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MUSICAL PRIMING BY THE RIGHT HEMISPHERE POST-CALLOSOTOMY

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Abstract—The hemispheric representation of auditory functions mediating the perception of harmony in music was investigated in two split-brain patients using a musical chord priming task. Previous experiments in normal subjects had demonstrated that the harmonic context established by a prime chord influences the accuracy of target chord intonation judgements. Only the right hemisphere of each callosotomy patient manifested the normal interaction between harmonic relatedness and intonation. The results raise the possibility that associative auditory functions which generate expectancies for harmonic progression in music are lateralized within the right hemisphere.

INTRODUCTION

ATTEMPTS TO lateralize musical functions to one or the other cerebral hemisphere by examining brain-damaged patients have yielded conflicting results (for reviews see [9, 19, 52, 66]). While the influences of many methodological and patient variables hamper a cohesive formulation of left–right differences, the literature indicates that a number of cognitive, perceptual, and motor subsystems contribute to musical experience, and that the sum of these is represented bilaterally in the brain. The left–right distribution of auditory functions mediating music perception may be organized in relation to psychoacoustic features of musical stimuli (e.g. spectral vs temporal), the experience, aptitude, or language lateralization of the listener, and/or broad dichotomies of perceptual organization (e.g. discriminative vs associative, analytic vs holistic). These issues bear upon the more general problem of hemispheric specialization for modality-specific functions lying outside the verbal domain.

Lesion studies in the cat [15, 65] and monkey [16, 30, 57] have demonstrated that certain aspects of spectral pattern perception rely on the integrity of auditory cortex. In man, studies of temporal lobectomy populations [39, 67], stroke populations [17, 54], and callosotomy patients [52, 53, 61, 62] suggest that fine-grained discriminative functions mediating the perception of complex tonal spectra—particularly spectra without cognitive referents in the verbal domain—are lateralized within the right auditory cortex.

The present split-brain experiments examine the degree to which cognitive representations of structural regularities in musical harmony are lateralized in the cerebral hemispheres. The perception of harmony in musical contexts relies on the capacity of the auditory system to analyze patterns in the pitch relationships among simultaneous components of individual

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spectra [31, 58, 59] and patterns in the harmonic relationships among successive spectra [1, 42, 46, 47]. Tonal spectra comprising musical chords, in particular the seven root triads of the major and minor diatonic scales, are the foundation of tonal harmony in Western music. Major and minor triads influence judgements about and generate expectancies for subsequent triads based on their harmonic relatedness ([6, 7, 34, 35]; for review see [33]). This empirical evidence for cognitive representations of chord relatedness supports the claims of formal music theory and likely reflects the transition probabilities that characterize harmonic progression in Western music [42]. It is hypothesized that these mental representations of harmonic structure are learned and internalized through extensive exposure to music in our cultural environment [3, 4].

In order to assess possible laterality effects in harmony perception, we examined two callosotomy patients using BHARUCHA and STOECKIG's musical chord priming task [7] (Fig. 1), modified to avail response choices to only one disconnected hemisphere on each trial (Fig. 2). In this task, a prime chord (e.g. C^{maj}) is followed by a target chord that is either

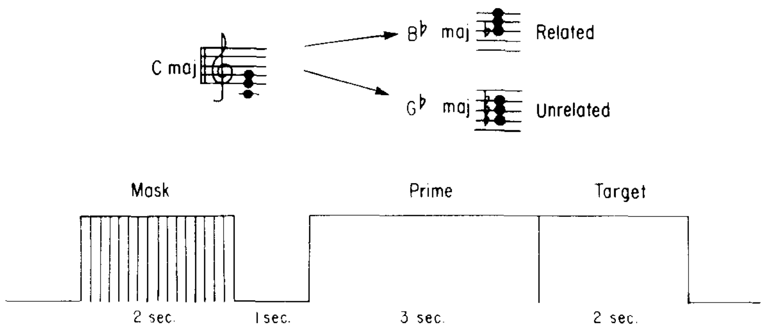

Fig. 1. Musical chord priming task. Each trial began with a 2 sec mask; following a 1 sec pause, a prime chord was presented for 3 sec and was immediately followed by a 2 sec target chord. The prime and target were either harmonically related or unrelated, and the target was either in-tune or mistuned by flattening the fifth a fraction of a semitone. The subject's task was to decide whether the target sounded "in-tune" or "out-of-tune". (See Methods for details.)

related ($B^{b\ maj}$) or unrelated ($G^{b\ maj}$) to the prime. On half the trials, the target is mistuned by altering the pitch of one component of the chord. Subjects are instructed to decide whether the target chord is in-tune or out-of-tune. In normals (both musicians and non-musicians), there is an interaction between harmonic relatedness (related vs unrelated major triad) and intonation (in-tune vs out-of-tune major triad), with higher accuracy in related trials when the target is in-tune, and higher accuracy in unrelated trials when the target is out-of-tune.* This interaction was used as an index of musical priming in the present split-brain experiments.

*Both accuracy data and reaction time data from normal subjects are characterized by an interaction between relatedness and intonation. In addition, reaction time data (but not accuracy data) show a small but significant main effect of relatedness, with related targets being judged more quickly than unrelated targets. The interaction between relatedness and intonation revealed by accuracy data represents a biasing of perceived intonation by the degree of relatedness, and the main effect of relatedness revealed by reaction time data represents an enhancement of sensitivity. In the present split-brain experiments, only accuracy could be measured because of methodological constraints; therefore, the interaction between relatedness and intonation was used to determine whether each hemisphere showed evidence of normal priming. It should be noted that the issue of whether the priming effect is a biasing effect or a sensitivity effect is orthogonal to the principal goal of the present study, in that both bias and sensitivity effects demonstrate the presence of an intact cognitive representation of the harmonic relationships among musical chords.

