

The sound of silence: an EEG study of how musicians time pauses in individual and joint music performance

Anna Zamm,¹ Stefan Debener,² Ivana Konvalinka,³ Natalie Sebanz,^{1,‡} and Günther Knoblich^{1,‡}

¹Department of Cognitive Science, Central European University, Budapest 1051, Hungary, ²Neuropsychology Lab, Department of Psychology, University of Oldenburg, Oldenburg 26129, Germany, and ³Section for Cognitive Systems, DTU Compute, Technical University of Denmark, Lyngby 2800, Denmark

Correspondence should be addressed to Anna Zamm, Nador Utca 9, Budapest 1051, Hungary. E-mail: zamma@ceu.edu.

‡Denotes joint final authorship.

Abstract

Pauses are an integral feature of social interaction. Conversation partners often pause between conversational turns, and musical co-performers often pause between musical phrases. How do humans coordinate the duration of pauses to ensure seamless interaction? A total of 40 trained pianists performed a simple melody containing fermatas (notated expressive pauses of unspecified duration) first alone (Solo) and then with a partner (Duet) while electroencephalography (EEG) was recorded. As predicted, Duet partners' tone onset synchrony was reduced for tones following pauses. Pauses were shorter in Duet relative to Solo performance, and synchrony of partners' Duet tone onsets was enhanced for tones following shorter pauses. EEG analysis revealed classic signatures of action preparation during pauses, namely decreases in the power of cortical beta oscillations (13–30 Hz, event-related desynchronization ERD). Beta ERD did not differ between pauses in Solo and Duet performance, but was enhanced for shorter relative to longer pauses, suggesting that reduced pause durations in Duet performance facilitated a neural state of enhanced action readiness. Together these findings provide novel insight into behavioural strategies by which musical partners resolve coordination challenges posed by expressive silence, and capture a clear neural signature of action planning during time-varying silences in natural music performance.

Key words: joint action; dual EEG; action prediction; music performance

Introduction

Pauses are an integral feature of social interaction. For instance, conversation partners often pause between conversational turns, and jazz improvisers often pause between musical phrases. These pauses present a difficult challenge, since partners must coordinate when a pause should end and who should end it. Successful coordination of pauses ensures seamless transitions between partners' action sequences and can promote trust (Brennan and Williams, 1995) and common ground (Beňuš *et al.*, 2011) between partners. In contrast,

failures to coordinate can significantly disrupt the flow of social interaction and adversely affect liking between partners (Koudenburg *et al.*, 2011). An open question is what behavioural and neural mechanisms allow individuals to determine when a partner will end a spontaneous pause in interaction, and how to time their own actions accordingly.

Pauses represent a unique challenge in ensemble music performance due to the millisecond-level temporal demands of music coordination. Musical scores often feature notation indicating that performers should pause at specified score

Received: 3 June 2020; Revised: 16 June 2020; Accepted: 11 July 2020

© The Author(s) 2020. Published by Oxford University Press. All rights reserved. For Permissions, please email: journals.permissions@oup.com
This is an Open Access article distributed under the terms of the Creative Commons Attribution NonCommercial-NoDerivs licence (<http://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits non-commercial reproduction and distribution of the work, in any medium, provided the original work is not altered or transformed in any way, and that the work is properly cited. For commercial re-use, please contact journals.permissions@oup.com

locations. These pauses are often intended as communicative or expressive gestures (Margulis, 2007a, 2007b; Acheson, 2008); in many cases, the duration of these pauses is not specified, in which case it is up to the performer's artistic discretion as to how long to pause for. In ensemble performance these self-paced pauses, which are known as 'fermatas' or 'caesuras,' pose a coordination challenge, particularly when they must be resolved simultaneously. To simultaneously resolve pauses, partners must mutually anticipate one another's actions with millisecond precision while planning their own actions accordingly. The current study investigates the behavioural and neural processes by which musicians determine the duration of self-paced pauses in ensemble and Solo performance. A broader goal of the study is to provide insight into how individuals navigate temporal uncertainty in social vs individual action contexts.

One process shown to support interpersonal action coordination is action prediction. Evidence suggests that individuals possess mental representations of their own and others' actions, and in coordination contexts, use these representations to simulate and predict a partner's actions and to coordinate their own actions accordingly (Novembre et al., 2012; Kourtis et al., 2013; Vesper et al., 2013). However, it is unclear how prediction might contribute to coordination in contexts where partners have little information about the timing of upcoming actions, as in the case of self-paced pauses, since these pauses are spontaneous and their duration is not known *a priori*.

In cases where individuals have sparse information about each other's actions, they often facilitate coordination by modifying their own behaviours so that they become more predictable (Vesper et al., 2011). This includes exaggerations of one's own movement trajectories and performing actions in a faster and less variable way (Goebel and Palmer, 2009; Vesper et al., 2011, 2016). Some of these behavioural modifications are displayed in non-human primates during cooperative tasks (Visco-Comandini et al., 2015), suggesting that they may constitute a basic evolutionary coordination strategy when more complex strategies are unnecessary or unavailable. In the context of self-paced musical pauses, when it is difficult to predict a partner's actions, individuals may try to facilitate coordination by falling back on behavioural strategies such as shortening the duration of pauses or decreasing their variability.

One means of assessing the mechanisms underlying coordination of self-paced musical pauses in ensemble performance is to measure known neural markers of action preparation and prediction while musicians are preparing to resolve self-paced pauses. If musicians predict one another's pause durations during ensemble performance, then neural markers of prediction should show different patterns of activity during pauses in Solo vs ensemble performance. One well-described neural marker of voluntary action preparation and execution that may provide insight into prediction processes is cortical beta activity (~13–30 Hz; Engel & Fries, 2010).

Cortical beta-band activity (BBA) is thought to reflect the activity state of the motor system (Pfurtscheller et al., 1996a). This functional interpretation of BBA arises from observed modulations of BBA during action execution (Stancák and Pfurtscheller, 1995), action imagery (Pfurtscheller et al., 2005; Zich et al., 2015) and action observation (Hari et al., 1998; Caetano, Jousmä, and Järveläinen et al., 2001; Koolewijn et al., 2008). Specifically, BBA power decreases relative to baseline levels during preparation of executed, imagined and observed actions. This phenomenon is referred to as event-related desynchronization (ERD). Subsequent increases of beta power after movement termination have also been observed and

are referred to as event-related synchronization (ERS; for a review see Pfurtscheller and Lopes Da Silva, 1999). Beta ERD/ERS is measured with electroencephalography (EEG) or magnetoencephalography (MEG), begins 1–2 s prior to an action, arises over sensorimotor areas (Salmelin et al., 1995), and is accompanied by ERD/ERS in the alpha frequency band (~8–12 Hz). In addition to capturing activity states of the motor system, beta ERD may reflect sensorimotor prediction processes, either about the consequences of one's own actions or actions that one observes another individual perform (Engel and Fries, 2010; Arnal, 2012; Arnal and Giraud, 2012). In the context of self-generated actions, evidence suggests that beta ERD reflects the predictability of actions one is about to perform. Specifically, a stronger beta ERD has been reported when individuals can fully predict the parameters of an action that they will perform, relative to when they have incomplete information (Tzagarakis et al., 2010; Zaepffel et al., 2013). Beta ERD is similarly modulated by predictability of observed actions. Here, beta power is lower than baseline during the observation of actions about which one has prior knowledge, such as actions that are in one's domain of expertise relative to actions outside of one's motor expertise (Orgs et al., 2008; Quandt and Marshall, 2014; Denis et al., 2017).

Beta oscillations may also reflect the prediction of a partner's actions during social motor coordination. The literature on speech turn-taking indicates that beta ERD reflects social motor dynamics of speech conversation. Listeners show beta ERD prior to the end of others' speech turns in conversation (Magyari et al., 2014; Gisladdottir et al., 2018), and prior to the onset of their own conversational utterances (Bögels et al., 2015). More recent evidence suggests that beta oscillations may even play a causal role in facilitating social motor coordination. Specifically, in-phase dual-brain beta-frequency stimulation over the left primary motor cortex has been shown to enhance synchrony of finger-tapping between partners relative to anti-phase stimulation and stimulation at other frequencies (Novembre et al., 2017).

