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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

learned to play an instrument, six had abandoned practicing more than 4 years before participating in the study, and two were still playing (one piano and one guitar) on an occasional basis (< 1 h per week). They all provided informed consent. The procedure was approved by the local ethics committee and the experiment was conducted in agreement with the University of Geneva guidelines and the ethical standards of the declaration of Helsinki. Two participants were excluded from the analyses, one because of a technical problem during recording, the other because of tapping coefficient of variation over two standard deviations above the mean in five of the six tapping conditions. Thus, the data of 14 participants were further processed (7 women; Mean age = 27.7 years; SD: 3.1 years).

2.2. Tasks and stimuli

The participants performed three rhythmic tasks at three different tempi. They either produced self-paced finger tapping (SP task), sensorimotor synchronization with a metronome (SMS task), or simply listened to the metronome (listen-only, LO task). The intermediate tempo corresponded to the participants' spontaneous motor tempo (SMT tempo), in other words, the tempo at which each individual spontaneously produces self-paced finger tapping. They were also asked to produce a faster tempo (FA) and a slower tempo (SL) as detailed in the Procedure section. During the synchronization conditions, the tempo of the metronome corresponded to the tapping speed of the self-paced condition. Thus, each participant completed nine conditions: three self-paced conditions (SP_{SMT}, SP_{FA}, SP_{SL}), three synchronization conditions (SMS_{SMT}, SMS_{FA}, SMS_{SL}), and three listen-only conditions (LO_{SMT}, LO_{FA}, LO_{SL}).

During the tapping tasks, the participants tapped with their right index finger on a response button (see Procedure section). The metronome sounds consisted of 500 Hz sine wave tones of 80 ms duration, emitted through loudspeakers at a level that the participant judged comfortable.

2.3. Procedure

After positioning the EEG cap and electrodes, the participants sat comfortably in a shielded room. They were instructed to minimize movements, muscle tension and eye blinks while executing the tasks. The response button was on a joystick positioned horizontally and adjustable in height, so that the participants could keep their arms as relaxed as possible, alongside their body. The screen displayed the instruction before the start of each condition, and turned black during execution of the task. A fixation point on top of the screen helped the participants to stabilize their gaze. Stimuli were presented and responses recorded using Presentation experimental software (version 12.2, Neurobehavioral System).

The first condition recorded was always SP_{SMT} to set the spontaneous motor tempo, followed by SP_{FA} and SP_{SL} in balanced order. For half the participants, the synchronization conditions (SMS_{FA}, SMS_{SMT}, and SMS_{SL}, in a balanced order) came next, followed by the listen-only conditions (LO_{FA}, LO_{SMT}, and LO_{SL}, in a balanced order). The other half did the listen-only conditions before the synchronization ones. Each condition was divided into three blocks of 40 intertap intervals (ITI or IOIs in the LO conditions). Thus, for each condition, 120 ITIs/IOIs were recorded. The participants performed all three blocks of each condition in a row to ensure that they produced the same tempo in each block.

Before recording, the experimenter explained the task to the participants. For the SP_{SMT} condition, they were asked to tap at their most natural pace, at a frequency they could maintain without mental effort and for a long period of time. For the SP_{FA} and SP_{SL} conditions, they were asked to tap at a significantly faster rate but not too fast, or at a significantly slower rate but not too slow. They were aware that they would have to synchronize at these frequencies later on and thus, the experimenter warned them that these faster and slower tempi should fit in a range where synchronization was possible. For the LO conditions, participants received the instruction not to move while listening to the beat. A webcam allowed on-line screening of overt movements. All participants satisfactorily followed this instruction.

2.4. EEG data acquisition and preprocessing

The EEG signal was continuously acquired from 64 active Ag–AgCl electrodes (BioSemi Active-Two, V.O.F., Amsterdam, the Netherlands) equally distributed over the scalp, with a sampling rate of 2048 Hz and impedances kept below 50 kΩ. Offline pre-processing was performed using the Matlab toolbox EEGLab (<http://scn.ucsd.edu>) and the Cartool software by Denis Brunet (cartoolcommunity.unige.ch).

First, the EEG data were imported into EEGLab, downsampled to 1024 Hz and filtered with a 0.1 Hz FIR high-pass filter. Then, we removed eye blinks from the EEG signal through an ICA procedure. In Cartool, electrodes with excessive noise were interpolated using a 3D spherical spline algorithm (mean: 2.5% of interpolated electrodes; Perrin, Pernier, Bertrand, Giard, & Echallier, 1987), and the data were recalculated against the average reference.

The data were then processed as a function of the comparisons of interest (SMS vs LO and SMS vs SP, see following sub-chapters and Fig. 1). For all behavioral and EEG analysis, the first three intervals of each block were discarded as several taps are necessary to adjust the finger tapping to the beat (Repp, 2005). The last interval was also removed as the script interrupted the presentation of the stimuli at the 41st tap, preventing the presentation of the last metronome tone in the SMS conditions when the tap preceded the tone.

2.4.1. SMS versus LO

Each condition was divided into nine epochs (three per block) of twelve metronome inter-onset intervals. After averaging these epochs to reduce non-stimulus locked oscillations, a Fast Fourier Transform Approximation (FFTA) was applied. The FFTA is an

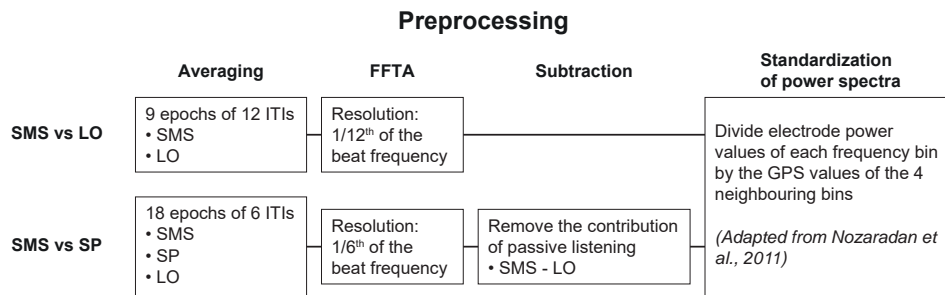


Fig. 1. EEG data preprocessing procedure as a function of the comparisons of interest (SMS vs LO and SMS vs SP, see Section 2.4.1 and following for details).

equivalent to the classical Fast Fourier Transform (FFT) that transfers the FFT power of each electrode into a sine-cosine space and uses the best fitting line of the plotted data as a reference to implement polarity in the output, necessary for source estimation (Lehmann & Michel, 1990). The resolution of the FFTA (as for the classical FFT) is calculated as the inverse of the period duration. Here, the period duration was equal to twelve beats, yielding a power spectra resolution of 1/12th of the beat frequency.

