SPECIAL ISSUE: POSITION PAPER

SIGNIFICANCE OF BROCA'S AREA AND VENTRAL PREMOTOR CORTEX FOR MUSIC-SYNTACTIC PROCESSING

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ABSTRACT

This paper suggests that a cortical network comprising inferior frontolateral cortex [IFLC, corresponding to Brodmann's area (BA) 44], ventrolateral premotor cortex (vlPMC), and anterior superior temporal gyrus (aSTG) is involved in the processing of musical structure. This network presumably calculates harmonic relations between a chord and a preceding harmonic sequence, is involved in the detection of music-structural irregularities, and organizes fast short-term predictions of upcoming musical events.

Key words: music, syntax, Broca's area, BA 44, ventral premotor cortex

In major-minor tonal music, chord functions are arranged within harmonic progressions according to regularities. For example, a dominant seventh chord at the end of a chord sequence is regularly followed by a tonic (top left of Figure 1). Chord functions other than the tonic represent structural irregularities, especially when they are only distantly related to the tonic (bottom left of Figure 1). The regularity-based arrangement of chord functions within harmonic progressions establishes a harmonic structure that may be considered as part of a musical syntax. Musical syntax also comprises other structural aspects, e.g. melodic, rhythmic, metric, and timbral structure. This paper mainly focuses on the processing of harmonic structure as one aspect of music-syntactic processing.

Some recent neurophysiological studies have used chord sequence paradigms to investigate neural correlates of the processing of structurally regular and irregular chord functions with electroencephalography (EEG; e.g., Patel et al., 1998; Koelsch et al., 2000, 2001; Koelsch and Mulder, 2002; see also Koelsch and Friederici, 2003), magnetoencephalography (MEG; Maess et al., 2001), and functional magnetic resonance imaging (fMRI; e.g., Koelsch et al., 2002, 2005; Tillmann et al., 2003; see Koelsch, 2005, for an overview). In the mentioned MEG and EEG studies, music-structurally irregular chords elicited anterior brain responses that had negative polarity over frontal regions, and emerged around 150-350 msec after the onset of an irregular chord. These negativities were denoted as early right anterior negativity (ERAN, maximal around 200 msec; Koelsch et al., 2000; Maess et al., 2001), or right anterior-temporal negativity (RATN, maximal around 350 msec; Patel et al., 1998; Koelsch and Mulder, 2002). Especially the ERAN is reminiscent to other deviance-related negativities, e.g. the mismatch negativity (MMN, which reflects the detection of irregularities on a sensory level; Näätänen, 1992), the early left anterior negativity (ELAN, which reflects processing of structure in language; Friederici, 2002), and the phonological MMN (related to expectancies for the sound of a phoneme; Connolly and Phillips, 1994).

The main generators of the ERAN were localized with MEG in the inferior frontolateral cortex (IFLC – inferior pars opercularis – corresponding to inferior BA 44; Maess et al., 2001). Additional contributions from generators located in the anterior portion of the superior temporal gyrus (aSTG) have been suggested by source localizations using EEG data (Koelsch et al., submitted). These source localizations have been corroborated by functional imaging studies from Koelsch et al. (2002, 2005); in these studies, the pars opercularis (both inferior and superior BA 44), as well as anterior superior temporal lobe structures were found to be activated. Moreover, activations of IFLC in relation to the processing of musical syntax have also been shown in other fMRI studies investigating the processing of harmonic structure (Parsons, 2001; Tillmann et al., 2003), melodic structure (Janata et al., 2002a; Parsons, 2001), rhythmic structure (Platel et al., 1997; Parsons, 2001), timbral structure (Janata et al., 2002a, 2002b), as well as in fMRI studies investigating listening to music under the instruction to track one voice within a multipart composition (Janata et al., 2002b; Satoh et al., 2001). These findings indicate that IFLC is important for the processing of musical structure in general, and not only important for the processing of harmonic structure.

