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Research Report

Specific contributions of basal ganglia and cerebellum to the neural tracking of rhythm

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ABSTRACT

How specific brain networks track rhythmic sensory input over time remains a challenge in neuroimaging work. Here we show that subcortical areas, namely the basal ganglia and the cerebellum, specifically contribute to the neural tracking of rhythm. We tested patients with focal lesions in either of these areas and healthy controls by means of electroencephalography (EEG) while they listened to rhythmic sequences known to induce selective neural tracking at a frequency corresponding to the most-often perceived pulse-like beat. Both patients and controls displayed neural responses to the rhythmic sequences. However, these response patterns were different across groups, with patients showing reduced tracking at beat frequency, especially for the more challenging rhythms. In the cerebellar patients, this effect was specific to the rhythm played at a fast tempo, which places high demands on the temporally precise encoding of events. In contrast, basal ganglia patients showed more heterogeneous responses at beat frequency specifically for the most complex rhythm, which requires more internal generation of the beat. These findings provide electrophysiological evidence that these subcortical structures selectively shape the neural representation of rhythm. Moreover, they suggest that the processing of rhythmic auditory input relies on an extended cortico-subcortico-cortical functional network providing specific timing and entrainment sensitivities.
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1. Introduction

Auditory perception excels in tracking rhythmic features of the sensory input over time (Joris, Schreiner, & Rees, 2004). However, the actual neural substrate of this rhythmic process remains largely unknown. Although auditory cortical activity faithfully tracks rhythmic temporal fluctuations of acoustic input (e.g. Brugge et al., 2009; Ding, Melloni, Zhang, Tian, &

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Poeppel, 2016; Eggermont, 2001; Gourévitch, Le Bouquin Jeannès, Faucon, & Liégeois-Chauvel, 2008; Liégeois-Chauvel, Lorenzi, Trébuchon, Régis, & Chauvel, 2004; Pantev et al., 1988; Picton, Skinner, Champagne, Kellett, & Maiste, 1987), this neural activity may constitute the final product of preceding and interactive processing stages (Large, Herrera, & Velasco, 2015; Patel & Iversen, 2014). More specifically, auditory cortices may interact with subcortical areas that have been shown to engage in temporal processing such as the basal ganglia and the cerebellum. The basal ganglia are claimed to play a key role in predicting upcoming events on the basis of a relative timing mechanism, possibly supporting the internal generation of a periodic pulse-like beat when listening to musical rhythms (Grahn and Brett, 2009; Grahn, 2009; Teki, Grube, Kumar, & Griffiths, 2011; Schwartze, Keller, Patel, & Kotz, 2011; Schwartze & Kotz, 2013). In contrast, the cerebellum is considered to play a critical role in absolute duration based mechanisms (Grube, Cooper, Chinnery, & Griffiths, 2010; Grube, Lee, Griffiths, Barker, Woodruff, & 2010; Knolle, Schröger, Baess, & Kotz, 2012; Knolle, Schröger, & Kotz, 2013; Teki et al., 2011; Teki, Grube, & Griffiths, 2012) and in the encoding of the precise timing of events particularly in the subsecond range (Ivry, Keele, & Diener, 1988; Ivry & Keele, 1989; Ivry & Schlerf, 2008).

The main goal of the current study was to specify the role of the basal ganglia and the cerebellum in the neural tracking of rhythmic streams. Uncovering these mechanisms would provide important insight into the operating principles of a cortico-subcortico-cortical network that has been proposed as the functional substrate of rhythm and timing processes (Schwartze & Kotz, 2013). To this end we recorded electroencephalographic activity (EEG) from patients with lesions in the basal ganglia or the cerebellum and from healthy matched controls while they listened to different rhythmic sequences. These rhythms were specifically selected on the basis of previous work indicating that particular frequencies of the continuous EEG activity elicited by these rhythms are amplified when they correspond to the frequency of a most-often perceived periodic pulse-like beat, even when a sound does not occur on each beat, i.e. in syncopated rhythms (Nozaradan, Peretz, & Mouraux, 2012b; Nozaradan, 2014; Nozaradan et al., 2016a). These rhythms were presented at different rates, either well within the musical tempo range promoting beat perception (<5 Hz) or at the upper limit of this range as such faster tempi requires the perceptual grouping of events into larger number of events to entrain to the beat (Nozaradan et al., 2012b; Repp, 2005).

First, neural tracking of the rhythm was compared across patients and controls based on a frequency-tagging approach measuring the amplitude of the responses expected at frequencies corresponding to the frequency components of the rhythmic contour of the sequences (Nozaradan, 2014). The average amplitude of these frequency-tagged responses provides an index for the general capacity of the auditory system to respond to the sequences, regardless of the relative amplitude of each frequency component elicited by the rhythmic sequences. Most importantly, while we did not expect to find differences in this average amplitude of the responses across the different groups of participants, we hypothesized to find finer-grained differences in these response patterns, in the form of an altered selective neural tracking at beat frequency in patients compared to controls. Specifically, we predicted basal ganglia patients to show reduced relative amplitude at beat frequency, especially for a more complex rhythm, in which a sound does not systematically coincide with a beat, thus relying more on endogenous beat generation. In contrast, we predicted cerebellar patients to display reduced relative amplitude at beat frequency, especially for the sequences played at the fastest tempo, as this tempo requires rapid and precise encoding of temporal events and a switch to a slower frequency of perceptual grouping in order to entrain to the beat. This dissociation between the three groups of participants would indicate a specific contribution of each of these subcortical structures to the neural tracking of rhythmic sensory input.

2. Materials and methods

2.1. Participants

Eleven patients with lesions in the basal ganglia (mean age 50.9, range = 30–64 years), eleven patients with lesions in the cerebellum (mean age 52.6, range = 37–64 years), and eleven healthy controls (mean age 52.1, range = 28–63 years) took part in the experiment after providing written informed consent. The controls were recruited via a database at the Max-Planck Institute for Human Cognitive and Brain Sciences (Leipzig, Germany) and matched the patients in age, education (in years), gender (5 males per group), and handedness (all right-handed). Structural neuroimaging techniques (MRI and brain CT) were used to locate and manually delineate lesions in MRIcron, thus generating volumes of interest for each patient (Rorden, Karnath, & Bonilha, 2007). Focal vascular lesions typically resulted from an ischemic or hemorrhagic stroke that had occurred 9.5 years before on average (see Table 1 for details on the age of the patients, the date of the incident, and on the topography and volume of the lesions). The structural overlay of the lesions is depicted in Fig. 1. Additional lesions outside the cerebellum and basal ganglia were present in some patients (see Table 1). All participants received a compensatory fee. None of the participants were professional musicians or had prior experience with the auditory sequences used in the experimental setting. They had no self-reported history of hearing or psychiatric disorder. The study was conducted in accordance with the declaration of Helsinki, and approved by the Ethics Committee of the University of Leipzig with respect to testing of patients and healthy controls.

2.2. Auditory stimuli

The auditory stimuli were created in Audacity 1.2.6 (http://audacity.sourceforge.net/) and presented binaurally through earphones at a comfortable hearing level (via Presentation Software 14.2, Neurobehavioral Systems, Inc., Berkeley, USA). The audio files are available on the following website (https://www.dropbox.com/sh/wnn2gzmpwv0u7x3/AABvk4jCBhP9TT1xpksCh_rba?dl=0).

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