If individuals focus on predicting a partner's actions during self-paced pauses, then beta ERD magnitude should be reduced during pauses in interpersonal relative to individual action contexts, since predictability of a partner's actions is lower than predictability of one's own actions; this hypothesis is based on the assumption that beta ERD magnitude is correlated with action predictability. However, if individuals focus on their own actions and adopt a strategy of modifying their own behaviour to simplify coordination during self-paced pauses in interpersonal coordination contexts, then beta ERD may not differ between pauses in social vs individual action contexts.

We tested these hypotheses in an EEG study of music performance. Beta oscillations have been linked to auditory prediction in music-related contexts such as perception of musical rhythms (Fujioka et al., 2012; Doelling and Poeppel, 2015), production of sound-making actions in non-musicians (Bauer et al., 2015; Ross et al., 2017), and sensorimotor synchronization with an auditory stimulus (Morillon and Baillet, 2017). We provide the first extension of this work to the context of natural music performance in expert musicians. We measured EEG from trained pianists while they performed a piece of music containing pauses of unspecified duration from memory, first alone (Solo) and then with a partner (Duet). In Solo performance, pause durations were entirely up to the individual performer, whereas in Duets partners had to mutually coordinate the duration of pauses in order to synchronously recommence tone onset production after each pause. On a behavioural level, we tested the hypothesis that pauses represent a coordination challenge. This was done by measuring tone onset asynchronies for tones immediately

following each pause. The magnitude of tone onset asynchronies immediately following each pause should be higher than asynchronies at other melody locations if pauses truly reflect a social coordination challenge. In addition, we tested whether individuals modified pause characteristics, such as duration and variability, in Duet relative to Solo performance, as can be predicted if individuals adopt a strategy where they modify their own actions to facilitate interpersonal coordination. On a neural level, we compared beta ERD dynamics across Solo and Duet performance within each performer, to investigate the distinct processes that underlie the resolution of self-paced pauses in individual vs interpersonal contexts.

Methods

Participants

A total of 40 participants [22 female; M age = 25.63 years, standard deviation (s.d.) = 5.49 years, range = 18–45] with a minimum of 6 years of musical training on the piano (M musical training = 12.13 years, s.d. = 4.27 years, range = 6–22 years) were included in the current study sample.¹ Participants completed the study in pairs (N = 20 pairs), and sample size was determined *a priori* based on previous studies of interpersonal synchrony between pairs of performing musicians with comparable sample size (Loehr and Palmer, 2011; Zamm et al., 2014; Zamm et al., 2016). Participants were recruited through an online participant database (SONA systems, www.sonasystems.com) and from local conservatories in Budapest.

All participants in the current sample reported basic English language skills, right-hand dominance, normal hearing, normal or corrected-to-normal vision, and no current use or history of psychiatric medication. All participants provided informed consent prior to the experiment and received gift vouchers for their participation. The study was approved by the United Ethical Review Committee for Research in Psychology (EPKEB), and was conducted in accordance with the Declaration of Helsinki (1991). Four additional pairs were recruited but excluded from the current sample. One of these pairs was excluded due to technical issues during data acquisition. Two of these pairs were excluded because at least one pair member did not pass the screening tests (see Procedure below). Finally, one pair was run in the study after reaching the target N of 20 pairs and was therefore excluded from analysis.

Musical stimulus

The musical stimulus used in the current study comprised a simple melody for piano, as shown in Figure 1. The melody was adapted from the theme of a major motion picture film score, and was selected because it featured a rhythmic structure that could be easily divided into segments delineated by pauses, making it well suited to the goals of the study. Specifically, the melody comprised 12 segments, each with a comparable rhythmic structure, where the structure featured a two- to three-measure sequences of continuous short-duration tones (quarter and half notes) followed by a sustained tone (dotted half note). Sustained tones in music often indicate phrase boundaries (Riemann, 1900), and pauses often accompany phrase boundaries (Neuhaus et al., 2006), so pauses were inserted in the melody after each sustained tone. Pauses were notated as

‘caesuras’ with ‘fermata’ markings over them, where ‘caesuras’ typically indicate that performers should insert a silence at a given score location (Merriam Webster Online Dictionary, 2020), and ‘fermatas’ typically indicate that performers should pause for an unspecified period of time (Fermata | Grove Music, 2020). Thus, a ‘caesura’ with a ‘fermata’ marking indicates that performers should sustain a silence for a time duration of their discretion (McGrain, 1990). Pause locations are indicated in Figure 1 by red arrows. Further details about the stimulus are provided in the Supplementary data.

Equipment

Keystroke recording

Two identical Akai Professional MAX25 USB-powered keyboards were used to record Duet piano performances (see Supplementary data for settings). Keyboards were placed on adjacent wooden tables with a cardboard screen between them to prevent Duet partners from seeing one another’s hand movements. Musical Instrument Digital Interface (MIDI) information (timing, pitch, velocity) was sent from each keyboard over a separate MIDI channel; data from the two keyboards were merged via a MIDI merger (MIDI Solutions Inc., Canada) and sent via a MIDI-USB interface to a Linux computer (Fedora 28, kernel 4.16.3-301.fc28.x8664) running FTAP MIDI recording software (Finney, 2001; see Supplementary data for further information about the version of FTAP used).

MIDI information associated with each keystroke was sent from FTAP via MIDI-USB to a battery-powered tone generator (Roland SD50 Mobile Studio Canvas, Roland Corporation, Japan), which produced the corresponding tone in a piano timbre (see Supplementary data for timbre details). FTAP was also used to generate metronome pacing sequences using the tone generator’s built-in woodblock timbre (see Supplementary data for timbre details). Audio from the tone generator was delivered to participants via EEG-compatible earbuds (ER3C Tubal Insert Earphones, Etymotic Research Inc., USA). Earbuds were connected to a battery-powered headphone distributor/amplifier (M-Audio Bass Traveller, M-Audio Inc., USA) that amplified and distributed audio to each pianist’s earbuds.

EEG recording

EEG data were recorded simultaneously from Duet pianists using two 32-channel BrainAmp DC EEG amplifiers (BrainProducts GmbH, Germany). Each pianist’s data were recorded with 32 active electrodes placed on a nylon 32ch Standard Cap for ActiCap from Easycap (EASYCAP, GmbH, Germany), which uses an extended 10–20 layout (see Supplementary data). Reference and ground electrodes were placed at FCz and AFz sites respectively. With one exception, electrode impedances were kept <25 kOhm (manufacturer-recommended threshold) at the beginning of each task.

Each pianist’s electrodes were connected to a separate ActiCap control box which performed referencing/grounding, ensuring galvanic isolation between the two subjects’ EEG data. Referenced data from each control box were sent to a 32-channel amplifier (high-pass filter = 10s time-constant/0.0159 Hz, low-pass filter = 250 Hz, sampling rate = 5000 Hz, 0.1 μ V resolution, \pm 3.28 mV range). Amplifiers were connected to a USB2 Adapter Box from Brain Products, which synchronized incoming data streams by providing a shared clock.

The USB2 Adapter Box also received TTL triggers from MIDI recordings over a parallel port allowing for full synchronization of behavioural and EEG data; timing tests were conducted

¹ Two participants could not report precise years of musical training and indicated only 10+ years, so they were excluded from the means reported here.



Fig. 1. Melody stimulus notation. Locations of the 12 pauses included in analyses are indicated by red arrows. The final indicated fermata was not analysed because there were no subsequent tone onsets and is therefore not indicated with an arrow.

to ensure synchronization between EEG and behavioural data streams. TTL triggers from MIDI keystrokes were sent at every keystroke onset. These triggers were 0.5 milliseconds in duration, hence the acquisition of EEG data at 5000 Hz. All EEG data and MIDI TTL triggers were sent from the USB2 adapter to BrainVision Recorder Software from Brain Products (v1.20.0801) running on a Windows OS (Win 7 Professional SP1).

Design. Participants completed two experimental tasks: Solo and Duet piano performance. As is common in music Duet studies (Goebel and Palmer, 2009; Davidson, 2012; Palmer et al., 2019), these tasks were completed in a fixed order (Solo followed by Duet) to ensure that participants' Solo performances were not influenced by how their partner performed the melody. Each task comprised five valid trials of piano performance, where one trial corresponded to a single performance of the stimulus melody (for an explanation of trial validity, see Procedure below). A single performance of the melody featured 12 pauses (see Stimulus section). Therefore, the experiment comprised a 2 (Task) \times 2 (Pause location) within-subject design.

