ELSEVIER

Cognitive Brain Research 16 (2003) 145–161

COGNITIVE BRAIN RESEARCH

www.elsevier.com/locate/cogbrainres

Research report

Activation of the inferior frontal cortex in musical priming

Barbara Tillmann*, Petr Janata, Jamshed J. Bharucha

Department of Psychological and Brain Sciences and Center for Cognitive Neuroscience, Dartmouth College, Hanover, NH 03755, USA

Accepted 1 October 2002

Abstract

Behavioral studies have provided evidence that the processing of a musical target is faster and more accurate when it is harmonically related to the preceding prime context. We investigated the neural correlates of processing related and unrelated musical targets that were presented at the end of musical sequences. Participants were scanned with functional magnetic resonance imaging (fMRI) while performing speeded intonation judgments (consonant versus dissonant) on the target chords. Behavioral results acquired in the scanner replicated the facilitation effect of related over unrelated consonant targets. The overall activation pattern associated with target processing showed commonalities with networks previously described for target detection and novelty processing. The blood oxygen level-dependent (BOLD) signal linked to target processing revealed activation of bilateral inferior frontal regions (i.e. inferior frontal gyrus, frontal operculum, insula) that was stronger for unrelated than for related targets. We discuss our results with regard to the role of these areas in the processing and integration of temporal information.

Theme: Neural basis of behavior

Topic: Cognition

Keywords: Context effects in music perception; Inferior frontal regions; Prefrontal cortex; Target processing; fMRI

1. Introduction

The processing of an event is influenced by the context in which it occurs. Context effects have been well established in language perception and more recently in music perception with priming paradigms. In language, the processing of a target word is facilitated (i.e. responses are faster and more accurate) if this word is semantically related to the prime context or if it is more frequently associated to it [69,73,78]. Similarly, in music perception the processing of a target chord is facilitated if this chord is harmonically related to the prime context. Harmonic relatedness means that, in pieces from the Western tonal repertoire, the type of chord used as a target is frequently associated to events belonging to the prime context. In language, the prime context can consist of a single word, a sentence or a paragraph [45,74,92]. In music, it can consist of a single chord or a chord sequence [15,16]. Neural correlates of context effects have been investigated extensively with both electrophysiological (ERP) and brain imaging (PET, fMRI) methods for language perception (e.g. Refs. [8,9,25,37,38,58,59,66,72,82,88,93]), but relatively infrequently for music perception [10,11,46,52,77,87]. Our present study investigates with fMRI the neural correlates of priming effects in musical contexts.

The relationships that are manipulated between the

Abbreviations: BA, Brodmann area; BOLD, blood oxygen level dependent; EPI, echo-planar imaging; ELAN, early left anterior negativity; ERAN, early right anterior negativity; ERP, event-related potential; fMRI, functional magnetic resonance imaging; HRF, haemodynamic response function; IFG, inferior frontal gyrus; IFS, inferior frontal sulcus; IPG, inferior parietal gyrus; IPS, intraparietal sulcus; LPC, late positivity component; mERAN, magnetic early right anterior negativity; MEG, magnetoencephalography; MFG, middle frontal gyrus; MIDI, musical instrument digital interface; RATP, right early frontal negativity; RC, related consonant; RD, related dissonant; SFG, superior frontal gyrus; SMA, supplementary motor area; SPM, statistical probability map; STG, superior temporal gyrus; STS, superior temporal sulcus; UC, unrelated consonant; UD, unrelated dissonant

*Corresponding author. Present address: Université Claude Bernard–Lyon I, CNRS UMR 5020, Neurosciences et Systèmes Sensoriels, 50 Av. Tony Garnier, F-69366 Lyon Cedex 07, France. Tel.: +33-4-3728-7493; fax: +33-4-3728-7601.

E-mail address: barbara.tillmann@olfac.univ-lyon1.fr (B. Tillmann).

0926-6410/02/$ – see front matter
doi:10.1016/S0926-6410(02)00245-8

prime context and the to-be-processed target event are based on regularities of Western tonal music. These regularities are mainly based on associative combinations (i.e. frequencies of co-occurrence and frequency of occurrence) between musical events. The basis of the Western tonal system is a set of twelve tones (*C–C♯–D–D♯–E–F–F♯–G–G♯–A–A♯–B*) that is combined into subsets of seven tones, the scales. For each tone of a scale, chords (combinations of three tones, for example *C–E–G* for a C Major chord) can be defined. The tones in a scale and their associated chords define a higher level of organization in the tonal system: the keys. The seven tones that belong to the underlying scale are in-key tones, the remaining five tones are out-of-key tones. Similarly for chords, in-key chords are differentiated from out-of-key chords. Hierarchies of functional importance exist among tones and chords belonging to a given key, with the tonic tone and tonic chord (based on the first degree of the scale) being at the top of tonal and harmonic hierarchies, respectively (i.e. representing the most important events of a key). In a given musical piece, tones and chords belonging to one key are frequently associated together. As the tonal system is based on a restricted set of events, the same event can define an in-key or an out-of-key event or can take different levels of functional importance—always depending on the established key. Extensive behavioral research has provided evidence that even nonmusician listeners are sensitive to the context dependency of musical events and the associated changes in tonal functions depending on the context [5,13,27–29,35,44,55–57,95].

Musical priming research concentrates on the influence of a harmonic context on the processing of a target chord. For this purpose the harmonic relationship between the target chord and its preceding prime context (that can be either a single chord or a chord sequence) is systematically manipulated. For example, the same target chord can be preceded by either a prime chord belonging to the same key (harmonically related context) or a prime being outside this key (unrelated context). In the experimental session, half of the target chords are mistuned or rendered acoustically dissonant. Participants make speeded accuracy judgments about the consonance/dissonance of the targets. Results with single-prime contexts showed that consonant (in-tune) target chords are processed faster and more accurately if they are preceded by a harmonically related prime than by an unrelated prime [14,15]. The influence of the prime context has also been shown for longer chord sequences with the target chord being the last chord of the sequence. Facilitated processing has been reported not only for in-key chords over out-of-key chords [98] but also for in-key-chords with a more important harmonic function (tonic chord) over in-key chords with a less important harmonic function (subdominant chord) in the established key [16,17,20,97]. The musical priming effects have been observed for both musician and nonmusician listeners, an outcome suggesting that implicit knowledge of tonal harmonic structures has been acquired through mere exposure of musical pieces obeying these regularities (see Ref. [96] for a formal account). The tonal knowledge is activated by the context and allows the listener to develop expectations for further musical events. These expectations are then more or less fulfilled (or even violated), which influences the processing of the musical event as reflected in the priming data.

The influence of a musical context has also been shown with neurophysiological measurements: the same musical event evokes a stronger P3b or late positive component LPC (peaking around 500 and 600 ms) when it is unrelated to the context than when it is related ([10–12] for tones; [46,77] for chords). The amplitude of the LPC increases with increasing harmonic violation: the positivity is larger for distant-key targets than for closely-related key targets which in turn is larger than for in-key tonic targets [46,77]. Neurophysiological correlates of musical expectancy are reported also for finer harmonic differences between target chords. Based on the priming material of Bigand and Pineau [17], Regnault et al. [87] reported that less related, weakly expected target chords (i.e. subdominant chord) evoked a P3 component (200–300 ms latency range) with larger amplitude than did strongly related tonic targets. Both musician and nonmusician listeners were sensitive to changes in harmonic function of the target chord due to the established harmonic context.

In a similar vein, Koelsch et al. [52] reported nonmusicians' sensitivity to violations of musical expectancies in chord sequences. Independently of the task (i.e. detecting timbral deviances while ignoring harmonies (exp. 1 and 2) or explicitly detecting harmonic chord structures (exp. 3 and 4)), an early right-anterior negativity (named ERAN, maximal around 150 ms) reflects the expectancy violation in the key context. A right-hemisphere negativity in response to out-of-key target chords (N350) has been also observed by Patel et al. [77] (right antero-temporal negativity RATN) who suggested links between the RATN and the right fronto-temporal circuits implicated in working memory for tonal material [103]. Both groups (see Refs. [52] and [77]) suggested that the right early frontal negativity (named ERAN and RATN, respectively) could be related to the processing of syntactic-like musical structures. They compared this negativity with an ERP component observed in auditory language studies for syntactic incongruities: the left early frontal negativity ELAN (e.g. Refs. [36,37]) that is thought to arise in the inferior frontal regions around Broca's area. Converging evidence for the hypothesis on neural correlates of musical expectancy has been provided by a recent magneto-encephalography (MEG) study [64] using the musical material of Koelsch et al. [52]. The source localization of the MEG signal placed the generators for the mERAN (the magnetic equivalent of the ERAN) in Broca's area and its right hemisphere homologue. The deviant event elicited an increased bilateral mERAN with a slight asymmetry to the right for some of the participants. The source–localization data from experiments using musical stimuli suggests that Broca's area and its right-hemisphere homologue are not only involved in the processing of syntactic information specific to language, but also in the processing of musical structures and musical syntactic-like relationships.

In our present study, we further investigated the neural correlates of musical expectancy by using functional MRI associated with the harmonic priming paradigm. More specifically, we studied the role of right and left inferior frontal cortices in the processing of musical material. Eight-chord sequences were presented to the participants who made speeded intonation judgments on the last chord of the sequence, the target. The harmonic relationship of the target with its preceding prime context (the first seven chords of the sequence) was strongly manipulated: the target was either the most expected tonic chord of the prime key or an unrelated out-of-key chord. As in previous musical priming studies, half of the experimental sequences ended with a target chord that was rendered acoustically dissonant by adding an out-of-key tone to the chord (e.g. *C–E–G–G♯–C*). An event-related design allowed us to use the harmonic priming paradigm with random presentation of related and unrelated contexts associated with consonant and dissonant targets. For the behavioral data, we expected faster and more accurate responses for the consonant tonic chord (related context) than for the consonant out-of-key chord (unrelated context).[1] For the fMRI data, we investigated the overall network of activation for the processing of context and of each of the target chords. We focused one part of the analyses on the inferior frontal regions, bilaterally (i.e. in the vicinity of the inferior frontal gyrus, pars opercularis) in order to further investigate the sensitivity of these regions to the violation of harmonic relationships (related versus unrelated target) and the violation of the sensory consonance (consonant versus dissonant target). The unrelated target can be defined as a contextual deviance (i.e. the chord does not harmonically fit into the preceding context) and the dissonant target as an acoustical deviance (i.e. due to the out-of-key tone, the chord contains a sensory dissonance). Based on previously reported data on expectancy violation in music perception [52,64,77], the inferior frontal regions were expected to be sensitive to both types of deviances (i.e. stronger activation for a deviant event), with an asymmetry in favor of the right hemisphere [64].

