Spatial organization of EEG coherence during listening to consonant and dissonant chords

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Abstract

Theories of harmony state that the contribution of both sensory and cognitive components is important for musical consonance perception. The aims of the present study were to analyze (a) functional intra- and inter-hemispheric connectivity associated with listening to consonant and dissonant chords using EEG coherence method; (b) relationships between affective responsiveness, sensory aspects of perceived consonance and associated brain connectivity. We identified two lines of inter-hemispheric connectivity in the theta band; one localized anterior being sensitive to consonance and one localized posterior sensitive to dissonance. Stronger right intra-hemispheric connectivity for consonance than dissonance in the theta band was associated with higher pleasantness ratings. The relationship between sensory aspects of perceived consonance and left intra-hemispheric connectivity found in theta-2 was interpreted as processing of vertical harmony without emotional involvement. The stronger connectivity along the axis "left anterior-right posterior" for dissonance than consonance in the alpha-1 band is discussed as a correlate of novelty processing. By introducing a "auditory object dissociation" hypothesis we suggest to extend the present concept of harmony perception. We believe that "auditory object dissociation" is a component of "sensory dissonance."
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Harmony or vertical structure of music, i.e. the combination of simultaneous musical sounds into chords, is one of the fundamental principles of Western music. Central to harmony is the concept of a consonance–dissonance dimension. Theories of harmony [3,16,22] state that both sensory and cognitive components contribute to musical consonance perception. The sensory attributes of harmony processing labeled as "tonal consonance" [16] are related to roughness sensation [6,16] and pitch perception [23] and are thought to be based upon neural processes in peripheral [23] and central, including cortical [4,13] parts of the auditory pathway. The cognitive components refer to memory and emotion related mechanisms [3]. These are still largely unexplored. A single study utilizing PET demonstrated that affective responsiveness to consonance and dissonance was related to regional brain activity changes in paralimbic and neocortical areas [2].

In order to elaborate on this problem, we focused on the principle of "functional integration," considering a function in terms of informational exchange between brain areas. Using the EEG coherence method we analyzed functional connectivity associated with listening to consonant and dissonant chords.

Our hypothesis was that specific functional connections between four brain quadrants associated with harmony perception should be found. Those specific functional connections would be established differently depending on the degree of harmony of a stimulus, and the coherent dynamical changes reflecting such connections can be termed "connectivity correlates of harmony processing" (CCHP). Specifically we expected (1) qualitatively different CCHPs in anterior and posterior halves of the brain reflecting specific informational transfer within the posterior "perceptive" half where most of the sensory pathways converge and within the anterior "productive" half involved in integrative cognitive processing. This hypothesis is based on previous findings that sensory and cognitive processes are involved in harmony perception as qualitatively different mechanisms [3,16]. (2) The second expectation is that a left–right asymmetry should be found in CCHPs. This second hypothesis is related to the well-documented hemispheric asymmetry in emotional pro-

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cessing (e.g., [5,14]) and strong evidence for the contribution of emotional mechanisms to harmony processing [2,3,16].

The coherence analysis evaluates phase relationships within frequency bands between two spatially separated signals. Cooperative behavior between distant cortical sites was first described by Livanov and Anan'ev in 1955 [9], who assumed that coherent oscillations of spatially separate groups of neurons reflect their participation in the same function, viz., encoding various aspects of the processed information. Since that time the sensitivity and robustness of EEG coherence methods have been documented in a variety of research contexts [12], including musical perception [15] and emotional regulation [1,14].

In the current study, we examine coherence *differences* in theta, alpha, beta and gamma bands during listening to consonant and dissonant musical chords as well as to single notes. In addition, we explore the possibility of relationships between EEG coherence and the subjects' emotional judgment and judgment of harmony.

Fifteen healthy right-handed non-musicians (22–31-year-old; mean age 27.2 ± 4.1; seven males, eight females) with normal hearing participated in the study. They gave written informed consent to the study.