Procedure

Home melody practice. Participants were sent the stimulus melody in advance of their arrival at the laboratory with the instruction to practise the melody with their right hand at a rate of 75 beats per minute (800 milliseconds between successive quarter notes), both in the written octave (C4-C5) and one octave lower (C3-C4). See Supplementary data for detailed instructions.

Laboratory tasks. Upon arrival, each partner was assigned to perform the stimulus melody in a unique octave, i.e. one of the two octaves in which they had practiced (C4-C5 or C3-C4). Each partner was also assigned to one of the two piano keyboards, and used this keyboard throughout the study. Partners then completed a melody practice session, screening tests, a resting state EEG session, and piano performance tasks (Solo followed by Duet piano performance) during which EEG was recorded. EEG was recorded continuously within each performance task and paused between tasks while the experimenter delivered instructions.

Pianists sat side-by-side, and a shoulder-level screen was placed between them so that they could not see one another's hand movements, or any body movements below the shoulders, and could only peripherally observe one another's head and shoulders. It is known from previous studies that body sway can act as a coordination cue (Chang et al., 2017; Keller and Appel, 2010; for a review see Palmer, 2013). Our aim was to investigate predictive processes arising from primarily auditory information exchange between task partners, so we deliberately created an

experimental setup where pianists had limited access to visual information about one another's actions. Sound was delivered through insert earbuds. Instructions for all tasks were given verbally by a fully bilingual experimenter in either English or Hungarian, depending on the participants' preference.

Melody practice and screening. Partners took turns completing a melody practice session followed by a screening test (see Supplementary data for details). The screening test was implemented to ensure that all pianists included in the study performed the melody at ceiling and to thereby minimize possible influences of melody familiarity on performance fluency. After each partner completed the melody practice and screening, they were both asked to return to the testing room where they were prepared for EEG data acquisition. Participants were allowed to talk to the experimenters and one another during EEG preparation.

Resting state EEG. After EEG caps were prepared and impedances were reduced, participants completed a 3 min resting state recording in which they were instructed to stare at a fixation cross and minimize body movements. Resting data were included in data cleaning procedures as described in the Supplementary data.

Solo performance with EEG. After participants completed the resting state EEG, partners took turns completing a Solo piano performance task while EEG was measured. In the Solo performance task, participants performed the melody alone at the rate of an initial metronome cue, with the same instruction to observe musical pauses that they received in the stimulus notation sent for home practice. The instructions were as follows:

'We are studying musical silences, so please be sure to observe notated breaks in the score. The exact length is up to you. These breaks are defined as silences between the end of the note right before the break and the beginning of the note right after the break. Please use your intuition to determine the length of the pause; do not count. Each pause should be unique and expressive. Think of the pauses as brief suspensions of musical time'.

Participants were given an additional instruction that 'For technical reasons, we can only include performances in our analyses with breaks of an acceptably long duration, so we will have you repeat trials where breaks are too short.' This was to ensure that each participant performed enough pauses of sufficient duration to allow for capturing beta ERD in offline EEG analyses. Pause durations for each trial were assessed online by experiment scripts, and trials were defined as invalid if >25% of pauses were shorter than an *a priori* defined minimal duration

of 1.6 s, corresponding to two quarter notes at the cued tempo (see Data analysis).

Participants performed practise Solo trials followed by test trials. On each trial, participants heard the initial metronome cue and then performed the melody once from memory as instructed by the experimenter. After completing one valid Solo practice trial, participants completed five test trials. For each invalid test trial, participants were informed by the experimenter that their pauses were not long enough and were given one opportunity to repeat the trial. If participants were unable to produce a valid trial after a second attempt, they moved on to the next test trial.

While one partner completed the Solo task, the other partner remained seated at their piano and read magazines. Their earbuds were removed so that they could not hear their partner's performance, and the visual occluder prevented them from seeing their partner's hand movements.

Duet performance with EEG. After both partners completed the Solo performance task, partners produced the stimulus melody as a Duet in octave–unison while EEG was recorded. The instructions for the Duet performance task were identical to the Solo task, except that partners were given the additional instruction that 'your goal is to synchronize keystrokes while maintaining the tempo of the metronome (cue).'

The procedure for the Duet performance task was identical to the Solo task (practise the melody until producing one valid trial, then complete five test trials with one opportunity to repeat each invalid test trial). For Duets, valid trials were defined as trials where both partners produced >25% of pauses correctly (longer than the minimally acceptable duration of 1.6 s).

Data analysis

All data pre-processing steps and analysis details are described in the Supplementary data. Below is a general description of each measure entered into data analysis, as reported in Results.

Dependent measures

Duet tone onset asynchronies

Duet tone onset asynchronies on each trial were computed as the absolute (unsigned) temporal offset in milliseconds between partners' keystrokes at corresponding melody locations. Low absolute asynchrony values indicate high interpersonal synchrony, and high absolute asynchrony values indicate low interpersonal synchrony.

Pause duration and variability

Pause durations were defined for all valid pauses on valid trials as the duration in milliseconds (ms) between the final keystroke release before a given pause and the first key depression after the pause. For Duets, durations entered into behavioural analyses were defined within-subject (a given subject's key release prior to the pause to the time of their key depression after the pause).

The variability of each subject's pause durations within each task (Solo/Duet) was computed as their coefficient of variation (CV) of pause duration. The CV of pause duration was computed as the s.d. of duration across pauses for a given subject/Task, divided by the mean pause duration for that subject/Task, multiplied by 100. The CV therefore reflects the variability of each

subject's pause duration in a given Task as a percentage of their mean pause duration for that Task.

Event-related desynchronization (ERD) of cortical beta activity

ERD is typically expressed as the proportional difference between beta amplitude (or power) in a given time window of interest (e.g. prior to the onset of an action) and beta amplitude in a baseline period (Pfurtscheller and Da Silva, 1999). Beta ERD was therefore computed for each pause on each channel by dividing the pause into deciles, corresponding to 10 evenly spaced time bins reflecting 10% of the total duration of silence for a given pause (see Supplementary data). Beta amplitude was averaged across samples within each decile, and the percentage difference in mean beta amplitude between each decile and a corresponding baseline period (defined from -0.5 to 0 seconds relative to the pause epoching event) was subsequently computed. Pauses were divided into proportional time windows (deciles) to allow for comparison across pauses that varied in duration across epochs and subjects. Linear changes in beta ERD across time windows of musical pauses in Solo and Duet performance were assessed at two regions of interest (ROIs) commonly associated with beta ERD (Zaepffel et al., 2013), a parietal ROI and a central ROI using a linear mixed model.

The linear mixed model was implemented using the lmer function in the lmerTest package (version 3.1-0) in R Statistics, with single-trial beta ERD as outcome variable, and fixed effects of Time window (10 time windows, reflecting deciles 1–10), Task (Solo/Duet), ROI (Parietal/Central), and pause duration (trial-level). Random subject effects (correlated slopes and intercepts) were defined for all main effects and interactions between Time window, Task, and ROI (1 + Time window * Task * ROI | subject). Time window was defined as a continuous variable to estimate a continuous change in ERD across each pause; and pause durations entered into the model were standardized across subjects using the scale function in the base package (version 3.6.0, options: centre = TRUE, scale = TRUE), to express each subject's pause duration as a standard deviation from the grand mean pause duration across subjects. The overall model equation was therefore: $ERD \sim \text{time window} * \text{Task} * \text{ROI} * \text{standardized (pause duration)} + (1 + \text{Time window} * \text{Task} * \text{ROI} | \text{subject})$. The model optimizer used was 'nloptwrap' (calc.derivs = false to enhance computational performance, <https://cran.r-project.org/web/packages/lme4/vignettes/lmerperf.html>), and restricted maximal likelihood estimation was set to false to allow for subsequent comparison of maximal and reduced models (Bates et al., 2014). This full model failed to converge; a restricted model was therefore run that was identical to the full model but without Task as a fixed or random effect, since this was the only fixed effect that was not a significant predictor in the full model. Significance levels for fixed linear mixed model effects were computed using Satterthwaite's approximation for degrees of freedom ('anova' function in the lmerTest package, which returns a type III analysis of variance (ANOVA) table with significance levels for fixed and random effects).