2. Methods

2.1. Participants

Fifteen right-handed students from Dartmouth College (nine females, mean age 19.4 years, range: 18–27) participated in the experiment after having given written informed consent. Number of years of musical training, as measured by years of instrumental instruction, ranged from 4 to 12, with a mean of 8.2 (S.D.=2.54) and a median of 9.

2.2. Material

Sixteen eight-chord sequences were chosen from the material of Bigand and Pineau [17], Pineau and Bigand [79] and Bigand et al. [20]. They all ended on the tonic chord (i.e. the most important chord in the tonal hierarchy). Each sequence was transposed into two harmonically distant keys that are close in pitch height: C Major and B Major. The last chord of the sequence was defined as the target. For the related sequences, the target was the tonic chord (a C Major or B Major chord, respectively). For the unrelated sequences, the last chord was transposed a semitone up or down, resulting in a chord that is harmonically unrelated to the key established by the first seven chords (e.g. a sequence in C Major ended on a B Major chord). As all sequences in the keys of C Major and B Major were derived from the same original sixteen sequences, a physically identical chord, for example C Major (*C2–E3–G3–C4*), represented the related target in the C Major key sequence and the unrelated target in the B Major key sequence.

In order to create dissonant targets for the priming task, the sensory consonance of targets was altered by adding an augmented fifth (*G♯3*) to the root (i.e. *C2–E3–G3–G♯3–C4*). The stimuli were created in MIDI with Performer 5.3 Software (Mark of the Unicorn) and played with sampled piano sounds produced by a KORG New SG-1D. Velocity, a MIDI parameter related to the sound level, was constant for all pitches except for the added augmented fifth whose velocity was decreased to temper the salience of the dissonance and adjusted for comparable salience among dissonant targets. Each of the first seven chords sounded for 500 ms, the target chord sounded for 2000 ms and the inter-chord interval was set to 0. The sound stimuli were recorded with SoundEdit 16 software (MacroMedia), and the experiment was run using PsyScope software [26]. In the scanning session, the stimuli were presented over the left output channel and then split in stereo. The sound material was presented via

---

[1] In previous priming data, reliable context effects have been observed for consonant targets that correspond to lawful musical events in the Western tonal system. Dissonant targets were only weakly influenced by the harmonic context and this influence was not consistent over several experiments (with some showing crossover interactions between chord types and context).

insert earphones (Tubephone™ ER-30, Etymotic Research) after having been filtered with a 31-band 1/3-octave band equalizer (Model 351, Applied Research Technologies) to compensate for frequency attenuation due to the earphones. Participants wore ear-muffs (HB-1000, Elvex) through which the earphones had been inserted and responded via buttons of a response interface (MRA Inc.).

2.3. Procedures

2.3.1. Training phase

Participants were trained to differentiate between consonant and dissonant chords outside the scanner. They had to make a consonant/dissonant judgment as quickly and accurately as possible by pressing one of two keys of the computer keyboard. They were trained first with 32 isolated chords, then with 16 chord sequences. In both phases, stimuli were presented in random order and the next trial began when the participant pressed a third key. An incorrect response was accompanied by an alerting feedback signal.

2.3.2. Behavioral procedure in the scanner

Crossing the within-subject factors Harmonic Relatedness (related/unrelated) and Target Type (consonant/dissonant) produced four possible versions for each of the 32 (related) sequences (16 in C Major, 16 in B Major). Each participant heard 128 sequences, distributed over four runs. Each run lasted for 6 min 14 s, and contained two blocks of 16 chord sequences (four sequences for each of the four experimental conditions) presented in random order. The sequences within a block were in the same key (in C Major or in B Major). Half of the runs started with a block in C Major, followed by a block in B Major. Inside a block, the inter-trial interval (ITI) between sequences was set to 2500 ms in average (with a jitter of ±500 ms). Participants were required to judge as quickly and accurately as possible the consonance/dissonance of the target chord by pressing one of two buttons of the response box, using right and left thumb, respectively. No feedback was given. For each run (Fig. 1), the first block was preceded by a 30-s rest period, followed by a 250-ms noise burst indicating that the first sequence would start in 5 s. The first and second blocks were separated by a 41-s rest period. After a delay of 1 second, a noise burst indicated the beginning of the rest period. After 35 s, a second noise burst indicated the end of the rest period and the second block followed after 5 s. The end of the second block was followed by a noise burst and a final 35-s rest period.

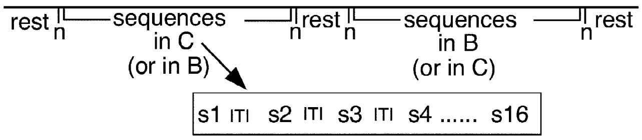

Fig. 1. Schematic presentation of the time course of one run. A run started either with 16 sequences (s1 to s16) in C Major followed by 16 sequences in B Major or the reverse. *n* represents the noise burst indicating beginning and ending of the blocs with chord sequences, ITI refers to inter-trial-interval.

2.4. Data acquisition

Data were acquired on a General Electric Signa Horizon Echospeed MRI scanner (1.5 T). During the functional scans, the BOLD response was measured using a single-shot gradient-echo-planar-imaging EPI sequence ($TR=2000$ ms; $TE=35$ ms; flip angle 90°; matrix 64×64; field of view 240×240 mm). Each volume was comprised of 27 contiguous axial slices with a resolution of 3.75×3.75×5.0 mm. Prior to the functional scans, an anatomical T1-weighted 2D-image (coplanar) was acquired with 27 contiguous slices (resolution: 0.937×0.937×5.0 mm) in the same planes as the functional images ($TR=650$ ms; $TE=6.6$ ms; flip angle 90°; matrix 256×256; FOV 240×240 mm). At the end of the scanning session, an anatomical high-resolution T1-weighted 3D-image was acquired with 124 contiguous sagittal slices ($TR=25$ ms; $TE=6$ ms; FOV 240×240 mm; flip angle 25°; matrix 256×256; resolution 0.937×0.937×1.2 mm). The functional scans were initiated using a TTL pulse delivered to the scanner from the computer running the experiment with Psyscope. During each run, the same computer sent event markers at the onset of every event to a second computer recording these markers together with the output of the response box.

2.5. Data processing and analysis

Data processing and analyses were conducted using SPM99 with default settings, unless further specified (http://www.fil.ion.ucl.ac.uk/spm). The first 15 EPI volumes acquired during the beginning rest period were discarded prior to data processing and analyses. For each functional run, the functional images were motion corrected relative to the first image of the first run. A mean functional image was created that allowed the coregistration of functional images to the coplanar T1-weighted image using a mutual information algorithm [63]. The coplanar images were coregistered to the high-resolution 3D-images that in turn were spatially normalized to the Montreal Neurological Institute (MNI) T1-template images [32,67]. The normalization parameters were applied to the functional images that retained the original voxel size. Normalized images were smoothed with a 6×6×8 mm (FWHM) gaussian smoothing kernel.

Functional data were analyzed for task-related activation using the general linear model and the theory of random fields [39]. Regression coefficients were estimated for the four target types of correct trials time-locked to the beginning of the target chord (related consonant, RC; related dissonant, RD; unrelated consonant, UC; unrelated dissonant, UD), for context sequences (the first seven chords), for noise bursts, for middle and ending resting periods and for target events of incorrect trials (regrouped together over experimental contexts in a single regressor). The onset times of events were determined with the recorded event markers relative to the beginning of each run. The regressors for the four target types of correct trials, the noise bursts and the error trials were modeled as events with the canonical haemodynamic response function in SPM99. The regressors for contexts and resting periods were modeled as epochs with a boxcar waveform convolved with the same haemodynamic response function. Additional regressors comprising a linear trend in each run and the estimated motion parameters were included in the model [40].

Statistical parametric maps SPMs were created for the following contrasts: Context minus Rest; Consonant targets (RC+UC) minus Dissonant targets (RD+UD), Dissonant targets (RD+UD) minus Consonant targets (RC+UC); RC minus UC; UC minus RC. In addition, SPMs were created for each of the four targets separately in order to identify regions that correlated, for each target type, with the convolution of the canonical haemodynamic response function and vector of target onsets. For each contrast, the statistical map from each participant was entered into a group analysis. Statistical parametric maps for the group data were projected on the averaged T1-weighted anatomical image (based on the T1 3D-images of all participants). Regions with activations significant at the cluster level were identified with the atlas of Duvernoy [30] and are listed in Tables 3–6.

3. Results

3.1. Pretest

Prior to the fMRI study, the experimental material and procedures were tested outside the scanner with 14 participants listening through regular headphones (Sony MDR-V600). Number of years of musical training, as measured by years of instrumental instruction, ranged from 0 to 9, with a mean of 4.1 (S.D.=3.82) and a median of 3.5. The pretest confirmed a strong influence of harmonic relatedness on target chord processing. For consonant targets, correct responses were more numerous and faster for related than for unrelated targets. The reverse relation was observed for dissonant targets. Percentages of correct responses and response times for correct responses (Table 1) were analyzed by two 2×2 ANOVAs with Relatedness and Target Type as within-subject factors. For accuracy data, the main effect of Relatedness and its interaction with Target Type were significant; $F(1,13)=17.58$; $P<0.01$ and $F(1,13)=26.46$; $P<0.001$, respectively. For response times, the effect of relatedness and its interaction with Target Type were also significant; $F(1,13)=56.74$; $P<0.001$ and $F(1,13)=46.35$; $P<0.001$, respectively. There were no other significant effects.

Table 1
Behavioral priming data (percentages of correct responses and correct response times) of the pretest

	% Correct Resp.	Response times
Consonant target		
Related	96.65 (1.06)	796.14 (40.73)
Unrelated	76.79 (4.03)	1079.61 (51.2)
Dissonant target		
Related	87.95 (3.65)	907.84 (51.48)
Unrelated	94.87 (1.69)	866.25 (44.62)

Standard errors are indicated in brackets.

