27, 10
	45/47	R. Inferior frontal gyrus	42, 11, 5
	45/47	L. Inferior frontal gyrus	-34, 15, 15
	22	R. Superior temporal gyrus	50, -41, 20
1d	22	L. Superior temporal gyrus	-54, -41, 20
	44/9	R. Medial frontal/inferior temporal	42, 19, 30
1e	44/9	L. Medial frontal/inferior temporal	-46, 11, 25
	45	L. Medial frontal gyrus	-42, 35, 15
1f	44/9	L. Medial frontal/inferior temporal	-38, 19, 40
	39	L. Angular gyrus	-34, -65, 30
	39	L. Medial temporal gyrus	-10, -57, 20
	35	R. Hippocampal gyrus	10, -21, -10
1g	35	L. Hippocampal gyrus	-22, -17, -10
	40	R. Inferior parietal lobule	34, -49, 50
1h	40	L. Inferior parietal lobule	-34, -53, 50
	18	R. Inferior occipital gyrus	26, -85, 0
1i	18	L. Inferior occipital gyrus	-30, -85, -5
	19	R. Lingual gyrus	18, -37, -5
	19	L. Lingual gyrus	-14, -41, -5
	37	L. Fusiform gyrus	-22, -41, -10
1j	37	R. Fusiform gyrus	18, -37, -10
	7	R. Precuneus	10, -53, 50
	7	L. Precuneus	-18, -57, 50
	8	R. Medial frontal gyrus	26, 35, 45
1k	8	L. Medial frontal gyrus	-30, 27, 45
	9	L. Medial frontal gyrus	-6, 55, 15

harmony (Satoh et al., 2001). The hypothesis that harmonic processing is connected with auditory imagery is also corroborated by an MEG study (Schurmann et al., 2002) showing activity bilaterally in the occipital lobes and precuneus after subjects were presented with visual notes and asked to imagine the corresponding sounds. For the components in Figs. 1g–i, the harmonic processing is very strongly associated with emotional affect and intensity, with no significant correlation remaining after effects due to emotion were removed. This is possibly due to a previously hypothesized relationship of musical expectation with emotion, related to tonal hierarchies (Beisteiner et al., 1999; Schinuckler, 1989). On the other hand, the components in Figs. 1j–k (with activation in the precuneus, prefrontal cortex, and medial frontal areas bilaterally) displayed a significant effect due to harmonic processing, even after removing effects due to emotion; components related to auditory imaging and attention are likely less strongly associated with emotion. Further research will be necessary to elucidate the precise relationship between harmonic processing, emotional commitment, and the neural substrates involved in each.

While ICA is not able to reveal the precise cognitive correlates of the found components, ICA is nevertheless able to provide evidence regarding their modularity. According to Peretz and Coltheart (2003), the mental information processing system for music may contain “smaller modules whose processing

domains may also be restricted to particular aspects of music. The possibility that such a cognitive architecture for music processing exists has been entertained for more than a decade.” The likely temporal dissimilarity in use of these smaller domains will lead to different functional time courses for BOLD activation. Operating under the assumption of spatial independence needed for ICA, the ICA algorithm will then separate out the spatial maps corresponding to the different processes. (Temporal independence, on the other hand, cannot be assumed since there may be some tasks for which both modules are needed in a specific temporal order.)

Thus, our results are able to provide some insight into the debate on modularity of music processing (Peretz and Coltheart, 2003) vs. the convergence of processing between language and music (Patel, 2003). The activation pattern in Fig. 1c (bilateral Broca’s and Wernicke’s areas) is quite similar to the activation observed in a previous fMRI study of a harmonic “oddball” paradigm (Koelsch et al., 2002), as well as that observed in a study investigating language syntactic processing for prosody (Holland et al., 2001b). The ICA algorithm was able to separate the syntactic processing module from other components with overlapping activated regions such as expressive language (Fig. 1e), where the activation pattern strongly resembles that previously found from an fMRI study of silent verb generation (Holland et al., 2001a). Hence, our results lend support to the hypothesis that, at least for syntactic processing, music and language have substantial overlap.

However, the existence of overlap between language and music for syntactic processing does not necessarily imply the non-domain specificity of other specific modules for music processing. For instance, a hypothesized distinction has been made (Patel, 2003) between (domain-specific) syntactic representation and (domain-general) syntactic processing; the distinction being that between “long-term structural knowledge in a domain (e.g., as instantiated in the strength of synaptic connections between neurons) and operations conducted on that knowledge for the purpose of building coherent percepts.” While the current study did not investigate syntax specifically, regions were detected to be involved in music perception, such as in the middle temporal gyrus, occipital lobe, and parietal lobe, which are not typically activated for language processing tasks. While further research will be necessary to precisely elucidate the significance of these regions, the results support the hypothesis (Peretz and Coltheart, 2003) that music processing involves the use of a number of different modules, some domain specific for music (or at least unrelated to language), others not. Since there is a wide variety in musical ability, the development of such representation should be experience dependent, and this is shown by some recent studies. For instance, early blindness has been shown (Rauschecker, 2001) to result in auditory stimulation activating parietal and occipital regions. Regarding synaptic connections, a diffusion tensor imaging study (Schmithorst and Wilke, 2002) has shown increased fractional anisotropy in musicians relative to controls, in the left and right inferior longitudinal fasciculi, which is consistent with the occipital lobes possessing an experience-dependent capability for musical representation.