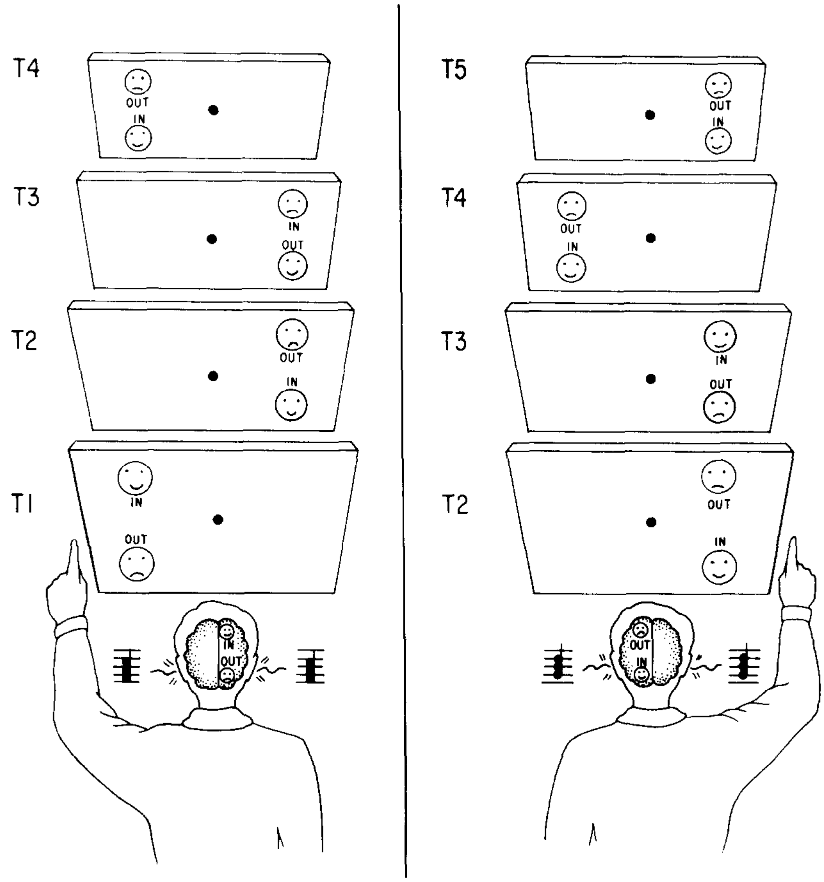

Fig. 2. Split-brain paradigm. At the onset of the target chord, response choices were tachistoscopically flashed in alternate quadrants of one visual field while the subject fixated a central point. The subject's task was to point to the correct response with the ipsilateral hand. Chords were presented in free field. T1 = Trial 1, T2 = Trial 2, and so on. (See Methods for details.)

EXPERIMENT 1: METHODS

Subjects

Case J.W. J.W. is a 36 year-old right-handed mechanic who 10 years ago underwent a two-stage callosotomy for intractable primary complex partial seizures with occasional generalization. Pre-operatively, the interictal neurological examination was normal; serial scalp electroencephalograms (EEGs) documented bilateral polyspike-and-wave paroxysms with a right anterior temporal predominance and occasional independent left frontoparietal spikes; contrast-enhanced computed tomography (CT) of the brain, technetium brain scan, and cerebrospinal fluid analysis were normal. After completing the second (anterior) stage of callosal transection, seizure frequency decreased to less than half the pre-operative baseline and EEG paroxysms became largely lateralized to the right. Extensive laboratory testing during the first year post-callosotomy showed left hemisphere speech lateralization and complete interruption of interhemispheric visual transfer and tactile-motor integration [55, 56]; subsequent mid-sagittal magnetic resonance imaging (MR) confirmed the surgical report and neuropsychological evidence that callosal transection was complete [23]. To date, evidence of paracallosal interhemispheric integration is limited to the observation that crude visuospatial information can be integrated across the midline [21].

Two years prior to the present experiments, the Verbal IQ was 97, Performance IQ 95, and Memory Quotient 102 [63, 64]. Previous work by GAZZANIGA and colleagues has documented that J.W.'s right hemisphere manifests good comprehension of spoken and written nouns, poor discrimination of consonant–vowel phonemes presented to the left ear under dichotic conditions, a limited capacity for syntactic manipulations, and no electrophysiological evidence of semantic priming on lexical decision tasks; J.W.'s left hemisphere is competent in all respects ([25, 36, 55, 56]; for review see [2]).

At the time of the present experiments, J.W. was medicated with phenytoin, carbamazepine, and valproic acid. He had not had a seizure in over a year. Aside from findings referable to callosotomy, the neurological examination was remarkable for a fine, rapid sustention tremor and end-gaze horizontal nystagmus.

While he has no musical training, J.W. listens to country, folk, and rock music several hours every day, goes dancing several times a month, attends several concerts a year, and has collected over 200 records and tapes. He meets criteria for GRISON's third level of musical culture [29], which lies in the middle of her musicality classification scheme.

Case V.P. V.P. is a 33 year-old right-handed cashier who 10 years ago underwent a two-stage callosotomy for a primary mixed seizure disorder with features of absence, myoclonic, and generalized tonic clonic seizures. At the time of her pre-operative work-up, EEG showed left temporal sharp waves superimposed on diffuse spike-and-wave activity in the theta range. CT and cerebral angiography were normal. Neuropsychological examination 4 months after the second (posterior) stage of callosal transection showed left hemisphere speech lateralization and complete interruption of interhemispheric visual transfer and tactile-motor integration [56]; 1 year after callosotomy, limited right hemisphere speech appeared [25]. Mid-sagittal inversion-recovery MR later showed midline signal intensities consistent with residual callosum at the extremes of the rostrum and splenium [23]. Subsequent experiments using elementary visual stimuli (e.g. geometric shapes [18] and letters [24]) have failed to document any evidence of visual transfer across the midline. The only evidence of interhemispheric integration to date is V.P.'s capacity to judge whether words presented in opposite visual fields rhyme; this observation holds only for word pairs that both look alike and sound alike (i.e. not for rhymes that differ orthographically) and has been attributed to the functional specificity of V.P.'s callosal remnants for the transfer of redundant phonological and orthographical information [24].