3.2. Behavioral data

The behavioral priming data of the scanning session confirmed pretest results and showed an influence of the harmonic context on target chord processing. Percentages of correct responses and response times for correct responses (Table 2) were analyzed by two 2×2 ANOVAs with Relatedness and Target Type as within-subject factors. For accuracy data, the main effect of Relatedness was significant; $F(1, 14)=12.75$; $P<0.01$; with more numerous correct responses for related contexts than for unrelated contexts. For response times, the main effect of Relatedness; $F(1,14)=41.22$; $P<0.0001$; and its interaction with Target Type were significant; $F(1,14)=68.87$, $P<0.0001$: For consonant targets only, responses were faster for related than for unrelated contexts. There were no other significant effects.

3.3. fMRI data

3.3.1. Context minus rest

When contrasting the context (the first seven chords of each sequence) with the rest sections, significant BOLD signal increases were observed in temporal, frontal and parietal areas (Table 3). Extensive areas of the superior temporal gyrus (STG) were activated bilaterally. Both medial and dorsal superior frontal gyrus (SFG) were activated during context listening. In addition, the posterior cingulate gyrus along the midline and the right angular

Table 2
Behavioral priming data (percentages of correct responses and correct response times) collected during the acquisition of functional MR images

	% Correct resp.	Response times
Consonant target		
Related	98.33 (0.80)	671.55 (33.63)
Unrelated	88.96 (3.62)	824.20 (45.29)
Dissonant target		
Related	96.04 (0.71)	747.42 (40.47)
Unrelated	91.88 (2.38)	761.17 (49.43)

Standard errors are indicated in brackets.

Table 3
Activations for the comparison context minus rest[a]

Lobe	Region	BA	Hemisphere	*x*	*y*	*z*	*Z*-score
Frontal	SFG medial	9/8	Left	−4	52	45	4.05
			Right	15	49	45	3.84
	SFG dorsal/SMA	6	Left	−4	0	65	3.67
	Precentral gyrus	6 (/4)	Left	−52	−8	50	4.21
Temporal	STG	41	Left	−49	−22	5	5.01
		42/41		−56	−15	5	4.83
		42/22		−60	−34	10	4.2
		42	Right	56	−19	5	5.67
		22/42		68	−30	5	3.91
Parietal	Posterior cing. gyrus	23	Left	−4*	−19	35	4.0
	Angular gyrus	39	Right	52	−60	35	3.54

* Denotes activation pattern that extends bilaterally. If for an anatomical location more than one set of coordinates is given, the coordinates denote the extent, rather than the center, of the activation.

[a] SPMs were thresholded at $P<0.001$ (uncorrected) and activation areas significant at cluster level are listed.

gyrus showed increased BOLD signal when listening to the context sequence.

3.3.2. Consonant versus dissonant targets

The comparisons between consonant and dissonant targets (averaged over related and unrelated contexts) reflected differences due to handedness of the responses (Table 4). Increased BOLD signal was observed in the left cerebellum and right precentral gyrus (with cingulate sulcus, postcentral sulcus and gyrus) for the Dissonant-minus-Consonant contrast and in the right cerebellum and left postcentral gyrus for the Consonant-minus-Dissonant contrast. Beyond these differences, the Dissonant-minus-Consonant contrast showed activation in both parietal and frontal areas, notably in the left inferior frontal gyrus (IFG), the right superior parietal gyrus (SPG) and the right parietal operculum. In addition, increased BOLD signal was observed in the left STG as well as the right insula and the right medio-dorsal thalamic nuclei. For the Consonant-minus-Dissonant contrast, additional BOLD signal increases were observed in right inferior temporal sulcus and left subiculum.

3.3.3. The four targets: RC, RD, UC, UD

Fig. 2 outlines the activation areas for each of the four targets. In parallel, Table 5 lists the regions significantly activated at the cluster level for each of the four targets. The four targets were associated with a network of activation including frontal and parietal areas as well as cerebellum and widespread thalamic activation. In the

Table 4
Activations for the comparisons between consonant and dissonant targets[a]

Contrast	Lobe	Region	BA	Hemisphere	*x*	*y*	*z*	*Z*-score
Consonant − Dissonant								
	Frontal	Postcentral gyrus	1/3	Left	−45	−22	60	5.08
					−52	−19	55	4.8
	Temporal	Inf. temp. sulcus		Right	60	−49	−10	4.5
	Other	Subiculum		Left	−15	−34	−5	3.52
		Cerebellum		Right	26	−60	−20	4.45
Dissonant − Consonant	Frontal	IFG/pars triangularis	45/47	Left	−41	26	5	3.93
		Cingulate sulcus		Right	8	−8	50	4.74
		Precentral gyrus	4	Right	26	−11	60	4.85
					34	−22	65	4.73
	Temporal	STG	22	Left	−64	−45	20	4.39
	Parietal	Postcentral sulcus		Right	56	−22	50	5.71
		Postcentral gyrus	3	Right	38	−30	65	4.66
		Sup. parietal gyrus	7	Right	30	−49	55	4.06
		Parietal operculum		Right	49	−22	25	4.7
	Other	Insula		Right	45	−4	15	4.37
		Thalamic nuclei		Right	11	−22	0	3.79
		Cerebellum		Left	−8	−52	−10	4.91
					−22	−52	−20	4.83

[a] SPMs were thresholded at $P<0.001$ (uncorrected) and activation significant at cluster level are listed.

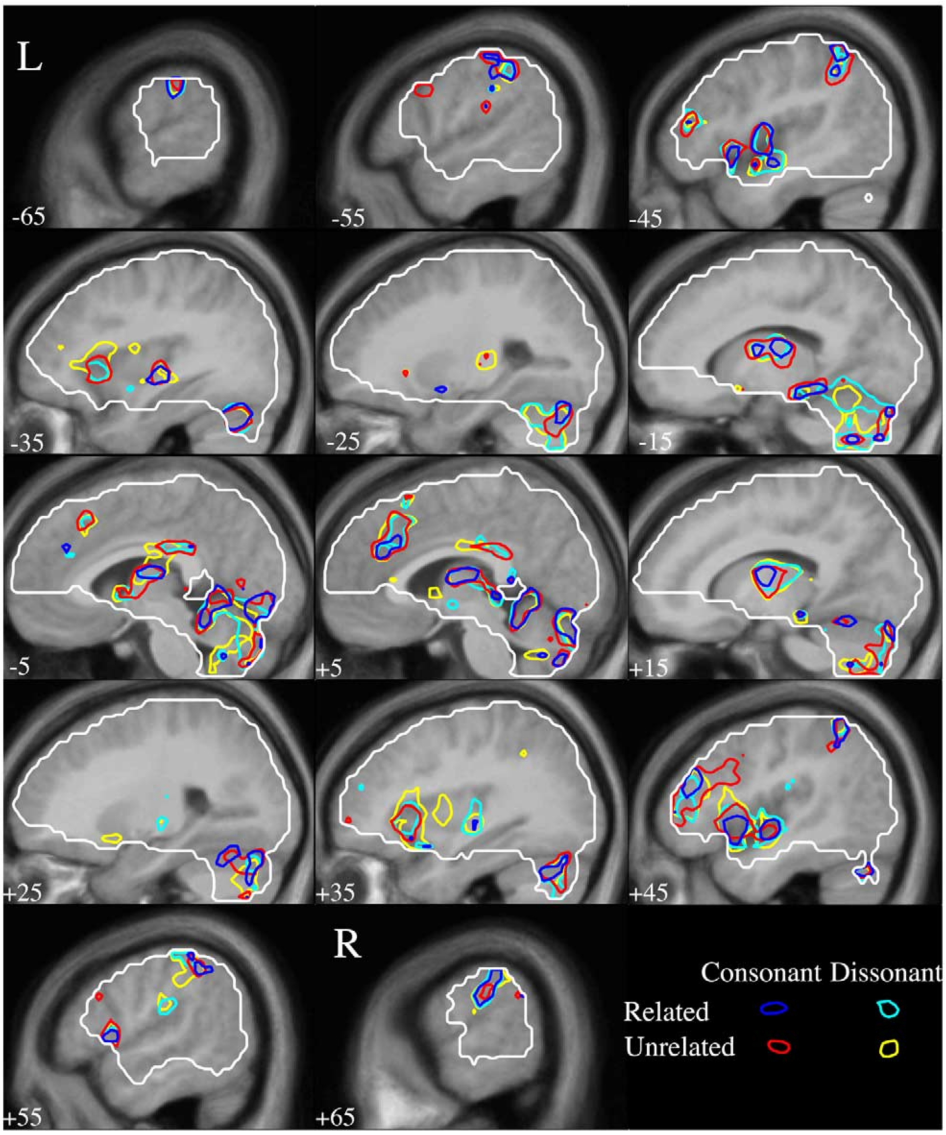

Fig. 2. Group ($N=15$) image showing significant correlations of the observed BOLD signal with the ideal haemodynamic response function for each of the four targets (RC, RD, UC, UD). Activations are thresholded at $P<0.01$ and superimposed on the average T1-weighted anatomical image based on all participants. The white contour is the inclusion mask which shows the edges of the volume that contained data from all participants.

frontal lobe, activation areas were found in the IFG bilaterally, the right middle frontal gyrus (MFG) as well as the superior medial frontal gyrus extending to the anterior cingulate sulcus and gyrus. In posterior areas, bilateral activation of the supramarginal and posterior cingulate gyri were observed for all targets. The supramarginal gyrus activation was widespread for all targets and extended to the intraparietal sulcus IPS. This area of activation extended over the IPS to the angular gyrus on the right for RC targets and spilled down to the right ascending segment of the superior temporal sulcus (STS) for UD targets. In addition, there was bilateral activation of insular regions: anterior insula adjacent to the frontal operculum (IFG, pars opercularis region) and more posterior insula regions including the circular insular sulcus (ventral and dorsal). Furthermore, all targets showed some activation in the left subiculum (activation was not significant at the cluster level for RD).

