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# Neural tracking and integration of 'self' and 'other' in improvised interpersonal coordination

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ABSTRACT

Humans coordinate their movements with one another in a range of everyday activities and skill domains. Optimal joint performance requires the continuous anticipation of and adaptation to each other's movements, especially when actions are spontaneous rather than pre-planned. Here we employ dual-EEG and frequency-tagging techniques to investigate how the neural tracking of self- and other-generated movements supports interpersonal coordination during improvised motion. LEDs flickering at 5.7 and 7.7 Hz were attached to participants' index fingers in 28 dyads as they produced novel patterns of synchronous horizontal forearm movements. EEG responses at these frequencies revealed enhanced neural tracking of self-generated movement when leading and of other-generated movements when following. A marker of self-other integration at 13.4 Hz (intermodulation frequency of 5.7 and 7.7 Hz) peaked when no leader was designated, and mutual adaptation and movement synchrony were maximal. Furthermore, the amplitude of EEG responses reflected differences in the capacity of dyads to synchronize their movements, offering a neurophysiologically grounded perspective for understanding perceptual-motor mechanisms underlying joint action.

## 1. Introduction

Humans extend everyday action capabilities by coordinating their actions with one another. Heavier and more distant objects can be moved or reached when two or more people cooperate (Sebanz et al., 2006; Schmidt and Richardson, 2008; Keller et al., 2014). Creative possibilities in music and dance increase when involving multiple co-performers (Phillips-Silver and Keller, 2012; D'Ausilio et al., 2015). The capacity for coordinating with each other develops at an early age, supports feelings of interpersonal connectedness, communication, and pro-social behavior (Richardson et al., 2007a; Hove and Risen, 2009; Marsh et al., 2009; Wiltermuth and Heath, 2009; Valdesolo et al., 2010; Cirelli et al., 2014). Coordination skills are often impaired in social pathologies such as autism or schizophrenia, and, conversely, can be enhanced with expertise (Charman et al., 1997; Varlet et al., 2012; Marsh et al., 2013; Keller et al., 2014). Optimal coordination in time and space requires individuals to continuously anticipate and adapt to each other's ongoing actions (Sebanz et al., 2006; Knoblich et al., 2011; Coey et al., 2012; Keller et al., 2014). Here we investigate the advanced neural mechanisms that allow humans to engage in efficient self-other anticipation and adaptation and the production of highly coordinated cooperative behaviors.

Amongst the multimodal sensory arrays that are typically available during joint action, visual information is often crucial when precise spatiotemporal coordination with others is required (e.g., dancing or team sports). In such situations, vision allows access to information about others' movements in relation to one's own movements with high resolution in space and time, allowing movement trajectories to be anticipated and joint action outcomes to be monitored (Schmidt and Richardson, 2008; Knoblich et al., 2011; Keller et al., 2014). Visual information often plays an influential role even in activities that are primarily driven by auditory information, such as ensemble musical performance, where visual cues support the coupling of musicians' expressive body movements and thereby facilitate the interpersonal synchronization of tempo fluctuations used to convey affective and aesthetic intentions (D'Ausilio et al., 2015; Chang et al., 2017; MacRitchie et al., 2017).

The need for anticipation and adaptation is heightened in joint tasks that are improvised and require ongoing planning, as is often the case in everyday activities, than for fully pre-planned and rehearsed tasks. Noy

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and colleagues recently developed the 'mirror game' paradigm to examine interpersonal coordination dynamics during joint improvisation (Noy et al., 2011). In this seminal study, dyads were asked to produce creative and synchronized upper-limb body movements together with and without a designated leader. The results revealed that, when leader and follower roles were given, adaptation to each other's movement trajectories became asymmetrical and interpersonal synchrony tended to degrade, in contrast with conditions in which no leadership instruction was given to the dyads. The benefits of no leadership instruction were found in expert improvisers (actors and musicians with over 10 years of experience in joint improvisation) and were interpreted as indicating that the task was being performed in the manner of two leaders in implicit agreement about their future motion patterns, possibly attaining a subjective state that corresponds to the state of 'togetherness' often experienced by ensemble musicians and actors.

