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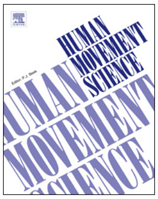

Steady-state evoked potentials distinguish brain mechanisms of self-paced versus synchronization finger tapping

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ABSTRACT

Sensorimotor synchronization (SMS) requires aligning motor actions to external events and represents a core part of both musical and dance performances. In the current study, to isolate the brain mechanisms involved in synchronizing finger tapping with a musical beat, we compared SMS to pure self-paced finger tapping and listen-only conditions at different tempi. We analyzed EEG data using frequency domain steady-state evoked potentials (SSEPs) to identify sustained electrophysiological brain activity during repetitive tasks. Behavioral results revealed different timing modes between SMS and self-paced finger tapping, associated with distinct scalp topographies, thus suggesting different underlying brain sources. After subtraction of the listen-only brain activity, SMS was compared to self-paced finger tapping. Resulting source estimations showed stronger activation of the left inferior frontal gyrus during SMS, and stronger activation of the bilateral inferior parietal lobule during self-paced finger tapping. These results point to the left inferior frontal gyrus as a pivot for perception–action coupling. We discuss our findings in the context of the ongoing debate about SSEPs interpretation given the variety of brain events contributing to SSEPs and similar EEG frequency responses.

1. Introduction

Sensorimotor synchronization (SMS) refers to the act of synchronizing motor actions with external events such as auditory beats (see Repp, 2005; Repp & Su, 2013 for exhaustive reviews). Neuroimaging studies of beat processing reported combined cortical activation of the pre-supplementary and supplementary motor areas (pre-SMA/SMA), premotor cortex (PMC), inferior frontal gyrus (IFG), and superior temporal gyrus (STG) in detecting and synchronizing with the beat (e.g. Chen, Penhune, & Zatorre, 2008; De Pretto & James, 2015; Grahn & McAuley, 2009; Kung, Chen, Zatorre, & Penhune, 2013). Motor areas also responded during pure perceptual tasks in both musicians and non-musicians (e.g. Bengtsson et al., 2009; Chen et al., 2008; Grahn & Brett, 2007; James, Michel, Britz, Vuilleumier, & Hauert, 2012; Teki, Grube, Kumar, & Griffiths, 2011), suggesting a strong inclination of the motor

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system to respond to rhythmic events. Thus, comparing SMS to self-paced finger tapping is crucial to isolate the brain mechanisms involved in auditory-motor coupling.

Compared to rest, self-paced finger tapping involved the pre-supplementary motor area (pre-SMA), left primary sensorimotor cortex, and left middle cingulate motor area (Kawashima et al., 1999). However, neuroimaging studies yielded contrasting results when comparing SMS to a continuation phase, where participants had to continue tapping at the same tempo after the stimulus was turned off (e.g. Bijsterbosch et al., 2011; Jantzen, Oullier, Marshall, Steinberg, & Kelso, 2007; Jantzen, Steinberg, & Kelso, 2004; Rao et al., 1997). Jantzen et al. (2004, 2007) showed that brain activation differences during on-beat synchronization versus off-beat (syncopated) finger tapping persisted during the continuation phase. These results indicate that the cognitive resources engaged during continuation depended on the previous context, suggesting that self-paced finger tapping performance might be influenced by a previously heard metronome. Thus, the synchronization-continuation paradigm might not be well suited for the evaluation of spontaneous self-paced rhythm production.

Here, we used EEG steady-state evoked potentials (SSEPs; Regan, 1989) – frequency domain representations of stable neural responses to a periodic stimulus – to compare the brain electrophysiological responses to spontaneous self-paced finger tapping, SMS, and passive beat perception. SSEP analysis provides a powerful tool to study modulations of brain activity without the need to isolate specific events and is therefore especially adapted to the study of sustained rhythmic tasks (Zhou, Melloni, Poeppel, & Ding, 2016).