One year prior to the present experiments, the Verbal IQ was 81 and the Memory Quotient 93. Previous work by GAZZANIGA and colleagues has documented that V.P.'s right hemisphere manifests good comprehension of spoken and written nouns, good discrimination of consonant vowel phonemes presented to the left ear under dichotic conditions, a limited capacity for syntactic manipulations, and electrophysiological evidence of semantic priming on lexical decision tasks; her left hemisphere is competent in all respects ([25, 36, 56]; for review see [2]).

At the time of the present experiments, V.P. was medicated with phenytoin and valproic acid. She had not had a generalized convulsion in over a year, nor a witnessed "minor" attack during 2 days of close observation. Aside from findings referable to callosotomy, the neurological examination was remarkable for end-gaze horizontal nystagmus.

V.P. took piano lessons for 1 year at age 14 and sang in a choral group during high school. She can read music but is not trained in music theory. At present she plays the piano about once every other month, frequently sings along with the radio when driving, occasionally listens attentively to classical and popular music while relaxing at home, and rarely attends concerts or dances. She meets criteria for the second highest level of musicality in GRISON's scheme [29].

Stimuli and apparatus

The 12 musical chords used in the present experiment have been previously detailed by BHARUCHA and STOECKIG [7]. Each prime chord and "in-tune" target chord was a major triad composed of 15 frequency components – the tonic, third and fifth across five octaves (range = 65.41–4186.24 Hz; equal-tempered scale; $A_4 = 440$ Hz). The amplitude envelope was shaped so as to approach the loudness threshold at either end of the frequency range. This procedure obscures pitch height effects [49]. Each "out-of-tune" target chord was a major triad that was mistuned by flattening the fifth by one or more eighths of a semitone (i.e. by a frequency factor of $2^{1/96}$). Harmonic relatedness between the prime and target was defined empirically in accordance with data obtained in previous experiments [6, 7, 34, 35]. Related pairs (e.g. C^{maj} and $B^{b\ maj}$) shared parent keys (F^{maj}), but they did not share component tones (C, E, G and B^{b}, D, F, respectively). Primes were 3 sec in duration and targets were 2 sec in duration.

In-tune and out-of-tune response choices were made available to only one hemisphere on each trial by lateralizing them tachistoscopically within alternate quadrants (Fig. 2; visual angle = 1.5°; duration of flash = 150 msec; adapted from [22]). As in "same" "different" response paradigms used to study aphasic patients with limited reading ability (e.g. [37]), "in" choices were presented together with a line drawing of a happy face and "out" choices with a line drawing of a sad face so that both verbal and non-verbal referents were available to each hemisphere. The face always appeared above the word in the upper quadrant of the hemifield and below the word in the lower quadrant.

Each subject performed two blocks of 96 trials. Each block was presented in random order, with brief pauses lasting up to 1 min interspersed approximately every 12 trials. Each of the 12 major chords occurred four times as a prime for each hemisphere. The prime was followed equally frequently by each of the following target conditions: in-tune/related; in-tune/unrelated; out-of-tune/related; and out-of-tune/unrelated.

Chords were synthesized using an Apple Macintosh microcomputer and presented in free field through a Sansui A-707 amplifier and speaker system at a level well above hearing threshold that was comfortable for each subject and customary for his/her music listening. Response choices were tachistoscopically lateralized via the computer and internally synchronized with target chord onset.

Procedure

An informal training session was conducted in order to assess whether each patient—and, in particular, each right hemisphere—understood the task. First, the two response choices were presented on a sheet of paper lying in free field. A single in-tune or out-of-tune chord was presented. Subjects were asked to point to the correct response. The response hand was alternated approximately every 10 trials and the orientation of the response choices approximately every five trials ("in"—happy face above, "out"—sad face below, and vice versa). Feedback, visual and prosodic as well as verbal, was given after each practice trial, and the amount of mistuning was increased by a factor of $2^{1/96}$ (beginning at $2^{2/96}$ below the fifth) until each subject performed several consecutive trials correctly. For J.W. the fifth was mistuned by $2^{3/96}$ and for V.P. $2^{5/96}$. Thereafter, approximately 20 practice trials were presented in which the response choices were tachistoscopically lateralized simultaneously with the onset of each chord. Subjects were instructed to point to the correct response with the hand on the same side as the visual stimulus (Fig. 2). To insure that there was no difference between the hemispheres in their ability to accurately identify tachistoscopic response choices, a separate set of 20 visual matching trials were run in which J.W. and V.P. had to point to the flashed response choice corresponding to the choice previously pointed out by the examiner in free field; both subjects performed this task flawlessly.

To begin each trial, the examiner pressed the space bar on the computer keyboard. The trial began with a 2 sec mask consisting of 16 tones of random pitch, followed by a 1 sec pause, then the prime chord, then the target chord (Fig. 1). The response choices were flashed simultaneously with the onset of the target chord, and the subject was asked to point to the correct response with the ipsilateral hand (Fig. 2). During the pause, subjects were intermittently reminded to fixate an orange dot placed in the center of the visual field. J.W. performed 96 trials in each of two 1 hr morning sessions conducted 2 months apart; V.P. performed 96 trials in each of two 1 hr sessions conducted on the same day, one in the morning and one in the afternoon.

EXPERIMENT 1: RESULTS

Accuracy in left visual field (LVF) and right visual field (RVF) trials in each of the four target conditions is illustrated in Fig. 3. Error rates were analyzed using replications as the random factor. For each patient, a three-way analysis of variance (ANOVA) was performed with relatedness (related vs unrelated), intonation (in-tune vs out-of-tune), and visual field (LVF vs RVF) as factors, followed by a two-way ANOVA for each visual field.