Previous research has suggested that leadership roles can influence the degree to which individuals monitor self- and other-generated movements, as well as the degree to which these two sources of information are integrated (Keller et al., 2016; Novembre et al., 2016). It has been proposed that adopting the role of follower encourages greater monitoring of other actions and self-other integration, whereas adopting the role of leader encourages greater monitoring of self actions and self-other segregation (Keller et al., 2016). Therefore, undesignated leadership roles might be key to achieving an optimal balance in joint improvisation by favoring self-other integration, and thus, enhancing mutual adaptation and the experience of a state of 'togetherness'. However, the neural mechanisms underlying the tracking of self- and other-generated movements and their integration remain unclear. A particular challenge is to disentangle responses related to self versus other in recordings of brain activity, to examine their dynamics separately and how they are integrated to support dyadic coordination performance.

Here, in order to investigate these mechanisms and their role in interpersonal coordination, we combined dual-EEG recording with frequency-tagging techniques in a joint improvisation scenario inspired by the 'mirror game' paradigm. Participants in dyads were required to create novel movement patterns by producing horizontal forearm oscillations in synchrony as leadership instructions were manipulated. Frequency-tagging techniques were employed because they allow the neural processing of multiple stimuli presented concomitantly in the visual environment to be disentangled in the EEG signal, based on different frequencies associated uniquely with each stimulus (Di Russo et al., 2007; Ales et al., 2012; Painter et al., 2014; Norcia et al., 2015; Renton et al., 2018). A light-emitting diode (LED) was attached to each participant's index finger within a dyad as they synchronized their movements together (see Fig. 1). The LEDs continuously flickered at a specific frequency that differed for each participant within a dyad – 5.7 Hz (Person 1) and 7.7 Hz (Person 2). The neural tracking of self- and other-generated movements could be indexed with high signal-to-noise ratio by the amplitude of the responses at those specific frequencies (and respective harmonics) in participants' EEG (i.e., Steady State Visual Evoked Potentials). The amplitude of *self* and *other* responses was expected to be selectively modulated depending on leadership instructions, with participants exhibiting larger *other* responses when following and larger *self* responses when leading. *Self* and *other* responses were expected in primary visual areas, as indicated by different topographical distributions for *self* and *other* responses reflecting the relative positions of self- and other-generated movements in the lower or upper parts of participants' visual fields, respectively, due to our task setup, and their projection onto the superior and inferior lips of the calcarine sulcus (due to the inversion of the visual field).

An advantage of implementing this method is that it allows neural responses related to the integration of multiple sources of environmental information to be measured. Indeed, previous research has revealed EEG responses not only at the fundamental frequencies of flickering stimuli but also at *inter*-modulation frequencies. These responses occur as a result of nonlinear interactions between separate fundamental frequencies (Zemon and Ratliff, 1982, 1984; Regan and Regan, 1988; Norcia et al.,

