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Cortical deafness to dissonance

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Summary

Ordinary listeners, including infants, easily distinguish consonant from dissonant pitch combinations and consider the former more pleasant than the latter. The preference for consonance over dissonance was tested in a patient, I.R., who suffers from music perception and memory disorders as a result of bilateral lesions to the auditory cortex. In Experiment 1, I.R. was found to be unable to distinguish consonant from dissonant versions of musical excerpts taken from the classical repertoire by rating their pleasantness. I.R.'s indifference to dissonance was not due to a loss of all affective responses to music, however, since she rated the same excerpts as happy or sad, as normal controls do. In Experiment 2, I.R.'s lack of responsiveness to varying degrees of dissonance was replicated with chord sequences which had been used in a previous study using PET, in examining emotional responses to dissonance. A CT scan of I.R.'s brain was co-registered with the PET activation data from normal volunteers. Comparison of I.R.'s scan with the PET data revealed that the damaged areas overlapped with the regions identified to be involved in the perceptual analysis of the musical input, but not with the paralimbic regions involved in affective responses. Taken together, the findings suggest that dissonance may be computed bilaterally in the superior temporal gyri by specialized mechanisms prior to its emotional interpretation.

Keywords: perception of dissonance; auditory disorder; auditory cortex; musical emotions; amusia

Abbreviation: rCBF = regional cerebral blood flow

Introduction

Perception of dissonance is a striking and distinct experience in music listening. To experience it, it suffices to play together two adjacent keys on a keyboard—forming a minor second in musical terminology—or to imagine the initial tuning of an orchestra. Both sound complexes are dissonant, and usually judged unpleasant by ordinary listeners. In contrast, striking together two keys that lie 12 keys apart, i.e. an octave apart, or hearing the first chord of Beethoven's fifth symphony produce sound experiences that are usually judged pleasing or consonant. Despite the saliency of dissonance, its functional and neural origins are still a matter of controversy. The goal of the present study is to provide new evidence for these origins, by exploring the processing specificity of dissonance and by trying to identify the essential neural elements associated with this experience.

The present investigation grew out of the observation of a remarkable indifference to dissonance in a brain-damaged patient who otherwise showed largely preserved emotional responses to music (Peretz *et al.*, 1998). The patient who exhibits this curious pattern is a middle-aged woman, I.R., without formal musical education, who suffers from irreversible deficits in music perception and expression as a consequence of bilateral damage to the auditory cortex (Peretz *et al.*, 1997; Peretz and Gagnon, 1999). In a previous study (Peretz *et al.*, 1998), I.R. was found to be able to use the mode (major or minor) in which a musical excerpt is played in order to judge if its emotional tone is happy or sad, as normals do. It is important to note that distinguishing the major and minor modes requires fine discrimination of musical pitch intervals. A distinctive feature of the two modes lies in the respective use of major and minor thirds that stand in semitone distance from one another. Yet, in a separate experiment, I.R.'s performance was at chance when required to detect an obvious dissonant change, created by a local semitone pitch shift of the upper voice, in an otherwise consonant musical excerpt (Peretz *et al.*, 1998). Therefore, I.R. exhibits a non-trivial dissociation on the musical pitch dimension. The main purpose of the present study was to document better the selectivity of I.R.'s deficit in processing dissonance.

Examination of I.R.'s responsiveness to dissonance was deemed worthwhile for several reasons. First, we wished to examine her responses to dissonance using emotional judgements, since this type of processing appears largely spared (Peretz *et al.*, 1998; Peretz and Gagnon, 1999). The common label attached to consonance and dissonance by naive listeners is pleasant and unpleasant, respectively. These judgements have been shown to index dissonance reliably in ordinary listeners (Plomp and Levelt, 1965). Secondly, we wished to compare I.R.'s behavioural responses and the location of her brain lesions with a recent PET study, examining emotional responses to consonant and dissonant chord sequences (Blood *et al.*, 1999). In this study, normal subjects rated the pleasantness of chord sequences that varied in the degree of dissonance.

By combining the evidence obtained from the lesion method with the outcome of cerebral imagery, it was hoped to gain insight into the way in which dissonance is processed in the auditory cortex. There is suggestive evidence that dissonance might be a by-product of a peripheral sensory organ that is pre-wired for consonance. Many psychoacousticians (e.g. Plomp and Levelt, 1965) adhere to this view in following von Helmholtz's proposal that dissonance results largely from the distortion created by the poor resolution power of the ear (Helmholtz, 1954). By this view, tones (or tone components) that are too close in pitch (e.g. the minor second) will create roughness tones when sounding together because the human sensory system does not have enough spatial resolution at the level of the basilar membrane to separate the tones. Although this mechanical built-in account of dissonance is appealing, it cannot be the whole story. It fails to explain why successive pure tones, that are processed one at a time and thus can be normally resolved by the basilar membrane, are judged following the same criteria of pleasantness as are simultaneous sounds (e.g. Schellenberg and Trehub, 1996*a*). One possibility is that the principles underlying dissonance perception at the level of the sensory organ are generalized to all pitch intervals at later, more centrally located, neural stages.

Indeed, there are ample opportunities for consonance calibration at all levels along the auditory pathways. Consonance is ubiquitous in the auditory environment. Most natural sounds, and speech in particular, are composed of consonant intervals. Thus, central neural networks may be attuned preferentially to consonant intervals by a process of generalization because of their prevalence or biological significance in the environment, and not simply because of hard-wired constraints of the peripheral hearing system.

Such a fine attunement of the neural system for consonance is echoed by the precocious role played by consonance in shaping perceptual as well as emotional responses to music. Infants exhibit heightened discrimination abilities for consonant over dissonant intervals even when intervals are matched in size (e.g. Schellenberg and Trainor, 1996; Schellenberg and Trehub, 1996*a*, *b*; for related but indirect evidence in birds see also Hulse *et al.*, 1995). Infants even exhibit a preference for consonant over dissonant music (Zentner and Kagan, 1996, 1998; replicated by Trainor and Heinmiller, 1999). Using a procedure similar to the one used in the present investigation, Zentner and Kagan presented 4-month-old infants with consonant and dissonant versions of the same musical excerpt. Infants were found to look longer to the side of the consonant than the dissonant version (Zentner and Kagan, 1996, 1998). Although this preference bias for consonance may result from a mere exposure effect, it is remarkable that such learning occurs so quickly.

Taken together, dissonance appears to be a basic attribute of pitch complexes that is shared by all auditory systems, from birds to mammals, and that may, in part, be determined by the mechanisms of the peripheral sensory system. This early constraint in the neural transmission of pitch information is likely to have later repercussions, at the perceptual level in the auditory cortex. We hypothesize that the cortical relay of pitch information would not only maintain its sensory input pattern, but would also elaborate it further by a process of calibration due to prior exposure to natural, consonant sounds. Accordingly, it is likely that the auditory cortex is equipped with neural networks that compute consonance or dissonance in musical sounds. What is unclear presently is to what extent a cortical relay is necessary. It is still plausible that such a relay is by-passed during emotional evaluation, i.e. dissonance might be detected and responded to subcortically, in the limbic system, without cortical contribution. The present study with a patient with lesions confined to cortical structures should shed light on this issue.