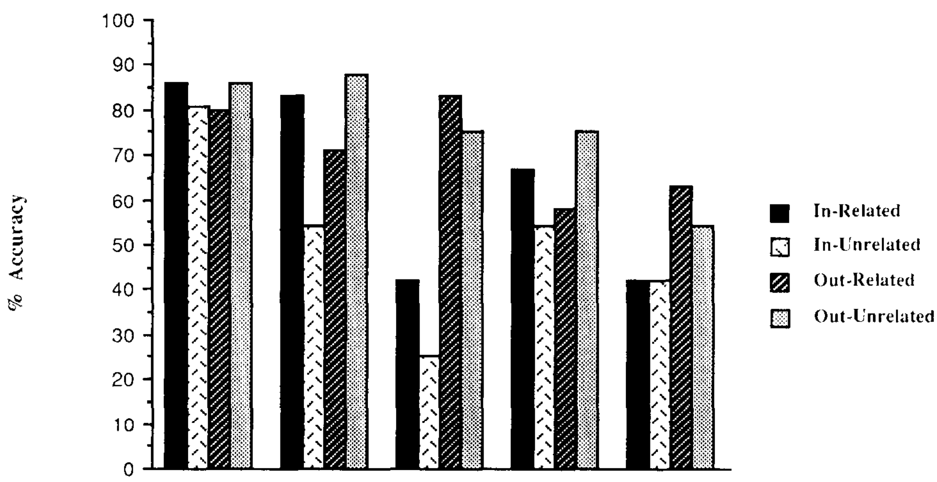

Fig. 3. Experiment 1: J.W. and V.P.'s per cent accuracy in left visual field (LVF) and right visual field (RVF) trials in each of the four target conditions. The previously reported data from 13 normal subjects [7] are shown for comparison.

For J.W., the three-way analysis yielded a significant main effect of visual field [F (1, 23) = 12.06, $P = 0.002$], with greater accuracy in LVF than RVF trials [LVF = 74%, significantly greater than chance, t (95) = 4.67, $P < 0.0005$; RVF = 56%, not significantly greater than chance, t (95) = 1.17, $P > 0.1$]. There was a significant main effect of intonation [F (1, 23) = 24.41, $P = 0.0001$], with higher accuracy in out-of-tune trials consistent with a response bias in favor of out-of-tune judgements; there was a significant interaction between intonation and visual field [F (1, 23) = 7.11, $P = 0.01$], indicating that the intonation effect occurred in RVF trials. There was a significant interaction between relatedness and intonation in the same direction as the normal priming effect [F (1, 23) = 4.05, $P = 0.05$]; a significant three-way interaction between relatedness, intonation, and visual field [F (1, 23) = 3.96, $P = 0.05$] indicated that priming occurred in LVF trials. Separate analyses for each visual field confirmed that the interaction between relatedness and intonation occurred in the same direction as the normal priming effect in LVF trials only [F (1, 23) = 8.31, $P = 0.008$; for RVF, F (1, 23) < 1]. The bias in favor of out-of-tune responses was significant in RVF trials only [F (1, 23) = 29.29, $P < 0.0001$; for LVF, F (1, 23) = 1.33, $P = 0.26$].

For V.P., the three-way ANOVA also yielded a significant main effect of visual field [F (1, 23) = 4.77, $P = 0.04$], again with greater overall accuracy in LVF than RVF trials [LVF = 63%; significantly greater than chance, t (95) = 2.53, $P < 0.01$; RVF = 50%, at chance]. The main effect of intonation was not significant [F (1, 23) = 2.64, $P = 0.11$] but suggested a trend in favor of higher accuracy in out-of-tune trials. The two-way interaction between relatedness and intonation was not significant [F = (1, 23) < 1], but the three-way interaction between relatedness, intonation, and visual field raised the possibility of a relatedness–intonation interaction in LVF trials in the same direction as the normal priming effect [F (1, 23) = 1.56, $P = 0.22$]. Separate analyses for each visual field revealed a strong trend consistent with normal priming in LVF trials [F (1, 23) = 3.14, $P = 0.08$] but not in RVF trials [F (1, 23) < 1]. Although there were more out-of-tune responses than in-tune responses on RVF trials, this bias did not reach statistical significance [F (1, 23) = 1.96, $P = 0.17$]; there was no hint of a response bias in LVF trials [F (1, 23) < 1].

Given the tachistoscopic presentation of lateralized response choices for durations less than the latency of saccadic eye movements, the existing evidence against any inter-hemispheric transfer of complex visual information in each patient, and the consistent left–right performance asymmetries observed, accuracy in LVF trials likely reflects right hemisphere performance and accuracy in RVF trials left hemisphere performance. Given the complex nature of the visual stimuli, the absence of any known connections between auditory thalamus and visual cortex, and the connectivity patterns and physiological characteristics of heteromodal association cortex, it is likely that performance reflected the integration of auditory and visual processes at the level of the cerebral cortex. The ease with which J.W. and V.P.'s left and right hemispheres performed visual matching during our practice session and the documented capacity of each patient's two half-brains to accurately perform picture–picture, word–word, picture–word, and word–picture matching tasks (for review see [20]) argues that the difference in response accuracy between the left and right hemispheres is not a result of visual processing differences *per se*, but arises from left–right asymmetries in auditory pattern perception, in cross-modal integration, or in both.