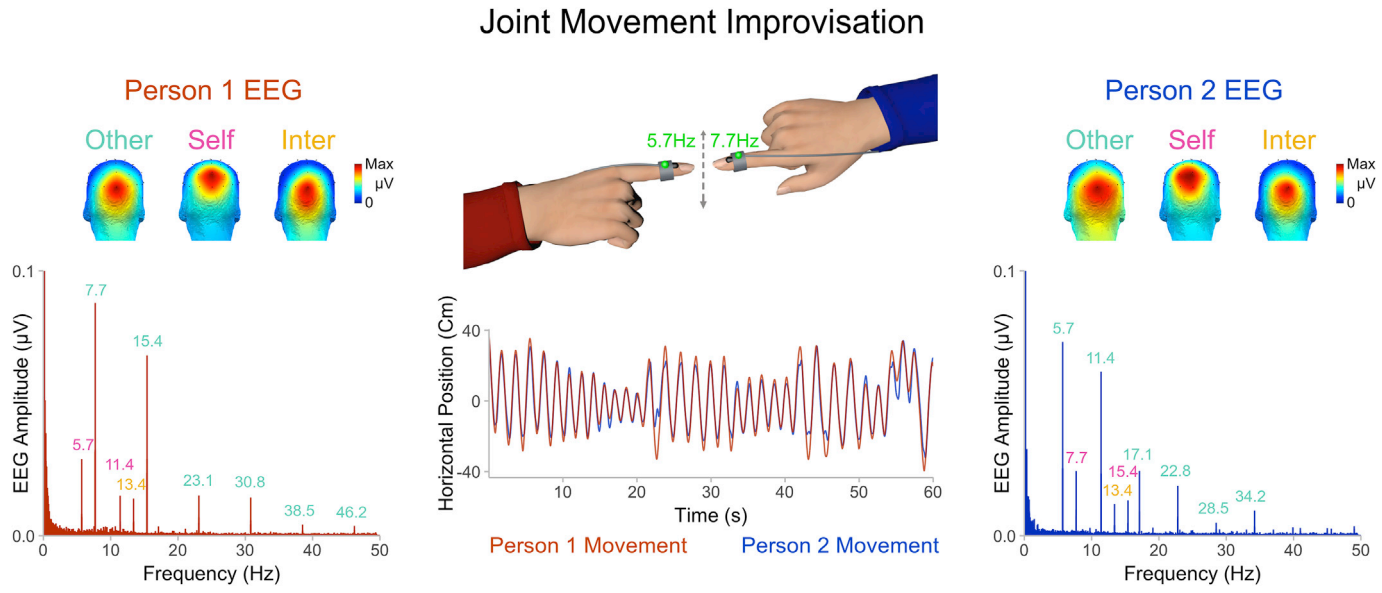


**Fig. 1.** Illustration of the joint movement improvisation task, and movement and EEG responses of paired participants. The panel at the center represents typical movement time series exhibited by paired participants instructed to produce novel movement patterns in synchrony by varying forearm motion speed and amplitude along the horizontal axis. The left and right panels represent the EEG frequency-domain amplitude spectra (with baseline subtracted) averaged across all channels, leadership conditions, and dyads (Person 1 and 2 separately). Spectra indicate large EEG responses at *other*, *self* and *inter* (self-other integration) frequencies (and corresponding harmonics) evoked by the 5.7 Hz and 7.7 Hz flickering LEDs attached to participants' right index fingers. The corresponding grand-averaged topographies represented above the EEG spectra generally show medial occipital distributions for the *other*, *self* and *inter* responses, with a more superior, parietal distribution for *self* responses than *other* and *inter* responses. *Other*, *self* and *inter* responses for the topographies correspond to the sum of the amplitude of all the significant frequency peaks at the group level (see method section for further details): sum of the fundamental and its first 5 harmonics for *other*, sum of the fundamental and its first 3 harmonics for *self* and amplitude at 13.4 Hz (fundamental only) for *inter*. The color-scales of the topographies are adjusted separately for *other*, *self,* and *inter* to the maximal value.

2015; Alp et al., 2018) and have been recently reported as markers of integration in the context of face and biological motion perception (Boremanse et al., 2013, 2014; Alp et al., 2017). We hypothesized that *inter*-modulation frequencies at 13.4 Hz [5.7 + 7.7] and/or 2 Hz [7.7–5.7] (and respective harmonics) will occur in the EEG as markers of self-other integration, with maximal amplitude in the Joint condition where no leader was designated.

## 2. Material and methods

### 2.1. Participants

Twenty-eight dyads (56 participants in total) volunteered to take part in the experiment (36 females and 20 males aged from 18 to 45 years; $M = 24.70$, $SD = 5.63$). Eleven female-female, three male-male and fourteen female-male dyads were composed by random assignment. All participants were right handed, had normal or corrected-to-normal vision, and provided written informed consent prior to the experiment, which was approved by the Human Research Ethics Committee at Western Sydney University.

### 2.2. Stimuli

Flickering lights ('flickers') attached to each participant's right index finger were Kingbright LEDs (L-7104ZGCK 3 mm Green [525 nm] InGaN Solid State Lamps, Kingbright, Taipei, Taiwan). The flickers were attached to the finger facing upwards using Velcro cuffs. The LEDs were powered by a 9 V alkaline battery and driven at a constant current of approximately 13 mA, producing a luminous intensity of 5 cd. The tops of the LEDs were ground down, leaving a flat matt surface, in order to more uniformly scatter the light and to increase the viewing angle. The LEDs were driven by a Microchip ATmega32U4 microcontroller to flicker at 5.70 Hz for Person 1 and 7.70 Hz for Person 2 (with accuracy better than ± 4.2 mHz and period uniformity better than ± 63 ns) with a 50% duty cycle (i.e., turned on for half of the time and turned off for half of the time) square-wave. The flickering lights were manually turned on by the experimenter at the beginning of the experiment and turned off at the end.

### 2.3. Procedure

On arrival, the participants were provided with an information sheet that described the joint movement synchronization task, and the EEG and motion capture equipment used. Written informed consent was then invited and in all cases obtained.