The patient I.R. was tested here in two experimental settings. In the first experimental situation, the same musical selections which I.R. previously had been able to rate as happy or sad (Peretz *et al.*, 1998) were exploited to assess the influence of dissonance on pleasantness judgements. In half the trials, a pitch shift of one semitone was applied to the leading voice of the musical excerpts so as to create dissonance, following the procedure used with infants by Zentner and Kagan (Zentner and Kagan, 1996, 1998). In contrast to infants, I.R. was expected to show little sensitivity to the presence of dissonance in her pleasantness judgements. In order to show that this impairment was specific to dissonance, I.R. was also required to perform happy–sad judgements on the same musical excerpts. These happy–sad judgements were expected to be performed as easily as in the past (Peretz *et al.*, 1998; Peretz and Gagnon, 1999) and hence served here as a control task.

In the second experiment, I.R. was tested with the same chord sequences, varying in degrees of dissonance, that elicited variations in regional cerebral blood flow (rCBF) in the brains of normal subjects (Blood *et al.*, 1999). In addition, by overlapping the CT scan of I.R.'s brain with the normal PET data, we hoped to determine whether I.R.'s lesions coincided with those regions found to be active in the perceptual analysis of the stimuli or rather in the affective analysis of the musical input.

Case description

The patient, I.R., is an amusic person who has been studied extensively over the last 6 years (Patel *et al.*, 1998; Peretz

Table 1 *I.R.'s performance in the detection of pitch-related changes applied to a single measure of a multiple-measure excerpt, and in the recognition of the emotional tone conveyed by spoken sentences and by music*

	I.R.	Normal controls
Change detection task (proportion of hits–false alarms)*		
Pitch shift	20.0	62.2
Mode change	40.0	39.8
Emotion recognition (percentage correct)		
Spoken sentences		
Happy	90%	97%
Sad	100%	95%
Fear	90%	84.5%
Anger	90%	96%
Surprise	100%	85.5%
Disgust	100%	92%
Music*		
Happy	94% (rating: 9.1)	100% (rating: 8.7)
Sad	100% (rating: 2.2)	90% (rating: 3.6)

I.R.'s scores are compared with the averaged performance of matched controls. *From Peretz *et al.* (1998).

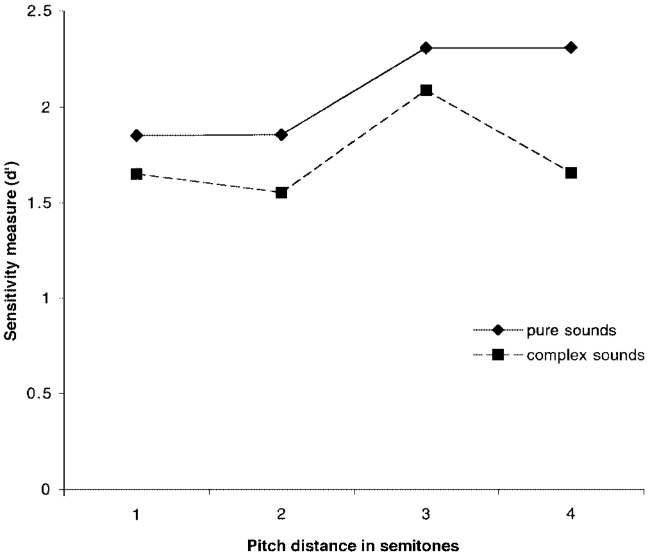


Fig. 1 I.R.'s sensitivity, expressed in d′ measure, to the pitch distance between two successive tones, each lasting 0.5 s. Each data point represents 48 trials, with half containing the same tones and half different ones. Chance level corresponds to a d′ value of zero.

et al., 1997, 1998; Peretz and Gagnon, 1999; Griffiths *et al.*, 2000). The case is remarkable in that 15 years after the brain damage she still experiences severe difficulties with music, while her language abilities and her general intellectual and memory abilities are normal. I.R.'s musical deficit has been characterized over the years, and only the aspects of her condition most relevant to the present study will be summarized here (Table 1).

I.R. is a 40-year-old, right-handed woman who has 10 years of education. She is musically untrained, although she was musically inclined and grew up in a musical environment. On the pitch dimension with which we are concerned in the present study, I.R. has difficulties. These impairments are not simple to describe, as suggested earlier. I.R. previously failed to detect local pitch shifts that created dissonance in the musical selections used here in Experiment 1, whereas she could detect changes in mode as normals do (Peretz *et al.*, 1998; see Table 1 for a summary of the results). This pattern cannot be explained by a simple defect in pitch discrimination since I.R. is able to distinguish as 'same' or 'different' isolated tones across varying pitch distances and complexity (Fig. 1). It is the musical quality of these pitch differences that seems to matter.

I.R.'s global emotional responses appear normal, although her usual mood is somewhat upbeat. On formal testing, I.R. has no difficulty selecting the appropriate written label describing the emotional tone conveyed by both the content and the intonation of 120 spoken sentences. Above all, as mentioned earlier and as summarized in Table 1, I.R. is able to recognize the happy or sad character of music. Performance is expressed both in percentage of correct classification, to allow comparison with emotional evaluation of the other materials, and in mean ratings on a 10-point scale (with 1 meaning very sad, and 10 very happy), to allow comparison with the measures collected in Experiment 1.

All normal scores presented in Table 1 and in Experiment 1 were provided by four neurologically intact women whose ages and socio-economic backgrounds closely matched those of I.R. (age mean = 41.2 years; education mean = 12.7 years; all were right-handed and non-musicians). These matched controls have been tested almost as regularly as I.R. over the last 6 years. All subjects' informed consent was obtained to participate in this project, which was approved by the ethical committee of the Institut universitaire de gériatrie de Montréal.

The extent and localization of I.R.'s lesions have been re-assessed recently and are illustrated in Fig. 2. All or most of the superior temporal gyrus in the left hemisphere is infracted. Heschl's gyrus and the anterior portion of the planum temporale have been completely destroyed (for identification of damage to the auditory regions of the temporal lobe with special attention to Heschl's gyri see Griffiths *et al.*, 2000). The temporal lobe lesion extends inferiorly into the middle temporal gyrus, superiorly into the parietal operculum (supramarginal gyrus) and anteriorly into the pre- and post-central gyri, and also destroys the posterior half of the insula. There appears to be no damage to the inferior temporal gyrus or to medial temporal lobe structures, such as the parahippocampal gyrus, the hippocampus or the amygdala.

In the right hemisphere, the temporal lobe damage appears to be confined to the most anterior and superior portion of the superior temporal gyrus near the pole. Heschl's gyrus is entirely spared, as is the planum temporale behind it. In this hemisphere, the anterior portion of the insula is infracted,