In addition to the activation pattern that was common to all four target types, differences among responses to the targets were observed. Overall, the extent of activation was smaller for RC targets than for RD, UC and UD (the three targets representing either an acoustical or contextual deviance). For example, the right MFG activation was extended and included rostral activation in the inferior frontal sulcus (IFS), bilaterally, for RD, UC and UD targets (but not for RC targets). In addition, the cingulate sulcus and gyrus were activated in response to RD, UC and UD targets (cf. $y=+5$, Fig. 2). A third area showing differences in the extent of activation as a function of

Table 5
Activations for the four targets: related consonant (RC), related dissonant (RD), unrelated consonant (UC) and unrelated dissonant (UD)[a]

Lobe	Region		Hemisphere	RC				RD				UC				UD			
				x	*y*	*z*	*Z*-score	*x*	*y*	*z*	*Z*-score	*x*	*y*	*z*	*Z*-score	*x*	*y*	*z*	*Z*-score
Frontal	IFG	44/45	Right	56	11	5	3.39	52	15	5	3.49	56	11	10	3.75	56	11	5	3.4
	IFG/Insula		Left	−49	15	−5	3.55	−38	15	0	3.54	−38	15	0	4.36	−34	19	10	4.15
																−38	15	0	3.81
			Right	45	11	−5	4.09	45	11	0	3.99	49	15	−5	4.37	41	15	−5	4.37
												41	11	5	4.05	45	8	5	3.92
	MFG/IFS	46/10	Left					−45	41	15	3.44	−41	38	15	3.36	−41	38	15	3.44
			Right					49	41	5	3.23	49	38	10	3.72				
	MFG	46/9	Right	49	38	25	3.58	38	38	25	3.2	49	38	25	3.9	49	38	25	2.99
								38	49	20	2.94	52	22	35	3.35	49	41	10	3.45
	SFG medial	8	Left	0*	22	45	3.23	0*	26	45	3.74	0*	30	50	3.67	0*	26	45	3.23
		6	Right													0	15	60	3.6
	Cingulate sulcus		Left	0	38	25	3.41												
			Right					4	34	25	3.45	8	30	35	3.87				
	Cingulate gyrus	24/32	Left									0	15	35	3.15	−4	41	15	2.54
			Right					0	0	40	3.1								
Parietal	Post. cing. gyrus	23/31	Left	0*	−34	30	4.13	0*	−22	30	4.08	−4	−26	30	4.13	−4	−22	30	4.13
			Right									4	−38	25	4.3	4	−11	30	3.82
	Supramarg. gyrus	40	Left	−64	−26	35	4.34	−64	−26	35	4.2	−49	−49	50	4.14	64	−22	30	4.12
				−45	−49	60	3.33	−49	−49	55	2.83	−64	−30	40	3.48	−64	−30	40	4.04
			Right	68	−26	30	4.05	68	−26	30	4.48	68	−26	30	3.26	64	−34	40	4.18
				56	−38	55	2.87	45	−52	60	3.17°	49	−52	55	3.23	45	−52	60	3.68
	Angular gyrus/IPG		Right	52	−52	50	3.5												
Other	Insula anterior		Right	41	11	−15	3.56	34	22	5	3.86	34	22	5	3.68				
	Insula posterior		Left	−41	−8	10	3.35	−41	0	−10	3.33	−45	−4	5	3.89	−41	−4	10	3.62
				−41	−8	−5	3.03	−41	−15	10	3.10					−45	−15	−5	3.2
			Right	41	−11	0	3.91	45	−11	0	3.86	45	−8	−5	3.65	45	−11	0	3.61
																38	0	5	3.46
	Thalamic nuclei		Left	−15	−15	15	4.17	−11	−11	15	4.23	−19	−15	15	4.54	−11	−11	15	4.29
				−11	−4	15	4.13	−11	0	10	4.10					−11	0	10	4.39
			Right	11	−4	15	3.85	11	−4	10	4.53	11	4	0	3.53	8	4	0	3.86
								11	−19	15	4.79	11	−4	10	3.86	15	−8	15	4.9
	Caudate nucleus		Left									−11	4	10	4.14	−8	8	0	4.67
	Subiculum		Left	−15	−34	−10	3.53					−19	−26	−10	3.94	−15	−26	−15	3.27
	Lingual gyrus	17/18	Left	0	−86	−5	3.42					0	−86	−5	3.49				
	Cerebellum		Left	−34	−68	−25	4.58	−8	−52	−5	5.36	−34	−60	−30	5.15	−8	−45	−15	5.04
				−19	−75	−20	3.06	−34	−60	−30	5.35	−8	−79	−35	4.07	−34	−60	−30	4.58
								−8	−79	−35	5.2								
			Right	4	−45	−15	4.02	4	−75	−15	5.08	22	−79	−20	4.3	4	−45	−15	4.58
				45	−68	−30	3.97	38	−68	−30	4.8	34	−64	−30	3.8	22	−68	−35	

If $x=0$: activation pattern is classified to the hemisphere where it extends to, except if activation pattern extends bilaterally, then *. °Indicates that the p-value for this activation is 0.051.

[a] SPMs were thresholded at $P<0.01$ (uncorrected) and activation significant at cluster level are listed.

target type was the inferior frontal region: the bilateral activations of an area around the frontal operculum (IFG, pars opercularis, extending to anterior insula) were larger for RD, UC and UD targets than for RC targets. Finally, right angular gyrus activation was observed for RC only.

3.3.4. Consonant targets: related versus unrelated

The direct comparisons between RC and UC controlled for handedness as all correct responses to consonant targets involved the right thumb. Both contrasts (RC−UC and UC−RC) included frontal and parietal activation areas, but in different regions. The UC-minus-RC contrast showed more extensive activation than the opposite contrast (Table 6 and Fig. 3). For RC relative to UC targets, significant BOLD signal increases were observed in the left SFG, right postcentral gyrus and, bilaterally, in angular gyrus and precuneus along the midline. When comparing UC to RC targets, bilateral activations in posterior cingulate gyrus and IPS were observed (right IPS activation failed to reach significance at the cluster level; $P=0.067$; $Z=3.89$; $x=30$, $y=-60$, $z=50$). In frontal areas, right lateralized activation was observed in the MFG, IFS and anterior cingulate gyrus. Bilateral activation was observed in the medial SFG that extended on the right into the cingulate sulcus. The extended activation in inferior frontal regions observed for UC targets (Fig. 2) was confirmed in the present contrast relative to RC targets: The IFG, pars opercularis, activation extending to the anterior insula was significantly stronger for UC than for RC targets. In addition, bilateral activation was observed in the thalamic nuclei and caudate nucleus.

3.3.5. Region of interest analyses

In right and left hemispheres, a region of interest around the frontal operculum was defined on the basis of the mean T1-weighted anatomical MR image. The region was centered on the frontal operculum and encompassed inferior parts of the inferior frontal gyrus, pars opercularis, and the anterior insula. Anterior ($y=+30$) and medial ($x=+30/-30$ between $y=+30$ and $+18$, $x=\pm35$ between $y=+8$ and $+18$) borders were limited by adjacent white matter. The posterior end was defined on the basis of coronal slices in the Duvernoy [30] atlas reporting frontal operculum areas up to $y=+10$. Dorsal and ventral borders were set to $z=+10$ and $z=-10$, respectively. The lateral borders were defined at $x=\pm60$. For areas more posterior than $y=+18$ and more lateral than $x=\pm45$, the ventral border was restricted to $z=-5$ in order to avoid the temporal lobe.

For each participant, contrast images of the four targets (RC, RD, UC, UD) were analyzed inside the defined region ($P<0.05$). Fig. 4 shows the numbers of significantly activated voxels (Fig. 4a) and the Z-scores for these

Table 6
Activations for the comparisons between related consonant and unrelated consonant[a]

Contrast	Lobe	Region	BA	Hemisphere	x	y	z	Z-score
Related consonant − unrelated consonant								
	Frontal	SFG medial	10	Left	−8	64	5	2.9
		SFG	10/9	Left	−11	60	25	2.76
	Parietal	Postcentral gyrus	3	Right	60	−19	35	3.28
		Angular gyrus		Left	−45	−75	30	3.1
			39	Right	52	−56	45	3.45
		Precuneus	7	Left	−11	−52	50	2.98
				Right	0	−45	55	3.05
Unrelated consonant − related consonant								
	Frontal	IFG/pars opercularis	44/45	Left	−52	8	0	3.08
				Right	49	15	0	4.04
		IFG/insula		Left	−38	19	5	4.17
				Right	34	22	0	3.89
		IFS		Right	45	26	20	3.9
		MFG	46/9	Right	41	34	25	3.62
		SFG medial/SMA	6	Left	−8	4	60	3.34
				Right	8	8	60	3.29
		Cingulate sulcus		Right	4	4	45	3.36
		Cingulate gyrus	31	Right	15	0	40	3.73
			32		11	19	35	3.03
	Parietal	Post. cingulate gyrus	23/31	Left	−4	−34	30	4.26
		IPS		Left	−34	−60	55	2.96
	Other	Thalamic nuclei		Left	−15	−11	5	3.46
				Right	11	−15	−5	3.48
		Caudate nucleus		Left	−8	8	5	3.23
				Right	15	11	15	3.36
		Cerebellum		Left	−19	−41	−20	3.42

[a] SPMs were thresholded at $P<0.01$ (uncorrected) and activation significant at cluster level are listed.

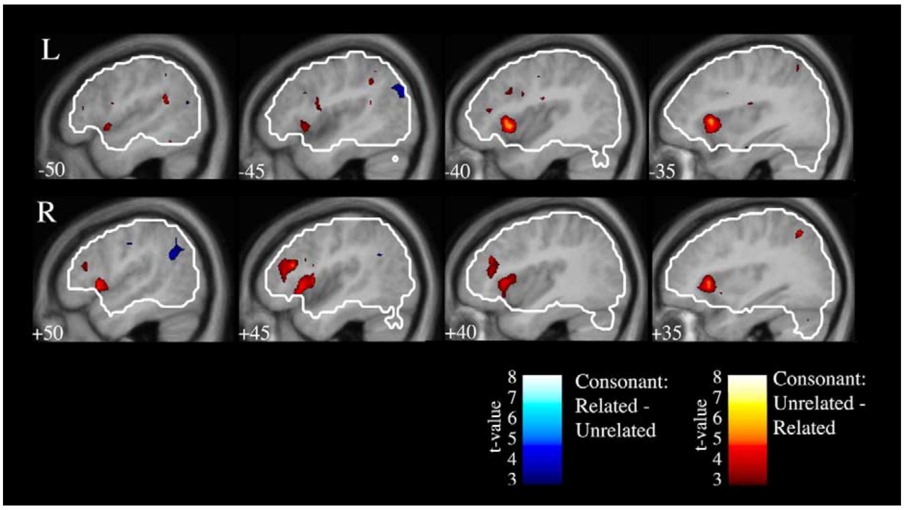

Fig. 3. Group ($N=15$) image showing significant differences in BOLD signal ($P<0.01$) between RC targets (blue) and UC targets (red). Activations are superimposed on the average T1-weighted anatomical image based on all participants. The white contour is the inclusion mask showing the edges of the volume that contained data from all participants.