Participants were then fitted with the EEG caps and electrodes before being asked to sit in two chairs positioned in front of each other. Participants were asked to point their right index finger (hand positioned horizontally and index finger extended) in front of each other as close as possible without contact. The position of the chairs was adjusted to have participants seated comfortably with their right index finger positioned at upper-abdomen height with the right elbow bent at approximately 90–120°, in order to remain still and relaxed while producing horizontal forearm oscillations.

Motion capture sensors and flickers were then attached on the Distal phalanx of each participant's right index finger (between the Distal interphalangeal joint and the fingernail with the LED facing up) and the participants were asked to perform continuous forearm oscillations together along the horizontal axis with minimum distance between their fingers and minimal deviations along the other axes (see Fig. 1). Participants were told to keep their movement amplitude within a comfortable 80 cm range (limits were shown visually by the experimenter at the beginning of the experiment). They were asked to do their best to produce movements that were synchronized (mirrored each other) and novel by varying their speed and amplitude along the horizontal axis. The experimenter monitored participants' movements to make sure that they followed these instructions and produced novel motion patterns continuously throughout the trials.

The participants were instructed to perform the task in three different conditions – the Follower-Leader condition, in which Person 2 was asked to lead the joint performance; the Leader-Follower condition, in which Person 1 was asked to lead the joint performance; and the Joint condition, in which no leader or follower roles were given and participants were asked to perform together. Participants were allowed one practice trial for each of the three conditions. They then performed 12 trials of 180 s in total (i.e., 4 trials in each condition), which were presented in a randomized order. The total duration of the experiment, including EEG preparation and breaks, was approximately 100 min.

### 2.4. Movement recording and analyses

Index finger movements of the two participants were recorded at a sampling rate of 240 Hz with 0.01 mm spatial resolution via a Polhemus LIBERTY motion tracker (Polhemus Ltd., VT, USA) and saved on a PC computer for off-line analyses. The recorded movement time series were bandpass filtered between 0.1 and 15 Hz using a bidirectional Butterworth filter to remove very slow and high frequency fluctuations. Different dependent variables were then computed to assess movement synchronization performance of the dyads.

We first computed the 3D distance between the index fingers of the two participants and calculated its *mean* and *standard deviation* to assess the accuracy and stability of the synchronization in each trial. We also computed the continuous phase of participants' horizontal movements using a Hilbert transform, and then calculated the relative phase angles between the two participants (phase of Person 1 – phase of Person 2) (Kelso, 1995; Pikovsky et al., 2003). Negative relative phase angles indicated that Person 2 led in time, and positive relative phase angles indicated that Person 1 led in time. Using circular statistics, we then computed the *mean* and *standard deviation* of the relative phase angles to assess leader-follower phase relations and their stability throughout each trial (Batschelet, 1981; Pikovsky et al., 2003). Although the mean and standard deviation of relative phase both constitute measures of synchronization performance, these measures can reflect different mechanisms underlying movement synchronization. Mean relative phase (or, alternatively, asynchronies as computed in traditional finger-tapping studies) mainly varies as function of global temporal parameters such as the period of internal timekeepers or oscillatory processes (i.e., period matching), whereas the standard deviation of relative phase (or asynchronies) varies as a function of noise in the system and error correction processes that counteract it locally (Schulze and Vorberg, 2002; Richardson et al., 2007b; Repp and Keller, 2008; Varlet et al., 2012). Finally, individual continuous phase time series were used to compute the directionality of the coupling between the two participants using the evolution map approach (Rosenblum and Pikovsky, 2001; Novembre et al., 2015; Richardson et al., 2015). This technique provides a measure of the directionality of the coupling between two self-sustained oscillators by estimating the ratio of the coupling terms from the phase time series. The aim of this method is to model the phase dynamics of the two oscillators to determine how much the phase of one oscillator predicts the phase of the other oscillator and vice versa (see Rosenblum and Pikovsky (2001) and Rosenblum et al. (2002) for further details). The coupling asymmetry index $d(1, 2)$ obtained with this method varies between −1 and 1, with −1 and 1 corresponding to perfectly unidirectional coupling and 0 corresponding to perfectly symmetrical bidirectional coupling. Negative values indicated greater adaptation of Person 1 towards Person 2, while positive values indicated the opposite.