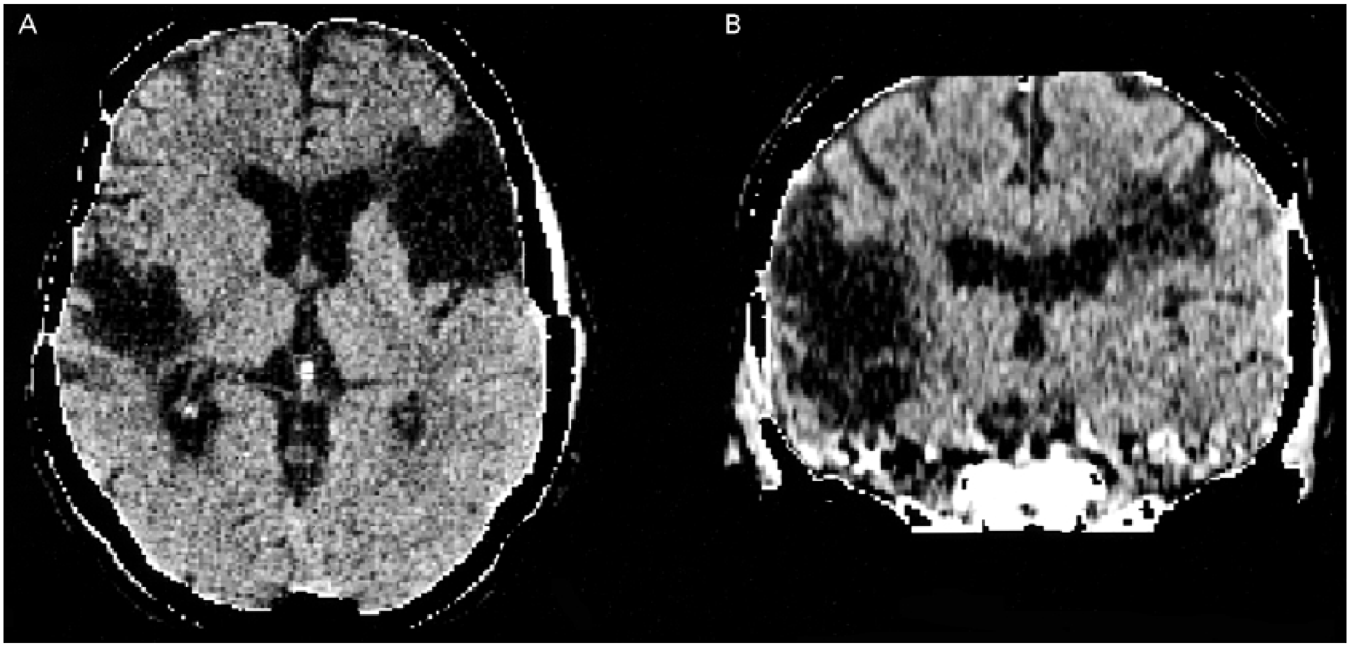


Fig. 2 CT scan (1.5 mm slices) of I.R.'s brain, transformed into the standardized stereotaxic space of Talairach and Tournoux (Talairach and Tournoux, 1988; following the procedure of Collins *et al.*, 1994). The right side of the image corresponds to the right side of the brain. The horizontal slice (z = 7) in **A** and coronal slice (y = –15) in **B** show the differing locations of temporal and frontal lobe damage in the left and right hemispheres. See text for details.

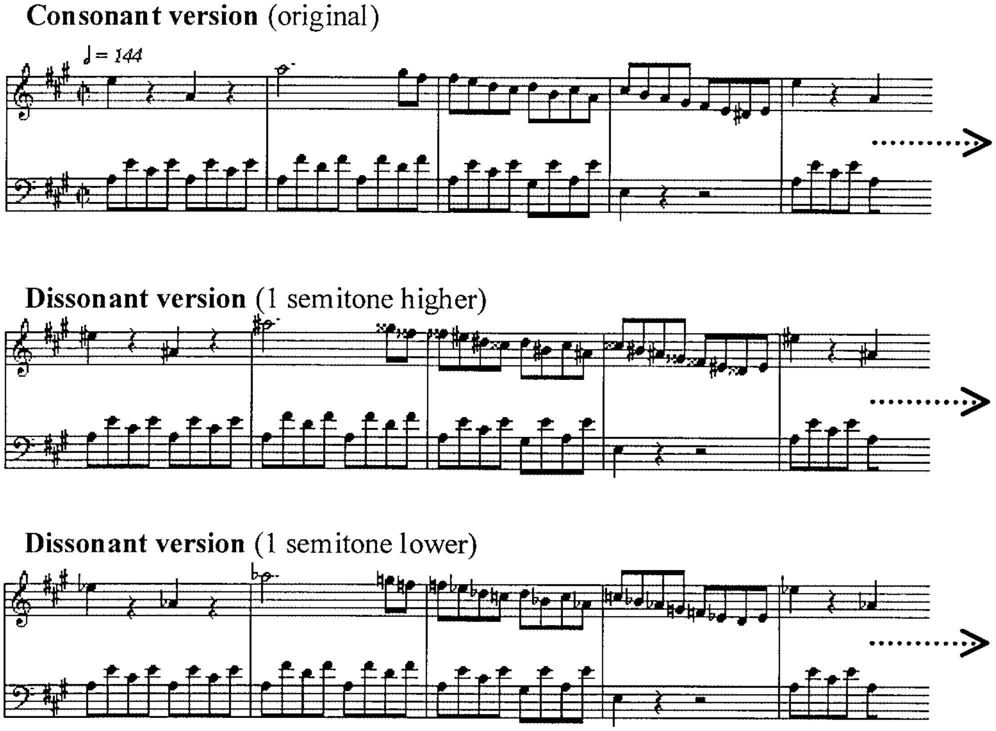


Fig. 3 First bars of the excerpt taken from Concerto no. 23 from Mozart in its original consonant version and in its two altered dissonant versions used in Experiment 1. The stimuli can be heard at http://www.fas.umontreal.ca/psy/iperetz.html

and the lesion encroaches medially into a small portion of the putamen. There is also a large frontal lobe lesion, including most of the precentral and inferior frontal gyri, as well as the white matter underlying them. Damage also encroaches on small regions of the lateral orbitofrontal and middle frontal gyri.