The EEG was recorded during an experimental session, which consisted of 12 stimulus blocks alternating with periods of silence, 64 s of each. There were three different types of stimulus blocks (conditions), each type was presented four times in random order. In consonant blocks (CONS), all stimuli were four-note consonant chords, created on the basis of the Western classical theory of harmony, either in major or in minor mode. In dissonance blocks (DISS), four-note dissonant chords were created from the consonant chords by shifting the tone on the bass position upward by one semitone. In control blocks (CONT), the stimuli were the individual notes of which the chords were made up. Each stimulus block contained 32 different chords or 36 different notes covering three octaves (from C3 (130.8 Hz) to C6 (1046.5 Hz)), 700 ms duration. All stimuli were presented in random order with inter-stimulus intervals varying randomly between 700 and 1400 ms. All stimuli were created to be of piano timbre using the CubasisVST-4.0® software and were run by Presentation®. Stimuli were presented binaurally via headphones with sound levels adjusted individually to be of comfortable loudness.

The EEG was recorded by means of the 32-channel BrainAmpMR system (Brain Products, Germany), with vertex reference, 500 Hz of sampling rate, bandwidth 0.3–70 Hz. Electrode impedances were kept below 2 kΩ.

EEG data were processed using the Analyzer 1.03® software (Brain Products). Analytically derived average reference (Avg) was calculated. Artifact free 2 s epochs overlapped by 50% were multiplied by Hanning window and Fourier transformed. Coherence (C) was computed for all possible pairs of the 24 EEG electrodes (Fig. 1D) ($n = 276$) for theta-1 (4–6 Hz), theta-2 (6–8), alpha-1 (8–10.5), alpha-2 (10.5–13), beta-1 (13–20), beta-2 (20–40), gamma-1 (40–50), and gamma-2 (50–70) frequency bands ([14], for details). We calculated the *differences* between the Fisher z-transformed C obtained from the various stimulus conditions and those measured
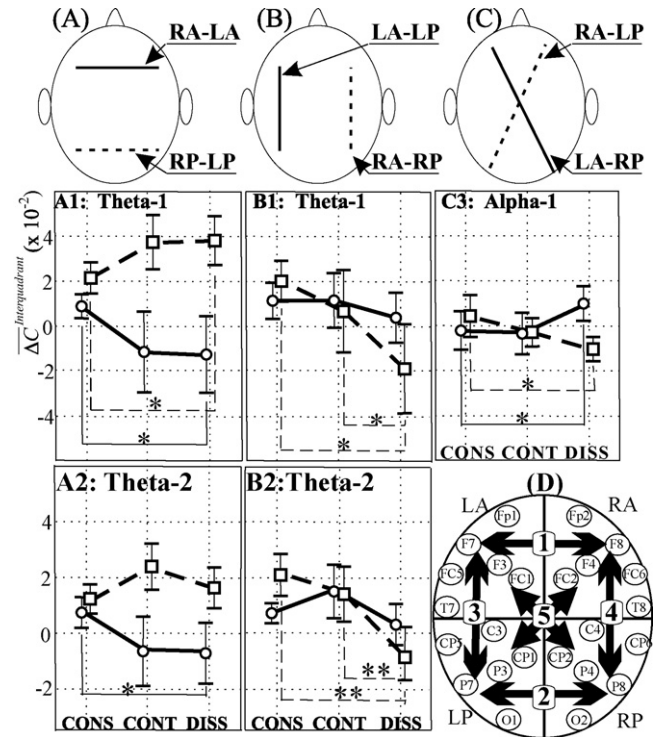

Fig. 1. ANOVA effects of inter-quadrant coherence differences, $\overline{\Delta C}^{\text{Interquadrant}}$, for three experimental conditions: CONS, CONT, DISS. Brackets denote significance obtained using the planned comparison method, $^{*}p < 0.05$; $^{**}p \leq 0.005$. Vertical bars denote standard errors. On the top: schematic two-way decomposition for ANOVAs. (D) Schematic representation of parcellation of electrodes into four quadrants: 1—*Homotopic heterolateral anterior*, 2—*Homotopic heterolateral posterior*, 3—*Heterotopic homolateral left*, 4—*Heterotopic homolateral right*, 5—*Heterotopic heterolateral*.

during the periods of silence $[C_{\text{CONS}} - C_{\text{Silence}} = \Delta C_{\text{CONS}}$; $C_{\text{DISS}} - C_{\text{Silence}} = \Delta C_{\text{DISS}}$; $C_{\text{CONT}} - C_{\text{Silenc}} = \Delta C_{\text{CONT}}]$.