2.4.2. SMS versus SP

The preprocessing steps followed the procedure used in the comparison between SMS and LO. However, for the SMS versus SP comparison, each condition was divided into 18 epochs (six per block) of six ITIs. Thus, after averaging these epochs to reduce non-tapping locked oscillations, the FFTA yielded a power spectra resolution of 1/6th of the tapping frequency. This lower resolution compared to the SMS versus LO comparison compensated the tapping variability (see Results section below). Indeed, to reconstruct the original signal, FFT (and FFTA) uses pure sinewaves at frequencies equal to the frequency bins of the power spectra. If the signal oscillates at a frequency not represented in the power spectra, it will leak in the neighboring frequency bins (Lyon, 2009). If the FFTA resolution is lower, each frequency bin accounts for a bigger range of frequencies present in the EEG signal. Thus, we took advantage of this phenomenon to compensate for the behavioral variability.

In order to extract synchronization-related brain activity of the SMS and SP tasks, we recomputed the FFTA of the LO conditions with the same parameters as the SP condition and subtracted it from the FFTA of the corresponding SMS conditions to remove the contribution of passive listening. In other words, the results of this subtraction will highlight specific brain activations reflecting the sound-to-action processes during SMS, and removing brain activations associated with passive beat perception.

Because, for the SMS versus SP comparison, the signal on which we applied the FFTA was time-locked to the finger taps, we recomputed the FFTA of the LO conditions to virtual finger taps. Specifically, to determine the onset of each epochs of the LO conditions, we calculated the deviation between the first metronome sound and associated finger tap for each epoch of the SMS conditions, and we used these values to calculate the distance between the first sound of the LO epochs and onsets of the epochs.

2.4.3. SMS versus LO and SMS versus SP

Once we obtained the FFTA power spectra of each electrode for both SMS versus LO and SMS versus SP comparisons, the data went through a standardization procedure adapted from the method of Nozaradan et al. (2011). Assuming that, in the absence of an SSEP at a given frequency bin, the power of the neighboring frequency bins are similar, we divided for each electrode the frequency power at each frequency bin by the mean of the four neighboring bin values of the global power spectra (GPS, i.e., the average across all electrodes of the frequency power absolute values; Sallard, Spierer, Ludwig, Deiber, & Barral, 2014), such as:

$$NP_f = \frac{P_f}{(GPS_{f-2} + GPS_{f-1} + GPS_{f+1} + GPS_{f+2})/4}$$

where P_f is the power, at a given frequency bin, of a single electrode, GPS_f is the GPS power at a given frequency bin, and NP_f is the normalized power.

In order to preserve brain topography, which is crucial for source localization, our procedure included the following changes compared to that of Nozaradan et al. (2011): 1) We normalized the data by division rather than by subtraction, as subtraction might reverse the polarity of the values inconsistently throughout the electrode setting. 2) For each frequency bin, rather than normalizing the power of a given electrode by the average value of the neighboring frequency bins from that same electrode, we used the GPS values so to normalize the data by the same value throughout the scalp.

2.5. Data analysis

2.5.1. Behavioral data

For the tapping tasks (SMS and SP), the behavioral performances were evaluated by the ITI mean and variability, and the lag-1 autocorrelation. Given that tapping variability increases linearly as the tempo decreases (Madison, 2001), the coefficient of variation (CV = Std/mean) was used to allow between-tempo comparisons. The lag-1 autocorrelation function is defined by:

$$r_k = \frac{\sum_{i=1}^{n-k} (x_i - \bar{x})(x_{i+k} - \bar{x})}{\sum_{i=1}^n (x_i - \bar{x})^2}$$

where \bar{x} is the average of the n observations and k is the time lag.

We performed a 2×3 ANOVA on those variables using SPSS (Version 23; IBM Corp., Armonk, NY) with the following factors: Task (SMS; SP), Tempo (FA; SMT; SL). The reported p-values were corrected for sphericity violation using the Greenhouse-Geisser estimates depending on the results of Mauchly's test.

For the synchronization conditions, we also tested the mean and variability of the asynchrony (i.e., the distance between finger taps and metronome onsets). In order to neutralize effects due to tempo differences (Semjen et al., 2000), the variability was estimated by dividing the standard deviation from the ITI mean. We performed a one-way ANOVA over the factor Tempo (FA; SMT; SL).

2.5.2. EEG data

EEG data were analyzed using the Cartool software programmed by Denis Brunet (cartoolcommunity.unige.ch), the STEN toolbox developed by Jean-François Knebel and Michael Notter (<http://doi.org/10.5281/zenodo.1164038>), and the RAGU toolbox (Koenig, Kottlow, Stein, & Melie-Garcia, 2011).

To test for between-condition modulations of the EEG frequency response, we performed statistical analyses on the GPS and the Global Map Dissimilarity index (GMD). These global measures of the EEG frequency response offer reference independent, and data-driven analyses preventing from pre-selecting a subset of electrodes of interest. GMD quantifies topographic differences between two electric fields and thus indicates modulations in the EEG scalp topography (Tzovara, Murray, Michel, & De Lucia, 2012). It is calculated as the root mean square of the difference between conditions, electrode by electrode, of the normalized voltage potentials. Normalization prevents significant differences due to the amplitude of the signal. Between-condition GPS modulations alone represent differences in the activation strength of a given brain network. GMD modulations indicate differences in the underlying brain sources of the signal (Michel & Murray, 2012; Murray, Brunet, & Michel, 2008; Tzovara et al., 2012).

To statistically evaluate between-condition GMD differences, the scalp topographies went through a bootstrapping procedure (Koenig et al., 2011): the GMD values were compared with an empirical distribution based on randomly reassigning each participant's data across the electrode montage to any of the conditions (5000 permutations per data point).

2.5.2.1. SMS versus LO. We performed a $2 \times 3 \times 2$ ANOVA on the GPS and GMD data with the following factors: Task (SMS; LO), Tempo (FA; SMT; SL), Harmonic (F0; H1). Because the influence of ERPs on the amplitude of the power spectra at F0 and H1 varied with tempo (Zhou et al., 2016), we considered neither the main effects of Tempo and Harmonic, nor the Tempo \times Harmonic and Task \times Tempo \times Harmonic interactions.

2.5.2.2. SMS versus SP. For the comparison of SMS and SP conditions, we analyzed F0 only, due to the variability of the tapping, and its impact on the corresponding higher-order harmonics. Indeed, if the tapping frequency varied from the average used to determine the FFTA resolution, each multiplication of the fundamental frequency increased the difference between the target FFTA power spectra frequency bin and the corresponding tapping frequency multiples. Thus, we performed a 2×3 ANOVA on the GPS and GMD at F0 with the following factors: Task (SMS; SP), Tempo (FA; SMT; SL). We did not consider the main effect of Tempo for the same reasons as for the SMS versus LO comparison.

