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Special issue: Research report

Predictive coding of music – Brain responses to rhythmic incongruity

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ARTICLE INFO

Article history:
Received 11 January 2007
Reviewed 29 May 2007
Revised 20 July 2007
Accepted 7 May 2008
Published online 14 November 2008

Keywords:
Music
MEG
Meter
Predictive coding
MMN

ABSTRACT

During the last decades, models of music processing in the brain have mainly discussed the specificity of brain modules involved in processing different musical components. We argue that predictive coding offers an explanatory framework for functional integration in musical processing. Further, we provide empirical evidence for such a network in the analysis of event-related MEG-components to rhythmic incongruence in the context of strong metric anticipation. This is seen in a mismatch negativity (MMNm) and a subsequent P3am component, which have the properties of an error term and a subsequent evaluation in a predictive coding framework. There were both quantitative and qualitative differences in the evoked responses in expert jazz musicians compared with rhythmically unskilled non-musicians. We propose that these differences trace a functional adaptation and/or a genetic pre-disposition in experts which allows for a more precise rhythmic prediction.

1. Introduction

Models of music processing in the brain have primarily discussed specificity of brain modules involved in processing musical components. In contrast to language processing, primarily located in the left hemisphere, music processing was originally suggested to be right-lateralized (Luria et al., 1965; Signoret et al., 1987). A more detailed modular viewpoint was recently expressed by Peretz and Coltheart (2003) who demonstrated that anatomically distinct sub-modules were not necessarily confined to one hemisphere to process different aspects of music. The Peretz–Coltheart model, based mainly on lesion studies and on studies of acquired and congenital amusia, emphasizes modular specificity at the expense of brain integration. It adequately accounts for certain aspects of neural musical processing particularly processing of pitch (Liegeois-Chauvel et al., 1998; Mendez, 2001; Peretz et al., 1994). However, it fails, Peretz et al. acknowledge, to fully account for processing of rhythm and meter. This appears problematic, as rhythm and meter are constitutive elements of musical structure, and influence how music is perceived and

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0010-9452/$ – see front matter
doi:10.1016/j.cortex.2008.05.014

understood (Benjamin, 1984; Dalla and Peretz, 2005; Schmuckler and Boltz, 1994).

Recently, Friston (2002) provided a promising model of brain function, in which predictive coding, as a central principle of brain organization, provides a link between segregation and integration (for similar viewpoints see Shepard, 2001; Tononi and Edelman, 1998). The model proposes that the interaction between segregation and integration may be described by predictive coding, interpreted in a hierarchical brain organization whereby lower level brain areas estimate predictions of their expected input based on contextual information through backward connections from higher level areas. A comparison between prediction and actual input produces an error term that, if sufficiently large, will be fed forward to call for an update of the model. This generates a recursive process, which aims at minimizing the difference between input and prediction. As representational capacity of any neuronal assembly in this model is dynamic and context sensitive, it addresses the issue of top–down processing (Frith and Dolan, 1997; Roepstorff and Frith, 2004).

The predictive coding model entails that the brain constantly tries to extract structural regularities from the surroundings. This concept is well-established in psychology and neurobiology (Mehta, 2001; Schultz and Dickinson, 2000), and has been successfully applied in several fields, e.g., motor control and social interaction (Blakemore et al., 1998; Wolpert et al., 2003), object perception (Kersten et al., 2004) and visual integration (Rao and Ballard, 1999). In this study, we have employed magnetoencephalography (MEG) to test two hypotheses: (1) that neuronal markers of rhythmic incongruities behave in accordance with a predictive coding framework, (2) that musical competence affects the composition of the neuronal networks involved in the processing of rhythm by affecting the neuronal integration.

The human auditory system appears to segregate the auditory environment into meaningful streams according to specific rules, and this forms the basis of a prediction of the near auditory future (Bregman, 1990). As a special case, the rhythmic regularity in music is generated by expectations created in different layers of the musical structure (Bharucha and Stoeckig, 1986; Meyer, 1956; Sloboda, 1985). This depends critically on the timing structure provided by the meter, which is based on a fundamental opposition between strong and weak beats (see, e.g., Cooper and Meyer, 1960; Vuust, 2000). Meter provides the listener with a temporal, hierarchical expectancy structure, underlying the perception of music, in which each musical time-point encompasses a conjoint prediction of timing and strength (Large and Kolen, 1994).

When metric expectancy structure is violated, it may elicit strong perceptual responses including sensation of tension (Vuust et al., 2006), shift of attention (Jones and Boltz, 1989) and laughter (Huron, 2004). Violations of meter, especially in music favouring a regular beat, therefore appear particularly well suited as substrate for critical examination of the predictive coding model of brain function. If the predictive coding theory is correct, we hypothesize that meter violation generates an error term at the neural level, the size of which depends on degree of violation. If the violation is sufficiently large, it may cause a subsequent evaluation that involves higher level neuronal structures. The first error term should occur locally, while the putative subsequent evaluation would involve integration across hierarchies of neuronal processing. We therefore created rhythm sequences of increasing rhythmic incongruence and measured brain responses with MEG to test the hypothesis that pre-attentive neural responses to increasing rhythmical incongruity could be identified, and would be congruent with an error term and subsequent evaluation.

We hypothesized that rhythmic incongruities would elicit the magnetic counterpart of the mismatch negativity (MMNm), an event-related field (ERF), peaking around 100–200 ms from change onset, an index of pre-attentive detection of change in some repetitive aspect of auditory stimulation (Naatanen, 1992), accompanied by a later component the P3a: usually associated with the evaluation of that change for subsequent behavioral action and believed to indicate activity in a network which contains frontal, temporal and parietal sources (Friedman et al., 2001).

According to Winkler et al. (1996), MMN reflects a modification of the pre-attentive model of the acoustic environment. This is caused by the incorporation of a new auditory event that mismatches the actual inferences of the model (the model adjustment hypothesis). This is highly compatible with the predictive coding theory which implies that the error term to unexpected events depends on an interaction between the objective differences in stimulus structure and the degree of detail in the expectancy structure. Musicians are known to have longer and more precise temporal integration windows compared to non-musicians (Russeler et al., 2001), more fine-grained representation of temporal structure (Jongsma et al., 2004) and higher sensitivity when detecting small time changes embedded within simple rhythmic patterns (Jones and Yee, 1997). If the predictive coding theory is correct, then the more detailed expectancy structure in musicians should influence both neuronal markers of the prediction error and the neuronal markers of evaluation. We therefore compared rhythmically unskilled non-musicians with expert jazz musicians. Jazz musicians use challenging rhythmic material in their musical performance and are therefore ideal candidates for identifying putative competence dependent differences in the processing of metric violations. We have previously described a leftward lateralization in musicians compared to non-musicians when exposed to rhythmically challenging material (Vuust et al., 2005). We here extend the analysis to the P3a component and demonstrate how the findings may be explained by a predictive coding framework.

2. Materials and methods

2.1. *Subjects, stimuli and task*

Nine expert jazz musicians (8 men and 1 woman; mean age = 27.22, SE = 1.68; from the Sibelius Academy of Music, Helsinki, Finland), scoring more than 14 in a modified version of the rhythm imitation test employed at the entry examination for Danish music conservatories, and eight rhythmically unskilled non-musicians (6 men and 2 women; mean age = 24.5, SE = 0.87), scoring less than 3 in the rhythm test,