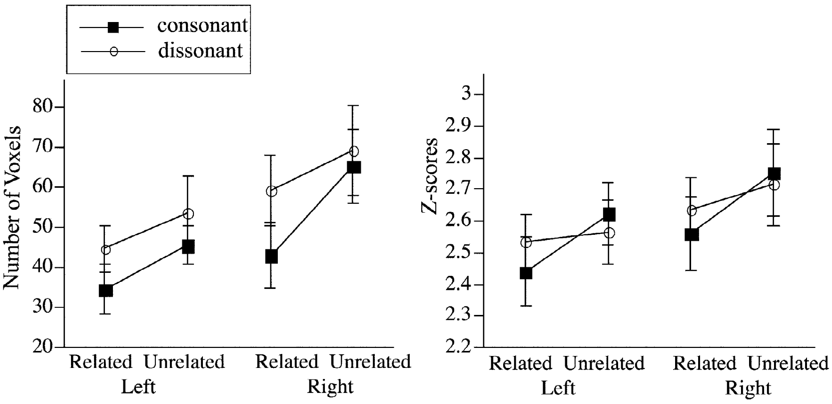

Fig. 4. Number of significantly activated voxels (left) and Z-scores of these activated voxels (right) in the defined region of interest around the frontal operculum. Data are presented as a function of hemisphere (left/right), harmonic relatedness (related/unrelated) and target type (consonant/dissonant) and are averaged over all participants ($N=15$).

activated voxels (Fig. 4b) for each target averaged over participants.[2] Two 2×2×2 ANOVAs were performed with Relatedness (related/unrelated), Target Type (consonant/dissonant) and Hemisphere (left/right) as within-subject factors with voxel counts and Z-scores as dependent variables, respectively. For both dependent variables, the main effect of Relatedness was significant; $F(1,14)=6.89$, $P<0.05$ for voxel counts and $F(1,14)=18.46$, $P<0.001$ for Z-scores. Activated voxels were less numerous and showed a weaker average Z-score in the related context than in the unrelated context. Planned comparisons indicated that this relatedness effect was observed essentially for consonant targets ($F(1,14)=17.42$, $P<0.001$ for voxel numbers and $F(1,14)=18.44$, $P<0.001$ for Z-scores) and not for dissonant targets. However, the interaction between Relatedness and Target Type was significant neither for voxel counts ($F<1$) nor Z-scores ($F=1.95$, $P=0.18$). For the number of activated voxels, the relatedness effect was more pronounced in the right hemisphere than in the left hemisphere, as expressed in the significant interaction between Relatedness and Hemisphere; $F(1,14)=4.71$, $P<0.05$. In addition, more voxels were activated overall in the ROI of the right hemisphere than of the left hemisphere; $F(1,14)=10.69$; $P<0.01$. The main effect of Hemisphere failed to reach significance for Z-scores, $F(1,14)=3.14$, $P=0.098$, as did the main effect of Target for the number of activated voxels ($F(1,14)=2.83$, $P=0.11$).

---

[2] The activated areas and associated Z-scores reflect the degree to which the observed BOLD signal fit with the ideal haemodynamic response function that was used to define the target events in the design matrix.

4. Discussion

In previous research on music perception, it has been well established that a musical context influences the processing of a target event. In the present study, we investigated the neural correlates of musical priming. Participants judged the sensory consonance of a target that was either harmonically related to the context and fit the established expectations, or unrelated to the context and violated expectations. The behavioral data acquired during the scanning session replicated previously observed facilitation effects due to harmonic relatedness: the processing of a consonant target was faster and more accurate if it was related to the context than if it was unrelated. In the following, we discuss first the overall network of activation that has been observed for the four target types and highlight some of the involved brain structures (e.g. posterior cingulate, MFG). We then discuss the involvement of the inferior frontal areas in target chord processing and integrate the musical priming data into data sets previously reported for both music and language perception.

4.1. The four targets—a network of activation involved in musical priming

The processing of the four targets was associated with bilateral activation in frontal (IFG, MFG, SFG, insular, anterior cingulate) and parietal areas (IPG, posterior cingulate) as well as in the thalamic nuclei and the cerebellum. Comparable activation networks have been recently reported for target detection and novelty processing in both visual and auditory modalities [51,61]. With the goals of understanding further target detection networks and localizing P300 generators, Linden et al. [61] used the oddball paradigm with auditory (1000 Hz tones versus 2000 Hz target tones) and visual (sequences of small angles) stimuli while recording ERPs and BOLD responses. For visual and auditory stimuli, the target versus non-target comparison revealed a network including bilateral supramarginal gyrus, frontal operculum, insula as well as frontal midline SMA (supplementary motor area) and anterior cingulate. When participants had to mentally count the targets (instead of pressing a button) the posterior cingulate (BA23) and right MFG were additionally activated for auditory targets. A similar network involved in target detection and novelty processing has been reported with a variation of the classical oddball [51]. A stream of non-target stimuli (1000-Hz tones) was interrupted every three to five stimuli either by a target stimulus (1500-Hz tones) that participants had to detect with a button press or by a novel stimulus (e.g. tone sweeps) that did not require a response. Target processing activated bilateral IFG, MFG, anterior STG, inferior and superior parietal lobes, anterior and posterior cingulate, lateral frontal cortex, thalamus, caudate and amygdala/hippocampal complex. The direct comparison between novel and non-target stimuli revealed bilateral activation in the IFG, insula, inferior parietal lobe and in inferior, middle and superior temporal gyri. We did not observe STG activation for the four targets nor in the direct comparison between RC and UC. In contrast to Kiehl et al. [51], the four targets were not presented in isolation, but followed directly the seven-chord context. It can be suggested that due to the preceding context STG activation did not result in an additional activation peak in response to the target as modeled by the event-related haemodynamic function in the design matrix.

The target chord processing in the musical priming task was associated with an activation pattern that contained network components observed in target and deviance detection in oddball paradigms. This outcome suggests that the neural circuitry observed for simple oddballs is activated for acoustically complex events in musical sequences. In addition, the activation of some components depended on the target's characteristics, notably in how far the chord fit or violated the expectations built up by the prime context. The expectancy violation was either sensory-acoustic or based on harmonic relationships. The dissonant-versus-consonant contrast showed for example, that activation in the IFG and parietal areas (parietal operculum, SPG) was stronger for dissonant than for consonant targets. Similarly, IFG, MFG, anterior and posterior cingulate, thalamic nuclei, caudate, IPS and cerebellum were more strongly activated for UC targets which violated harmonic relationships with the prime than for RC targets. Furthermore, the overall network of bilateral activation and, more specifically, the implication of bilateral IFG (see below) suggest that neural correlates of music perception (i.e. here the processing of musical target events) are not restricted to the right hemisphere, but are distributed throughout left and right cerebral and cerebellar hemispheres (see also Refs. [2,47,76]).

The processing of targets in oddball paradigms and the musical priming paradigm was associated with activation in the posterior cingulate (BA23/31). Posterior cingulate activation has been reported in experimental situations investigating processes that might also be involved in music perception and target chord processing. In auditory discrimination tasks, increased posterior cingulate activation has been observed for phoneme discrimination or judgments of rising and falling pitches [85]. One hypothesis about posterior cingulate activation in our priming task (for both context and target processing) is that the posterior cingulate may be involved in perceptual processes aimed at increasing the perceptibility of the musical material against the background noise of the MRI system. This hypothesis is based on Lockwood et al. [62] who reported activation in middle and posterior portions of the cingulate gyrus (BA23) (4 −38 24) for the perception of sounds at different intensities. As activation was maximal for sound stimuli at low sound intensities (30 dB HL for

0.5 kHz) and less prominent at higher intensities, the authors suggested that posterior cingulate regions act as gain or volume control. In our study, this gain control would become even more important in cases with expectancy violation, notably a harmonically unrelated chord that was consonant (UC−RC, Table 5).

An alternative hypothesis for posterior cingulate activation is derived from studies on cognitive processes (such as text comprehension or memory), notably because it might be argued that listeners integrate incoming sounds with previously heard ones. When unusual stories were processed and the narrative information had to be linked to prior knowledge and integrated into a previously established situation model of the story, activation was reported in the posterior cingulate, though in even more posterior regions (0 −46 28, BA31) [65]. In other studies on language processing and memory, posterior cingulate activation was reported in similar regions as in our study. However, in contrast to the observed stronger activation for UC than RC, stronger posterior cingulate activation was reported for coherent than for incoherent sentence pairs in text comprehension (BA23/31, −5 −34 39) [33], for real words in contrast to random letter strings (−3 −36 24) [48] and for correct responses to previously seen ('old') words in recognition memory (−2 −33 33, BA23) [99].

Aside from language processing, posterior cingulate activation has been observed during emotional responses to consonant and dissonant musical material. Blood et al. [22] reported positive correlations between increasing unpleasantness ratings of musical stimuli and posterior cingulate activation (BA23/31, −3 −33 32). If we argue that a strong expectancy violation (as with UC targets) is an unpleasant experience for the listener in comparison to a fulfilled ending (as with RC targets), then increased posterior cingulate activation for UC is consistent with Blood et al. [22].

The activation network in the priming task is comparable not only to networks implicated in target detection and novelty processing, but contains components that have been reported for selective attention and general attentional demands of tasks. A right hemispheric fronto-parietal activation pattern that included right IFG (BA45) and IPG (BA40) was observed in neuroimaging studies involving sustained or selective attention to sensory input patterns, as for example to auditory stimuli in a sound intensity discrimination task [7] or to visual and sensory stimuli in detection of changes [75]. In the musical priming task, IFG and IPG were activated bilaterally for target chord processing. Bilateral activation of inferior frontal and parietal networks involved in auditory attention has been reported for syllables [85] and for musical streams [47]. In the musical priming task, the target processing involved also activation of the anterior cingulate, more specifically in its dorsal, 'cognitive' division that is part of a distributed attentional network [23].