To make sure that volume conduction is not misinterpreted as functional connectivity [12] we calculated both (1) relative phase shifts ($\Delta \varphi$) between the two signals at each frequency and (2) ΔC from current source densities (CSD).

For ANOVA, the 24 EEG electrodes were subdivided into four quadrants: left anterior (LA), right anterior (RA), left posterior (LP) and right posterior (RP) (Fig. 1D). This division allowed us to simplify the statistical model by reducing the number of variables and test the null hypothesis that functional connectivity between quadrants was equal with respect CONS/DISS/CONT conditions. This reduction was achieved by averaging the 36 possible inter-quadrant ΔC for each condition to yield a mean inter-quadrant coherence difference, $\overline{\Delta C}^{\text{Interquadrant}}$. The following inter-quadrant combinations and locations were examined (See Fig. 1D): (1) homotopic heterolateral quadrants at anterior and posterior locations (LA–RA vs. LP–RP), (2) heterotopic homolateral quadrants in the left and right hemisphere (i.e., LA–LP vs. RA–RP) and (3) heterotopic heterolateral quadrants along the two diagonals (LA–RP vs. RA–LP). For each frequency band and for the six inter-quadrant combinations two-way ANOVAs were run independently, involving factors of the *Experimental condition* (Con)

(3: CONS, CONT, DISS) and *Location* (Loc) at two levels, and followed by planned comparison. In addition, ΔC for all possible electrode pairs within a given quadrant ($n = 15$) were averaged and the resulting mean intra-quadrant coherence difference, $\overline{\Delta C}^{\text{Intraquadrant}}$, was subjected to a two-way ANOVA with the factors of Con (3: as above) and Loc (4: LA, LP, RA, and RP). To explore gender differences three-way ANOVAs were run with the *Sex* as an additional between-subjects factor in the above ANOVAs. The Greenhouse–Geisser epsilon correction was used where appropriate; the corrected *p*-values are presented.

To examine the topographic representation of all possible single differences of ΔC between selected conditions, Student's *t*-tests for dependent samples were run.

During the EEG sessions and at the end of each stimulus block participants had been instructed to rate, how pleasant they considered the stimuli in that block to have been overall, by pressing a button from once (very pleasant) to six times (very unpleasant). As the semantic field of emotions has multi-dimensional structure and is composed of several complimentary word pairs [19], participants were asked, after the EEG experiment, to listen to the same stimulus material again and to rate each stimulus block along four additional scales with the extremes defined as "*interesting–boring*," "*happy–sad*," "*new–known*," "*calm–upset*" and to repeat the rating along the "*pleasant–unpleasant*" scale. To obtain a rating on a more "sensorial" aspect of harmony processing [16], CONS and DISS blocks had to be also rated along a "*degree of harmony*" scale with the extremes defined by "*harmonic–disharmonic*."

The ratings of "*pleasantness*" obtained by the two methods were closely correlated (Spearman $R = 0.749$; $p = 0.004$). Therefore, only the ratings made after the EEG experiments were used further, since they were obtained under the same conditions as the other four emotional and the harmony ratings.

Only the ratings of "*pleasantness*," "*familiarity*" *(new-known)* and "*degree of harmony*" differed for CONS, DISS and CONT conditions (Wilcoxon test). CONS was rated significantly more pleasant than DISS ($p = 0.003$) and more pleasant than CONT ($p = 0.009$). DISS was rated significantly more unpleasant than CONT ($p = 0.007$). The DISS was rated to be less familiar than CONS ($p = 0.01$) and CONT ($p = 0.02$). The difference between ratings of CONS, DISS, and CONT along the other scales were non-significant. The "*degree of harmony*" of CONS was rated higher than that of DISS ($p = 0.01$). The rating of "*familiarity*" was positively correlated with that of "*pleasantness*" when CONS blocks were treated separately (Spearman's coefficient, $R = 0.64$, $p = 0.01$) and when CONS and DISS blocks were combined ($R = 0.490$, $p = 0.003$), It is noteworthy that the ratings of "*pleasantness*" and of "*degree of harmony*" were not significantly correlated. This result was unexpected and disagreed with previous data of 1965 [16]. Upon inquiry, some subjects reported a preference for modern music in which dissonance dominates. Such ratings may reflect differences in the musical taste between the young generation now and that in the 1960s.