In recent years, an increasing number of studies analyzed the neural correlates of beat processing using SSEPs (e.g.; Celma-Miralles, de Menezes, & Toro, 2016; Nozaradan, Peretz, Missal, & Mouraux, 2011; Nozaradan, Zerouali, Peretz, & Mouraux, 2015; Stupacher, Witte, Hove, & Wood, 2016; Stupacher, Wood, & Witte, 2017; Tierney & Kraus, 2014), suggesting direct entrainment of neural oscillations to the frequency of the beat. However, SSEP often reflect complex waveforms aligned on the interonset interval (IOI) and repeating over time, rather than pure sinewave oscillations (Regan, 1989; Zhou et al., 2016). Pure neural oscillations at the frequency of the beat will show power spectra peaks restricted to the frequency of the oscillation (F0), whereas complex waveforms will also show peaks at higher-order harmonics (integer multiples of the stimulus' frequency; H1, H2, etc.). Indeed, Fourier transform is a mathematical conversion from time to frequency domain. The resulting power spectra do not report the exact oscillatory content of the analyzed signal, but rather the frequencies necessary to reconstruct that signal (Luck, 2014).

Additionally, transient event-related potentials (ERPs), such as auditory evoked potentials in response to the perceived beats, might induce peaks in the power spectra at the frequency of the beat and/or at its higher-order harmonics depending on the tempo (Zhou et al., 2016). Transient ERPs are discrete waveforms, not taking advantage of the repetition of the events to which they are related (Regan, 1989), in contrast to SSEPs. At faster tempi, the rapid succession of events will prevent the brain mechanisms to return to resting state between each repetition, resulting in power spectra peaks at F0. At slow tempi, transient ERPs are less likely to induce peaks at the frequency of the stimuli and will rather increase power at higher-order harmonics.

Thus, the effect of event-related potentials on the resulting power spectra has to be taken into account when designing a study, analyzing the data, and interpreting the results. To cancel out overlap between SSEPs and transient ERPs, the tasks were performed at three different tempi. Additionally, by performing scalp topography analysis and computing source estimations, we were able to evaluate whether the observed SSEPs relied on distinct brain mechanisms and identify potential brain sources specifically involved in auditory-motor coupling.

Previous SSEP studies of beat processing showed that synchronizing finger taps to every other beat resulted in increased SSEP peak amplitude at the frequency of the tapping, centered at electrodes above the contralateral primary motor area (Nozaradan et al., 2015). Tierney and Kraus (2014) showed that top-down processes may modulate frequency peak amplitudes. Listening to musical excerpts with added emphasis on the first beat of the metrical grid (strong beat) induced strong SSEP peaks at the frequency of the beat (F0) and at its first harmonic (H1; i.e., twice the stimulus' frequency). If the second beat of the metrical grid (weak beat) was accentuated, the power spectra showed a peak at F0 only. According to the authors, this may reflect reduced attention to the metrical grid when accents occurred on the weak beat. Similarly, studies in the visual domain showed that peaks at H1 increased when participants paid attention to the stimuli (Kim, Grabowecky, Paller, & Suzuki, 2010) and were associated with different brain sources than at F0 (Heinrichs-Graham & Wilson, 2012; Pastor, Valencia, Artieda, Alegre, & Masdeu, 2007).

Our original paradigm allowed investigating SMS and its basic components, namely, beat perception and finger tapping. First, at the behavioral level, we hypothesized greater stability of tapping during SMS than during self-paced finger tapping, due to the presence of the metronome (Semjen, Schulze, & Vorberg, 2000), and at relatively fast tempi. Indeed, the estimation of the intervals is more difficult at slower tempi (Lewis & Miall, 2003; Madison, 2001). Second, we hypothesized that auditory-motor coupling during sensorimotor synchronization would induce SSEPs reflecting more than the sum of auditory and movement-related brain activity. We expected associated activations within pre-SMA/SMA, PMC, IFG and STG. Third, we hypothesized stronger brain activity associated to H1 when the attentional demands of the tasks increased, that is, during SMS compared to passive listening, and at slower tempi. Based on previous findings, we expected associated source estimations within the inferior parietal lobule (Bolger, Coull, & Schön, 2013; Konoike et al., 2012; Rao, Mayer, & Harrington, 2001) and/or middle/posterior cingulate gyrus (Leech & Sharp, 2014; Vogt, 2009).

2. Material and methods

2.1. Participants

Sixteen right-handed young adults (8 women; Mean age = 27.7 years; SD: 3.3 years), without any history of neurological or psychiatric illness, participated in the study. Six of them had never received extracurricular musical education. Of the eight who had