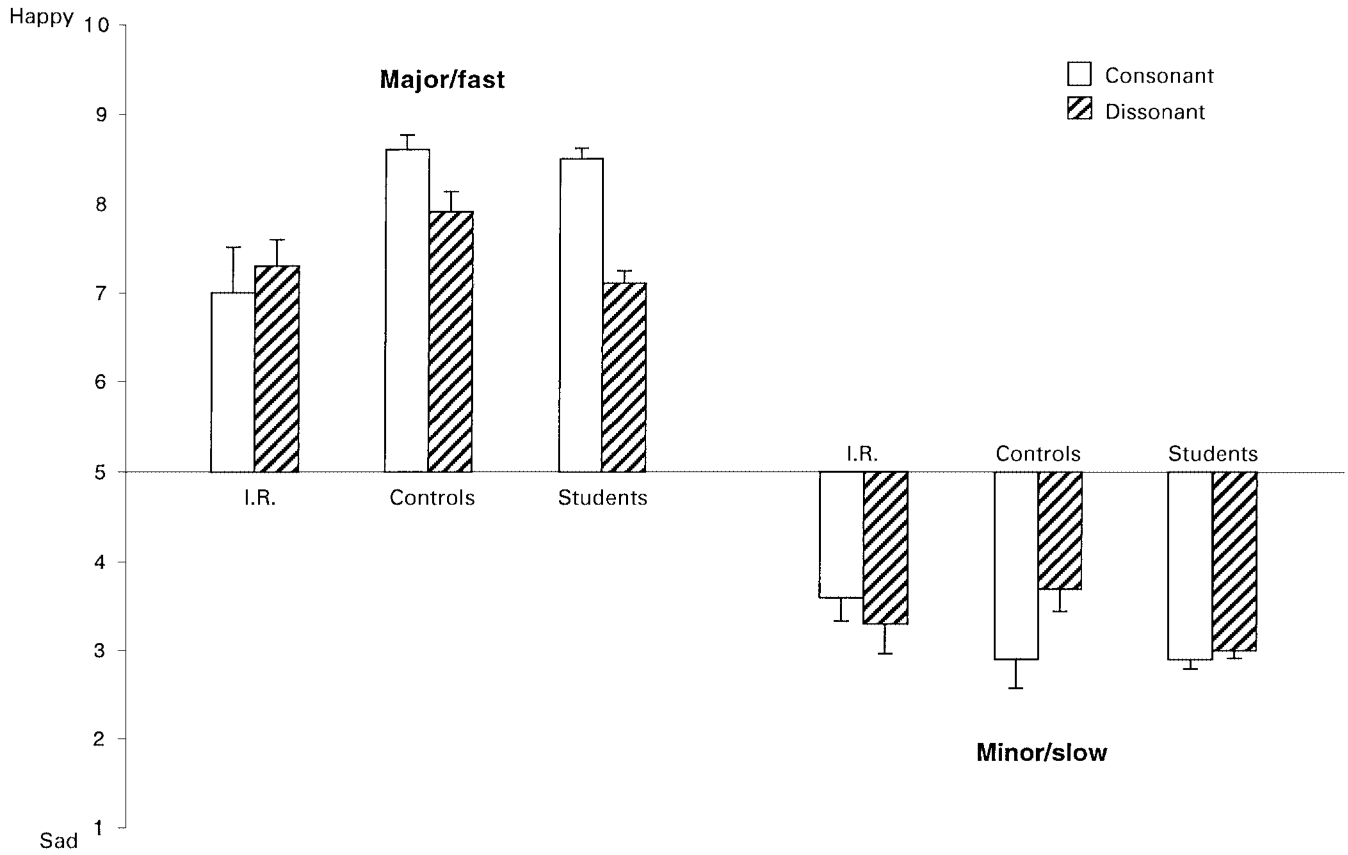


Fig. 4 Average ratings obtained by I.R., her matched controls and students in the 'happy– sad' task of Experiment 1, as a function of the structure of the piece (major/fast versus minor/slow) and of the version presented (consonant versus dissonant).

Experiment 1: behavioural responses

Method

Participants

I.R. and two control subjects were tested. The control subjects also participated in the previous study (Peretz *et al.*, 1998) in which the same material was used, and closely matched I.R. in age, gender and occupation. Thus, the two matched controls and I.R. were equally familiar with the material and the testing situation. Twenty university students, having little or no musical education, were also tested in order to assess the effects of secondary variables, such as order of task presentation, on judgements.

Material and apparatus

Twenty-four excerpts were taken from the set used in our previous study (Peretz *et al.*, 1998). These excerpts were all instrumental in that they were not originally sung with lyrics; they were drawn from the corpus of Western classical music, from baroque (e.g. Bach and Albinoni), classical (e.g. Mozart), romantic (e.g. Verdi) and early 20th century (e.g. Ravel) periods. Twenty-four were selected so that half evoked a sense of happiness (they were all played in the major mode with a median tempo of 138) and the other half a sense of sadness (they were played in the minor mode at a median tempo of 53). These excerpts lasted from 6 to 32 s (mean 15 s) and corresponded to the consonant versions.

The dissonant versions were created by shifting the pitch of all tones of the leading voice by one semitone either upward or downward (see Fig. 3). This had the effect of creating many dissonant intervals, including minor seconds, major sevenths and minor ninths. Note that the pitch shift applied to the leading voice did not alter the mode of the leading voice or the mode of the accompaniment, when considered separately. The mode remained the same in the consonant and the dissonant versions. However, when both parts are considered together, then the pitch shift did create ambiguity in the overall mode of the excerpts by sometimes changing major thirds into minor thirds, and vice versa. This ambiguity was, however, equivalent in the major and minor excerpts.

Four equivalent sets of stimuli were constructed with these excerpts. Each set comprised 48 excerpts, half happy and half sad. In each category, half the excerpts were presented in their consonant version, half in their dissonant version. The consonant versions were presented twice in order to match the number of dissonant versions. However, stimulus repetition was avoided in a given set. In each set, the 48 excerpts were presented in a random order.

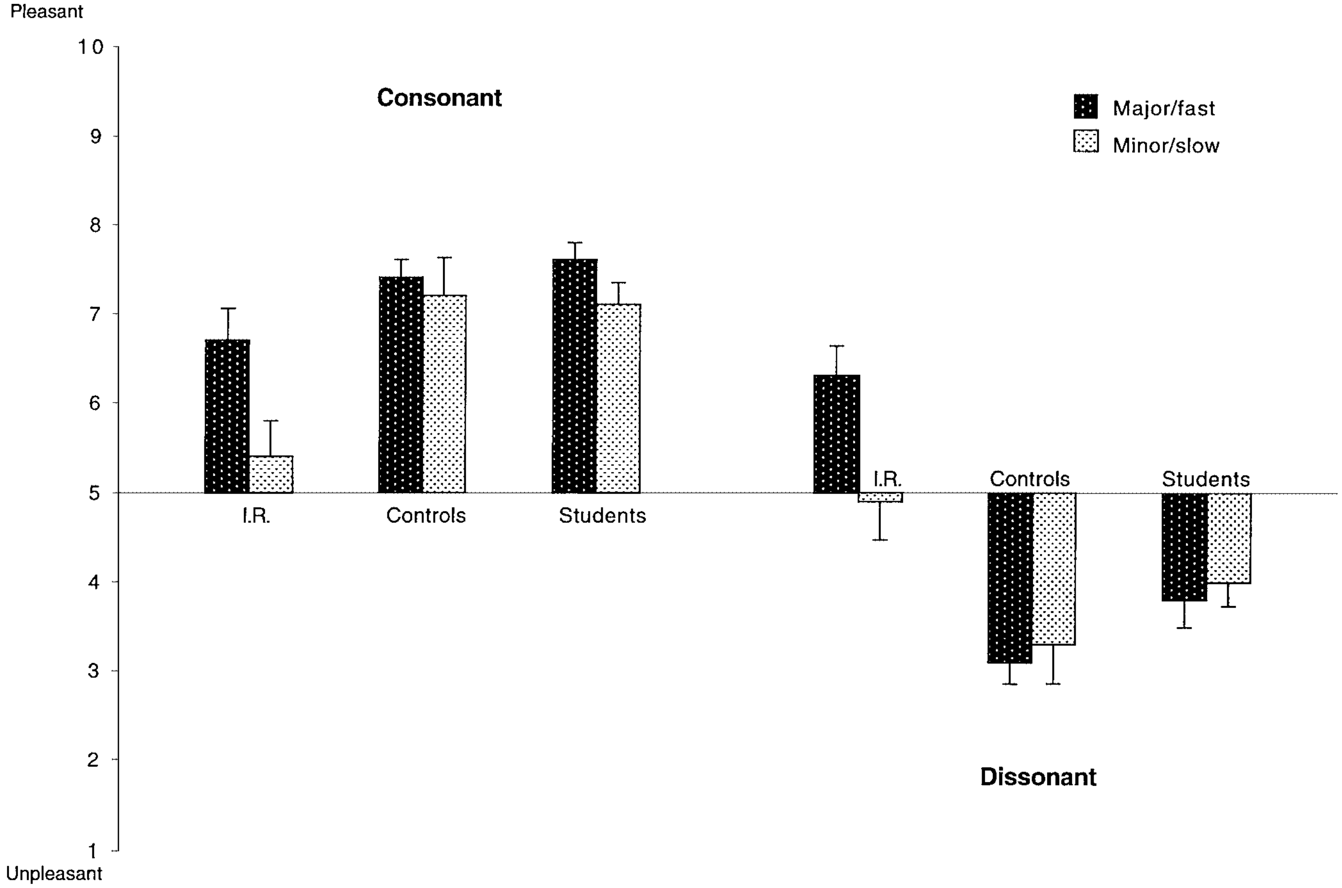


Fig. 5 Average ratings obtained by I.R., her matched controls and students in the 'pleasant–unpleasant' task of Experiment 1, as a function of the version presented (consonant versus dissonant) and the structure of the piece (major/fast versus minor/slow).