In the mentioned studies from Parsons (2001),

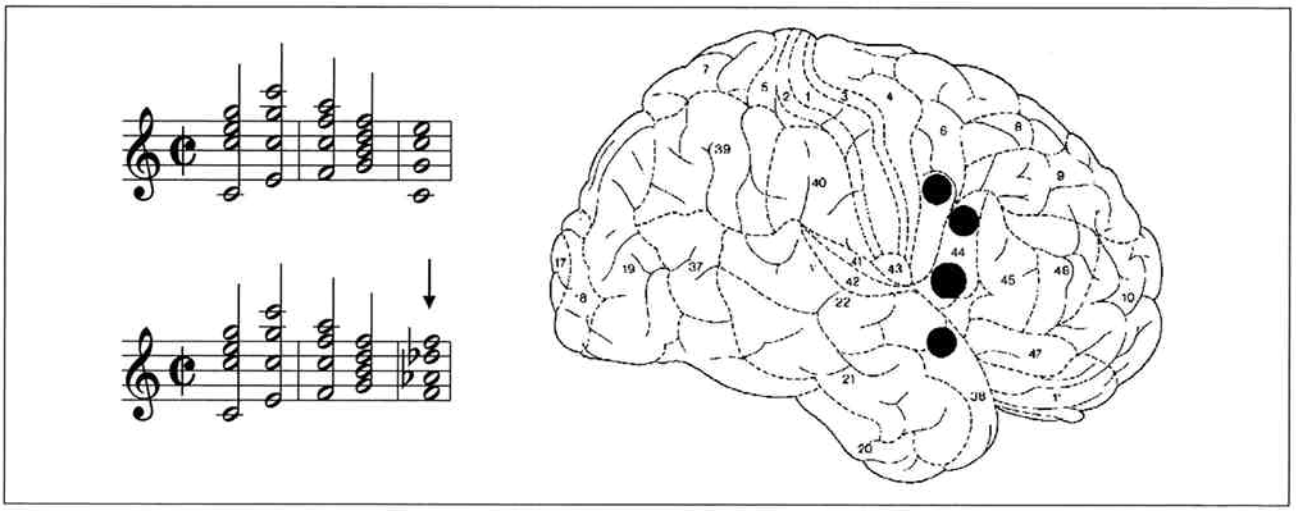

Fig. 1 – *Left: Sequences ending on music-structurally regular (top) and irregular chords (bottom, the irregular chord is indicated by the arrow). Right: Brain structures that are presumably involved in the processing of musical structure: vlPMC, IFLC, and aSTG.*

Janata et al. (2002b), Koelsch et al. (2002, 2005), and Satoh et al. (2001), additional frontal activations were observed in the ventrolateral premotor cortex (vlPMC). The data reported by Tillmann et al. (2003) indicate that not only processing of music-syntactically irregular, but also processing of regular chord functions activates premotor cortex (PMC), and unpublished data from our lab suggest that BA 44 is also activated by the processing of normal musical structure (i.e., not only by the processing of music-structural irregularities).

In the studies from Koelsch et al. (2002, 2005), and Satoh et al. (2001), activations were also observed in posterior temporal areas; these activations appear to be involved in processes of harmonic integration, and possibly the processing of musical semantics (this issue will not further be discussed in this article, for more detailed discussions see Koelsch, 2005). With this respect it is important to note that processing of musical syntax usually also activates other brain functions such as processing of semantics, attention, memory, and emotion, making it challenging to pin down brain activations that are specifically related to music-syntactic processing.

However, the combined findings obtained with EEG, MEG, and fMRI suggest that the processing of musical structure involves a cortical network comprising IFLC (BA 44, inferior and superior pars opercularis), vlPMC, and aSTG (right of Figure 1). Activations of IFLC (BA 44) and vlPMC have been reported in some functional imaging studies on auditory processing using musical stimuli (see above), linguistic stimuli (Friederici, 2002), auditory oddball paradigms (Opitz et al., 2002), pitch discrimination tasks (Zatorre et al., 1992, 1994; Griffith, 2001, 2003; Gandour et al., 2000; Gaab et al., 2003), and serial prediction tasks (Schubotz and von Cramon, 2002a).

On a more abstract level, IFLC (BA 44), and the vlPMC have been considered to be involved in the analysis, recognition and prediction of sequential auditory information (Schubotz and von Cramon, 2002a; Schubotz et al., 2003; Conway and Christiansen, 2001; Huettel et al., 2002): fronto-opercular cortex, along with vlPMC, recognizes structural properties (rather than simple acoustic properties) of complex auditory sequences, and these areas are involved in a fast short-term prediction of upcoming events. The processing of events that violate a prediction activates these areas (compared, e.g., to events that are predicted).

The processing of structural properties, and the detection of structural irregularities, requires the computation of structural relations between sequential events. In the mentioned music experiments that used chord sequence paradigms to investigate the processing of harmonic structure, the music-structural analysis of the chord functions required a computation of the harmonic relation between a chord and the preceding harmonic context. This computation is more difficult for the irregular chord functions than for the regular chord functions, because (a) the harmonic relation was more distant between the irregular chords and the preceding harmonic context (compared to the close harmonic relation between regular chords and preceding harmonic context; for further explanations see Koelsch et al., 2000), and (b) the computation of the relation is less common for irregular than for regular chords. This increased difficulty in computing the relation between the irregular chord function and the preceding harmonic context possibly led to a stronger activation of BA 44 and vlPMC. As a result, the irregular chords may be perceived consciously as unexpected.

Whether neural substrates of the computation of harmonic relations, the detection of a structural irregularity, and processes of (serial) prediction during the processing of chord sequences can

functionally and anatomically be distinguished from each other remains to be specified. Likewise, it remains to be specified if the areas in which knowledge about musical syntax is stored are identical with areas that are involved in the analysis of music-syntactic information (see also Patel, 2003).

Interestingly, it has been suggested that there might be an immediate link between the prediction of upcoming events and a representation of corresponding motor schemas in the lateral PMC to enable an immediate mapping of perception onto action, in the mentioned music-studies premotor programs for articulation, or *vocal plans* (Schubotz and von Cramon, 2002b). Such a mapping is needed, e.g., when singing along in a group. Note that during the observation of actions in the visual domain, the activation of premotor representations is regarded to provide a neurophysiological basis for the understanding and learning of these actions (e.g., Fadiga et al., 2000). Similarly, activations of PMC during the processing of music structural irregularities (possibly related to programs for articulation) might also play a role for the learning and understanding of musical structure.

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