Results

Number of pauses in analyses

The mean number of pauses included in behavioural analyses per subject after pre-processing (see Supplementary data) was 54.83 for the Solo Task (range = 29–60) and 53 for the Duet Task

(range = 34–60). Additional pauses were removed for EEG analyses because these pauses contained artefactual activity. The mean number of pauses retained for EEG analyses per subject was 49.38 for the Solo task (range = 27–56), and 47.35 for the Duet task (range = 32–54).

Effect of pauses on Duet synchronization

Figure 2A shows grand average asynchronies for each subject, and Figure 2B shows the mean asynchrony profile for each pair. Peaks in partners' Duet asynchronies are clearly visible after each pause location. A one-way repeated-measures analysis of variance (ANOVA) on Duet asynchronies (see Supplementary data for full details of ANOVA model) with Pause location (1 = tone onset immediately following a pause, 0 = non-pause location) as factor indicated a significant main effect of pause location on Duet asynchrony, $F(1, 19) = 265.03$, $p < 0.0001$, $\eta^2_G = 0.84$, with higher asynchronies for tone onsets following pauses relative to onsets at other melody locations.

Effect of Task on Pause duration

Figure 2C shows grand average pause durations in the stimulus melody for Solo and Duet performance. Pause durations are visibly reduced for Duet relative to Solo performance. A two-way repeated-measures ANOVA (see Supplementary data for full details of ANOVA model) on Pause duration with Task and Pause number as factors and Pair as ID variable indicated a significant main effect of Task on Pause duration, $F(1, 19) = 5.99$, $p = 0.02$, $\eta^2_G = 0.08$, with reduced Pause durations for Duet relative to Solo performance. In addition, a significant main effect of Pause number on Pause duration was observed, $F(5.10, 96.92) = 16.64$, $p < 0.0001$, $\eta^2_G = 0.09$, where Pause durations differed depending on where the Pause occurred in the melody. The interaction between Task and Pause number did not reach significance ($p = 0.12$).

Effect of Task on Pause variability

A two-way repeated-measures ANOVA (see Supplementary data for full details of ANOVA model) on the CV of Pause duration with Task and Pause location as factors and pair as ID variable revealed no effect of Task on the CV of Pause duration after removing outliers in Pause duration, $F(1, 19) = 0.39$, $p = 0.54$, $\eta^2_G = 0.003$. A significant main effect of Pause location on the CV of Pause duration was observed, $F(6.55, 124.53) = 3.19$, $p = 0.005$, $\eta^2_G = 0.04$, where variability of Pause duration varied by Pause number. The interaction between Task and Pause location did not reach significance ($p = 0.77$).

Relationship between Duet Pause duration and synchrony

Figure 2D displays the relationship between Duet Pause duration and Asynchronies. A Spearman's correlation (see Supplementary data for full details of calculation) between Duet pause duration and Duet asynchronies revealed a significant positive relationship between these two variables, $\rho(18) = 0.824$, $p < 0.0001$, where asynchronies increase with increases in pause duration.

Effect of Task and Pause duration on beta ERD

Figure 3A displays changes in beta ERD across Time windows of musical pauses in Solo (top panel) and Duet (bottom panel) tasks. Figure 3B displays the grand average time-course of beta

ERD for the Solo task at Central and parietal ROIs, and Figure 3C displays the grand average time-course of beta ERD for the Duet task (right) at central and Parietal ROIs. Corresponding linear mixed model predictions from the full model of Task and ROI are overlaid on these figures for comparison (see Supplementary data for details of the linear mixed model). Figure 3D displays linear mixed model predictions (from the full model, see below) for the main effect of Pause duration (standardized) on beta ERD; model predictions indicate that beta ERD is more negative on average during shorter relative to longer pauses. Significance levels for fixed linear mixed model effects were computed using Satterthwaite's approximation for degrees of freedom ('anova' function in the stats package, which calls the lmerTest method for computing ANOVAs on mixed models, returning type III ANOVA table with significance levels for fixed and random effects, with degrees of freedom computed using Satterthwaite's method). The full model yielded significant main effects of Time window, ROI, Pause duration (standardized), and a significant interaction between Time window and ROI. No other main effects or interactions were observed. This full model did not converge. To confirm the observed main effects, a restricted model was subsequently implemented without Task as a fixed or random effect, since Task did not show a significant main effect or interaction with any, and other variable in the full model. This restricted model did converge, and confirmed the main effects of time window $F(1, 40) = 30.12$, $p < 0.0001$, Pause duration (standardized), $F(1, 7465.9) = 9.931$, $p = 0.002$, and ROI $F(1, 95.7) = 15.095$, $p = 0.0002$, observed in the full model, as well as the interaction between Time window and ROI, $F(1, 198.5) = 5.55$, $p = 0.02$. There were no other main effects or interactions in the restricted model (all p values > 0.25).

Discussion

The current study investigated the behavioural and neural correlates of action preparation during musical pauses of unspecified duration. These pauses—'fermatas' and 'caesuras'—naturally occur in music as expressive and rhetorical gestures and pose a challenge for coordination in ensemble music, as partners must determine—often without explicit communication—when to resolve the silence. We investigated how musicians resolve these silences in Solo and Duet music performance. Our first aim was to determine whether musicians adopt different behavioural strategies for resolving pauses in individual vs joint performance contexts. Our second aim was to assess whether known neural correlates of action preparation—namely desynchronization of cortical beta oscillations (beta ERD)—occur when musicians prepare to resolve pauses of uncertain duration. Moreover, we assessed whether beta ERD reflects potential differences in how musicians resolve temporal uncertainty in individual vs joint action contexts.

In terms of behaviour, we found that pauses did indeed pose a challenge to interpersonal coordination. Duet synchronization was reduced (higher tone onset asynchronies) for tones following pauses relative to tones at other melody locations. Partners navigated this challenge by reducing the duration of pauses in Duets. Specifically, pauses were shorter on average in Duet relative to Solo performance, and pairs whose pauses were shorter on average displayed enhanced synchronization for tones following pauses relative to pairs who produced longer pauses. Together, these findings are consistent with previous work indicating that individuals modify their own actions to facilitate joint action coordination in contexts where it is difficult to predict a partner's actions (Vesper et al., 2011, 2016). While