The musical excerpts were transcribed for piano and computer generated on a microcomputer running a MIDI sequencing program (Sequencer Plus Gold) feeding into a sample playback digital synthesizer (Roland Sound Canvas SC 50). All stimuli were recorded with a piano timbre onto digital tapes and presented via a Tascam DAT-30 digital recorder in free field at a loudness level that was comfortable for the listener.

Procedure

Each subject was tested individually in two sessions, each lasting ~1 h, following an ABBA design. In each session, they were required to perform two tasks, a happy–sad judgement task (e.g. A) or a pleasant–unpleasant judgement task (e.g. B). For each task requirement (A and B), subjects were presented with one of the four sets, hence with 48 musical selections to evaluate. They were required to evaluate the emotional tone that they felt corresponded to the presented selection and to respond on a 10-point rating scale. For the happy–sad judgement task, 1 meant 'triste'/sad and 10 meant 'gai'/happy. For the pleasant–unpleasant judgement task, 1 meant 'désagréable'/unpleasant and 10 meant 'agréable'/pleasant. No further information or feedback was given to the participant.

I.R. and her matched controls were tested in the AB and then BA orders, where A corresponds to the happy–sad judgements and B to the pleasant–unpleasant judgements. I.R. was tested in two sessions, 6 months apart. The 20 university students were also tested in two sessions, about 3 days apart. In this group, order of task and stimuli sets were fully counterbalanced across subjects.

Results and comments

The results are presented for the happy–sad judgements and for the pleasant–unpleasant judgements in Figs 4 and 5, respectively. The responses of I.R. and her matched controls were analysed by separate ANOVAs (analyses of variance) considering items (F_2) as the random variable. Students' responses were analysed with ANOVAs considering subjects (F_1) as the random factor. All ANOVAs were performed on ratings by taking three factors into consideration: task (happy–sad versus pleasant–unpleasant judgement), dissonance (consonant versus dissonant) and structure (major/fast and minor/slow). In the analysis per

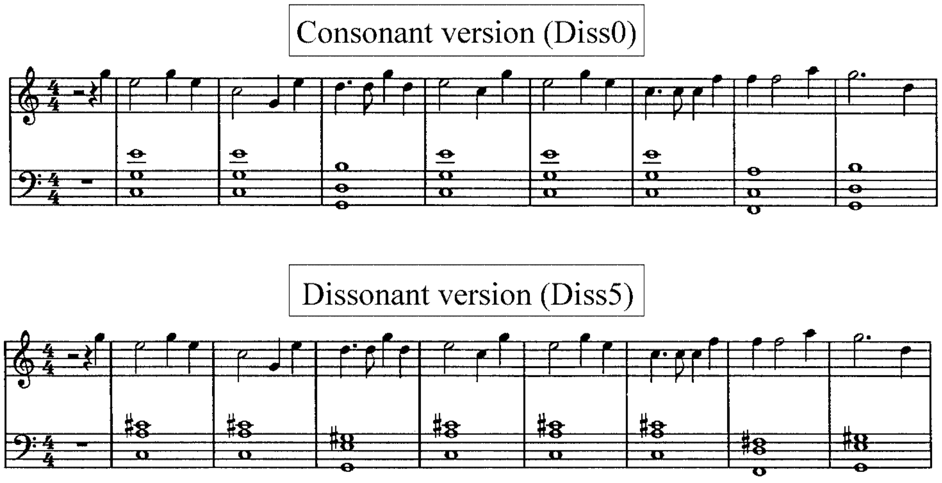


Fig. 6 First bars of the most consonant version (Diss0) and the most dissonant version (Diss5) of the musical passage used in Experiment 2.

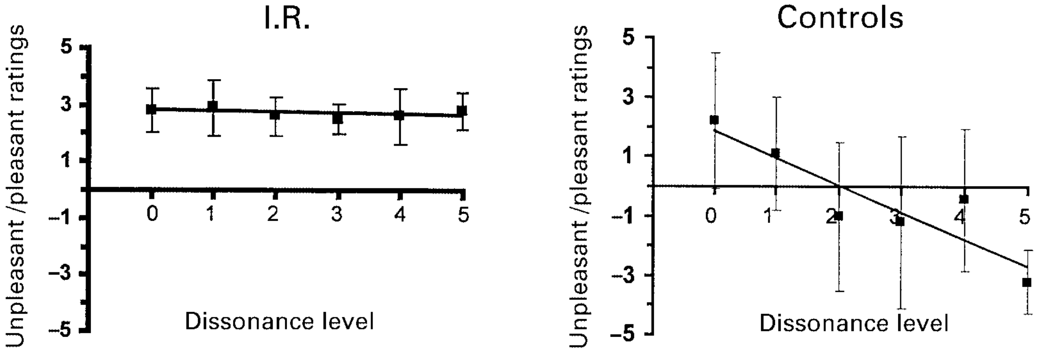


Fig. 7 Average ratings obtained by I.R. (left panel) and non-musician students (right panel) for the six versions differing in degrees of dissonance (from Diss0 to Diss5) used in Experiment 2. Error bars indicate standard error of the mean for each data point.

items, task and dissonance were considered as within-items variables, and structure as the between-items variable. In the analysis per subjects, all three factors were within-subjects variables.

Controls' judgements

Controls' judgements were found to be influenced differently by dissonance and structure. The different patterns were supported by several interactions in the overall ANOVAs. Therefore, the happy–sad task (presented in Fig. 4) was analysed separately from the pleasant–unpleasant task (presented in Fig. 5). In the happy–sad task, an interaction between dissonance and structure was present, with $F_2(1{,}22) = 17.31$, and $F_1\ (1{,}19) = 95.51$, both $P < 0.001$, for the matched controls and students, respectively. *Post hoc* comparisons revealed that both happy and sad judgements were significantly influenced by dissonance (Tukey, $P < 0.05$), i.e. consonant music was found to sound happier or sadder than dissonant music. In other words, the happy–sad tone of music was better perceived in consonant than in dissonant music. This might be related to the fact that mode is more ambiguous due to the pitch shift applied to the leading voice.

The pleasantness ratings reveal a similar pattern (see Fig. 5). Pleasantness judgements are, as expected, determined by dissonance, since a simple and highly robust effect of dissonance was obtained [$F_2(1{,}22) = 176.97$; $F_1(1{,}19) = 86.89$; both $P < 0.001$, for matched controls and students, respectively] which did not interact with structure for matched controls ($F_2 < 1$). For students, the interaction between structure and dissonance reached significance, with $F_1(1{,}19) = 13.60$; $P < 0.005$. However, this interaction was not robust since simple effects did not reach significance (i.e. although major/fast excerpts appear more pleasant than minor/slow ones when consonant, the difference was not significant by Bonferroni corrected *t*-tests). It is worth mentioning that, in general, the effect of structure on pleasantness judgements was weak (F_2 and $F_1 < 1$). This result stands in sharp contrast to I.R.'s data.