2.5.2.3. Source estimations. In order to identify potential differences in the underlying brain generators of the signal recorded at the scalp, we performed source estimations for contrasts showing significant GPS or GMD effects. First, a LAURA (local autoregressive average) distributed linear inverse solution (Grave de Peralta Menendez, Gonzalez Andino, Lantz, Michel, & Landis, 2001; Grave de Peralta Menendez, Murray, Michel, Martuzzi, & Gonzalez Andino, 2004) yielded source estimations for each condition and harmonic of each participant. The solution space included 3005 nodes spread over a realistic head model on a $6 \times 6 \times 6$ mm grid. The solution points were equally distributed within the grey matter of the Montreal Neurological Institute (MNI) average brain. Even though EEG source estimation has been applied successfully in various clinical and fundamental studies (e.g. Britz, Landis, & Michel, 2009; Corrigan et al., 2009; De Pretto, Rochat, & Spierer, 2017; Geukes et al., 2013; James, Britz, Vuilleumier, Hauert, & Michel, 2008; James et al., 2012; James, Oechslin, Michel, & De Pretto, 2017; Rihs et al., 2013; Sallard et al., 2014), such method only guarantees a 1–2 cm spatial accuracy (Martuzzi et al., 2009; Plomp, Michel, & Herzog, 2010).

We performed ANOVAs on the current density of each solution point including the same factors as for GPS and GMD ($2 \times 3 \times 2$ ANOVA for SMS vs LO, and a 2×3 ANOVA for SMS vs SP). To correct for multiple testing, we applied a cluster extent threshold of at least 15 contiguous nodes with $p < 0.05$. This spatial criterion was determined using the AlphaSim program (available from the Analysis of Functional NeuroImages website: <http://afni.nimh.nih.gov>). This program computed 10,000 Monte Carlo permutations over the 3005 nodes masked within our lead field matrix, and assuming a spatial smoothing of 6 mm FWHM and a cluster connection radius of 8.5 mm. For clusters of at least 15 nodes, the output yielded a cluster-level likelihood of $p < 0.05$, and a corresponding node-level false positive probability of $p < 0.0001$.

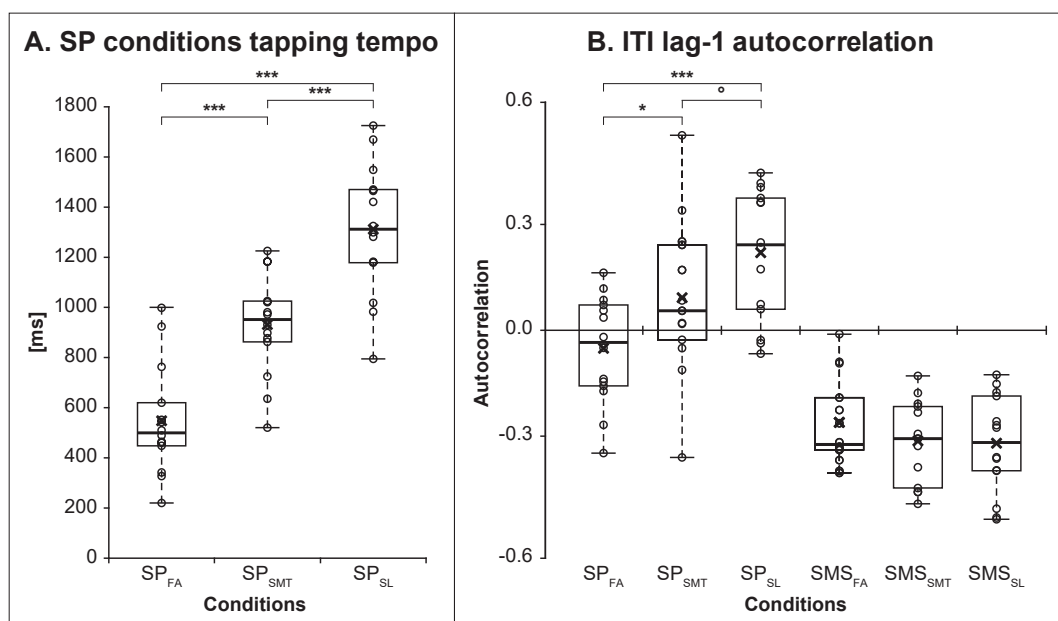


Fig. 2. Behavioral results. The graphs show the individual performances (grey circles), the median (thick horizontal line), and the mean (cross). A. Spontaneous self-paced tapping intertap intervals for each tempo condition. B. ITI lag-1 autocorrelation for each tempo of the SMS and SP conditions. $^{\circ}p = 0.072$, $^*p < 0.05$, $^{***}p < 0.001$.

3. Results

3.1. Behavioral results

During the self-paced conditions, the participants produced a wide range of tapping frequencies with some overlap between tempo conditions (Fig. 2A, Table 1). The Task (2) \times Tempo (3) ANOVA (Table 2) showed a significant effect of Tempo. Post-hoc analyses using Fisher's Least Significant Difference (LSD) indicated that each tempo was significantly different from the others ($p < 0.001$). The 2 \times 3 ANOVA on the ITI CV showed no significant effect (Table 2).

The 2 \times 3 ANOVA on the ITI lag-1 autocorrelation (Table 2) showed a main effect of Task, illustrating higher values during the SP conditions compared to the SMS conditions, and a main effect of Tempo. This result was driven by the SP conditions, as illustrated by an interaction effect between Task and Tempo (Fig. 2B). Post-hoc analyses using Fisher's LSD indicated that the values were significantly different during SP_{FA} from the values during SP_{SMT} ($p < 0.05$) and SP_{SL} ($p < 0.001$), and marginally different between SP_{SMT} and SP_{SL} tempi ($p = 0.072$). Because ITI lag-1 autocorrelation values increased with longer ITIs (as tempo became slower), and because each participant produced his/her own tempo, we computed the correlation between ITI and lag-1 autocorrelation to verify whether the ITI lag-1 autocorrelation increase was associated with between-subject differences in ITI. A positive correlation was statistically significant in the SP_{SL} condition ($r = 0.71$, $p = 0.014$, Bonferroni corrected).

The one-way ANOVA on the asynchrony mean and variability showed no statistically significant effect of tempo (Table 2).

Table 1
Behavioral results.

Condition	Tempo	Intertap intervals		Lag-1 autocorr.	Asynchrony	
	Mean (Std)	Mean (Std)	CV (Std)	Mean (Std)	Mean (Std)	Var. (Std)
	[Hz]	[ms]	[%]	[au]	[ms]	[%]
SP _{FA}	2.1 (0.9)	548 (219)	5.6 (1.5)	−0.05 (0.14)	−	−
SP _{SMT}	1.1 (0.3)	931 (204)	5.6 (1.3)	0.08 (0.20)	−	−
SP _{SL}	0.8 (0.2)	1312 (265)	5.9 (1.6)	0.20 (0.17)	−	−
SMS _{FA}	2.1 (0.9)	549 (220)	5.4 (1.4)	−0.25 (0.12)	−36 (43)	7.3 (6.3)
SMS _{SMT}	1.1 (0.3)	936 (204)	5.9 (1.4)	−0.29 (0.11)	−48 (40)	5.1 (1.0)
SMS _{SL}	0.8 (0.2)	1306 (262)	5.9 (1.8)	−0.30 (0.13)	−37 (41)	5.2 (1.7)

CV = coefficient of variation; Std = between-subject standard deviation; Var. = average within-subject variability.