Only when response choices were presented to the right hemisphere of each patient was there evidence of an interaction between relatedness and intonation in the same direction as that previously found in normal subjects [7]: (1) higher accuracy in related than in unrelated trials when target chords were in-tune; and (2) higher accuracy in unrelated than in related trials when target chords were out-of-tune. It is highly unlikely that left hemisphere accuracy was compromised by the nature of the response choices or by a general limitation in information processing capacity, given our presentation of the visual–verbal referents "in" and "out", and given the well-documented cognitive and perceptual resources of each patient's left hemisphere. Similarly, it is unlikely that the cross-modal nature of our task would put the left hemisphere at a disadvantage relative to the right hemisphere, given previous data concerning the same patients' left hemisphere competence in speech–picture, speech–word, sound–picture, and sound–word matching tasks [20, 25, 61, 62]. It is unlikely that the side of the seizure focus can account for the absence of left hemisphere priming since J.W. has predominantly right-sided paroxysms. That the left hemisphere of each patient did not perform significantly above chance raised the possibility that priming failed to occur in the left hemisphere because the left hemisphere was simply not able to perform a spectral intonation judgement. Furthermore, the significant bias in favor of out-of-tune responses in RVF trials for J.W. and the trend in the same direction for V.P. suggested that left hemisphere priming might have been precluded by an inability to perceive tonal consonance. In order to address these concerns, a second experiment was performed which analyzed the ability of each hemisphere to make target intonation judgements in the absence of a prime.

EXPERIMENT 2: METHODS

The subjects, stimuli, apparatus and procedure were the same as described in Experiment 1, except that the mask was followed by a single chord—i.e. an in-tune or out-of-tune major triad target without a prime. Each hemisphere heard each target twice (one block of 96 trials for each patient, 48 for each hemisphere).

EXPERIMENT 2: RESULTS

The results are summarized in Table 1. For J.W., overall response accuracy was significantly better than chance in LVF trials [65%; t (47) = 2.06; $P<0.05$] but not in RVF trials [54%; t (47) < 1]. There was no significant difference in accuracy between LVF and RVF trials [F (1, 23) = 1.09]. There was no significant effect of intonation in LVF trials [F (1, 23) = 1], but there was a strong trend suggesting a bias in favor of out-of-tune judgements in RFV trials [F (1, 23) = 3.29; $P=0.08$]. There was a significant interaction between intonation and visual field [F (1, 23) = 6.67; $P=0.02$], indicating a differential intonation effect between the two hemispheres.

Table 1. Experiment 2: J.W. and V.P.'s per cent accuracy in left visual field (LVF) and right visual field (RVF) trials in the two target conditions

	LVF		RVF	
	In	Out	In	Out
J.W.	71	58	42	67
V.P.	83	67	71	54

For V.P., overall response accuracy was significantly better than chance in LVF trials [75%; t (47) = 3.43, $P<0.005$] and marginally better than chance in RVF trials [62%; t (47) = 1.65; critical value = 1.68 for $P=0.05$]. Accuracy was significantly greater in LVF trials than RVF trials [F (1, 23 = 7.67, P = 0.01]. There was a significant bias in favor of in-tune judgements in both LVF trials [F (1, 23) = 4.60, P = 0.04] and RVF trials [identical F (1, 23) = 4.60, P = 0.04]. Obviously, there was no interaction between intonation and visual field.

These results confirm the evidence of right hemisphere competence for spectral intonation judgements in Experiment 1 and establish that the right hemisphere of each patient was able to distinguish between tonal consonance and dissonance in the absence of contextual cues.

The performance of the left hemisphere differed between patients. For J.W., the chance performance and out-of-tune response bias observed in RVF trials suggests an inability to perceive tonal consonance. The absence of an interaction between relatedness and intonation in RVF trials in Experiment 1 may thus be attributed to a lack of perceptual capacities rather than a failure to prime *per se*.

For V.P., the better-than-chance performance in RVF trials and significant difference in accuracy in RVF vs LVF trials indicate, respectively, that: (1) her left hemisphere was able to distinguish between tonal consonance and dissonance; and (2) her left hemisphere was inferior to the right. For V.P., it is therefore unlikely that the absence of an interaction between relatedness and intonation in RVF trials in Experiment 1 can be attributed solely to an inability of her left hemisphere to distinguish in-tune from out-of-tune targets. V.P.'s left hemisphere performed above chance without the prime but at chance with the prime; this may reflect an inability to offset the greater task difficulty in the two-chord priming experiment by the facilitation which priming offers in the related/in-tune and unrelated/out-of-tune conditions.

DISCUSSION

Only the right hemisphere of each split-brain patient showed evidence of the musical chord priming effect previously found in normal subjects. When response choices were presented to the right hemisphere, the normal interaction between harmonic relatedness and intonation was observed: (1) intonation judgements were more accurate in related than in unrelated trials when target chords were in-tune; and (2) intonation judgements were more accurate in unrelated than in related trials when target chords were out-of-tune. No such interaction was apparent when response choices were presented to the left hemisphere.

The right hemisphere interaction between harmonic relatedness and intonation in our split-brain patients is unlikely to be a manifestation of frequency-specific repetition priming. BHARUCHA and STOECKIG [7] showed that removing the non-octave harmonics of prime and target chords had no effect on the response accuracy of normal subjects; likewise, the related chords used in the present experiment did not share component tones. Therefore, the facilitation of target perception by the prime appears to occur at an associative level of auditory processing.

The influence of harmony on target chord perception and the modality-specific nature of this interaction are interpreted as evidence for spreading activation within a cortical auditory network that contains an internalized representation of harmonic regularities in music. These regularities form the basis of formal theoretical accounts [42, 46, 47], psychological models [38, 49], and neural net models [3, 10] of harmony perception in music that have been substantiated by empirical studies of normal populations (for reviews see [3, 13, 33]). Our results indicate that this network is lateralized within the right hemisphere of each of our patients.

It remains unclear if the failure of the left hemisphere to prime reflects: (1) the absence of cognitive processes mediating chord priming; and/or (2) the absence of sensory or perceptual processes mediating tonal consonance perception, thereby precluding the activation of cognitive processes mediating chord priming. The ability of V.P.'s left hemisphere to perceive tonal consonance in the no-prime experiment undermines the latter interpretation in her case. In addition, we have observed priming despite severely impaired tonal consonance perception in a patient with bilateral auditory cortex lesions that spared portions of auditory association and heteromodal association areas in both hemispheres [60].