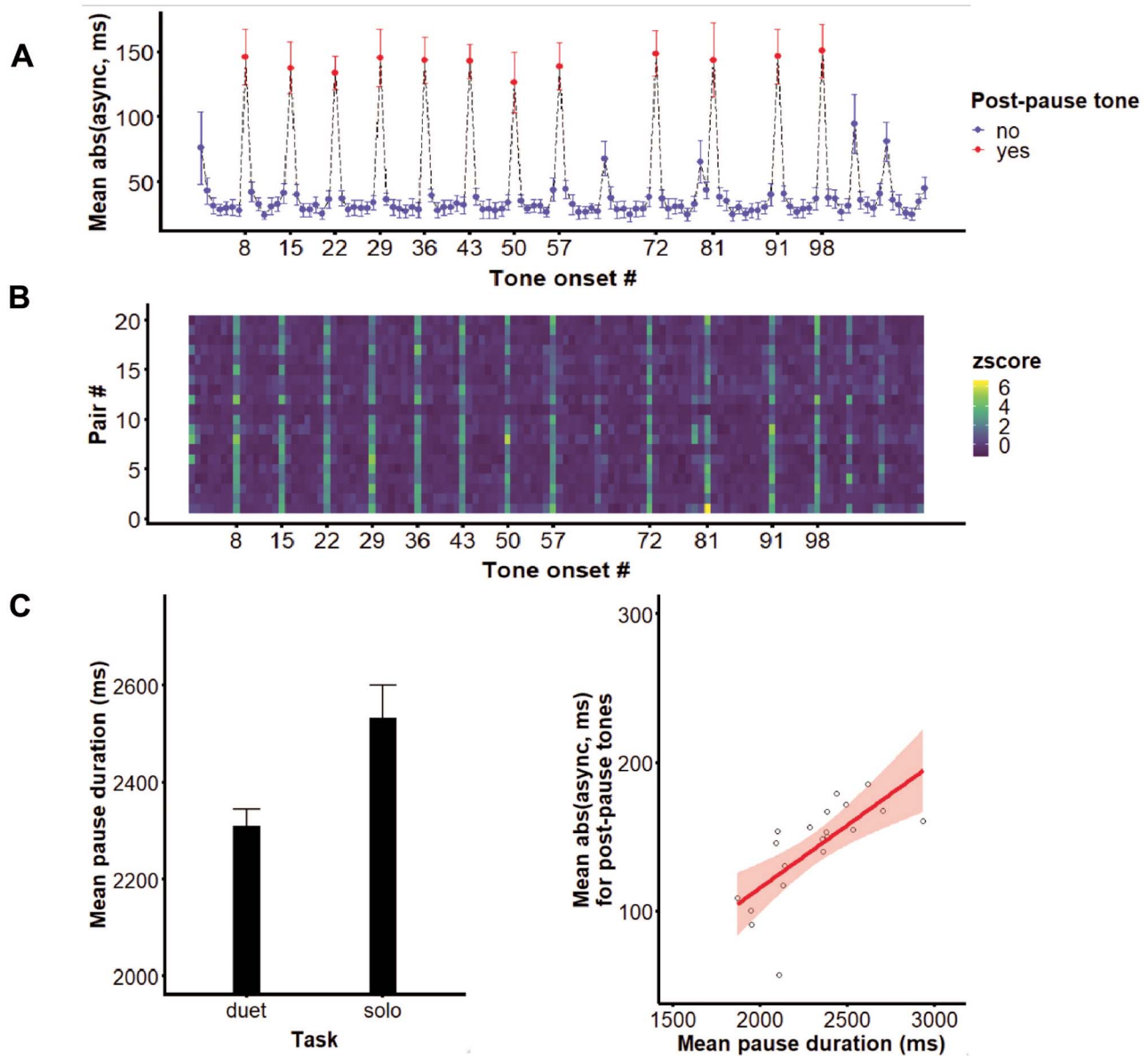


Fig. 2. Behavioural results summary. Panel A: Grand average asynchrony profile across pairs. Panel B: Mean asynchrony profiles for each pair, where asynchrony is represented as a z-score to allow for visual comparison across pairs with different asynchrony scales. Panel C: Main effect of Task on pause duration. Panel D: Correlation between mean Duet pause duration and mean asynchrony for post-pause tones (tones coloured red in Panel A).

earlier studies have focused on simple actions in non-artistic contexts, we extend these findings to the context of Duet music performance. It should be noted that Figure 2A and B indicates that half notes (sustained tones that are measured in duration) also posed a challenge for Duet synchronization, as evidenced by higher tone onset asynchronies following these notes. It is known that action variability increases at slower rates of movement (Semjen et al., 2000), possibly due to increasing cognitive involvement in timekeeping processes (Lewis and Miall, 2003); therefore, it is possible that any joint action context in which partners must simultaneously sustain temporal intervals without producing timekeeping actions pose a coordination challenge, regardless of whether the sustained interval is a measured tone or an unmeasured silence.

In contrast with previous work, the decrease in pause duration from Solo to Duet performance was not accompanied by

a decrease in variability of pause duration. Successive pauses in the current task were spaced apart in time and separated by intervening events, which may have made it difficult for musicians to remember the duration of pauses with high enough accuracy to reduce variability over time. In addition, the experimental instructions—which emphasized that each pause be unique and expressive—may have discouraged any strategy for coordination involving reduction of variability. Regardless of these caveats, the current behavioural findings clearly support the hypothesis that increasing the speed of one’s own behaviour, if not reducing the variability—is a means of facilitating coordination with an unpredictable partner.

In terms of EEG findings, musicians displayed neural signatures of action preparation, namely beta ERD, during pauses in Solo and Duet performance. Although beta ERD has been shown to proceed actions in simple tasks such as

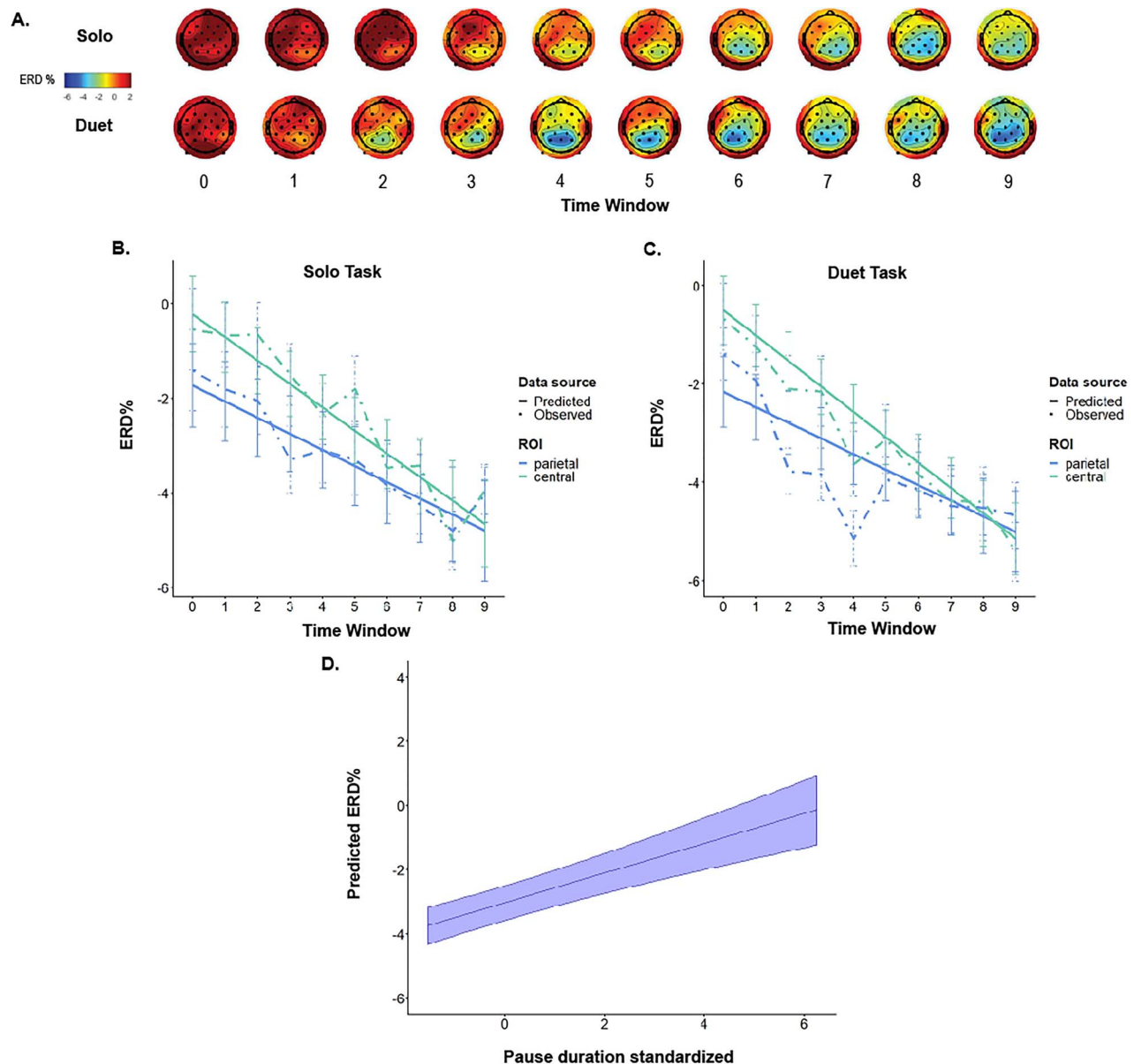


Fig. 3. EEG results summary. Panel A: Mean ERD% topographies in each time window of musical pauses for Solo (top) and Duet (bottom). Outliers were not removed for this visualization (Panels B and C show ERD% after removing outliers; these reflect the data submitted to analyses). Panel B: Observed (dashed lines) and Predicted (solid lines) ERD% data for the Solo task. Predicted data are predicted from the full Linear Mixed Model on beta ERD (see Methods). Panel C: Same as Panel B, but for the Duet task. Panel D: Predicted relationship between pause duration (standardized) and beta ERD% from the full Linear Mixed Model.

finger tapping and grasping (Pfurtscheller *et al.*, 1996a), and also in music-related contexts involving perception (Fujioka *et al.*, 2012; Doelling and Poeppel, 2015) and production of simple rhythms (Bauer *et al.*, 2015; Morillon and Baillet, 2017), and sound-making actions (Ross *et al.*, 2017), the current study is to our knowledge among the first to capture beta ERD during online music performance. In contrast with these previous music-related tasks investigating beta ERD, natural music performance involves the production of stimuli at different time-scales across participants, posing a challenge for time-locking. The current method of computing beta ERD across proportional time windows of musical pauses (deciles) allowed for comparing beta ERD across musicians performing pauses of time-varying duration. This method successfully captured classic signatures of motor preparation (beta ERD) previously

observed in time-locked tasks. The observed beta ERD was maximal at parietal channels at pause onset, and clearly anteriorized to more central sites over the pause time-course. This centro-parietal ERD topography is consistent with previous work investigating action planning in contexts where parameters of an upcoming action are not fully known (Zaepffel *et al.*, 2013). This pattern is compatible with the involvement of parietal areas in the resolution of action uncertainty and decision-making (Andersen and Cui, 2009). However, source modelling of high-density EEG data would be needed to verify this association.