Table 2
ANOVA results for behavioral measures.

	F	df	p-val	ηp^2	ϵ^*
<i>ITI MEAN</i>					
Task	0.00	1,13	0.986	0.00	–
Tempo	96.14	1.27,16.53	0.000	0.88	0.64
Task \times Tempo	3.32	1.32,17.17	0.077	0.20	0.66
<i>ITI CV</i>					
Task	0.01	1,13	0.927	0.00	–
Tempo	0.44	1.22,15.80	0.554	0.03	0.61
Task \times Tempo	0.64	2,12	0.545	0.10	–
<i>ITI LAG-1 AUTOCORRELATION</i>					
Task	80.48	1,13	0.000	0.86	–
Tempo	5.05	2,12	0.026	0.46	–
Task \times Tempo	7.79	2,12	0.007	0.56	–
<i>ASYNCHRONY MEAN</i>					
Tempo	1.26	2,12	0.318	0.17	–
<i>ASYNCHRONY VARIABILITY</i>					
Tempo	1.83	1.09,14.15	0.199	0.12	0.54

* Greenhouse-Geisser Epsilon reported for effects violating sphericity assumption and corrected using Greenhouse-Geisser estimates of sphericity.

3.2. EEG results

3.2.1. SMS versus LO

3.2.1.1. *Global frequency indices (SMS vs LO).* The GPS of each task and tempo showed prominent peaks at the frequency of the tapping and higher-order harmonics (Fig. 3). The Task (2) \times Tempo (3) \times Harmonic (2) ANOVA on GPS resulted in a main effect of

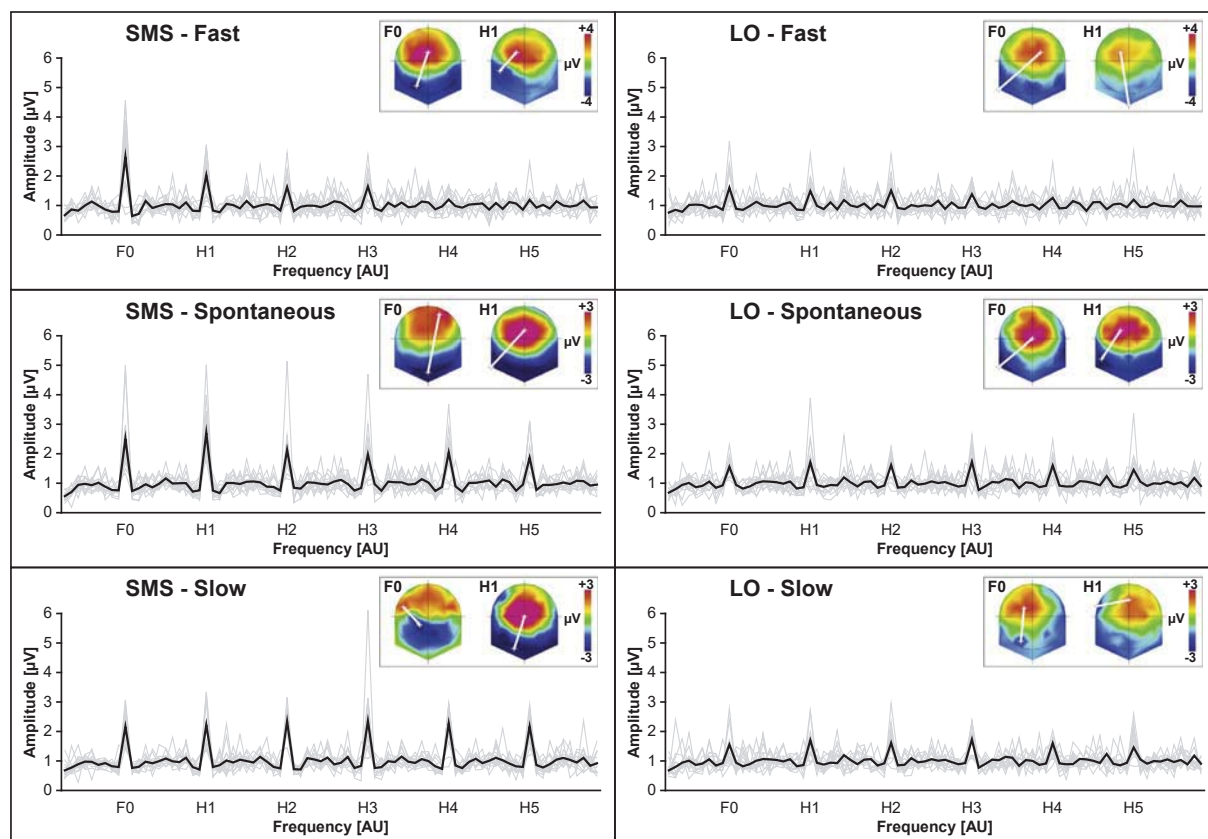


Fig. 3. SSEPs for each tempo of the SMS and LO conditions. The thin grey power spectra represent each participant and the thick black power spectra represent the inter-individual averages.

Table 3

Results for the global frequency indices comparing SMS versus LO.

	GPS					GMD
	F	df	p-val	η^2	ε^*	p-val
Task	24.94	1,13	0.000	0.66	–	0.007
Task \times Tempo	0.32	2,12	0.735	0.05	–	0.497
Task \times Harmonic	1.60	1,13	0.228	0.11	–	0.000

* Greenhouse-Geisser Epsilon reported for effects violating sphericity assumption and corrected using Greenhouse-Geisser estimates of sphericity.

Task reflecting higher GPS amplitude during SMS than LO (Table 3). GMD analysis indicated significant Task main effect and Task \times Harmonic interaction effect (Table 3).

3.2.1.2. Electrical source estimations (SMS vs LO). The main effect of Task showed significant differences at the bilateral middle/posterior cingulate gyrus, and SMA; left IFG; and the right STG (Table 4; Fig. 4A). The average current density (CD, expressed in $\mu\text{A}/\text{mm}^3$) for all these sites was stronger during SMS than LO. The Task \times Harmonic interaction yielded significant differences at the bilateral middle/posterior cingulate gyrus (Table 4; Fig. 4B). Post-hoc analyses using Fisher's LSD indicated that during SMS, CD was significantly higher at H1 than F0 ($p < 0.005$); and during LO, the CD values did not differ significantly between F0 and H1.

3.2.2. SMS versus SP

3.2.2.1. Global frequency indices (SMS vs SP). For the SMS task, the GPS of each tempo showed prominent peaks at the frequency of the tapping and higher-order harmonics (Fig. 5). For the SP task, peaks appeared at F0 in the fast condition and at F0 and H1 in the spontaneous condition. In the slow condition, only small peaks emerged from the inter-individual noise at H1 and H2. The Task (2) \times Tempo (3) ANOVA on GPS at F0 yielded no significant effect (Table 5). GMD analyses yielded significant Task \times Tempo interaction effect and a marginal main effect of Task (Table 5). As the behavioral results indicated a significant lag-1 autocorrelation main effect of Task, we analyses electrical source estimation for this contrast too.