ANOVAs of mean inter-quadrant differences, $\overline{\Delta C}^{\text{Interquadrant}}$, revealed significant main effects or interactions only in theta-1, theta-2, and alpha-1 frequency bands (Fig. 1).

Homotopic heterolateral quadrants: Significant Con × Loc (2: *anterior, posterior*) interactions were found in both theta-1 ($F(2, 28) = 4.40$; $p = 0.03$) (Fig. 1, A1) and theta-2 ($F(2, 28) = 3.64$; $p = 0.048$) (Fig. 1, A2) bands. Significant Loc effect was found in theta-1 band ($F(1, 14) = 7.59$; $p = 0.015$). For thetha-1, the interactions were due to the fact that $\overline{\Delta C}^{\text{Interquadrant}}$ between heterolateral quadrants at the anterior positions were larger for CONS than for DISS (Planned comparison: $F(1, 14) = 4.65$; $p = 0.049$), whereas at posterior positions it was larger for DISS than for CONS ($F(1, 14) = 4.79$; $p = 0.047$). For thetha-2, differences were limited to anterior positions ($F(1, 14) = 5.12$; $p = 0.04$).

Heterotopic homolateral quadrants: the ANOVAs revealed a significant Con effect in both theta-1 ($F(2, 28) = 3.87$; $p = 0.05$) (Fig. 1, B1) and theta-2 $F(2, 28) = 4.83$; $p = 0.03$ bands (Fig. 1, B2). Con × Loc (2: *Left, Right*) interaction was found in theta-2 band, $F(2, 28) = 4.89$; $p = 0.02$. The planned comparison confirmed significant larger $\overline{\Delta C}^{\text{Interquadrant}}$ for CONS than for DISS ($F(1, 14) = 13.0$; $p = 0.003$) and for CONT than for DISS ($F(1, 14) = 10.8$; $p = 0.005$) only in the right hemisphere.

Heterotopic heterolateral quadrants: The significant Con × Loc (2: LA–RP, RA–LP) interaction ($F(2, 28) = 5.00$; $p = 0.01$) in the alpha-1 band was due to a larger $\overline{\Delta C}^{\text{Interquadrant}}$ for CONS than for DISS along the axis "RA–LP" ($F(1, 14) = 4.76$; $p = 0.04$), and a larger $\overline{\Delta C}^{\text{Interquadrant}}$ for DISS than for CONS along the axis "LA –RP" $F(1, 14) = 6.0$; $p = 0.028$ (Fig. 1, C3).

ANOVAs of mean intra-quadrant differences, $\overline{\Delta C}^{\text{Intraquadrant}}$, revealed a significant interaction Con × Loc (4: LA, RA, LP, RP) in theta-1 ($F(6, 84) = 2.95$; $p = 0.01$) and theta-2 ($F(6, 84) = 2.79$; $p = 0.02$) bands. The planned comparison demonstrated a larger $\overline{\Delta C}^{\text{Intraquadrant}}$ for CONS than for DISS in the RA quadrant in both theta-1 ($F(1, 14) = 8.72$; $p = 0.01$) and theta-2 $F(1, 14) = 5.92$; $p = 0.03$ bands and in the RP quadrant in the theta-2 band ($F(1, 14) = 3.89$; $p = 0.05$). A larger $\overline{\Delta C}^{\text{Intraquadrant}}$ for DISS than for CONS was found in the LP quadrant in the theta-1 band ($F(1, 14) = 4.79$; $p = 0.047$).