A further region involved in target processing is the MFG whose activation was mostly right-lateralized, but also present on the left for RD, UC and UD targets. In the direct comparison between UC and RC, MFG activation was significantly stronger for UC targets in the right hemisphere. This activation might be linked to monitoring demands of the task that were higher for consonant judgments of UC targets because of the contextual expectancy violation. In a recognition memory task where participants had to recognize 'old' words from the previous study phase and to distinguish them from new words that were either related or unrelated to the old words, von Zerssen et al. [99] reported activation of the right MFG (BA9/46) for correct rejections of related new words.

The right angular gyrus was activated significantly only for RC targets. The RC target respected harmonic relations and fulfilled listeners' expectations—in contrast to the incorrect UC ending. In an implicit learning study using artificial grammars, Skosnic et al. [91] reported right angular gyrus activation when contrasting grammatical versus non-grammatical trial types after the learning phase. In language processing, however, it is essentially the left angular gyrus that is described as part of a semantic processing network (see Ref. [21] for a review): increased activation is reported when sentences have to be processed [6], unrelated words are presented slowly [84] and the meaning of words has to be accessed [83]. A neurological case suggests that the inferior parietal regions in the right hemisphere also play a role in music understanding and music appreciation: lesions close to the angular gyrus (i.e. supramarginal gyrus, temporo-parietal areas) caused altered perception of musical form and of emotional components of music [68].

The processing of the four targets was associated with activation in anterior insula (in combination with inferior frontal activation, see below) and posterior insula. Activation of the insula was observed in the oddball tasks discussed above, but also in the processing of melodies [80,103], of moving sound stimuli [42] and in the detection of auditory–visual stimulus onset asynchronies [50]. For melody processing, insula activation was observed in a task on rhythm processing [80] and in a task in which the first and last notes of a melody were compared [103]. Platel et al. [80] suggested that the (left) insula and Broca's area are involved in the processing and memorizing of sequential sound information. Griffiths et al. [42] suggested that the insula is acting as an auditory association cortex involved in sound movement analysis. Connections have been described between the insula and auditory regions [60], and with the frontal operculum, the medial area BA6 as well as orbital cortex and cingulate gyrus [3]. In the musical priming paradigm, we observed insula activation in combination with frontal operculum activation. The outcome suggests that these structures are involved in the integration of incoming sound stimuli over time (including the comparison of new sounds with previously heard ones). We turn to this point in the next section.

4.2. Inferior frontal activation in target processing

The processing of the four targets was associated with bilateral activation in the frontal operculum area (including ventral IFG and anterior insula). These frontal areas were sensitive to the manipulation of target type and prime context, with a weak hemispheric asymmetry to the right. The RC target that fulfilled expectations and represented a deviant neither on an acoustic level (as dissonant targets) nor on a contextual level (as unrelated targets) activated the fewest voxels and with the lowest *Z*-scores. The number of activated voxels increased for unrelated targets and acoustic deviants. The data are in agreement with the mERAN source localization in bilateral inferior frontal regions with a weak right-hemispheric asymmetry [64]. The two data sets provide converging evidence that Broca's area and its right-hemisphere homologue are not involved solely in language processing. This finding can be integrated with a variety of other results showing that Broca's area and its right homologue participate in non-linguistic processes [1,43,61,71,85] besides their roles in semantic [81,100], syntactic [25,31] and phonological functions [34,81,85].

As reported above, the inferior frontal areas are also associated in target detection and novelty processing [51,61]. These activation patterns suggest the role of these areas in processing and integrating (auditory and visual) information over time and the comparison of older stored information with newer incoming information—processes that include time and memory. More specifically, bilateral frontal opercular activation was reported for the processing of timing information [90], when movements had to be synchronized to a sensory event [86] or when participants had to time the perceptual anticipation of a sensory event [80,89]. Fuster [41] summarizes the higher integrative functions of the prefrontal cortex and underlines its importance in temporal information processing. The lateral prefrontal cortex has both retrospective and prospective roles in integrative temporal functions. The retrospective role is specifically analyzed in studies on working memory (see Ref. [24], for a review) observing, for example, increased inferior frontal activation with increased sentence complexity [49]. The prospective role shows its involvement in expectation and preparation of anticipated events (e.g. planning steps [4]). In the musical priming paradigm, chords of the sequence are stored in sensory memory, activate a given key representation and give rise to expectations for further events, notably for consonant events that are harmonically related to the prime context. If the incoming chord does not fit with previous information and expectations, the integration demands necessary for this event are more complex and inferior frontal activation is increased.

The harmonic relatedness of the target chord manipulated in the present study is based on music theoretic rules (i.e. 'musical syntax'): the related target belongs to the same key as the chords of the prime context, the unrelated target is an out-of-key chord belonging to a very distant key. This manipulation implies that (a) the related target is frequently associated with events of the prime context when musical pieces of the Western tonal repertoire are analyzed, and (b) tones of the related target occur in the prime context. The first aspect of the musical material means that our harmonic priming situation opposes target events that have strong versus weak association strengths in musical pieces obeying the Western tonal system. The fMRI data showed increased BOLD signal in the IFG (ventral regions) for target events that are weakly associated with the prime context (e.g. UC targets). Interestingly, IFG activation has also been reported in language studies manipulating the associative strengths of words. Bilateral IFG activation was increased when the word serving as cue was weakly associated to the to-be-selected target word [101] and when categorically related word pairs were compared to unrelated pairs [53]. In a lexical decision task, increased left IFG activation was observed for semantically unrelated pairs in comparison to related pairs [102].

The second aspect of the musical material suggests that a component of repetition priming might be involved in our data. In repetition priming for objects and words, decreased inferior frontal activation (including the bilateral frontal operculum) was reported for repeated items in comparison to novel items [54] or for familiar words in comparison to novel words [82]. In our study, the frequency of occurrence of tones of the target was not kept constant between related and unrelated conditions, but the tones of the related target occurred more often in the prime context than those of the unrelated target. The link with repetition priming data suggests that the weaker activation of the IFG area for RC targets might also involve repetition priming for neural correlates in musical priming. However, this suggestive hypothesis needs further investigation by systematically manipulating the musical material, especially in the light of recent behavioral studies providing evidence that harmonic priming is not only based on sensory priming components (e.g. repetition of tones), but includes a cognitive priming component. The musical sequences were constructed in such a way that less related targets shared more tones with the context than did related targets [18] or that the target was immediately preceded by the same chord [19]. The behavioral data always show facilitated processing for related targets, supporting the hypothesis that listeners have internalized Western tonal regularities by mere exposure.

With regard to the neural substrates of target detection and processing of novel or unrelated events, the question is raised in how far the inferior frontal activation observed in musical priming is specific to musical syntax processing or if it is more generally linked to musical deviance processing (i.e. sensory dissonance). If considering consonant targets only (RC versus UC), results suggest that inferior frontal regions are sensitive to harmonic expectancy violation and imply a processor of music-syntactic relationships. However, data of dissonant targets suggests that these regions are also sensitive to other types of violations, notably the violation of sensory consonance. More voxels were also activated for acoustically deviant targets without syntactical violation (the RD targets), even if this increase was weaker than for contextual deviance (UC, UD). In addition, it is important to note that due to the strong harmonic manipulation, the unrelated target (even if it is consonant in itself) creates a harmonic dissonance with the preceding context since it does not share as many harmonics with the context as does the related target. Because of this contextual dissonance, our musical material does not allow extracting solely expectancy violation due to harmonic relationships (see Ref. [94], for a definition of two components of musical consonance). Interestingly, mERAN and ERAN activity were observed with a chord that (even if consonant in itself) was deviant not only because of its harmonic structure, but also because of two out-of-key tones [52,64]. Overall, the data suggest that the inferior frontal regions are sensitive to strong violations of harmonic relationships and also to violations of sensory features. The harmonic manipulation of our study does not allow us to make strong inferences about subtle syntactic changes in musical structures that do not include contextual dissonance. Further studies are investigating whether the inferior frontal regions are sensitive to different degrees of harmonic relatedness. For this purpose, two in-key target chords that differ in harmonic functions are opposed to each other as in Bigand and Pineau [17] with behavioral and in Regnault et al. [87] with electrophysiological measures.

The present data obtained with musical material are in agreement with previous studies pointing to a role of inferior frontal regions for the integration of information over time. The integrative role includes storing previously heard information (i.e. a component linked to working memory) and comparing the stored information with further incoming events. The processing of structural relations between sequentially presented events in language and music relies on integrative processes and on listener's knowledge about grammatically correct relations. In language, inferior frontal activation is reported for the processing of syntactic and also semantic relations in the left hemisphere, though in some cases also in the right [70,81,101]. In music, the processing of structural, syntactic-like relations between musical events evokes bilateral inferior frontal activation with a weak asymmetry to the right ([64]; our data). The activations observed in the musical priming study encompass also areas activated in semantic processing in language, as for example the processing of semantic relations and associations [101]. The data obtained with semantic material [101] and with musical material suggest an influence of the association strengths of to-be-processed events, notably weakly associated events are linked with stronger activation of the inferior frontal areas than frequently associated events. These findings suggest a link to long-term memory: previously stored knowledge about possible relations and their frequency of occurrence influences the processing of incoming events. Depending on the current context, the listener's knowledge allows the development of expectations for typical future events. The comparison of expected versus incoming events (i.e. via integrative processes) allows the detection of a potential deviant, incoherent event (in our case the deviance in musical syntax and acoustic consonance). The processing of deviants, or more generally of less frequently encountered event groups may then require more neural resources than processing of more familiar or prototypical stimuli.

Acknowledgements

We thank Lauren Fontein for help with testing participants. This research was supported by NIH grant P50 NS17778-18 to Jamshed J. Bharucha.

References

[1] R.B. Adams, P. Janata, A comparison of neural circuits underlying auditory and visual object categorization, NeuroImage 16 (2002) 361–377.

[2] E.O. Altenmüller, How many music centers are in the brain, in: R. Zatorre, I. Peretz (Eds.), The Biological Foundations of Music, Vol. 390, New York Academy of Sciences, New York, 2001, pp. 273–280.