3.2.2.2. Electrical source estimations (SMS vs SP). The main effect of Task showed significant differences at the bilateral inferior parietal lobule (IPL); and a cluster centered on the left IFG and encompassing the insula and STG (Table 6; Fig. 6A). The average CD for each cluster indicated stronger activation of the bilateral IPL during SP than SMS, and stronger activation of the left IFG during SMS than SP. The Task \times Tempo interaction yielded significant differences at the bilateral IPL; right pre-SMA; and left fusiform gyrus, and a cluster centered on the inferior temporal gyrus and encompassing the parahippocampal gyrus (Fig. 6B). Post-hoc analyses using Fisher's LSD indicated stronger CD during SP than SMS at spontaneous tempo for the bilateral IPL and left fusiform gyrus ($p < 0.05$); stronger CD during SMS than SP at slow tempo for the right pre-SMA, and left IFG ($p < 0.05$).

We also computed the SMS versus SP analysis without subtraction of the LO signal, in order to verify the influence of the subtraction on the results, and compared the results of both analyses (see Supplementary Material).

4. Discussion

By contrasting neurophysiological activity of beat perception, self-paced finger tapping, and sensorimotor synchronization, we could isolate brain activity related to synchronizing finger movement with a steady beat. Comparing SMS versus SP we showed stronger activation of the left IFG during synchronization and of the bilateral IPL during self-paced finger tapping. At the behavioral level, the results suggested the use of two different timing modes for successive intertap intervals. The negative lag-1 autocorrelation values for SMS seems associated with event-based timing, whereas positive ITI lag-1 autocorrelation values may represent emergent timing (Delignières & Torre, 2011; Dione & Delevoeye-Turrell, 2015; Ivry, Spencer, Zelaznik, & Diedrichsen, 2002). Event-based timing supposes an internal representation of temporal intervals, informing the nervous system on the timing of the upcoming beat.

Table 4Main Brain Region Activations for the 2 Task \times 3 Tempo \times 2 Harmonic ANOVA on current density for SMS versus LO.

Brain region	Hemisphere	x	y	z	F-values	Cluster size
TASK						
Middle/Posterior Cingulate Cortex	bilateral	–15	–28	41	27.47	154
Supplementary Motor Area	bilateral	–3	–21	64	12.66	
Superior Temporal Gyrus	right	45	–27	15	21.31	106
Inferior Frontal Gyrus	left	–41	5	29	9.79	31
TASK \times HARMONIC						
Middle/Posterior Cingulate Cortex	bilateral	–3	–16	28	23.66	89

Note. Talairach x y z coordinates of local maxima for each significant cluster at $p < 0.05$. Minimal cluster size: 15 solution points. Brain areas are grouped by cluster.

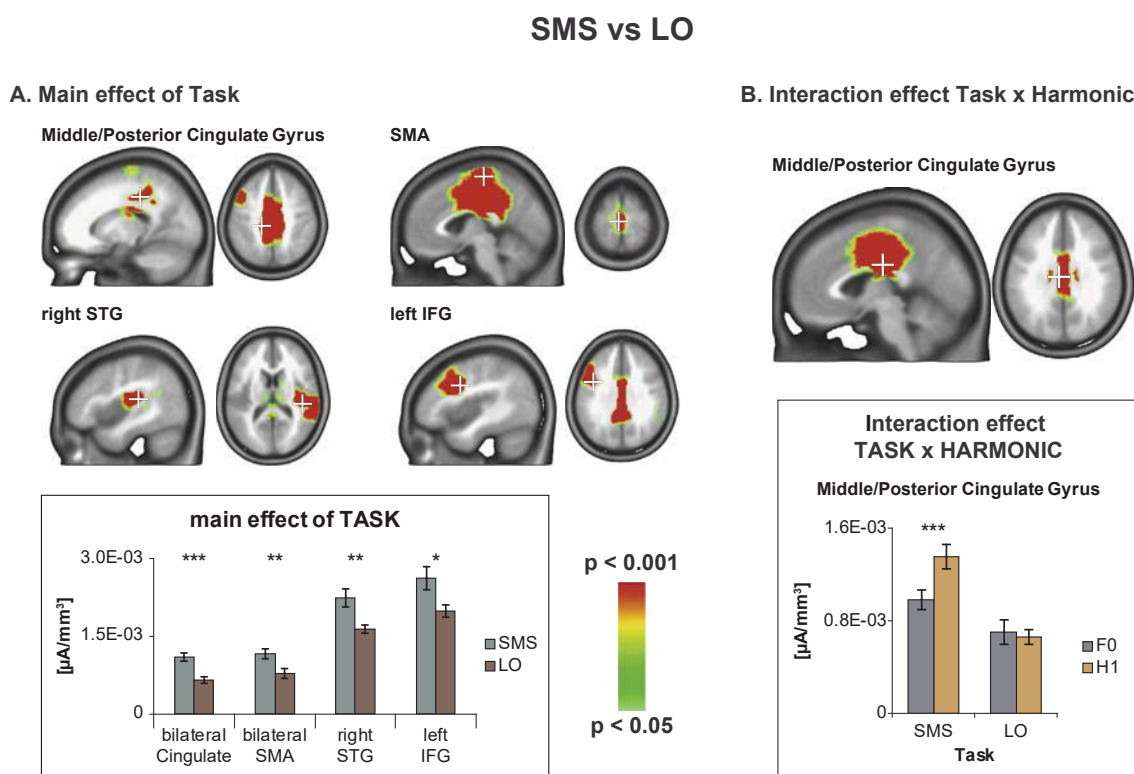


Fig. 4. Distributed electrical source estimations for the main and interaction effects of significant GPS or GMD differences between SMS and LO. The bar graphs depict the current density mean and standard error for each cluster. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

In emergent timing, temporal information arises from the dynamic of the movement, requiring less cognitive involvement (Delignières & Torre, 2011; Repp & Su, 2013).

Here, compared to SMS, SP conditions showed an implication of the bilateral IPL during SP_{SMT} and reduced cerebral activation, including pre-SMA, during SP_{SL} – where behavioral data suggest the predominant use of emergent timing (see Behavioral Findings section). Compared to passive beat perception (LO conditions), SMS involved more strongly auditory, motor, and prefrontal regions, including the bilateral SMA; left IFG; and the posterior part of the right STG. These brain areas have recurrently been associated to beat processing and sensorimotor synchronization tasks (e.g. Chen et al., 2008; De Pretto & James, 2015; Grahn & McAuley, 2009; James et al., 2012; Konoike et al., 2012; Kung et al., 2013).

Taken together, these results partly confirm the findings of Coull and Nobre (2008). In their review, these authors suggested that event-based timing may rely on the basal ganglia, SMA, IFG, and cerebellum, whereas emergent timing may rely on left-lateralized IPL and premotor cortex. We propose the alternative hypothesis that the IPL pattern of activation observed here reflects increased engagement of attentional resources for interval retention.

