CrossMark

Neural networks for harmonic structure in music perception and action

R. Bianco [a,*], G. Novembre [b], P.E. Keller [b], Seung-Goo Kim [a], F. Scharf [a], A.D. Friederici [a], A. Villringer [a], D. Sammler [a]

[a] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany
[b] The MARCS Institute for Brain, Behaviour and Development, Western Sydney University, Sydney, Australia

ABSTRACT

The ability to predict upcoming structured events based on long-term knowledge and contextual priors is a fundamental principle of human cognition. Tonal music triggers predictive processes based on structural properties of harmony, i.e., regularities defining the arrangement of chords into well-formed musical sequences. While the neural architecture of structure-based predictions during music *perception* is well described, little is known about the neural networks for analogous predictions in musical *actions* and how they relate to auditory perception. To fill this gap, expert pianists were presented with harmonically congruent or incongruent chord progressions, either as musical actions (photos of a hand playing chords) that they were required to watch and imitate without sound, or in an auditory format that they listened to without playing. By combining task-based functional magnetic resonance imaging (fMRI) with functional connectivity at rest, we identified distinct sub-regions in right inferior frontal gyrus (rIFG) interconnected with parietal and temporal areas for processing action and audio sequences, respectively. We argue that the differential contribution of parietal and temporal areas is tied to motoric and auditory long-term representations of harmonic regularities that dynamically interact with computations in rIFG. Parsing of the structural dependencies in rIFG is co-determined by both stimulus- or task-demands. In line with contemporary models of prefrontal cortex organization and dual stream models of visual-spatial and auditory processing, we show that the processing of musical harmony is a network capacity with dissociated dorsal and ventral motor and auditory circuits, which both provide the infrastructure for predictive mechanisms optimising action and perception performance.

© 2016 Elsevier Inc. All rights reserved.

1. Introduction

The brain shows a fine sensitivity to patterns and regularities that afford the prediction of incoming events in different domains (Tenenbaum et al., 2011). The theory of predictive coding (Friston, 2010) constitutes a unifying framework for human cognition and considers the brain as a "hypothesis tester" with the goal to optimise perception and action by constantly matching incoming sensory inputs with top-down predictions. Within a multi-level cascade of neural processes at different time scales, higher-level predictions act as priors for lower-level processes based on contextual information, previous exposure and acquired long-term knowledge. Recently, predictive coding theory has been used to explain predictions in the action domain (Kilner et al., 2007), as well as in music perception based on priors related to melodic (pitch) content (Pearce et al., 2010), metric structure (Vuust and Witek, 2014), or harmony (Rohrmeier and Koelsch, 2012). The present study takes a comparative stance on predictions in both music perception and action, with a specific focus on Western tonal harmony.

Theoretical accounts refer to harmony as combinatorial arrangement of chords within musical sequences characterized by local and non-local dependencies (Swain, 1995). An instance of these dependencies is that a typical chord progression in Western tonal harmony starts and ends with a reference chord to which some chords are overwhelmingly likely to move to, while they rarely move to others (Tymoczko, 2003). Psychologically, these dependencies are predicted and perceived as tension-resolution patterns by listeners who have been sufficiently exposed to the prevailing musical system (Krumhansl, 1983; Lerdahl and Jackendoff, 1983). Convention in the field of music cognition has that the harmonic principles that govern musical structure are considered as part of a musical "syntax" (Bharucha and Krumhansl, 1983; Koelsch and Siebel, 2005; Patel, 2003), that also includes melodic and/ or rhythmic principles of music (Large and Palmer, 2002; Rohrmeier and Koelsch, 2012). Here, we consider "syntax" generally as the knowledge of regularities that control the integration of smaller units into larger musical phrases (Swain, 1995) and thereby support predictions. It is well established that tacit knowledge about structural regularities of music 1) is acquired implicitly (Loui et al., 2009; Rohrmeier and

Rebuschat, 2012; Tillmann et al., 2000), 2) largely shapes our musical competence across different musical systems and cultures (Eerola et al., 2006; Lartillot and Ayari, 2011), and 3) enables listeners to cognitively link current auditory items to past events and to generate predictions on forthcoming events (Patel, 2003; Tillmann, 2012). In the present study we will focus on harmonic regularities and investigate how they govern predictions during (auditory) music perception and (silent) musical actions.

Harmony not only defines the sequence of musical *sounds* but also co-determines the associated chain of musical *actions*. Therefore, the implicit knowledge of harmonic regularities might influence not only *listeners*' predictions, but also musicians' *action* planning during performance (Palmer and van de Sande, 1995). While regularity-based predictions during music *listening* have already been thoroughly investigated (Rohrmeier and Koelsch, 2012; Tillmann, 2012), the neural basis of motor predictions in musical *actions* has not been explored in depth (Maidhof et al., 2009; Ruiz et al., 2009). Recent behavioural (Novembre and Keller, 2011) and electrophysiological studies on music production (Bianco et al., 2016; Sammler et al., 2013b) revealed slower response times, higher number of errors and neural processing costs (a centro-parietal negativity) in expert pianists when asked to silently execute harmonically incongruent compared to congruent chord progressions. These costs were associated with the motor reprogramming of a pre-planned, congruent, action in face of an unexpected incongruity, and were taken as indirect evidence that pianists' action planning was based on musical context and internalised knowledge of harmony. In other words, these findings imply that harmonic structure might implicitly regulate mechanisms of motor control to improve music performance beyond fine movement optimization (Bianco et al., 2016; Novembre and Keller, 2011).