The right hemisphere of each of our patients has previously been shown to be superior to the left on the Timbre Test of the Seashore Measures of Musical Talents [61, 62], which requires same–different discriminations of six-element harmonic spectra that vary in the relative intensities of two frequency components [48]. V.P.'s left hemisphere performed at chance and J.W.'s left hemisphere was marginally better than chance on this task. Given the absence of diffuse cerebral dysfunction in our patients, these findings are consistent with MILNER's original observation [39] that right but not left temporal lobectomy causes a significant drop in Timbre Test performance, and they argue against the presence of anomalous asymmetries for auditory non-verbal functions in our patients.

SIDTIS and colleagues [50–54] have previously reported evidence that auditory functions mediating complex pitch perception are lateralized within the right hemisphere. In the original dichotic complex tone experiment, an interaction between the number of overtones in the test stimuli and the magnitude of the left ear advantage was found [50]. Subsequently, the musical interval formed by the dichotic complex tone pair was noted to influence laterality effects in normals [51] and overall response accuracy in patients with right hemisphere stroke [54]. ZATORRE [67] has recently published evidence that associative auditory functions mediating spectral pattern recognition are lateralized within the right hemisphere. The capacity to abstract the pitch of the "missing" fundamental frequency of a harmonic series was lost in the majority of temporal lobectomy patients whose excision included all or part of the right transverse gyrus(i) of Heschl (as well as the superior temporal gyrus lying anteriorly); the performance of patients with left-sided excisions did not differ significantly from that of normal controls. The observation of musical priming by the right hemispheres of our split-brain patients extends the claim of right hemisphere specialization in auditory non-verbal processing to include cognitive functions which hierarchically structure pitch information embedded in musical contexts.

Hemispheric differences in the perception of musical chords have previously been inferred from ear-of-presentation differences measured in monaural [32, 44] and dichotic [26–28, 40, 41, 45] listening experiments in normal subjects. In the original dichotic experiment, GORDON [26] presented a pair of musical chords (in various combinations of major triads, major sevenths, minor triads and minor sevenths) to 20 right-handed musicians and asked them to select the two chords that were played from among four response choices written in music notation; 71% of chords presented to the left ear and 64% of chords presented to the right ear were recognized—a statistically significant difference which was interpreted as evidence of right hemisphere superiority. Most subsequent dichotic studies of musical chord recognition have supported the notion of a right hemisphere advantage, with some controversy concerning the influence of task-related differences and of musicality on the presence (e.g. [27] vs [41] vs [45]) and magnitude [28] of laterality effects. However, a number of investigators have raised concerns about the reliability of dichotic listening tests as measures of hemispheric differences in auditory perception (e.g. [8, 43]). In particular, the interaction reported by DEUTSCH [11, 12] between the pitches of dichotic tones and their perceived lateralization to one or the other ear is likely to confound the relationship between ear differences and hemispheric differences in dichotic musical tasks [14]. GORDON [28] has reported evidence of Deutsch's auditory illusion in a dichotic chord experiment, such that lower-pitch chords were referred to the left ear and higher-pitch chords to the right ear; this interaction reached statistical significance in musicians but not in non-musicians. SAN MARTINI *et al.* [45] recently found no significant interaction between musical chord pitch and perceived lateralization among amateur musicians and non-musicians using a monaural–dichotic chord recognition task. While these authors demonstrated that same–different judgements were significantly more accurate when the monaural standard chord was presented to the left ear, performance was well above chance on right as well as left ear trials, and the difference in mean accuracy for the two ears of 58 subjects was only 0.99 out of a possible 24 [17.14/24.00 (71%) in the right ear vs 18.13/24.00 (76%) in the left ear]. Among monaural listening studies, PREISLER *et al.* [44] recently reported significantly greater accuracy for left ear presentations on a task which required the manual tuning of musical intervals mistuned by a fraction of a semitone at the major second, major third, and fifth.

Our patient population and study design allowed us to avoid uncertainties about the relationship between ear differences and hemisphere differences in dichotic and monaural listening tasks: auditory stimuli were presented in free field and visual response choices were made available to only one disconnected hemisphere. Although our paradigm as well as our particular task differ greatly from those used in dichotic and monaural listening experiments, in general the data offer converging evidence to support the notion of right hemisphere specialization for harmony perception in music.

While the present observations indicate that auditory functions mediating chord priming are lateralized in the right hemispheres of our patients, they offer no insight concerning their localization within the right hemisphere. The modality-specific nature of the interaction between relatedness and intonation suggests that the right auditory cortex subserves at the very least sensory functions requisite for priming, if not priming itself. The participation of heteromodal structures subserving memory and multimodal integration cannot be ruled out. The previously cited case of preserved priming despite impaired tonal consonance perception following complete bilateral infarction of Heschl's gyri suggests that priming does not rely on the integrity of primary auditory cortex, and that priming and tonal consonance perception are neurologically dissociable functions [60].

Of course, a number of confounding variables compromise the interpretation of the present findings as evidence of right hemisphere specialization for harmony perception in the general population at large. Not the least of these is that the task requirements imposed a selection bias in favor of sampling only split-brain patients whose right hemispheres possess the cognitive, and perhaps linguistic, capacities to carry out sound–picture matching and perceptual-motor integration. However, in this regard it is noteworthy that even though each of our patients' left hemispheres is dominant for speech and language and is capable of cross-modal matching, J.W.'s left hemisphere was incompetent in both Experiment 1 and Experiment 2, and V.P.'s left hemisphere was incompetent in the former and inferior to the right in the latter. Studies of normal populations using lateralized response choice presentations and reaction time measures may help to assess the amount of variability existing in the general population.