4.1. Behavioral findings

The average SMT (SP_{SMT} condition) in this study (931 ms) was slow compared to the population mean (around 600 ms; Fraisse, 1982). However, the values measured here still fit within the range of inter-individual variability reported in the literature (Michaelis, Wiener, & Thompson, 2014; Monier & Droit-Volet, 2016; Schwartz, Keller, Patel, & Kotz, 2011; Sternad, Dean, & Newell, 2000). In the current study, the participants kept their arms along-side their body (sagittal plane). Recent evidence indicated lower corticomotor excitability in this position than if the arms were positioned on a table in front of the participant (Mogk, Rogers, Murray, Perreault, & Stinear, 2014), and that higher corticomotor excitability resulted in faster SMT (Bisio et al., 2015). The reverse may also be true (lower corticomotor excitability inducing slower SMT) and thus, the imposed position would explain the observed slow pace of SMT in the current experiment.

The ITI lag-1 autocorrelation showed consistent negative values for SMS associated with a stable representation of the beat (Dione & Delevoeye-Turrell, 2015), and increasing values for SP – from negative to positive – with reducing tempo (Fig. 2). Negative values of ITI lag-1 autocorrelation indicate that longer intervals are mostly followed by shorter ones and reversely, and reflect correction of interval length (Semjen et al., 2000). Positive values suggest that successive intervals tend to be of similar duration, and typically reflect slow temporal drifts (Collier & Ogden, 2004). The values close to zero in the SP_{FA} and SP_{SMT} conditions suggest a hybrid use of event-based and emergent timing (Dione & Delevoeye-Turrell, 2015; Repp & Steinman, 2010; though see Delignières & Torre, 2011).

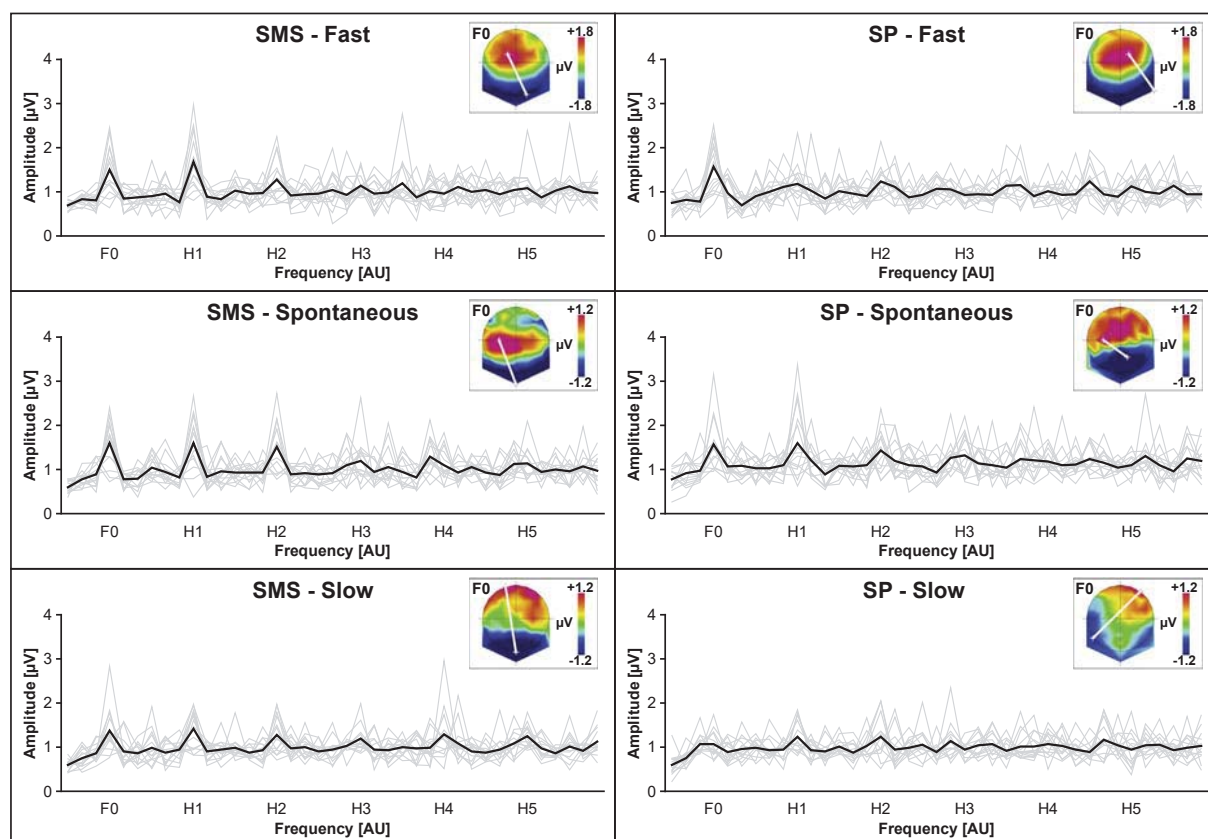


Fig. 5. SSEPs for each tempo of the SMS and SP conditions. The thin grey power spectra represent each participant and the thick black power spectra represent the inter-individual averages.

Table 5

Results for the global frequency indices comparing SMS versus SP.

	GPS					GMD
	F	df	p-val	η^2	ϵ^*	p-val
Task	1.16	1,13	0.302	0.08	–	0.059
Task \times Tempo	1.33	2,12	0.301	0.18	–	0.022

* Greenhouse-Geisser Epsilon reported for effects violating sphericity assumption and corrected using Greenhouse-Geisser estimates of sphericity.

Table 6

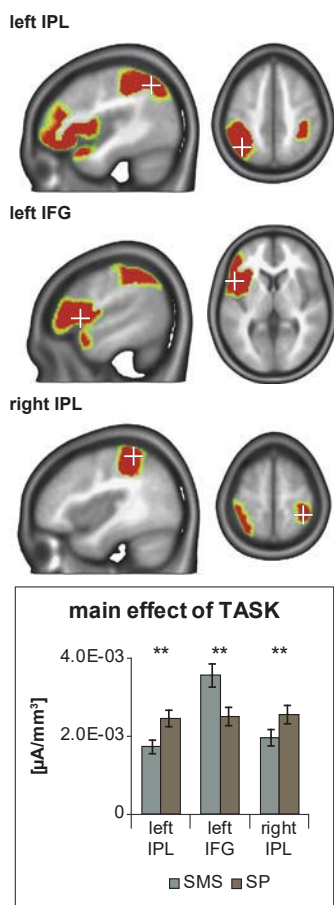
Main Brain Region Activations for the 2 Task \times 3 Tempo ANOVA on current density for SMS versus SP.