There were no significant gender differences.

The topographic pattern of individual coherence differences, ΔC, elicited by listening to CONS and DISS is shown in Fig. 2.

Inter-hemispheric differences: In the theta-1 band, listening to CONS compared to DISS was accompanied by significantly larger ΔC between electrodes over an anterior region of the right hemisphere (F4, FC2) and a cluster of electrodes over frontal, central and temporal areas of the left hemisphere (Fig. 2, A1; solid lines; areas filled with checkerboard pattern). In contrast, listening to DISS compared to CONS was accompanied by larger ΔC between electrodes over more posterior regions of the right hemisphere (CP2, P4) and a cluster of electrodes over central, parietal and occipital areas of the left hemisphere (Fig. 2, A1; dashed lines; hatched areas). In the theta-2 band, listening to CONS compared to DISS was accompanied by significantly larger ΔC between clusters of electrodes over frontal to central regions in both hemispheres (Fig. 2, A2: solid lines; areas filled with checkerboard pattern). In the alpha-1 band, listening to CONS compared to DISS was accompanied by
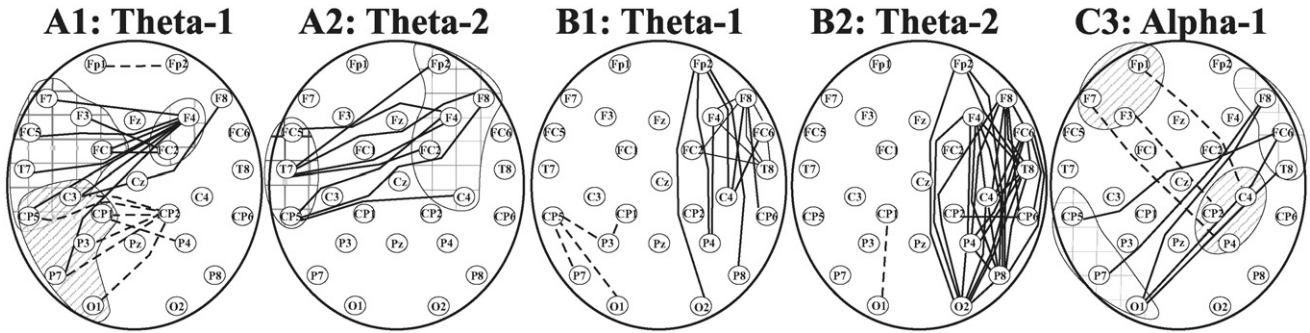
Fig. 2. Topographic representation of EEG coherence differences, ΔC, between CONS and DISS conditions. A solid line connecting two electrodes represents a significantly ($p < 0.05$) higher coherence for CONS than for DISS. A dashed line represents a significantly higher coherence for DISS than for CONS. Checkerboard pattern identifies two spatially separated areas between which inter-hemispheric coherence for CONS was higher than for DISS. Hatched pattern identifies two areas between which coherence for DISS was higher than for CONS.

stronger ΔC between electrodes along the axis "right anterior (F8, FC6, T8)—left posterior (CP5, P7, O1)" (Fig. 2, C3; solid lines; areas filled with checkerboard patterns) and listening to DISS compared to CONS was accompanied by stronger ΔC was accompanied between electrodes along the axis "left anterior (Fp1, F7, F3)—right posterior (C4, CP2, P4)" (Fig. 2, C3; dashed lines; hatched areas).

Intra-hemispheric differences: In the theta-1 and theta-2 bands listening to CONS compared to DISS was paralleled by higher ΔC exclusively in the right hemisphere and involved nearly all electrodes (Fig. 2, B1, B2; solid lines). CONT condition contrasted to DISS revealed higher ΔC for CONT, with very similar right inter-hemispheric topographic pattern to that found for CONS versus DISS (without picture). Listening to DISS compared to CONS was paralleled by stronger ΔC exclusively in the left hemisphere, but with an involvement of only few posterior electrodes (Fig. 2, B1, B2; dashed lines).