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REFERENCES

1. APEL, W. *Harvard Dictionary of Music*. Harvard University Press, Cambridge, Massachusetts, 1972.
2. BAYNES, K. Language and reading in the right hemisphere: Highways or byways of the brain? *J. Cognit. Neurosci.* **2,** 159–179, 1990.
3. BHARUCHA, J. J. Music cognition and perceptual facilitation: A connectionist framework. *Music Percept.* **5,** 1–30, 1987.
4. BHARUCHA, J. J. Pitch, harmony, and neural nets: A psychological perspective. In *Connectionism and Music*, P. TODD and G. LOY (Editors). M.I.T. Press, Cambridge, in press.
5. BHARUCHA, J. J. and KRUMHANSL, C. L. The representation of harmonic structure in music: Hierarchies of stability as a function of context. *Cognition* **13,** 63–102, 1983.
6. BHARUCHA, J. J. and STOECKIG, K. Reaction time and musical expectancy: Priming of chords. *J. exp. Psychol.: Hum. Percept. Perform.* **12,** 403–410, 1986.
7. BHARUCHA, J. J. and STOECKIG, K. Priming of chords: Spreading activation or overlapping frequency spectra? *Percept. Psychophys.* **41,** 519–524, 1987.
8. BLUMSTEIN, S., GOODGLASS, H. and TARTTER, V. The reliability of ear advantage in dichotic listening. *Brain Lang.* **2,** 226–236, 1975.
9. DAMASIO, A. R. and DAMASIO, H. Musical faculty and cerebral dominance. In *Music and the Brain*, M. CRITCHLEY and R. A. HENSON (Editors), pp. 141–155. Heinemann, London, 1977.
10. DEUTSCH, D. Music recognition. *Psychol. Rev.* **76,** 300–307, 1969.
11. DEUTSCH, D. An auditory illusion. *Nature* **251,** 307–309, 1974.
12. DEUTSCH. D. Two-channel listening to musical scales. *J. Acoust. Soc. Am.* **57,** 1156–1160, 1975.
13. DEUTSCH, D. The processing of pitch combinations. In *The Psychology of Music*, D. DEUTSCH (Editor), pp. 271–316. Academic Press, New York, 1982.
14. DEUTSCH, D. Dichotic listening to melodic patterns and its relationship to hemispheric specialization of function. *Music Percept.* **3,** 127–154, 1985.
15. DEWSON, J. H. Speech sound discrimination by cats. *Science* **144,** 555–556, 1964.
16. DEWSON, J. H., PRIBRAM, K. H. and LYNCH, J. C. Effects of ablations of temporal cortex upon speech sound discrimination in the monkey. *Exp. Neurol.* **24,** 579–591, 1969.
17. FAGLIONI, P., SPINNLER, H. and VIGNOLO, L. A. Contrasting behavior of right and left hemisphere damaged patients on a discriminative and semantic task of auditory recognition. *Cortex* **5,** 366–389, 1969.
18. FENDRICH, R. and GAZZANIGA, M. S. Evidence of foveal splitting in a commissurotomy patient. *Neuropsychologia* **27,** 273–281, 1989.
19. GATES, A. and BRADSHAW, J. L. The role of the cerebral hemispheres in music. *Brain Lang.* **4,** 403–431, 1977.
20. GAZZANIGA, M. S. Cognitive and neurologic aspects of hemispheric disconnection in the human brain. In *Discussions in Neurosciences* Vol. 4, P. J. MAGISTRETTI (Editor), pp. 7–72, 1989.
21. GAZZANIGA, M. S. Perceptual and attentional processes following callosal section in humans. *Neuropsychologia* **25,** 119–133, 1987.
22. GAZZANIGA, M. S., BOGEN, J. E. and SPERRY, R. W. Some functional effects of sectioning the cerebral commissures in man. *Proc. Nat. Acad. Sci.* **48,** 1765–1769, 1962.
23. GAZZANIGA, M. S., HOLTZMAN, J. D., DECK, M. D. F. and LEE, B. C. P. MRI assessment of human callosal surgery with neuropsychological correlates. *Neurology* **35,** 1763–1766, 1985.
24. GAZZANIGA, M. S., KUTAS, M., VAN PETTEN, C. and FENDRICH, R. MRI-verified neuropsychological functions. *Neurology* **39,** 942–946, 1989.
25. GAZZANIGA, M. S., SMYLIE, C. S., BAYNES, K., HIRST, W. and MCCLEARY, C. Profiles of right hemisphere language and speech following brain bisection. *Brain Lang.* **22,** 206–220, 1984.
26. GORDON, H. W. Hemispheric asymmetries in the perception of musical chords. *Cortex* **6,** 387–398, 1970.
27. GORDON, H. W. Hemispheric asymmetry for dichotically presented chords in musicians and non-musicians, males and females. *Acta psychol.* **42,** 383–395, 1978.
28. GORDON, H. W. Degree of ear asymmetries for perception of dichotic chords and for illusory chord localization in musicians of different levels of competence. *J. exp. Psychol.: Hum. Percept. Perform.* **6,** 516–527, 1980.
29. GRISON, B. Une étude sur les altérations musicales au cours des lésions hémisphériques. Thèse, Paris 1972, Cited by A. L. BENTON, The amusias. In *Music and the Brain*, M. CRITCHLEY and R. A. HENSON (Editors), pp. 378–397. Heinemann, London, 1977.
30. HEFFNER, H. E. and HEFFNER, R. S. Effect of unilateral and bilateral auditory cortex lesions on the discrimination of vocalizations from Japanese macaques. *J. Neurophysiol.* **56,** 683–701, 1988.