Brain region	Hemisphere	x	Y	z	F-values	Cluster size
TASK						
Inferior Parietal Lobule	left	–40	–58	47	19.71	79
Inferior Frontal Gyrus	left	–49	8	4	16.60	150
Inferior Parietal Lobule	right	40	–39	57	12.52	35
TASK \times TEMPO						
Inferior Parietal Lobule	left	–34	–64	47	15.18	112
Inferior Parietal Lobule	right	60	–38	43	8.79	90
pre-SMA (SFG)	right	9	25	54	8.51	16
Fusiform Gyrus	left	–42	–56	–8	6.18	156
Inferior Temporal Gyrus	left	–32	0	–35	5.89	

Note. Talairach x y z coordinates of local maxima for each significant cluster at $p < 0.05$. Minimal cluster size: 15 solution points. Brain areas are grouped by cluster.

SMS vs SP

A. Main effect of Task



B. Interaction effect Task x Tempo

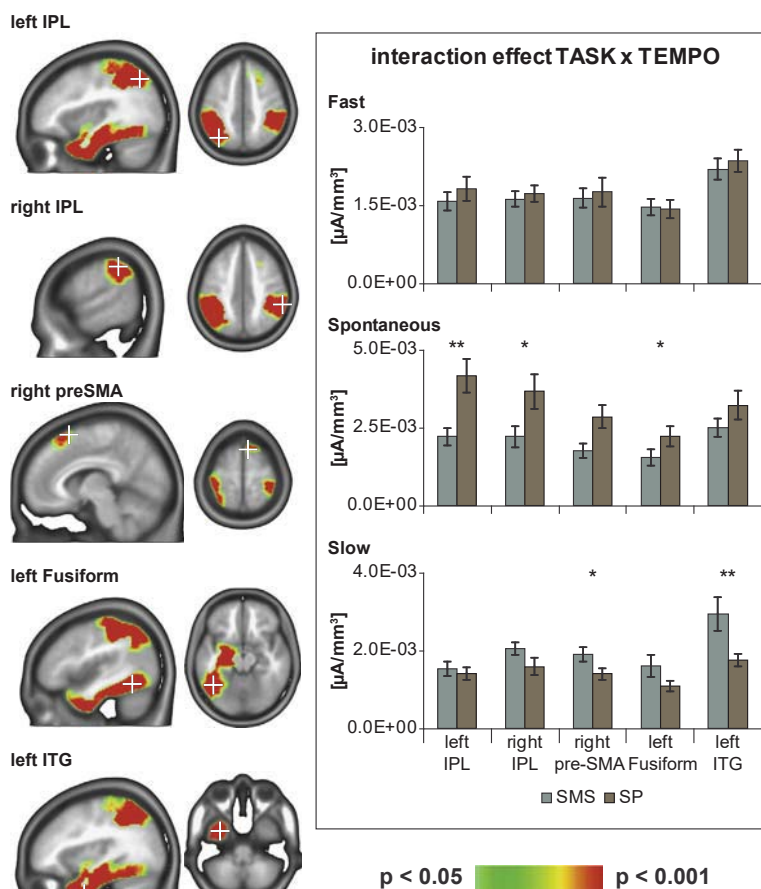


Fig. 6. Distributed electrical source estimations for the main and interaction effects of significant GPS or GMD differences between SMS and SP. The bar graphs depict the current density mean and standard error for each cluster. * $p < 0.05$, ** $p < 0.01$.

The absence of significant correlation between ITI and ITI lag-1 autocorrelation indicate that this was not directly related to the tapping frequency. However, during SP_{SL} most participants seemed to favor emergent timing (Fig. 2), and the slower the tapping tempo, the more they were likely to use this mode of timing control.

Our results imply a weaker representation of the ITIs during SP_{SL} , and that faster tempi facilitate the creation of an internal representation of the beat, even without external stimulation. Even though the tapping variability was similar between all conditions, these findings are consistent with our behavioral hypothesis predicting increased stability during SMS and at faster tempi. These findings are in line with distinction between sub-second (roughly corresponding to SP_{FA} and SP_{SMT}) and supra-second (roughly corresponding to SP_{SL}) timing (Lewis & Miall, 2003).

4.2. Cerebral correlates of event-based versus emergent timing

In the current study, the left IFG showed stronger activation in the SMS conditions compared to SP and to LO. However, the left IFG clusters of the SMS versus SP and SMS versus LO contrasts did not overlap. In SMS versus LO, the cluster was at the border with the premotor cortex, roughly corresponding to Broca's area. In the SMS versus SP comparison, the cluster was more ventral, corresponding to the activations identified by Coull and Nobre (2008) that they associated with event-based timing, corroborating our behavioral results. Thus, the ventral portion of the left IFG may play a central role in event-based timing, probably through its implication in working memory (Kumar et al., 2016; Strand, Forssberg, Klingberg, & Norrelgen, 2008). The increased cerebral

activation during event-based timing at slower tempi (SMS_{SL} vs SP_{SL}) supports the hypothesis of a greater need for brain resources during event-based than emergent timing (Delignières & Torre, 2011), and at slower tempo (Lewis & Miall, 2003).

On the other hand, our results do not confirm the association of the IPL with emergent timing suggested by Coull and Nobre (2008). Their conclusions on emergent timing were based on perceptual tasks only, justifying that the mechanisms involved differ significantly, whereas for event-based timing they reviewed both perception and production tasks, for which the mechanisms were considered similar. Alternatively, previous studies associated the IPL with the allocation of attentional resources during temporal processing and in the temporary retention of interval durations (Bolger et al., 2013; Konoike et al., 2012; Rao et al., 2001). As, for practical reasons, SP_{SMT} was always the first condition that the participants completed, this area might rather have been involved in the initial retention of the intervals.

The left fusiform gyrus activation, showing the same pattern of activation as IPL, is mainly associated with visual discrimination or categorization of letters strings (e.g. Pernet, Celsis, & Démonet, 2005), but also musical notation and notably rhythm (James et al., 2014; Proverbio, Manfredi, Zani, & Adorni, 2013; Stewart, 2005), suggesting that it may act as a pattern analyzer. Thus, this area may support the IPL in the initial evaluation of the intertap intervals.

4.3. Cerebral correlates of auditory-motor coupling

In accordance with our second hypothesis, we observed stronger involvement of the bilateral SMA, left IFG and right STG during SMS compared to LO. The dorsal stream, running from temporo-parietal to inferior and pre-frontal areas, was defined as the sound-to-action pathway supporting auditory-motor integration in language in the left hemisphere (Hickok & Poeppel, 2007, 2015), and in music processing in the right hemisphere (Oechslin, Gschwind, & James, 2018). Several studies of functional and anatomical connectivity pointed out a potential coordinated implication of SMA, IFG, and STG in SMS. We previously proposed that the network including the bilateral SMA, IFG and STG, along with cerebellar areas and the left premotor cortex may play a role in interfacing auditory and motor processing (De Pretto & James, 2015). Similarly, Kung et al. (2013) suggested that the right posterior STG and bilateral IFG were part of a network involved in finding and maintaining the beat. Using diffusion tensor magnetic resonance imaging, Blecher, Tal, and Ben-Shachar (2016) observed significant correlation between synchronization accuracy and fractional anisotropy of white matter tracks connecting the bilateral temporal lobes, and connecting the left STG to the left IFG and premotor areas, reflecting potential faster communication within these tracts in participants producing smaller SMS asynchrony. Taken together, these results provide converging evidence of a coordinated activity of the right STG and left IFG during SMS.