The results supporting modularity however must be interpreted within the limitations of the group ICA procedure. The strength of ICA lies in its ability to separate out different components without prior knowledge of the hemodynamic response, which is

useful especially when there is expected to be significant across-subject variance in the hemodynamic response for the various components. Post hoc testing may then be performed on the component maps for activation (by voxelwise random-effects analysis) and the time courses for task relatedness (according to some a priori criterion chosen by the investigator). The actual components found, however, are dependent on the data-driven ICA decomposition rather than a pre-specified time course, and hence some weak components might not be found via ICA. A further limitation of ICA is that due to the finite number of voxels sampled in the spatial dimension, spatial independence of the found components cannot be assumed with absolute certainty, and moreover, certain assumptions must be made (e.g., Calhoun et al., 2004; Duann et al., 2002) in order to link spatial independence to modularity of the found components. Hence, the technique is only able to provide supporting, not probative, evidence of modularity. However, the results found for the small sample of subjects ($N = 15$) used in the current study seem to indicate that ICA may be a feasible post-processing method for group fMRI studies of complex cognitive tasks such as math processing (Schmithorst and Brown, 2004) or music perception, even with large intersubject variability in the associated time courses (Fig. 2). Hence, group ICA may be useful for analysis of neuroimaging data obtained from more complex music perception tasks, such as listening to a Beethoven symphony or Bach fugue.

Conclusion

Group ICA analysis was performed on fMRI data obtained from a cohort of subjects performing a passive music perception task. In addition to auditory processing areas, activation was found in regions consistent with syntactic processing, expressive language, and visual association. The results indicate that group ICA is a feasible method for analysis of data from complex tasks involving many cognitive components, and that while some components for music processing overlap with language, many appear to be unique to music, supporting the hypothesis of modularity for music processing.