[3] A. Ardila, The role of insula in language: an unsettled question, Aphasiology 13 (1999) 79–87.

[4] S.C. Baker, R.D. Rogers, A.M. Owen, C.D. Frith, R.J. Dolan, H. Frack-Damasio, T. Grabowski, R.S.J. Frankowiak, T.W. Robbins, Neural systems engaged by planning: A PET study of the Tower of London task, Neuropsychologia 34 (1996) 515–526.

[5] J.C. Bartlett, W.J. Dowling, The recognition of transposed melodies: A key-distance effect in developmental perspective, J. Exp. Psychol. Hum. Percept. Perform. 6 (1980) 501–515.

[6] D. Bavelier, D. Corina, P. Jezzard, S. Padmanabhan, A. Prinster, A. Braun, Sentence reading: A functional MRI study at 4 Tesla, J. Cogn. Neurosci. 9 (1997) 664–686.

[7] P. Belin, S. McAdams, B. Smith, S. Savel, L. Thivard, S. Samson, Y. Samson, The functional anatomy of sound intensity discrimination, J. Neurosci. 18 (1998) 6388–6394.

[8] S. Bentin, M. Kutas, S.A. Hillyard, Electrophysiological evidence for task effects on semantic priming in auditory word processing, Psychophysiology 30 (1993) 161–169.

[9] S. Bentin, G. McCarthy, C.C. Wood, Event-related potentials, lexical decision and semantic priming, Electroencephalogr. Clin. Neurophysiol. 60 (1985) 343–355.

[10] M. Besson, F. Faïta, An event-related potential (ERP) study of musical expectancy: Comparison of musicians with nonmusicians, J. Exp. Psychol. Hum. Percept. Perform. 21 (1995) 1278–1296.

[11] M. Besson, F. Faïta, J. Requin, Brain waves associated with musical

incongruities differ for musicians and nonmusicians, Neurosci. Lett. 168 (1994) 101–105.
[12] M. Besson, F. Macar, An event-related potential analysis of incongruity in music and other non-linguistic context, Psychophysiology 24 (1987) 14–25.
[13] J.J. Bharucha, C.L. Krumhansl, The representation of harmonic structure in music: Hierarchies of stability as a function of context, Cognition 13 (1983) 63–102.
[14] J.J. Bharucha, K. Stoeckig, Reaction time and musical expectancy: Priming of chords, J. Exp. Psychol. Hum. Percept. Perform. 12 (1986) 403–410.
[15] J.J. Bharucha, K. Stoeckig, Priming of chords: Spreading activation or overlapping frequency spectra?, Percept. Psychophys. 41 (1987) 519–524.
[16] E. Bigand, F. Madurell, B. Tillmann, M. Pineau, Effect of global structure and temporal organization on chord processing, J. Exp. Psychol. Hum. Percept. Perform. 25 (1999) 184–197.
[17] E. Bigand, M. Pineau, Global context effects on musical expectancy, Percept. Psychophys. 59 (1997) 1098–1107.
[18] E. Bigand, B. Poulain, B. Tillmann, D. D'Adamo, Cognitive versus sensory components in harmonic priming effects. J. Exp. Psychol. Hum. Percept. Perform. (2002) in press.
[19] E. Bigand, B. Tillmann, D. Manderlier, B. Poulin, Harmonic priming versus chord repetition effect in music. Manuscript submitted for publication (2002).
[20] E. Bigand, B. Tillmann, B. Poulin, D.A. D'Adamo, The effect of harmonic context on phoneme monitoring in vocal music, Cognition 81 (2001) B11–B20.
[21] J. Binder, C.J. Price, Functional neuroimaging of language, in: R. Cabeza, A. Kingstone (Eds.), Handbook of Functional Neuroimaging of Cognition, MIT Press, Cambridge, MA, 2001, pp. 187–252.
[22] A.J. Blood, R.J. Zatorre, P. Bermudez, A.C. Evans, Emotional responses to pleasant and unpleasant music correlate with activity in paralimbic brain regions, Nature Neurosci. 4 (1999) 382–387.
[23] G. Bush, P. Luu, M.I. Posner, Cognitive and emotional influences in anterior cingulate cortex, Trends Cogn. Sci. 4 (2000) 215–222.
[24] R. Cabeza, L. Nyberg, Imaging cognition II: an empirical review of 275 PET and fMRI Studies, J. Cogn. Neurosci. 12 (2000) 1–47.
[25] D. Caplan, N. Alpert, G. Waters, PET studies of syntactic processing with auditory sentence presentation, NeuroImage 9 (1999) 343–351.
[26] J. Cohen, B. MacWhinney, M. Flatt, J. Provost, PsyScope: An interactive graphic system for designing and controlling experiments in the psychology laboratory using Macintosh computers, Behav. Res. Methods Instrum. Comput. 25 (1993) 257–271.
[27] L.L. Cuddy, B. Badertscher, Recovery of the tonal hierarchy: Some comparisons across age and levels of musical experience, Percept. Psychophys. 41 (1987) 609–620.
[28] L.L. Cuddy, W.F. Thompson, Asymmetry of perceived key movement in chorale sequences: Converging evidence from a probe-tone analysis, Psychol. Res. 54 (1992) 51–59.
[29] L.L. Cuddy, W.F. Thompson, Perceived key movement in four-voice harmony and single voices, Music Percept. 9 (1992) 427–438.
[30] H.M. Duvernoy, The Human Brain: Surface, Three-dimensional Sectional Anatomy With MRI, and blood Supply, 2 Edition, Springer, Wien, 1999.
[31] E. Embick, A. Marantz, Y. Miyashita, W. O'Neil, K.L. Sakai, A syntactic specialization for Broca's area, Proc. NY Acad. Sci. 97 (2000) 6150–6154.
[32] A. Evans, M. Kamber, D.L. Collins, D. Macdonald, An MRI-based probabilistic atlas of neuroanatomy, in: S. Shorvon, D. Fish, F. Anderman, G.M. Byder, H. Stefan (Eds.), Magnetic Resonance Scanning and Epilepsy, Vol. 264, Plenum Press, New York, 1994, pp. 263–274.
[33] E.C. Ferstl, Y.D. von Cramon, The role of coherence and cohesion in text comprehension: an event-related fMRI study, Cogn. Brain Res. 11 (2001) 325–340.
[34] J.A. Fiez, D.A. Balota, M.E. Raichle, S.E. Petersen, Effects of lexicality, frequency and spelling-to-sound consistency on the functional anatomy of reading, Neuron 24 (1999) 205–218.
[35] R. Francès, La Perception de la Musique, 2nd Edition, Vrin, Paris, 1958.
[36] A.D. Friederici, The time course of syntactic activation during language processing: A model based on neuropsychological and neurophysicological data, Brain Lang. 50 (1995) 259–281.
[37] A.D. Friederici, M. Meyer, D.Y. van Cramon, Auditory language comprehension: An event-related fMRI study on the processing of syntactic and language information, Brain Lang. 74 (2000) 289–300.
[38] A.D. Friederici, E. Pfeifer, A. Hahne, Event-related brain potentials during natural speech processing: effects of semantic, morphological and syntactic violations, Cogn. Brain Res. 1 (1993) 182–192.
[39] K.J. Friston, A.P. Holmes, K.J. Worsley, J.P. Poline, C.D. Frith, R.S.J. Frackowiak, Statistical parametric maps in functional imaging: a general linear approach, Hum. Brain Mapping 2 (1995) 189–210.
[40] K.J. Friston, S. Williams, R. Howard, R.S.J. Frackowiak, R. Turner, Movement-related effects in fMRI time-series, Magn. Reson. Med. 35 (1996) 346–355.
[41] J.M. Fuster, The prefrontal cortex—An update: Time is of the essence, Neuron 30 (2001) 319–333.
[42] T.D. Griffiths et al., Human cortical areas selectively activated by apparent sound movement, Curr. Biol. 4 (1994) 891–895.
[43] T.D. Griffiths, I. Johnsrude, J.L. Dean, G.G.R. Green, A common neural substrate for the analysis of pitch and duration pattern in segmented sound?, NeuroReport 10 (1999) 3825–3830.
[44] S. Hébert, I. Peretz, L. Gagnon, Perceiving the tonal ending of tune excerpts: The roles of pre-existing representation and musical expertise, Can. J. Exp. Psychol. 49 (1995) 193–209.
[45] D.J. Hess, D.J. Foss, P. Carroll, Effects of global and local context on lexical processing during language comprehension, J. Exp. Psychol. Gen. 124 (1995) 62–85.
[46] P. Janata, ERP measures assay the degree of expectancy violation of harmonic contexts in music, J. Cogn. Neurosci. 7 (1995) 153–164.
[47] P. Janata, B. Tillmann, J.J. Bharucha, Listening to polyphonic music recruits domain—general attention and working memory circuits, Cogn. Affect. Behav. Neurosci. 2 (2002) 121–140.
[48] F. Jessen, M. Erb, U. Klose, M. Lotze, W. Grodd, R. Heun, Activation of human language processing brain regions after the presentation of random letter strings demonstrated with event-related functional magnetic resonance imaging, Neurosci. Lett. 270 (1999) 13–16.
[49] M. Just, P. Carpenter, T. Keller, W. Eddy, K. Thulborn, Brain activation modulated by sentence comprehension, Science 274 (1996) 114–116.
[50] O.B. Khalafalla, J. Grafman, M. Hallett, Neural correlates of auditory–visual stimulus onset asynchrony detection, J. Neurosci. 21 (2001) 300–304.
[51] K.A. Kiehl, K.R. Laurens, T.L. Duty, B.B. Forster, P.F. Liddle, Neural sources involved in auditory target detection and novelty processing: An event-related fMRI study, Psychophysiology 38 (2001) 133–142.
[52] S. Koelsch, T. Gunter, A.D. Friederici, Brain indices of music processing: 'nonmusicians' are musical, J. Cogn. Neurosci. 12 (2000) 520–541.
[53] A.S. Kotz, A.D. Friederici, S.F. Cappa, D.Y. von Cramon, Task demands influence the activation pattern of auditory semantic priming in fMRI, Brain Lang. 74 (2000) 412–414.
[54] W. Koustaal, A.D. Wagner, M. Rotte, A. Maril, R.L. Buckner, D.L. Schacter, Perceptual specificity in visual object priming: functional magnetic resonance imaging evidence for a laterality difference in fusiform cortex, Neuropsychologia 39 (2001) 1.
[55] C.L. Krumhansl, The psychological representation of musical pitch in a tonal context, Cogn. Psychol. 11 (1979) 346–374.
[56] C.L. Krumhansl, J.J. Bharucha, M. Castellano, Key distance effects

on perceived harmonic structure in music, Percept. Psychophys. 32 (1982) 96–108.