Regarding the implication of SMA, a wide range of studies associated it to beat processing, along with the basal ganglia (e.g. Grahn & Brett, 2007; Schwartz et al., 2011; Teki et al., 2011). In particular, Grahn and McAuley (2009) observed combined stronger activation of left IFG and SMA in participants with better ability to extract the beat of complex stimuli, suggesting a potential joint role of these areas in beat processing.

Confirming our third hypothesis, the cingulate gyrus showed stronger activation during SMS at H1 than F0 and no difference during LO. The activation cluster encompassed the posterior and middle cingulate cortices. Activation of these areas have been reported during self-paced finger tapping (Kawashima et al., 1999), temporal sensory prediction (James et al., 2012), and beat perception (Grahn & Rowe, 2013). The cingulate cortex seems to play a key role in attention-related motor control (Leech & Sharp, 2014; Vogt, 2009). Thus, the current result is compatible with the findings of Kim et al. (2010) showing stronger peaks at H1 when paying attention to the stimuli, and supports the notion that modulations of H1 in SSEP analysis provide information on the attentional processes involved. In our case, the differences between F0 and H1 occurred at the level of brain topography, indicating that these modulations accompanied changes in the underlying brain sources and are consistent with findings in the visual domain showing different brain sources for F0 and H1 (Heinrichs-Graham & Wilson, 2012).

4.4. Neural processes contributing to SSEPs

Some authors hypothesized the existence of endogenous oscillators involved in beat processing (e.g. Large, 2000; McAuley, Jones, Holub, Johnston, & Miller, 2006; Michaelis et al., 2014; Repp, 2008), and it may be tempting to interpret the SSEPs as reflecting neural oscillations at the frequency of the beat and higher-order harmonics. However, SSEPs often reflect complex waveforms (Regan, 1989) and other factors may influence the configuration of peaks in the power spectra, such as the presence of transient ERPs or the acoustic features of the sound, (for discussions, see Henry, Herrmann, & Grahn, 2017; Nozaradan, Keller, Rossion, & Mouraux, 2017; Zhou et al., 2016).

In the current study, the power spectra of the SMS and LO conditions showed high F0 peaks at all tempi relative to the peaks at higher-order harmonics (Fig. 4), indicating the presence of SSEPs. It most likely reflects a neural linkage between the beats, also during passive listening, consistent with the notion of induced feeling of a regular pulsation (Honig, 2013).

In the SMS versus SP comparison, the pattern of peaks in SP (Fig. 6) was consistent with the idea that the peaks are the consequence of regularly occurring transient ERPs. No clear evidence occurred that the SP condition induced SSEPs. This observation can be explained by the emergent timing mode dominating in SP, showing a more instinctive functioning that requires less cognitive involvement. Here, the participants produced self-paced tapping before being exposed to an auditory beat. The results might have been different in the context of a synchronization-continuation paradigm, where the continuation phase might require an internal

representation of the previously heard beat (Jantzen et al., 2007, 2004). This could explain the contrasting neuroimaging results when comparing SMS to a continuation phase (e.g. Bijsterbosch et al., 2011; Jantzen et al., 2007, 2004; Rao et al., 1997), as the internal persistence of the auditory beat might vary depending on the task or instruction.

On the other hand, in SMS the power spectra at all three tempi showed a similar pattern, especially peaks at F0, indicating the presence of SSEPs. Even though we cannot disentangle whether this result derives from pure oscillatory neural entrainment or more complex waveforms, source localization suggest that auditory-motor coupling is mediated by the left ventral IFG, making it the best candidate for the hypothesized endogenous oscillation generator related to beat processing.

4.5. Limitations

First, although we controlled for overt movements during the LO conditions by means of a webcam, we cannot exclude that micro-movements were produced in response to the auditory beats. Such movements during the LO conditions may have reduced the differences between conditions. However, the differences that we did observe are unlikely induced by the presence of unwanted movements in the LO conditions. Indeed, the differences were either showing stronger activation in SMS than LO, or, in the case of SMS vs SP after subtraction of LO, were also observable before the subtraction (see Supplementary Material).

Second, asking participants to tap at their own pace resulted in a wide range of inter-individual tapping frequencies overlapping between tempo conditions. This prevented from fully analyzing the GPS differences between tempi and interpreting them in relation with potential effects of ERPs. We would like to underline that the different inter-individual tempi highlighted cognitive effects of the task rather than physiological effects, given the fact that SMT (SMS_{SMT} and SP_{SMT} conditions) represented the “most natural” to the participants, as instructed.

Third, as SSEP analysis transfers the EEG signal into the frequency domain, the temporal information is lost. Temporal resolution is one of the main advantages of EEG over other neuroimaging technics such as fMRI. However, whereas fMRI reflects slow hemodynamic processes (Huettel, Song, & McCarthy, 2014), SSEPs represent events occurring within the millisecond range (Zhou et al., 2016). Moreover, because the tempo differences might modulate the latency or amplitude of classical ERP components (Jongsma, Meeuwissen, Vos, & Maes, 2007; Snyder & Large, 2004), SSEPs are more robust than ERPs to this issue.

Finally, regarding spatial resolution, EEG source estimation can only guarantee a 1–2 cm spatial accuracy (Martuzzi et al., 2009; Plomp et al., 2010), as compared to the millimeter precision of fMRI. This holds true especially for deeper brain sources (Sohrabpour et al., 2015; Song et al., 2015). Thus, our design could not evaluate the implication of brain areas such as the basal ganglia and the cerebellum, which influence in timing and SMS is well established (e.g. Grahn & Brett, 2007; Kung et al., 2013; Schwartz et al., 2011; Teki et al., 2011). In conclusion, EEG and fMRI measure different brain mechanisms and provide complementary information (Disbrow, Slutsky, Roberts, & Krubitzer, 2000).

5. Conclusion

This study investigated the still under explored neurophysiological correlates of self-paced finger tapping in comparison with SMS. By comparing SMS to auditory perception and isochronous motor action at different tempi, we could highlight brain areas involved in perception-action coupling. Based on previous findings, we hypothesized the use of two attentional processes: one associated with the middle/posterior cingulate cortex and oriented towards the external beats; and one associated with the inferior parietal lobules and oriented towards the internal retention of intervals. Most importantly, the comparison of SMS versus LO suggests a role of the dorsal stream in SMS supporting sound-to-action processes, whereas the comparison of SMS versus SP pointed to the left inferior frontal gyrus as playing a key role in beat-based auditory-motor coupling. We hypothesize that this brain area acts as a working memory structure by aligning its neural activity to the beat frequency.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version

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