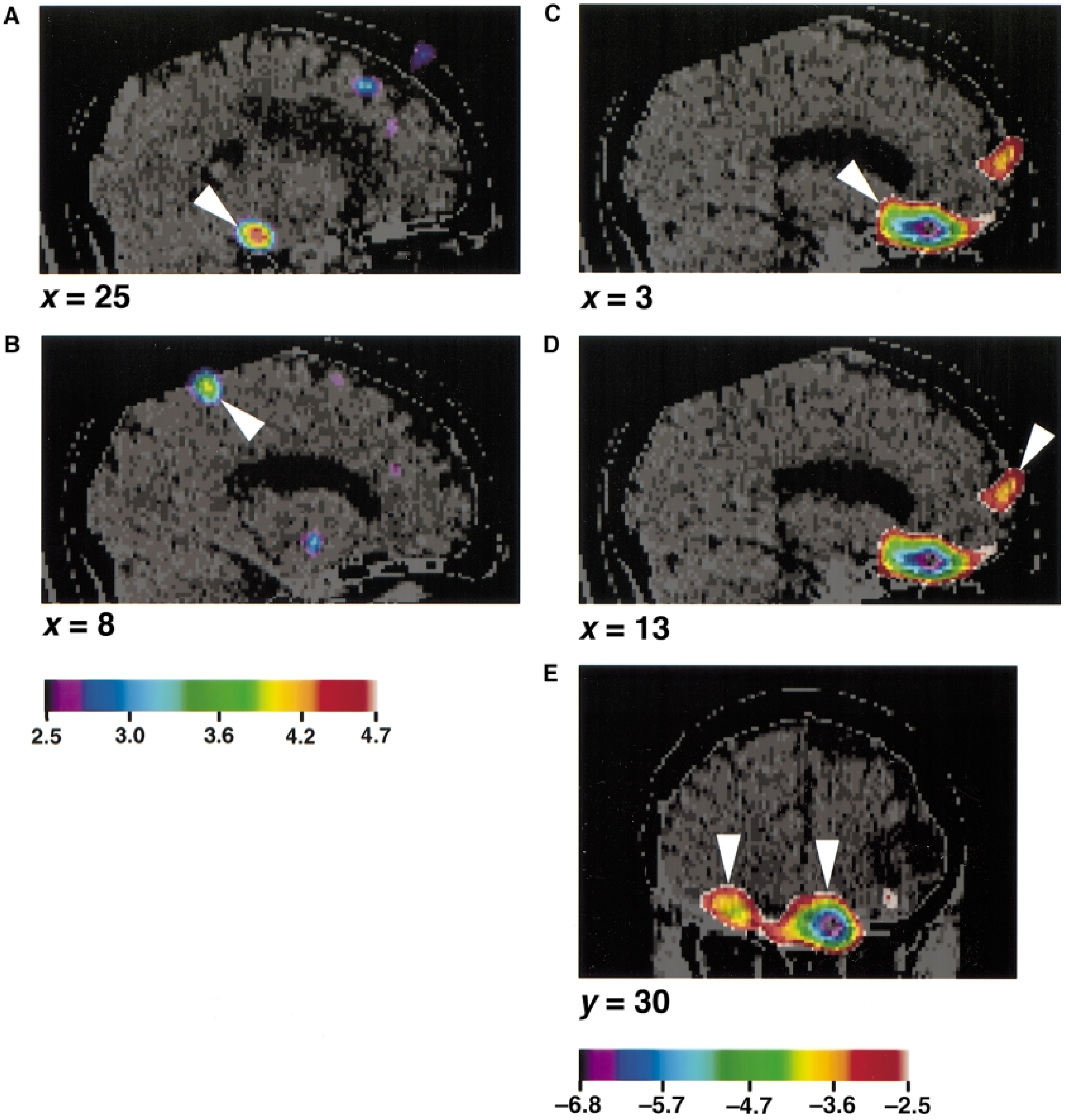
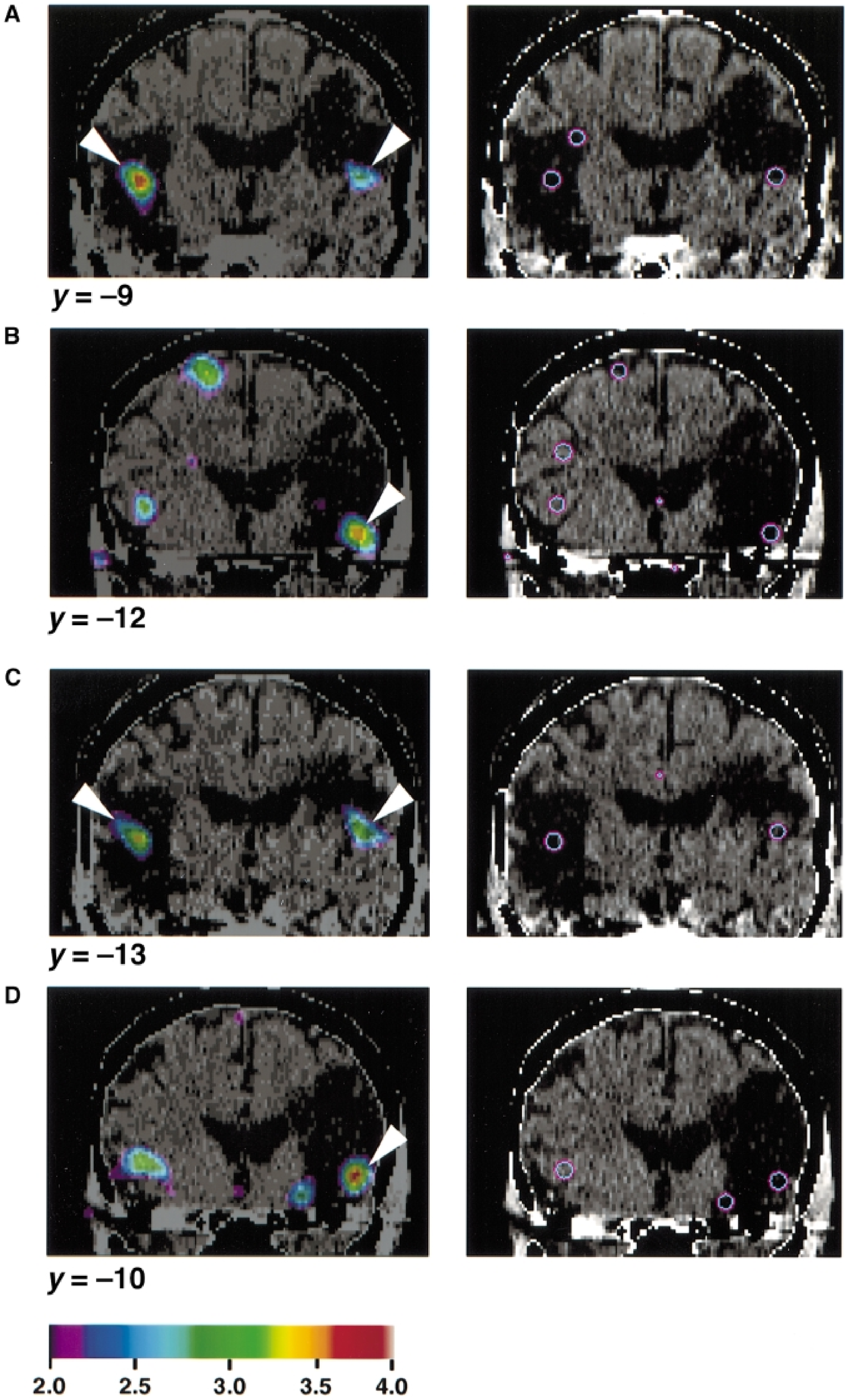


Fig. 8 PET data from a group of normal subjects superimposed on the CT scan of I.R.'s brain. The PET data indicate areas of significant CBF co-variation as a function of parametric change in the dissonance level of a melodic stimulus. PET data are shown as *t*-statistic images; the ranges for each set of images are coded by colour scales below each column. **A** and **B** show areas whose CBF increases as a function of increasing dissonance; arrowheads in the two sagittal sections show the parahippocampal area (**A**) and the precuneus (**B**). **C–E** show areas whose CBF decreases as a function of increasing dissonance; arrowheads in sagittal sections **C** and **D** show the subcallosal and frontal polar regions, respectively; arrowheads in coronal section **E** show the subcallosal area and the left orbitofrontal areas. Note that none of the paralimbic or neocortical regions recruited by the dissonance manipulation in normals overlapped with the lesions in I.R.'s brain, with the exception of a small region of orbitofrontal cortex (**E**).