[57] C.L. Krumhansl, E. Kessler, Tracing the dynamic changes in perceived tonal organization in a spatial representation of musical keys, Psychol. Rev. 89 (1982) 334–368.

[58] M. Kutas, S.A. Hillyard, Event-related brain potentials to semantically inappropriate and suppression large words, Biol. Psychol. 11 (1980) 99–116.

[59] M. Kutas, S.A. Hillyard, Brain potentials during reading reflect word expectancy and semantic association, Nature 307 (1984) 161–163.

[60] C. Liegeois-Chauvel, S. Trottier, A. Musolino, P. Chauvel, Organisation anatomique et fonctionnelle du cortex auditif chez l'homme, Rev. Neuropsychol. 4 (1993) 453–477.

[61] D.E.J. Linden, D. Prvulovic, E. Formisano, M. Vollinger, F.E. Zanella, R. Goebel, T. Dierks, The functional neuroanatomy of target detection: An fMRI study of visual and auditory oddball tasks, Cereb. Cortex 9 (1999) 815–823.

[62] A.H. Lockwood, R.J. Salvi, M.L. Coad, S.A. Arnold, D.S. Wack, B.W. Murphy, R.F. Burkard, The functional anatomy of a normal human auditory system: Responses to 0.5 and 4.0 kHz tones at varied intensities, Cereb. Cortex 9 (1999) 65–76.

[63] F. Maes, A. Collignon, D. Vandermeulen, G. Marchal, P. Suetens, Multimodality image registration by maximization of mutual information, IEEE Trans. Med. Imag. 16 (1997) 187–198.

[64] B. Maess, S. Koelsch, T. Gunter, A.D. Friederici, 'Musical syntax' is processed in the Broca's area: An MEG-study, Nature Neurosci. 4 (2001) 540–545.

[65] E.A. Maguire, C.D. Frith, R.G.M. Morris, The functional neuroanatomy of comprehension and memory: The importance of prior knowledge, Brain 122 (1999) 1839–1850.

[66] B.M. Mazoyer et al., The cortical representation of speech, J. Cogn. Neurosci. 5 (1993) 467–479.

[67] J.C. Mazziotta, A. Toga, A.C. Evans, P. Fox, J.A. Lancaster, Probabilistic atlas of the human brain: Theory and rationale for its development, NeuroImage 2 (1995) 89–101.

[68] M. Mazzoni, P. Moretti, L. Pardossi, M. Vista, A. Muratorio, A case of music imperception, J. Neurol. Neurosurg. Psychiatry 56 (1993) 325.

[69] D.E. Meyer, R.W. Schvaneveldt, Facilitation in recognizing pairs of word: Evidence of a dependence between retrieval operations, J. Exp. Psychol. 90 (1971) 227–234.

[70] M. Meyer, A.D. Friederici, D.Y. von Cramon, Neurocognition of auditory sentence comprehension: event-related fMRI reveals sensitivity to syntactic violations and task demands, Cogn. Brain Res. 9 (2000) 19–33.

[71] R.-A. Müller, N. Kleinhans, E. Courchesne, Broca's area and the discrimination of frequency transitions: A functional MRI study, Brain Lang. 76 (2001) 70–76.

[72] C.J. Mummery, T. Shallice, C.J. Price, Dual-process model in semantic priming: A functional imagining perspective, NeuroImage 9 (1999) 516–525.

[73] K. Nation, M.J. Snowling, Developmental differences in sensitivity to semantic relations among good and poor comprehenders: Evidence from semantic priming, Cognition 70 (1999) B1–B13.

[74] J.H. Neely, Semantic priming effects in visual word recognition: A selective review of current findings and theories, in: D. Besner, G.W. Humphreys (Eds.), Basic Processes in Reading: Visual Word Recognition, Lawrence Erlbaum, Hillsdale, NJ, 1991, pp. 264–336.

[75] J.V. Pardo, P.T. Fox, M.E. Raichle, Localization of a human system for sustained attention by positron emission tomography, Nature 349 (1991) 61–64.

[76] L.M. Parsons, Exploring the functional neuroanatomy of music performance, perception and comprehension, in: R. Zatorre, I. Peretz (Eds.), The Biological Foundations of Music, Vol. 930, New York Academy of Science, New York, 2001, pp. 211–231.

[77] A.D. Patel, E. Gibson, J. Ratner, M. Besson, P.J. Holcomb, Processing syntactic relations in language and music: An event-related potential study, J. Cogn. Neurosci. 10 (1998) 717–733.

[78] M. Perea, E. Rosa, The effects of associative and semantic priming in the lexical decision task, Psychol. Res. 66 (2002) 180–194.

[79] M. Pineau, E. Bigand, Effet des structures globales sur l'amorçage harmonique en musique, Année Psychologique 97 (1997) 385–408.

[80] H. Platel, C. Price, J.C. Baron, R. Wise, J. Lambert, R.S.J. Frackowiak, B. Lechevalier, F. Eustache, The structural components of music perception: A functional anatomical study, Brain 120 (1997) 229–243.

[81] R.A. Poldrack, A.D. Wagner, M.W. Prull, J.E. Desmond, G.H. Glover, J.D.E. Gabrieli, Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex, Neuroimage 10 (1999) 15–35.

[82] C. Price, R.J.S. Wise, E. Warburton, C.J. Moore, K. Patterson, D. Howard, Hearing and saying: the functional neuroanatomy of auditory word processing, Brain 119 (1996) 919–931.

[83] C.J. Price, The anatomy of language: Contributions from functional neuroimaging, J. Anat. 197 (2000) 335–359.

[84] C.J. Price, C.J. Moore, R.S.J. Frackowiak, The effect of varying stimulus rate and duration on brain activity during reading, NeuroImage 3 (1996) 40–52.

[85] K.R. Pugh, B.A. Shaywitz, R.K. Fulbright, D. Byrd, P. Skudlarski, L. Katz, R.T. Constable, J. Fletcher, C. Lacadie, K. Marchione, J.C. Gore, Auditory selective attention: An fMRI investigation, NeuroImage 4 (1996) 159–173.

[86] S.M. Rao, D.L. Harrington, K.Y. Haaland, J.A. Bobholz, R.W. Cox, J.R. Binder, Distributed neural systems underlying the timing of movements, J. Neurosci. 17 (1997) 5528–5535.

[87] P. Regnault, E. Bigand, M. Besson, Event-related brain potentials show top-down and bottom-up modulations of musical expectations, J. Cogn. Neurosci. 13 (2001) 241–255.

[88] S.L. Rossell, E.T. Bullmore, C.R. Williams, A.S. David, Brain activation during automatic and controlled processing of semantic relations: a priming experiment using lexical-decision, Neuropsychologia 39 (2001) 1167–1176.

[89] R.I. Schubotz, A.D. Friederici, D.Y. von Cramon, Time perception and motor timing: a common cortical and subcortical basis revealed by fMRI, NeuroImage 11 (2000) 1–12.

[90] R.I. Schubotz, D.Y. von Cramon, Functional organization of the lateral premotor cortex: fMRI reveals different regions activated by anticipation of object properties, location and speed, Cogn. Brain Res. 11 (2001) 97–112.

[91] P.D. Skosnic, P.J. Reber, D.R. Gitelman, T.B. Parrish, M.M. Mesulam, Examining the neural substrate of artificial grammar learning utilizing event-related fMRI, in: Proceedings of the 8th Annual Meeting of the Cognitive Neuroscience Society, Cognitive Neuroscience Society, New York, 2001, p. 64, 116B.

[92] K.E. Stanovich, R.F. West, Mechanisms of sentence context effects in reading: Automatic activation and conscious attention, Mem. Cogn. 7 (1979) 77–85.

[93] L.A. Stowe, C.A. Broere, A.M. Paans, A.A. Wijers, G. Mulder, W. Vaalburg, F. Zwarts, Localizing components of a complex task: Sentence processing and working memory, NeuroReport 9 (1998) 2995–2999.

[94] E. Terhardt, The concept of musical consonance: A link between music and psychoacoustics, Music Percept. 1 (1984) 276–295.

[95] W.F. Thompson, L.L. Cuddy, Sensitivity to key change in chorale sequences: A comparison of single voices and four-voice harmony, Music Percept. 7 (1989) 151–168.

[96] B. Tillmann, J.J. Bharucha, E. Bigand, Implicit learning of tonality: a self-organizing approach, Psychol. Rev. 107 (2000) 885–913.

[97] B. Tillmann, E. Bigand, Global relatedness effect in normal and scrambled chord sequences, J. Exp. Psychol. Hum. Percept. Perform. 27 (2001) 1185–1196.

[98] B. Tillmann, E. Bigand, M. Pineau, Effects of global and local contexts on harmonic expectancy, Music Percept. 16 (1998) 99–117.

[99] G.C. von Zerssen, A. Mecklinger, B. Opitz, D.Y. von Cramon,

Conscious recollection and illusory recognition: an event-related fMRI study, Eur. J. Neurosci. 13 (2001) 2148–2156.

[100] A.D. Wagner, W. Koustaal, A. Maril, D.L. Schacter, R.L. Buckner, Task-specific repetition priming in left inferior prefrontal cortex, Cereb. Cortex 10 (2000) 1176–1184.

[101] A.D. Wagner, E.J. Paré-Blagoev, J. Clark, R.A. Poldrack, Recovering meaning: Left prefrontal cortex guides controlled semantic retrieval, Neuron 31 (2001) 329–338.

[102] W.C. West, A.M. Dale, D. Greve, G. Kuperberg, G. Waters, D. Caplan, Cortical activation during a semantic priming lexical decision task as revealed by event-related fMRI. Poster #360 at the Human Brain Mapping Meeting, NeuroImage (2000) 360.

[103] R.J. Zatorre, A.C. Evans, E. Meyer, Neural mechanisms underlying melodic perception and memory for pitch, J. Neurosci. 14 (1994) 1908–1919.