Beta ERD did not differ between Solo and Duet performance, counter to our initial hypothesis that ERD might reflect potential differences in prediction processes between Solo and Duet performance. This hypothesis arose from the substantial

literature indicating that beta ERD reflects sensorimotor prediction processes, either about the consequences of one's own actions or actions that one observes another individual perform (Engel and Fries, 2010; Arnal, 2012; Arnal and Giraud, 2012). It is possible that the limited available Duet coordination cues in the current study—such as visual cues or assigned leader-follower roles—made it challenging or nearly impossible for partners to accurately predict one another's actions during pauses. Therefore, Duet partners may have facilitated coordination of pauses by individually modifying their own action characteristics (i.e. increasing their action speed, as mentioned previously) instead of actively predicting their partner. If each partner was not actively predicting when the other partner would end a pause, then there would be no reason to expect a difference in beta ERD between the two action contexts.

Had we allowed partners to more directly visually communicate in the current study, we may have made it easier for partners to predict one another's actions and thus observed corresponding differences in beta ERD between Duet and Solo performance. Ensemble musicians often use visual cuing to facilitate coordination (Camurri et al., 2009), particularly after long pauses in performance (Bishop and Goebel, 2015). The current study restricted visual cuing between Duet partners in order to investigate predictive processes under conditions where visual information exchange between task partners is limited. Future work should investigate whether direct visual feedback—such as face-to-face interaction between musical partners—facilitates prediction of a partner's pause durations and yields a corresponding enhancement of beta ERD in Duet relative to Solo performance, after controlling for potential artefacts caused by differences in eye movement. In addition, designated Leader-Follower roles are often used in ensemble performance to facilitate coordination and have been shown to modulate motor-related dynamics in the alpha frequency band during piano Duet performance (Washburn et al., 2019), which often closely follow beta dynamics (Pfurtscheller and Da Silva, 1999). Leader-Follower role assignment should be investigated in future work to determine whether the assignment of explicit roles boosts prediction of a partner's actions during Duet pauses—specifically in the Follower's brain—and might lead to corresponding modulations of beta ERD.

Beta ERD was modulated by pause duration, as indicated by linear mixed model predictions showing a main effect of pause duration on beta ERD. Specifically, the linear mixed model indicated that beta ERD was stronger (more negative) during shorter relative to longer pauses. Strong beta ERD is traditionally interpreted as an indicator of heightened 'action readiness', and strong beta ERS (positive beta amplitude relative to a baseline) is in contrast thought to represent an 'idling state' of the motor system (Pfurtscheller et al., 1996b; Engel and Fries, 2010). In accordance with an 'action readiness' interpretation of beta ERD strength, 'action readiness' may have been higher during shorter relative to longer pauses in performance. This could potentially explain why pianists reduced pause durations in Duet relative to Solo performance, i.e. shorter pauses may have facilitated action readiness so that pianists could resolve a pause as soon as their partner did so. An alternate interpretation of enhanced beta ERD for shorter pauses comes from work indicating that beta ERD is an index to estimated interval durations between a cue and a target (Kononowicz and van Rijn, 2015) and is specifically lower at the beginning of short relative to long intervals. In line with this work, pianists in the current study may have had an idea of how long they wanted to sustain a pause from the pause onset,

resulting in higher or lower beta ERD amplitude depending on the anticipated interval. The current study cannot disentangle these possibilities.

There was no interaction between pause duration and task in the linear mixed-effects model. Therefore, although pianists displayed shorter pause durations in Duet relative to Solo performance, the neural processes underlying reductions in pause duration may reflect task-general individual action timing processes. This interpretation is again consistent with the idea that Duet pianists may have focused on modifying their own actions to facilitate coordination rather than on predicting their partner. It is also possible that the lower time limit on pauses (1.6 s)—which was imposed to allow sufficient time for capturing beta ERD dynamics—may have placed a limit both on the extent to which Duet partners felt that they could be expressive and on the extent to which they could reduce pause durations. Therefore, the difference in pause durations between performance tasks may have been too small on a trial-by-trial level to give rise to an interaction between task and pause duration in a linear mixed model. Perhaps had this experimental constraint on pause durations been removed, we might have observed greater trial-level differences in pause duration between performance tasks and a resulting interaction between duration and task.

Taken together, the current findings indicate that when musical partners have limited means of predicting one another's actions—such as when they have no visual feedback about one another's behaviour or means of coordinating through mechanisms such as counting the duration of pauses—they fall back on simple strategies such as speeding up their actions, which have the effect of facilitating coordination, possibly by optimizing 'action readiness' in the brain. It should be noted that these findings were observed in a constrained musical context; partners had limited visual communication, the musical stimulus comprised a simple monophonic Duet, there was a lower limit on pause durations, etc. These constraints were in place to ensure optimal data quality that allowed for capturing a clear beta ERD time-course.

One major question going forward is how these findings might extend to real-world musical interaction, where there are fewer constraints on how partners coordinate expressive silences. An important direction is to determine how to measure these natural musical interactions while also being able to clearly distinguish unique neural responses to specific aspects of musical behaviour. The current study provides a step in this direction by describing a clear neural signature of a time-varying feature of natural music performance—expressive silence, while at the same time implementing appropriate constraints to ensure the measurement of this signal. Future work should aim to investigate not only how this neural signature might be modulated by more naturalistic performance scenarios, but also whether a similar signature of motor preparation might be observed during turn-taking silences in real-world musical interactions and speech, which may involve even stronger interpersonal prediction processes than simultaneous music performance.

Supplementary data

Supplementary data are available at SCAN online.

Acknowledgements

The authors thank the musicians who participated in the study, Alexander Demos and Oana Stanciu for consultation

on implementation of linear mixed models, Francis Spidle for input on musical stimuli, Dávid Csűrös for assistance with data collection, and Qualitis LTD for technical assistance with the EEG hardware set-up.

Conflict of interest: The authors declare no conflict of interest.

Funding

This work was supported by the European Research Council under the European Union's Seventh Framework Program (FP7/2007–2013) ERC grant agreement 616072, JAXPERTISE, and 609819, SOMICS.