We also found correlations between coherence and ratings of the stimulus material. Specifically, the $\overline{\Delta C}^{\text{Interquadrant}}$ in the

right hemisphere was positively correlated with the rating of "*pleasantness,*" in both theta-1 and theta-2 bands. This was true when CONS, DISS and CONT blocks were combined (for theta-1: Spearman's coefficient $R = 0.366$, $p = 0.013$; for theta-2: $R = 0.358$, $p = 0.015$) (Fig. 3A). In addition, for theta-1 significant correlations were also found also when the CONS condition was treated separately ($R = 0.521$, $p = 0.046$). The topography of significant relationships between ΔC and the rating of "*pleasantness*" (for combined CONS, DISS and CONT blocks) is presented on Fig. 3B (R: between 0.50 and 0.79).

Positive correlations of individual ΔC with the rating of "*degree of harmony*" were seen in the theta-2 band (Fig. 3C; solid lines), although for few anterior-frontal and occipital (Fp1-O1) and central-frontal and central-parietal (FC5-CP5) pairs within the left hemisphere ($R = 0.519$ and 0.641, respectively).

Significantly negative correlations of ΔC with the rating of "*familiarity*" were found in the alpha-1 band for electrodes of the LA quadrant (F3, FC1) and RP quadrant (CP2, P4, O2) (R between 0.787 and 0.514) (Fig. 3D, dashed lines).
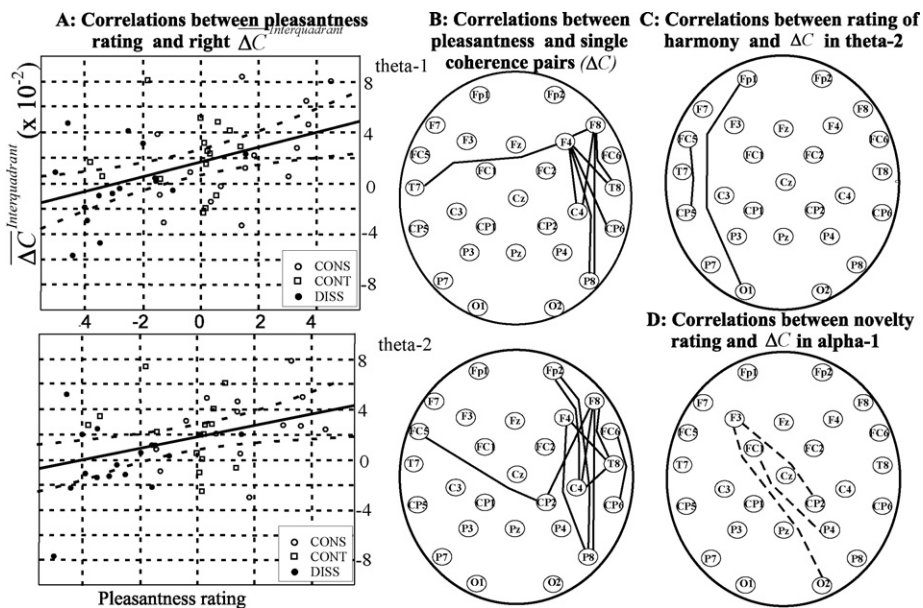

Fig. 3. (A) Correlations between pleasantness rating and right intra-hemispheric mean coherence, $\overline{\Delta C}^{\text{Interquadrant}}$. Correlations between individual EEG coherence, ΔC, and (B) pleasantness rating; (C) rating of harmony; (D) rating of novelty. A solid line connecting two electrodes represents significant positive correlations ($p < 0.05$). A dashed line represents significant negative correlations.

The patterns of significant ΔC found with CSD were very similar to the patterns found with the Avg. It is noteworthy that significance levels of consonance versus dissonance differences were generally higher for ΔC based on CSD than for ΔC based on Avg. Here, we only present the results based on Avg since this is the more conservative method.

The inspection of $\Delta\varphi$ revealed that it was not in the vicinity of 0 or $\pm\pi$ for the vast majority of pairs in theta-1, theta-2, alpha-1 bands, indicating no considerable effect of volume conductance.