References

- Beisteiner, R., Erdler, M., Mayer, D., Gartus, A., Edward, V., Kaindl, T., Golaszewski, S., Lindinger, G., Deecke, L., 1999. A marker for differentiation of capabilities for processing of musical harmonies as detected by magnetoencephalography in musicians. *Neurosci. Lett.* 277, 37–40.
- Bell, A.J., Sejnowski, T.J., 1995. An information maximization approach to blind separation and blind deconvolution. *Neural Comput.* 7, 1129–1159.
- Calhoun, V.D., Adali, T., McGinty, V.B., Pekar, J.J., Watson, T.D., Pearlson, G.D., 2001a. fMRI activation in a visual-perception task: network of areas detected using the general linear model and independent components analysis. *NeuroImage* 14, 1080–1088.
- Calhoun, V.D., Adali, T., Pearlson, G.D., Pekar, J.J., 2001b. A method for making group inferences from functional MRI data using independent component analysis. *Hum. Brain Mapp.* 14, 140–151.
- Calhoun, V.D., Pekar, J.J., McGinty, V.B., Adali, T., Watson, T.D., Pearlson, G.D., 2002. Different activation dynamics in multiple neural systems during simulated driving. *Hum. Brain Mapp.* 16, 158–167.
- Calhoun, V.D., Pekar, J.J., Pearlson, G.D., 2004. Alcohol intoxication effects on simulated driving: exploring alcohol-dose effects on brain activation using functional MRI. *Neuropsychopharmacology* 29, 2017–2097.
- Dehaene, S., Cohen, L., 1995. Towards an anatomical and functional model of number processing. *Math. Cogn.* 1, 83–120.
- Duann, J.R., Jung, T.P., Kuo, W.J., Yeh, T.C., Makeig, S., Hsieh, J.C., Sejnowski, T.J., 2002. Single-trial variability in event-related BOLD signals. *NeuroImage* 15, 823–835.
- Griffiths, T.D., 2003. Functional imaging of pitch analysis. *Ann. N. Y. Acad. Sci.* 999, 40–49.
- Griffiths, T.D., Rees, A., Witton, C., Cross, P.M., Shakir, R.A., Green, G.G., 1997. Spatial and temporal auditory processing deficits following right hemisphere infarction. A psychophysical study. *Brain* 120 (Pt. 5), 785–794.
- Holland, S.K., Plante, E., Weber Byars, A., Strawsburg, R.H., Schmithorst, V.J., Ball Jr., W.S., 2001a. Normal fMRI brain activation patterns in children performing a verb generation task. *NeuroImage* 14, 837–843.
- Holland, S.K., Plante, E., Weber-Byars, A.S., Schmithorst, V.J., Strawsburg, R.H., 2001b. Functional MRI of normal language development. *Human Brain Mapping 7th Annual Meeting*, Brighton, UK.
- Jeffries, K.J., Fritz, J.B., Braun, A.R., 2003. Words in melody: an H(2)150 PET study of brain activation during singing and speaking. *NeuroReport* 14, 749–754.
- Koelsch, S., Gunter, T.C., v Cramon, D.Y., Zysset, S., Lohmann, G., Friederici, A.D., 2002. Bach speaks: a cortical “language-network” serves the processing of music. *NeuroImage* 17, 956–966.
- Levitin, D.J., Menon, V., 2003. Musical structure is processed in “language” areas of the brain: a possible role for Brodmann area 47 in temporal coherence. *NeuroImage* 20, 2142–2152.
- Maess, B., Koelsch, S., Gunter, T.C., Friederici, A.D., 2001. Musical syntax is processed in Broca’s area: an MEG study. *Nat. Neurosci.* 4, 540–545.
- McKeown, M.J., Makeig, S., Brown, G.G., Jung, T.P., Kindermann, S.S., Bell, A.J., Sejnowski, T.J., 1998. Analysis of fMRI data by blind separation into independent spatial components. *Hum. Brain Mapp.* 6, 160–188.
- Mendez, M.F., 2001. Generalized auditory agnosia with spared music recognition in a left-hander. Analysis of a case with a right temporal stroke. *Cortex* 37, 139–150.
- Metz-Lutz, M.N., Dahl, E., 1984. Analysis of word comprehension in a case of pure word deafness. *Brain Lang.* 23, 13–25.
- Moritz, C.H., Rogers, B.P., Meyerand, M.E., 2003. Power spectrum ranked independent component analysis of a periodic fMRI complex motor paradigm. *Hum. Brain Mapp.* 18, 111–122.
- Patel, A.D., 2003. Language, music, syntax and the brain. *Nat. Neurosci.* 6, 674–681.
- Peretz, I., Coltheart, M., 2003. Modularity of music processing. *Nat. Neurosci.* 6, 688–691.
- Peretz, I., Kolinsky, R., Tramo, M., Labrecque, R., Hublet, C., Demeurisse, G., Belleville, S., 1994. Functional dissociations following bilateral lesions of auditory cortex. *Brain* 117 (Pt. 6), 1283–1301.
- Platel, H., Price, C., Baron, J.C., Wise, R., Lambert, J., Frackowiak, R.S., Lechevalier, B., Eustache, F., 1997. The structural components of music perception. A functional anatomical study. *Brain* 120, 229–243.
- Platel, H., Baron, J.C., Desgranges, B., Bernard, F., Eustache, F., 2003. Semantic and episodic memory of music are subserved by distinct neural networks. *NeuroImage* 20, 244–256.
- Rauschecker, J.P., 2001. Cortical plasticity and music. *Ann. N. Y. Acad. Sci.* 930, 330–336.
- Satoh, M., Takeda, K., Nagata, K., Hatazawa, J., Kuzuhara, S., 2001. Activated brain regions in musicians during an ensemble: a PET study. *Brain Res. Cogn. Brain Res.* 12, 101–108.
- Schinuckler, M.A., 1989. Expectation in music: investigation of melodic and harmonic processes. *Music Percep.* 7, 109–150.
- Schmithorst, V.J., Brown, R.D., 2004. Empirical validation of the triple-code model of numerical processing for complex math operations using functional MRI and group independent component analysis of

- the mental addition and subtraction of fractions. *NeuroImage* 22, 1414–1420.
- Schmithorst, V.J., Holland, S.K., 2003. Neural networks for language processing determined via group independent component analysis performed simultaneously on fMRI data from separate tasks. ISMRM 11th Scientific Meeting, Toronto, ON.
- Schmithorst, V.J., Holland, S.K., 2004. Comparison of three methods for generating group statistical inferences from independent component analysis of fMRI data. *J. Magn. Reson. Imaging* 19, 365–368.
- Schmithorst, V.J., Wilke, M., 2002. Differences in white matter architecture between musicians and non-musicians: a diffusion tensor imaging study. *Neurosci. Lett.* 321, 57–60.
- Schmithorst, V.J., Dardzinski, B.J., Holland, S.K., 2001. Simultaneous correction of ghost and geometric distortion artifacts in EPI using a multiecho reference scan. *IEEE Trans. Med. Imaging* 20, 535–539.
- Schurmann, M., Raij, T., Fujiki, N., Hari, R., 2002. Mind's ear in a musician: where and when in the brain. *NeuroImage* 16, 434–440.
- Sergent, J., 1993. Mapping the musician brain. *Hum. Brain Mapp.* 1, 20–38.
- Talairach, J., Tournoux, P., 1988. *Co-planar Stereotaxic Atlas of the Human Brain*. Thieme Medical Publishers, New York.
- Thevenaz, P., Unser, M., 1998. A pyramid approach to subpixel registration based on intensity. *IEEE Trans. Image Process.* 7, 27–41.
- Tillmann, B., Janata, P., Bharucha, J.J., 2003. Activation of the inferior frontal cortex in musical priming. *Brain Res. Cogn. Brain Res.* 16, 145–161.