A
y = –9
B
y = –12
C
y = –13
D
y = –10
2.0
2.5
3.0
3.5
4.0

I.R.'s judgements

I.R.'s judgements were not sensitive to dissonance, as can be seen in both Figs 4 and 5. Contrary to controls, her happy–sad judgements were not influenced by dissonance. There was no interaction between dissonance and structure ($F_2 < 1$). As expected, major/fast excerpts were clearly distinguished from minor/slow excerpts, with an effect of structure [$F_2(1,22) = 83.22$, $P < 0.001$]. I.R.'s pleasantness judgements were not sensitive to dissonance either, with $F_2(1,22) = 1.73$, NS. In general, she judged the consonant versions to be as pleasant as the dissonant versions [with 6.0 and 5.6 mean rating, respectively (when ratings were dichotomized into correct scores, by considering correct a rating below 6 for a dissonant stimulus and a rating above 5 for a consonant one, I.R. was only 57% correct while her matched controls achieved perfect scores)]. Curiously, her pleasantness judgements were influenced by the mode/tempo structure; I.R. found the major/fast excerpts slightly more pleasant than the minor/slow excerpts, with mean ratings of 6.5 and 5.1, respectively [$F_2(1,22) = 12.19$; $P < 0.005$]. This may reflect a refugee strategy since mode and tempo are the main cues available to her. Clearly, I.R. does not show any evidence of responsiveness to dissonance.

Experiment 2: behavioural and neural correlates

In Experiment 1, I.R. failed to exhibit normal sensitivity to dissonance, while each matched control and each student did. Thus, I.R.'s brain lesions are probably interfering with normal evaluation of dissonance. The goal of this second experiment was to compare the regions known to be damaged in I.R. and the results of a PET study of dissonance in normal subjects. In the PET study (Blood *et al*., 1999), rCBF changes were examined in neurologically intact non-musicians and related to the degree of dissonance of a novel musical passage and subjects' pleasantness ratings. rCBF changes were observed in several distinct paralimbic and neocortical regions of the brain. Activity in right parahippocampal gyrus and precuneus regions was associated with increasing dissonance, whereas activity in bilateral orbitofrontal, medial subcallosal cingulate and right frontal polar cortex correlated with decreasing dissonance (or increasing consonance). In contrast, activity in superior temporal cortices was observed bilaterally, independently of dissonance level. In order to facilitate comparisons across studies, I.R. was tested here with the same stimuli as those used by Blood and colleagues with normal subjects in the PET study (Blood *et al*., 1999). Then, PET data from the previous study were mapped onto the CT scan of I.R.'s brain to determine if her lesions overlapped with any of the regions associated with responses to dissonance in normals.

Method

I.R. was presented with each of the six versions of the musical passage used by Blood and colleagues (Blood *et al*., 1999). The same melody was presented in all six versions, while the harmonic structure of the accompanying chords was varied systematically between versions so as to increase the degree of dissonance. The three-note chord accompaniment consisted of major triads, dominant 7ths, 9ths, 11ths, 13ths or flattened 13ths, corresponding to dissonance levels 0–5 (see Fig. 6 for an example). The pieces were novel in that they were composed for experimental purposes. They were created as MIDI files on a PC platform with Cubase 3.5 by Steinberg software and were burned on a CD using the Kurzweil MASS synth engine with a piano timbre. A complete passage lasted 73 s.

I.R. was tested 10 times with each of the six versions; stimuli were presented in pseudo-random order. I.R. rated the emotional valence of each version on a bipolar scale of –5 to +5 for nine adjectives, including pleasant versus unpleasant, tense versus relaxed, irritated versus not at all irritated, annoyed versus not at all annoyed, dissonant versus consonant, out-of-tune versus in-tune, angry versus calm, bored versus interested and happy versus sad. Since it was soon apparent that she could not discriminate either the stimuli or their emotional valence, I.R. was presented with only one pair of adjectives such that –5 corresponded to 'très désagréable'/very unpleasant and +5 corresponded to 'très agréable'/very pleasant. Testing was interrupted several times because I.R. repeatedly reported that she could not hear any difference between versions. The experimenter encouraged her to continue by saying that there were subtle differences that she might pick up in her ratings.

Results and comments

I.R.'s pleasantness ratings did not vary with dissonance level, while the ratings of normal controls in the PET study clearly did (see Fig. 7). I.R.'s average responses did not reflect the use of a single neutral rating; I.R. tried to vary her ratings

Fig. 9 PET data from a group of normal subjects superimposed on the CT scan of I.R.'s brain. The left column illustrates PET images superimposed on a CT scan of I.R.'s brain, while the right column illustrates the corresponding peak of each active region (indicated with white circles) on the CT scan to view better the location relative to I.R.'s lesions. The PET data indicate areas of significant CBF increase in a subtraction analysis; **A** and **B** show the subtraction of a highly dissonant stimulus condition (Diss5) with a matched noise baseline condition, while **C** and **D** show the subtraction of the consonant stimulus condition with the matched noise. Each of the coronal sections shows areas of activity within the superior temporal gyri bilaterally (indicated by arrowheads). Note that these regions overlapped significantly with the lesions in I.R.'s brain. The *t*-statistic ranges are coded by the colour scale in the bottom left corner.

from trial to trial, as indicated by standard errors. However, these small variations were not significantly correlated with degree of dissonance ($r = 0.06$), in contrast to those of normal controls ($r = 0.56$; $P < 0.001$). Thus, I.R.'s lack of sensitivity to dissonance observed in Experiment 1 was replicated here with material that was novel to her.

When the regions of PET activation from the study of Blood and colleagues (Blood *et al.*, 1999) were mapped onto the CT scan of I.R.'s brain, the lesions did not overlap with regions found to vary as a function of dissonance level (see Fig. 8), except for a small region of the right orbitofrontal cortex. In contrast, the superior temporal gyri, which were activated in the most dissonant and most consonant versions of stimuli (i.e. in the dissonance levels 0 and 5 after subtraction of noise control conditions), clearly overlapped with I.R.'s lesions. This overlap is illustrated in Fig. 9. These results suggest that the superior temporal gyrus may be critically involved in I.R.'s deficit. Since, in the PET study, the superior temporal gurus appears involved in all judgements, independent of their emotional valence, its contribution is probably more related to the perception of dissonance than to its emotional evaluation. Thus, the results suggest that an intact neocortical processing of dissonance is necessary for adequate emotional evaluation.

General discussion and conclusions

In two distinct experimental settings, converging evidence for a loss of responsiveness to musical dissonance was gathered in an amusic subject, I.R. Although each control participant found the consonant excerpts more pleasant than the dissonant excerpts, I.R. did not manifest such a preference. I.R.'s indifference to dissonance cannot be ascribed to an attentional failure or to an absence of all affective responses to music. I.R. was able to distinguish the happy–sad character of the consonant and dissonant excerpts, as control participants did (Experiment 1). Thus, I.R.'s lack of responsiveness appears to be a selective disorder resulting from her damaged brain. The neural correlates of this new form of auditory impairment point to the auditory cortex on both sides of the brain as the critical regions. Taken together, the findings suggest that (i) dissonance is computed at the cortical level by specialized neural networks; and (ii) emotional evaluation requires initial cortical analysis of the input. These two major implications will be discussed in turn.