References

- Acheson, K. (2008). Silence as gesture: rethinking the nature of communicative silences. *Communication Theory*, *18*(4), 535–55. doi: 10.1111/j.1468-2885.2008.00333.x.
- Andersen, R.A., Cui, H. (2009). Intention, action planning, and decision making in parietal-frontal circuits. doi: 10.1016/j.neuron.2009.08.028.
- Arnal, L.H. (2012). Predicting 'when' using the motor System's beta-band oscillations. *Frontiers in Human Neuroscience*. doi: 10.3389/fnhum.2012.00225.
- Arnal, L.H., Giraud, A.-L. (2012). Cortical oscillations and sensory predictions. *Trends in Cognitive Sciences*, *16*(7), 390–8. doi: 10.1016/j.TICS.2012.05.003.
- Bates, D., Mächler, M., Bolker, B., Walker, S. (2014). Fitting linear mixed-effects models using lme4. arXiv preprint arXiv:1406.5823.
- Bauer, A.-K.R., Kreutz, G., Herrmann, C.S. (2015). Individual musical tempo preference correlates with EEG beta rhythm. *Psychophysiology*, *52*(4), 600–4. doi: 10.1111/psyp.12375.
- Beňuš, Š., Gravano, A., Hirschberg, J. (2011). Pragmatic aspects of temporal accommodation in turn-taking. *Journal of Pragmatics*, *43*(12), 3001–27. doi: 10.1016/j.pragma.2011.05.011.
- Bishop, L., Goebel, W. (2015). When they listen and when they watch: pianists' use of nonverbal audio and visual cues during Duet performance. *Musicae Scientiae*, *19*(1), 84–110. doi: 10.1177/1029864915570355.
- Bögels, S., Magyari, L., Levinson, S.C. (2015). Neural signatures of response planning occur midway through an incoming question in conversation. *Scientific Reports*, *5*, 1–11. doi: 10.1038/srep12881.
- Brennan, S.E., Williams, M. (1995). The feeling of another's knowing: prosody and filled pauses as cues to listeners about the metacognitive states of speakers. *Journal of Memory and Language*, *34*(3), 383–98. doi: 10.1006/jmla.1995.1017.
- Caesura. 2020. In Merriam Webster Online Dictionary. Retrieved from <https://www.merriam-webster.com/dictionary/caesura>.
- Camurri, A., Varni, G., Volpe, G. (2009). Towards analysis of expressive gesture in groups of users: computational models of expressive social interaction. In: *Lecture Notes in Computer Science (Including Subseries Lecture Notes in Artificial Intelligence and Lecture Notes in Bioinformatics)*, 5934 LNAI, Springer, Berlin, Heidelberg. 122–33. doi: 10.1007/978-3-642-12553-9(_11.
- Chang, A., Livingstone, S.R., Bosnyak, D.J., Trainor, L.J. (2017). Body sway reflects leadership in joint music performance. *Proceedings of the National Academy of Sciences*, *114*(21), E4134–41. doi: 10.1073/pnas.1617657114.
- Davidson, J.W. (2012). Bodily movement and facial actions in expressive musical performance by Solo and duo instrumentalists: two distinctive case studies. *Psychology of Music*, *40*(5), 595–633. doi: 10.1177/0305735612449896.
- Denis, D., Richard Rowe, A.M.W., Milne, E. (2017). The role of cortical sensorimotor oscillations in action anticipation. *NeuroImage*, *146*, 1102–14. doi: 10.1016/j.neuroimage.2016.10.022.
- Doelling, K.B., Poeppel, D. (2015). Cortical entrainment to music and its modulation by expertise. *Proceedings of the National Academy of Sciences*, *112*(45), E6233–42. doi: 10.1073/pnas.1508431112.
- Engel, A.K., Fries, P. (2010). Beta-band oscillations—signalling the status quo? *Current Opinion in Neurobiology*, *20*(2), 156–65. doi: 10.1016/j.conb.2010.02.015.
- Fermata | Grove Music. (2020). <https://www.oxfordmusiconline.com/grovemusic/view/10.1093/gmo/9781561592630.001.0001/omo-9781561592630-e-0000009487?rskey=h9Bg2M&result=1>.
- Finney, S.A. (2001). FTAP: a Linux-based program for tapping and music experiments. *Behavior Research Methods, Instruments, and Computers*, *33*(1), 65–72. doi: 10.3758/BF03195348.
- Fujioka, T., Trainor, L.J., Large, E.W., Ross, B. (2012). Internalized timing of isochronous sounds is represented in neuromagnetic beta oscillations. *Journal of Neuroscience*, *32*(5), 1791–802. doi: 10.1523/JNEUROSCI.4107-11.2012.
- Fuller, D. Fermata (It.: 'pause'). In *Grove Music Online*. Retrieved from <https://www.oxfordmusiconline.com/grovemusic/view/10.1093/gmo/9781561592630.001.0001/omo-9781561592630-e-0000009487>
- Gisladottir, R.S., Bögels, S., Levinson, S.C. (2018). Oscillatory brain responses reflect anticipation during comprehension of speech acts in spoken dialog. *Frontiers in Human Neuroscience*, *12*, 1–13. doi: 10.3389/fnhum.2018.00034.
- Goebel, W., Palmer, C. (2009). Synchronization of timing and motion among performing musicians. *Music Perception*. doi: 10.1525/mp.2009.26.5.427.
- Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., Rizzolatti, G. (1998). Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proceedings of the National Academy of Sciences*, *95*(25), 15061–5. doi: 10.1073/pnas.95.25.15061.
- Järveläinen, J., Schürmann, M., Avikainen, S., Hari, R. (2001). Stronger reactivity of the human primary motor cortex during observation of live rather than video motor acts. *Neuroreport*, *12*(16), 3493–5. doi: 10.1097/00001756-200111160-00024.
- Jasper, H., Penfield, W. (1949). Electrocorticograms in man: effect of voluntary movement upon the electrical activity of the precentral gyrus. *Archiv für Psychiatrie und Nervenkrankheiten*, *183*(1–2), 163–74. doi: 10.1007/BF01062488.
- Keller, P.E., Appel, M. (2010). Individual differences, auditory imagery, and the coordination of body movements and sounds in musical ensembles. *Music Perception: An Interdisciplinary Journal*, *28*(1), 27–46. doi: 10.1525/mp.2010.28.1.27.
- Koelewijn, T., van Schie, H.T., Bekkering, H., Oostenveld, R., Jensen, O. (2008). Motor-cortical beta oscillations are modulated by correctness of observed action. *NeuroImage*, *40*(2), 767–75. doi: 10.1016/j.neuroimage.2007.12.018.
- Kononowicz, T.W., van Rijn, H. (2015). Single trial beta oscillations index time estimation. *Neuropsychologia*, *75*, 381–9. doi: 10.1016/j.neuropsychologia.2015.06.014.
- Koudenburg, N., Postmes, T., Gordijn, E.H. (2011). Disrupting the flow: how brief silences in group conversations affect social needs. *Journal of Experimental Social Psychology*, *47*(2), 512–5. doi: 10.1016/j.jesp.2010.12.006.
- Kourti, D., Sebanz, N., Knoblich, G. (2013). Predictive representation of other people's actions in joint action plan-