We found anterior–posterior differences of CCHP, namely stronger connectivity between frontal regions for CONS compared to DISS, and stronger connectivity between posterior regions for DISS compared to CONS. This result is consistent with findings of Petsche and Etlinger [15]. They observed increased coherences in the theta band restricted to the anterior half of the brain for listening to classical and baroque music. The region of increased coherence extended more posteriorly for listening to music of Schönberg. The most significant differences between Schönberg's and baroque-classical music concern the harmony structure. Schönberg's musical style is characterized by non-resolved dissonance, which was avoided during the baroque and classical periods.

To explain both our data and literature [15] the functional role of theta oscillations deserves special consideration. A growing body of evidence shows that changes in the theta band may reflect an encoding and retrieval of information [8] and emotion-related processes [1,14]. It is generally accepted that theta-activity is induced in the cortex via limbic-hippocampal-cortical feedback loops ([8] for review],) which are traditionally regarded as being associated with fundamental memory related and emotional operations. Consonance is more abundant than dissonance in natural acoustic environments and in human speech [20]. This suggests that the consonance–dissonance distinction might recruit very basic aspects of implicit memory and related mechanisms of emotional regulation, which heavily rely on the integrative capability of frontal associative cortex. This line of argument can enlighten us to the role of theta-oscillating inter-hemispheric anterior networks in processing consonance, but cannot explain the contribution of posterior inter-hemispheric interaction in processing dissonance.

In order to deal with posterior interaction we suggest that the consonance–dissonance distinction should be viewed as an "attempt" at solving a general sensory problem before reaching the cognitive level, namely the problem of acoustical spatial processing and sound source segregation. This line of thought comes from the well-documented psychoacoustical phenomenon of mistuned complex tone perception [11]. The mistuning of a single harmonic component in harmonic tones results in a percept of two tones with two distinct pitches, one resulting from the fundamental frequency of the residual harmonic tone and one of the mistuned single harmonic [11]. Combinations of harmonic tones in which the fundamentals and harmonics do not show simple integer ratios (like dissonant chords in our experiment) produce not only the percept of disharmony [18], but also a breakdown of the percept of a unitary sound [11], leading to the impression that more than one auditory object is heard. The latter effect can be termed "auditory object dissociation."

Looking at natural sound environments, dissonant sounds are most likely produced by different sound sources with independent harmonic structures. Hence, the auditory system might be programmed to interpret dissonance as coming from a number of independent sources. Following our "auditory object dissociation" hypothesis, the dissonant chords might have been perceived accordingly. Hence, the listening to dissonant stimuli may lead to an increased coherent behavior of neural substrates specialized for spatial encoding in order to identify special positions of auditory objects. Results obtained in both animal and human studies indicate the involvement of the posterior cortex in the representation of space [10,17]. Therefore, higher inter-hemispheric coherence in posterior regions for dissonance found in our study may be associated with mechanisms of spatial encoding.

We have also shown left-right differences of CCHP. In the theta bands, the contrast yielded stronger right intra-hemispheric connectivity for CONS, which is associated with emotional appreciation of harmony. This is consistent with previous findings indicating the importance of the right hemispheric connectivity for emotional regulation [14] and is also in concordance with the concept of right hemisphere involvement in mediation of emotional arousal [5].

The transfer of information provided by theta-2 oscillators within the left hemisphere might play a role in differentiation of the degree of harmony without emotional interpretation. This finding is in line with our fMRI data showing the importance of the left auditory cortex in the CONS–DISS distinction [13].

Analysis of alpha-1-oscillation revealed higher coherence for DISS than for CONS along the axis "left anterior - right posterior" (Fig. 2, C3). We have also observed a significant negative relationship between familiarity ratings and coherence along this axis, pointing to a higher connectivity for less familiar, in our case dissonant, stimuli. Remarkably, connections between left anterior and right posterior regions were found to have functional importance in information processing, especially in non-standard novel situations [21]. As the alpha-1 band is sensitive to attention demands and reflects changes in phasic alertness [7], the observed pattern may also be discussed as a reflection of an alerting effect of dissonant stimuli.

Acknowledgments

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