The goal of the present study is to identify the brain areas involved in motor planning based on the regularities of Western tonal harmony, to explore the connectivity between these areas and to compare this network with the neural network sub-serving analogous processes in auditory music perception. The rationale behind this study is that expert pianists have internalised the rules of harmony not only auditorily but also in the hand action domain. Their substantial motor training should enable them to parse harmonic dependencies also in sequences of silent musical actions to facilitate prediction and planning of forthcoming motor acts during performance. This is because the same harmonic structure in sequences of sounds or sequences of actions without sound (i.e., those movements typically employed for producing these sounds) should trigger cognitive processes that are analogous with regard to the structural information. At the same time, processing should differ between perception and action with regard to the associated sensory and memory retrieval processes (i.e., auditory sound vs. motoric act). Here, we sought to isolate and compare the neural networks involved in harmony processing during either perception or (silent) actions, i.e. to probe the potential contribution of auditory and motor prediction of harmony that are otherwise co-occurring during real music production.

Neural hypotheses for musical syntax processing (i.e., harmony) in music *perception* (Koelsch, 2011; Patel, 2003; Tillmann, 2012) posited a special role of frontal computational regions that successively integrate incoming information into higher-order structures by drawing on knowledge about regularities stored in posterior brain regions. Neuroimaging research points to the inferior frontal gyrus (IFG) as the critical computational area that, together with a repository of regularities in posterior auditory regions superior temporal gyrus (STG), affords the prediction of future musical sounds based on the context and listener's long-term music structural knowledge (Kim et al., 2011; Koelsch et al., 2005; Maess et al., 2001; Musso et al., 2015; Sammler et al., 2011; Tillmann et al., 2006). Interestingly, IFG has been associated not only with structural integration and prediction of musical sequences, but also with structuring of complex *actions* (Fuster, 2001; Koechlin and Summerfield, 2007) outside the music domain. Lesions of the left IFG

cause impairment in sequencing pictures representing human actions (Fazio et al., 2009), and bilateral IFG are involved in evaluating whether constituent acts belong to the same or separate sub-goals (Farag et al., 2010). Moreover, bilateral IFG activations have been reported during execution of series of motor acts that were organised according to hierarchical action plans (Koechlin and Jubault, 2006). In sum, IFG has become central to hypotheses on processing of structured sequential information in perception and action (Fitch and Martins, 2014; Fiebach and Schubotz, 2006, for various perspectives see Cortex, 2006, vol.2, issue 42), making it conceivable that IFG is also involved in parsing and predicting structural information embedded in musical actions.

What has received less attention than the role of IFG, however, is its interaction with task-relevant posterior systems of knowledge during structural processing. In other words, apart from frequently reported co-activations of IFG and auditory temporal regions during music listening (Koelsch and Siebel, 2005), the characterization of other 'modality-specific regions', e.g., in musical action, and particularly their connectivity with frontal 'computational regions' remains uncertain. In this study, we tested whether pianists' action planning based on knowledge of Western tonal harmony involves (i) IFG in interaction with (ii) posterior visual-motor areas. Furthermore, we (iii) compared the functional connectivity profiles of IFG during the processing of musical actions and auditory sequences that contained similar harmonic violations.

We acquired resting state fMRI data from expert pianists, and then fMRI data during an audio and an action task in which the same harmonic sequences were either auditorily presented or had to be motorically imitated. In the audio task, pianists listened to 5-chord sequences (similar to Koelsch et al., 2005) in which the last chord was either harmonically congruent or incongruent with the preceding musical context. In the action task, in total absence of musical sound, participants were presented with series of photos of a pianist's hand performing the same congruent/incongruent chord progressions on a piano (Bianco et al., 2016). To engage the motor system in the processing of musical actions, pianists had not only to watch the movements, but also to manually reproduce them on a glass-board. The contrasts of incongruent minus congruent chords during listening or imitation were used to functionally segregate modality-specific areas and to isolate frontal computational areas. To demonstrate crosstalk between these regions, we used the latter as seeds in a functional connectivity analysis of the resting state fMRI data.

If harmonic violations of audio sequences activate IFG, then violations of action sequences with the same musical structure should also activate IFG as parser of harmonic regularities and top-down generator of predictions. On the other hand, we expected to find divergent activity in temporal auditory or parietal visual-motor regions associated with item identification and storage of knowledge in their modality-specific format. Finally, by mirroring task-based activation (Smith et al., 2009), the resting-state data should reveal processing streams involved in processing harmonic regularities in music perception and action.

2. Materials and methods

2.1. Participants

29 pianists (17 female) aged 20–32 years (mean age: 24.7, SD = 2.9) took part in the experiment. They had a minimum of 5 years of piano training in classical Western tonal music (range = 5–27 years, mean years of training = 17.2, SD = 4.8) and had started to play the piano at an average age of 7.3 years (SD = 3.08). None of the pianists had training in improvisation or other musical styles. All participants were naïve with regard to the purpose of the study. Written informed consent was obtained from each participant before the study that was approved by the local ethics committee.