The selectivity of I.R.'s deficit must be considered in the context of her general condition with regard to music processing. As traditionally construed, I.R. is one of the most severe cases of amusia that has been reported in the literature because she is severely impaired in discrimination tasks (requiring 'same–different' discrimination for musical sequences), in recognition tasks for both novel and familiar music, and in singing (Peretz *et al.*, 1997; Peretz and Gagnon, 1999). However, this massive loss of musical abilities has apparently spared some emotional evaluation of music. As mentioned in the Introduction, I.R. is able to distinguish happy from sad music normally (Peretz *et al.*, 1998; Peretz and Gagnon, 1999). This result was replicated here in Experiment 1. It was shown further that I.R. is able to use mode information in the excerpts to derive their emotional tone (Peretz *et al.*, 1998). Mode, like dissonance, is a pitch-based characteristic of music. Yet, I.R.'s judgements show normal sensitivity to a change of mode, from major to minor, and vice versa. This has been demonstrated in emotional judgements, when assessing the happy–sad character of the music (Experiment 2 in Peretz *et al.*, 1998), and in structural judgements, when requested to detect a change in the pianist's way of playing (Experiment 6 in Peretz *et al.*, 1998; see also Table 1). In this context, it is surprising that we observe a lack of sensitivity to the presence of dissonance.

I.R.'s failure to interpret dissonance as normals do is remarkable for a number of reasons. First, I.R. fails in tasks that infants succeed in performing at 4 months of age (e.g. Zentner and Kagan, 1996) whereas she succeeds in tasks that are mastered much later by children (Gerardi and Gerken, 1995; Dalla Bella *et al.*, 2001). As mentioned in the Introduction, 4-month-olds prefer listening to consonant rather than dissonant versions of Mozart minuets, thus showing a precocious preference for consonance. These biases are still present in adults, as observed here in each control participant. In contrast, the association of the major mode with happiness and the minor mode with sadness is an ability that seems to emerge much later than preference for consonance. Dalla Bella and colleagues, for instance, have presented the same musical material as used here to 3- to 8-year-old children (Dalla Bella *et al.*, 2001). The material was manipulated in order to assess the respective role of mode and tempo to the judgements, following the procedure of Peretz and colleagues (Peretz *et al.*, 1998, Experiment 2). The results showed that at 5 years of age, children are able to employ tempo but not mode for judging the happy–sad tone of the musical excerpts. Children display the adult-like ability to use mode, as well as tempo, for interpreting the 'happy–sad' tone of music slightly later, after the age of 6 years. In this context, it is striking that I.R. fails to use dissonance, while her ability to use mode is preserved because it violates normal acquisition order.

Secondly, indifference to dissonance in the presence of sensitivity to the major–minor mode differentiation is counterintuitive because dissonance is generally conceived of as more primitive or primary relative to mode. The major–minor mode differentiation is often viewed as a by-product of the consonance principle. By most accounts, the major mode is associated with happiness, or with a positive valence, because it is more consonant or 'natural'. Such an acoustic account goes back to Rameau and von Helmholtz (for a review, see Crowder, 1984). For example, von Helmholtz (1954, pp. 214–17) asserted that the negative connotation for minor harmonies is only a special case of the 'inherent distress' that listeners experience for dissonance. However, I.R.'s results suggest that consonance and major mode (or dissonance and minor mode) are separable phenomena of pitch perception.

Taken together, I.R.'s lack of responsiveness to dissonance can hardly be explained by a general effect of brain vulnerability account since perception of consonance appears to have pre-eminence over mode in ontogenetic development and is predominant in the environment. These two factors should have produced the reverse condition, i.e. preserved sensitivity to dissonance and impaired processing of mode, because the first would exhibit more stable and resistant neural representation than the latter. The fact that the opposite pattern was observed in I.R. provides compelling evidence for the existence of specific neural circuits that are devoted to dissonance computation and that can be disrupted selectively by brain damage.

The damaged neural networks critical to dissonance computation are in all likelihood located bilaterally in the superior temporal gyri. This conclusion derives from the comparison between I.R.'s lesion localization with normal cerebral regions activated by dissonance as measured by PET (Blood *et al.,* 1999). I.R.'s lesions are extensive and asymmetrically localized in her cerebral hemispheres. Therefore, it is not clear which of these damaged areas can be taken as being responsible for the observed deficit in responding to dissonance. Recently, Blood and colleagues identified a number of cerebral regions that are particularly active when normal listeners judge the affective value of musical versions differing in degree of dissonance (Blood *et al*., 1999). In that study, as in most functional brain imaging studies, a large number of subcortical and cortical areas were implicated. Hence, combining I.R.'s lesion localization with localized brain activity in different activation conditions provides a unique opportunity to identify which regions might be essential for responding to dissonance.

In Blood's PET study, a complex network involving paralimbic and neocortical regions was associated with perceived (un)pleasantness as a function of (diss)consonance. This complex network did not overlap significantly with I.R.'s lesions. In contrast, significant overlap was found between I.R.'s lesions and the pattern of activity elicited by all musical stimuli, irrespective of dissonance level (see Fig. 9). This overall activity involves the superior temporal gyri bilaterally (Brodmann areas 22 on the right and 41/22 on the left) and is obtained in both the most dissonant and the most consonant conditions after the activity related to the matched noise control condition was subtracted. The fact that these regions were activated similarly in the two extreme conditions (most dissonant and most consonant) suggests that similar computations are performed in these auditory cortical areas. Such computation probably represents perceptual processes, including those related to dissonance. Since these specific secondary auditory areas are damaged in I.R., we can infer both that these particular cortical regions are crucial for responsiveness to dissonance and that I.R.'s problem with dissonance lies at the perceptual level.

Ascribing I.R.'s indifference to dissonance to a perceptual defect is consistent with a number of independent observations. First, I.R.'s emotional processes in general appear fairly normal (see Table 1). Secondly, the neural network specifically associated with emotional evaluation of dissonance, which involves subcortical–frontal areas, seems largely spared in I.R.'s brain. Thirdly, I.R. was unable to discriminate the different versions of the same musical sequence that were used in Experiment 2 and that only differed in degrees of dissonance. Therefore, a plausible account of I.R.'s lack of responsiveness to dissonance is simply that she does not perceive it. Had she perceived it correctly, she should have judged its emotional valence accordingly. If this interpretation is correct, affective responses to dissonance are mediated via a cortical perceptual relay.

In summary, the present findings point to a particular functional architecture underlying emotional interpretation of dissonance. Taken together, the results suggest that the musical input first reaches the superior temporal gyri where perceptual organization takes place. The perceptual output is then relayed to emotional systems in the paralimbic structures or more frontal areas, depending on its valence. This two-stage model suggests that emotion and perception are not taking place along two parallel and independent pathways as some models (Zajonc, 1984; Ledoux, 2000) posit, at least in this type of affective process.

In conclusion, the findings suggest that dissonance may be computed bilaterally in the superior temporal gyri by specialized mechanisms prior to its emotional interpretation. Finding brain specialization for dissonance computation is consistent with the nativist view, by which the brain would be pre-wired for processing consonant pitch intervals. However, this brain specialization is suggestive but not conclusive. It will be necessary to demonstrate that all humans possess such specialized mechanisms for consonance and that these are located in fixed brain structures across cultures. Answers should not be long in coming, given the rapid development of brain imaging techniques.

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