- ning: an EEG study. *Social Neuroscience*, **8**(1), 31–42. doi: [10.1080/17470919.2012.694823](https://doi.org/10.1080/17470919.2012.694823).
- Lewis, P.A., Miall, R.C. (2003). Distinct systems for automatic and cognitively controlled time measurement: evidence from neuroimaging. *Current Opinion in Neurobiology*, **13**(2), 250–5. doi: [10.1016/s0959-4388\(03\)00036-9](https://doi.org/10.1016/s0959-4388(03)00036-9).
- Loehr, J.D., Palmer, C. (2011). Temporal coordination between performing musicians. *Quarterly Journal of Experimental Psychology*, **64**(11), 2153–67. doi: [10.1080/17470218.2011.603427](https://doi.org/10.1080/17470218.2011.603427).
- Loehr, J.D., Kourtis, D., Vesper, C., Sebanz, N., Knoblich, G. (2013). Monitoring individual and joint action outcomes in Duet music performance. *Journal of Cognitive Neuroscience*, **25**(7), 1049–61. doi: [10.1162/jocn.1a00388](https://doi.org/10.1162/jocn.1a00388).
- Margulis, E.H. (2007a). Moved by nothing: listening to musical silence. *Journal of Music Theory*, **51**(2), 245–76. doi: [10.1215/00222909-2009-003](https://doi.org/10.1215/00222909-2009-003).
- Margulis, E.H. (2007b). Silences in music are musical not silent: an exploratory study of context effects on the experience of musical pauses. *Music Perception: An Interdisciplinary Journal*, **24**(5), 485–506. doi: [10.1525/mp.2007.24.5.485](https://doi.org/10.1525/mp.2007.24.5.485).
- Mathias, B., Gehring, W.J., Palmer, C. (2017). Auditory N1 reveals planning and monitoring processes during music performance. *Psychophysiology*, **54**(2), 235–47. doi: [10.1111/psyp.12781](https://doi.org/10.1111/psyp.12781).
- Maygyari, L., Bastiannsen, M.C.M., de Ruiter, J.P., Levinson, S.C. (2014). Early anticipation lies behind the speed of response in conversation. *Journal of Cognitive Neuroscience*, **26**(11), 2530–9. doi: [10.1162/jocn](https://doi.org/10.1162/jocn).
- McGrain, M. (1990). *Music notation*, Hal Leonard Corporation, Boston, MA, USA.
- Morillon, Baillet, S. (2017). Motor origin of temporal predictions in auditory attention. *Proceedings of the National Academy of Sciences*, **114**(42), E8913–21. doi: [10.1073/pnas.1705373114](https://doi.org/10.1073/pnas.1705373114).
- Neuhaus, C., Knösche, T.R., Friederici, A.D. (2006). Effects of musical expertise and boundary markers on phrase perception in music. *Journal of Cognitive Neuroscience*, **18**(3), 472–93. doi: [10.1162/jocn.2006.18.3.472](https://doi.org/10.1162/jocn.2006.18.3.472).
- Novembre, G., Ticini, L.F., Schutz-Bosbach, S., Keller, P.E. (2012). Distinguishing self and other in joint action. Evidence from a musical paradigm. *Cerebral Cortex*, **22**(12), 2894–903. doi: [10.1093/cercor/bhr364](https://doi.org/10.1093/cercor/bhr364).
- Novembre, G., Knoblich, G., Dunne, L., Keller, P.E. (2017). Interpersonal synchrony enhanced through 20 Hz phase-coupled dual brain stimulation. *Social Cognitive and Affective Neuroscience*, **12**(4), 662–70. doi: [10.1093/scan/nsw172](https://doi.org/10.1093/scan/nsw172).
- Orgs, G., Dombrowski, J.H., Heil, M., Jansen-Osmann, P. (2008). Expertise in dance modulates alpha/beta event-related desynchronization during action observation. *European Journal of Neuroscience*, **27**(12), 3380–4. doi: [10.1111/j.1460-9568.2008.06271.x](https://doi.org/10.1111/j.1460-9568.2008.06271.x).
- Palmer, C. (2013). Music performance: Movement and coordination. In: Deutsch, D., editor. *The Psychology of Music*, Third edn, Amsterdam, The Netherlands: Elsevier Press, pp. 405–22.
- Palmer, C., Spidle, F., Koopmans, E., Schubert, P. (2019). Ears, heads, and eyes: when singers synchronise. *Quarterly Journal of Experimental Psychology*, **72**(9), 2272–87. doi: [10.1177/1747021819833968](https://doi.org/10.1177/1747021819833968).
- Pfurtscheller, G., Da Silva, F.H.L. (1999). Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clinical Neurophysiology*, **110**(11). doi: [10.1016/S1388-2457\(99\)00141-8](https://doi.org/10.1016/S1388-2457(99)00141-8).
- Pfurtscheller, G., Stancák, A., Neuper, C. (1996a). Post-movement beta synchronization. A correlate of an idling motor area? *Electroencephalography and Clinical Neurophysiology*, **98**(4), 281–93. doi: [10.1016/0013-4694\(95\)00258-8](https://doi.org/10.1016/0013-4694(95)00258-8).
- Pfurtscheller, G., Stancák, A., Neuper, C. (1996b). Event-related synchronization (ERS) in the alpha band — an electrophysiological correlate of cortical idling: a review. *International Journal of Psychophysiology*, **24**(1–2), 39–46. doi: [10.1016/S0167-8760\(96\)00066-9](https://doi.org/10.1016/S0167-8760(96)00066-9).
- Pfurtscheller, G., Neuper, C., Brunner, C., Da Silva, F.L. (2005). Beta rebound after different types of motor imagery in man. *Neuroscience Letters*, **378**(3), 156–9. doi: [10.1016/j.neulet.2004.12.034](https://doi.org/10.1016/j.neulet.2004.12.034).
- Quandt, L.C., Marshall, P.J. (2014). The effect of action experience on sensorimotor EEG rhythms during action observation. *Neuropsychologia*, **56**(1), 401–8. doi: [10.1016/j.neuropsychologia.2014.02.015](https://doi.org/10.1016/j.neuropsychologia.2014.02.015).
- Riemann, H. (1900). In: Hesse, M., editor. *Vademecum der phrasierung*.
- Ross, B., Barat, M., Fujioka, T. (2017). Sound-making actions lead to immediate plastic changes of neuromagnetic evoked responses and induced β -band oscillations during perception. *Journal of Neuroscience*, **37**(24), 5948–59. doi: [10.1523/JNEUROSCI.3613-16.2017](https://doi.org/10.1523/JNEUROSCI.3613-16.2017).
- Salmelin, R., Hämäläinen, M., Kajola, M., & Hari, R. (1995). Functional segregation of movement-related rhythmic activity in the human brain. *NeuroImage*, **2**, 237–243.
- Scheurich, R., Mathias, B., Demos, A.P., Zamm, A. (2018). Capturing intra- and inter-brain dynamics with recurrence quantification analysis. Available: <http://www.biosemi.com/faq/cms&drl.htm>.
- Semjen, A., Schulze, H. H., & Vorberg, D. (2000). Timing precision in continuation and synchronization tapping. *Psychological Research*, **63**, 137–147.
- Senkowski, D., Molholm, S., Gomez-Ramirez, M., Fox, J.J. (2005). Oscillatory beta activity predicts response speed during a multisensory audiovisual reaction time task: a high-density electrical mapping study. *Cerebral Cortex*, **16**(11), 1556–65. doi: [10.1093/cercor/bhj091](https://doi.org/10.1093/cercor/bhj091).
- Stancák Jr, A., & Pfurtscheller, G. (1995). Desynchronization and recovery of β rhythms during brisk and slow self-paced finger movements in man. *Neuroscience letters*, **196**, 21–24. doi: [10.1016/0304-3940\(95\)11827-j](https://doi.org/10.1016/0304-3940(95)11827-j).
- Tzagarakis, C., Ince, N.F., Leuthold, A.C., Pellizzer, G. (2010). Behavioral/systems/cognitive beta-band activity during motor planning reflects response uncertainty. doi: [10.1523/JNEUROSCI.6026-09.2010](https://doi.org/10.1523/JNEUROSCI.6026-09.2010).
- Vesper, C., Van Der Wel, R.P.R.D., Knoblich, G., Sebanz, N. (2011). Making oneself predictable: reduced temporal variability facilitates joint action coordination. *Experimental Brain Research*, **211**(3–4), 517–30. doi: [10.1007/s00221-011-2706-z](https://doi.org/10.1007/s00221-011-2706-z).
- Vesper, C., van der Wel, R.P.R.D., Knoblich, G., Sebanz, N. (2013). Are you ready to jump? Predictive mechanisms in interpersonal coordination. *Journal of Experimental Psychology*, **39**(1), 48–61. doi: [10.1037/a0028066](https://doi.org/10.1037/a0028066).
- Vesper, C., Schmitz, L., Safra, L., Sebanz, N., Knoblich, G. (2016). The role of shared visual information for joint action coordination. *Cognition*, **153**, 118–23. doi: [10.1016/j.cognition.2016.05.002](https://doi.org/10.1016/j.cognition.2016.05.002).
- Visco-Comandini, F., Ferrari-Toniolo, S., Satta, E., Papazachariadis, O., Gupta, R., Nalbant, L.E., Battaglia-Mayer, A. (2015). Do non-human primates cooperate? Evidences of motor coordination during a joint action task in macaque monkeys. *Cortex*, **70**, 115–27. doi: [10.1016/j.cortex.2015.02.006](https://doi.org/10.1016/j.cortex.2015.02.006).
- Washburn, A., Román, I., Huberth, M., et al. (2019). Musical role asymmetries in piano duet performance influence alpha-band neural oscillation and Behavioral synchronization. *Frontiers in Neuroscience*, **13**, 1088. doi: [10.3389/fnins.2019.01088](https://doi.org/10.3389/fnins.2019.01088).

- Zaepffel, M., Trachel, R., Kilavik, B.E., Brochier, T. (2013). Modulations of EEG Beta power during planning and execution of grasping movements. *PLoS One*, *8*(3). doi: [10.1371/journal.pone.0060060](https://doi.org/10.1371/journal.pone.0060060).
- Zamm, A., Pfordresher, P.Q., Palmer, C. (2014). Temporal coordination in joint music performance: effects of endogenous rhythms and auditory feedback. *Experimental Brain Research*, *233*(2). doi: [10.1007/s00221-014-4140-5](https://doi.org/10.1007/s00221-014-4140-5).
- Zamm, A., Wellman, C., Palmer, C. (2016). Endogenous rhythms influence interpersonal synchrony. *Journal of Experimental Psychology*. doi: [10.1037/xhp0000201](https://doi.org/10.1037/xhp0000201).
- Zich, C., De Vos, M., Kranczioch, C., Debener, S. (2015). Wireless EEG with individualized channel layout enables efficient motor imagery training. *Clinical Neurophysiology*, *126*(4), 698–710. doi: [10.1016/j.clinph.2014.07.007](https://doi.org/10.1016/j.clinph.2014.07.007).