31. HELMHOLTZ, H. *On the Sensations of Tone* (A. J. ELLIS, Translator). Dover, New York, 1954 (originally published 1863).
32. KELLAR, L. A. and BEVER, T. G. Hemispheric asymmetries in the perception of musical intervals as a function of musical experience and family handedness background. *Brain Lang.* **10,** 24–38, 1980.
33. KRUMHANSL, C. L. *Cognitive Foundations of Musical Pitch.* Oxford University Press, New York, 1990.
34. KRUMHANSL, C. L., BHARUCHA, J. J. and CASTELLANO, M. A. Key distance effects on perceived harmonic structure in music. *Percept. Psychophys.* **32,** 96–108, 1982.
35. KRUMHANSL, C. L., BHARUCHA, J. J. and KESSLER, E. J. Perceived harmonic structure of chords in three related musical keys. *J. exp. Psychol.: Hum. Percep. Perform.* **8,** 24–36, 1982.
36. KUTAS, M., HILLYARD, S. A. and GAZZANIGA, M. S. Processing of semantic anomaly by right and left hemispheres of commissurotomy patients. *Brain* **111,** 553–576, 1988.
37. LINEBARGER, M. C., SCHWARTZ, M. F. and SAFFRAN, E. M. Sensitivity to grammatical structure in so-called agrammatic aphasics. *Cognition* **13,** 361–392, 1983.
38. MEYER, L. B. *Emotion and Meaning in Music.* University of Chicago Press, Chicago, 1956.
39. MILNER, B. Laterality effects in audition. In *Interhemispheric Relations and Cerebral Dominance*, V. MOUNTCASTLE (Editor), pp. 177–195. Johns Hopkins University Press, Baltimore, 1962.
40. MORAIS, J., PERETZ, I. and GUDANSKI, M. Ear asymmetry for chord recognition in musicians and nonmusicians. *Neuropsychologia* **20,** 351–354, 1982.
41. PERETZ, I. and MORAIS, J. A left ear advantage for chords in non-musicians. *Percept. Mot. Skills* **49,** 957–958, 1979.
42. PISTON, W. *Harmony* (4th edn). Norton, New York, 1978.
43. PIZZAMIGLIO, L., DE PASCALIS, C. and VIGNATI, A. Stability of dichotic listening test. *Cortex* **10,** 203–205, 1974.
44. PREISLER, A., GALLASCH, U. and SCHULTER, G. Hemispheric asymmetry and the processing of harmonies in music. *Int. J. Neurosci.* **47,** 131–140, 1989.
45. SAN MARTINI, P., DE PASCALIS, V., MONTIROSSO, R. and SURIAN, A. Deutsch's anisotropy and ear advantage in a dichotic test of musical chords. *Neuropsychologia* **27,** 1109–1113, 1989.
46. SCHENKER, H. *Harmony* (O. JONES, Editor, E. M. BORGESE, Translator). M.I.T. Press, Cambridge, Massachusetts, 1954 (originally published 1906).
47. SCHOENBERG, A. *Structural Foundations of Harmony* (L. STEIN, Editor). Norton, New York, 1969 (originally published 1954).
48. SEASHORE, C. E., LEWIS, D. and SAETVEIT, J. *Seashore Measures of Musical Talents (Revised).* Psychological Corporation, New York, 1960.
49. SHEPARD, R. N. Circularity in judgments of relative pitch. *J. Acoust. Soc. Am.* **36,** 2346–2353, 1964.
50. SIDTIS, J. J. On the nature of the cortical function underlying right hemisphere auditory perception. *Neuropsychologia* **18,** 321–330, 1980.
51. SIDTIS, J. J. The complex tone test: Implications for the assessment of auditory laterality effects. *Neuropsychologia* **19,** 103–112, 1981.
52. SIDTIS, J. J. Music, pitch perception, and the mechanisms of cortical hearing. In *Handbook of Cognitive Neuroscience*, M. S. GAZZANIGA (Editor), pp. 91–114, 1984.
53. SIDTIS, J. J. and GAZZANIGA, M. S. Complex pitch perception after callosal section: Further evidence for a right hemisphere mechanism. *J. Acoust. Soc.* **69,** S119, 1981.
54. SIDTIS, J. J. and VOLPE, B. T. Selective loss of complex-pitch or speech discrimination after unilateral lesion. *Brain Lang.* **34,** 235–245, 1988.
55. SIDTIS, J. J., VOLPE, B. T., HOLTZMAN, J. D., WILSON, D. H. and GAZZANIGA, M. S. Cognitive interaction after staged callosal section: Evidence for transfer of semantic actication. *Science* **212,** 344–346, 1981.
56. SIDTIS, J. J., VOLPE, B. T., WILSON, D. H., RAYPORT, M. and GAZZANIGA, M. S. Variability in right hemisphere language function after callosal section: Evidence for a continuum of generative capacity. *J. Neurosci.* **1,** 323–331, 1981.
57. SYMMES, D. Discrimination of intermittent noise by macaques following lesions of the temporal lobe. *Exp. Neurol.* **16,** 201–214, 1966.
58. TERHARDT, E. Pitch, consonance, and harmony. *J. Acoust. Soc. Am.* **55,** 1061–1069, 1974.
59. TERHARDT, E. The concept of musical consonance: A link between music and psychoacoustics. *Music Percept.* **1,** 276–295, 1984.
60. TRAMO, M. J., BHARUCHA, J. J. and MUSIEK, F. E. Music perception and cognition following bilateral lesions of auditory cortex. *J. Cognit. Neurosci.* **2,** 195–212, 1990.
61. TRAMO, M. J. and GAZZANIGA, M. S. Discrimination and recognition of complex tonal spectra by the cerebral hemispheres: Differential lateralization of acoustic-discriminative and semantic-associative functions in auditory pattern perception. *Soc. Neurosci. Abstracts* **15,** 1060, 1989.
62. TRAMO, M. J. and GAZZANIGA, M. S. Cerebral specialization in auditory pattern perception: Timbre (Manuscript in preparation).
63. WECHSLER, D. A standardized memory scale for clinical use. *J. Psychol.* **19,** 87–95, 1945.

64. WECHSLER, D. *Wechsler Adult Intelligence Scale—Revised*. Psychological Corporation, New York, 1981.
65. WHITFIELD, I. C. Auditory cortex and the pitch of complex tones. *J. Acoust. Soc. Am.* **67,** 644–647, 1980.
66. ZATORRE, R. J. Musical perception and cerebral function: A critical review. *Music Percept.* **2,** 196–221, 1984.
67. ZATORRE, R. J. Pitch perception of complex tones and human temporal lobe function. *J. Acoust. Soc. Am.* **84,** 566–572, 1988.