### 2.5. EEG recording and analyses

EEG signals were recorded at a sampling rate of 2048 Hz using a Biosemi Active-Two system (Biosemi, Amsterdam, Netherlands) with 64 Ag-AgCl electrodes placed over the scalp of the two participants

according to the international 10/20 system. All electrodes were referenced to the Common Mode Sense (CMS) and their magnitude was kept below 50 μV. Four additional electrodes placed above and below the right eye and the external corner of the left and right eyes were used to record ocular movements and eye blinks.

Data were first high-pass filtered using a 4th order Butterworth filter with a cut-off frequency of 0.1 Hz, notch filtered to remove 50 Hz (and corresponding harmonics) electrical power contamination, and then downsampled to 1000 Hz and segmented into 180 s trials, thus corresponding to the 180 s sequences of joint movement. Channels containing excessive artifact or noise were then interpolated with the neighbouring channels (i.e., an average of 1.7 [$SD = 1.41$] interpolated electrodes per participant and never more than 5 electrodes). An independent components analysis (FastICA), as implemented in Fieldtrip (Oostenveld et al., 2011), was then used to remove eye blink artifacts. Based on visual inspection of the topography and time-course, one single component related to eye blinks was removed per participant (no such component was identified and removed for 8 participants). Lateralized eye movements were observed for most participants due to visual-tracking behavior but these components were not removed from the data. EEG data were then re-referenced to the average of all scalp electrodes.

At the next stage of data processing, we used a Fast Fourier Transformation (FFT) on each trial to compute the amplitude spectra up to 50 Hz with a frequency resolution of 0.0056 Hz (i.e., 1/180). In order to examine the occurrence of significant EEG responses at specific frequencies, we pooled the spectra of all EEG channels together and computed Z-scores at each frequency bin as the difference in amplitude between that frequency bin and the mean of the 20 neighbouring frequency bins (excluding the two immediately adjacent frequency bins), divided by the standard deviation of those 20 neighbouring bins. Z-scores were computed at the group-level (amplitude spectra averaged across conditions and participants [Person 1 and 2 separately]) and individual-level (amplitude spectra averaged across conditions). EEG responses at specific frequency bins were considered to be significant when the Z-score value was greater than 3.1 ($p < .001$, one-tailed), in line with previous studies that used frequency-tagging techniques (Jacques et al., 2016; Quek et al., 2018), which indicated signal amplitude significantly larger than the noise background.

In order to control for the effect of background noise (including muscular artifacts) on participants' EEG responses, we subtracted at each frequency bin of the amplitude spectra the average amplitude of the 20 neighbouring frequency bins excluding the two immediately adjacent frequency bins (Nozaradan et al., 2011; Jacques et al., 2016; Lenc et al., 2018). The baseline subtraction allowed background noise and muscular artifacts to be controlled for, as such irregularities affect amplitude spectra over a large range of frequency bins around those of interest. Finally, amplitude spectra averaged across all EEG channels with noise-subtraction were computed for each participant and condition, and used for further statistical analyses in order to compare the amplitude of participants' EEG responses across the different conditions and to calculate correlations with movement synchronization performance. Topographies presented in Figs. 1 and 3 were made using Letswave6 (Mouraux and Iannetti, 2008) (www.nocions.org/letswave).

### 2.6. Statistical analyses

All statistical analyses were conducted using R version 3.4.3 (Team, 2017) and graphics were made with the package ggplot2 (Wickham, 2016). Repeated-measures ANOVAs were performed with the package "afex" version 0.19–1 (Singmann et al., 2015) with Greenhouse-Geisser correction applied when the assumption of sphericity was violated. Pairwise contrasts were used to examine the significant effects further, with Bonferroni adjustment for multiple comparisons.

To compare movement synchronization performance across the different conditions, one-way repeated-measures ANOVAs with the factor Leadership (Follower-Leader, Joint, and Leader-Follower) were conducted on the *mean* and *standard deviation* of the distance and relative phase angles between participants' fingers, and the coupling asymmetry index values. Follower-Leader and Leader-Follower conditions were kept separate because *mean* relative phase values and coupling asymmetric index values could not be averaged, as they were either positive or negative. One-sample t-tests were also used on the *mean* relative phase and directionality index values for the different leadership conditions, with Bonferroni adjustment to test for differences from 0.

To compare the amplitude of individual EEG *other* and *self* responses across the different conditions, two-way repeated-measures ANOVAs were performed with the factors Leadership (Leader, Follower and Joint) and Harmonic (which included harmonics that were significant at the group level, i.e., the fundamental and the 1st-5th harmonics for *other* and fundamental and 1st-3rd harmonics for *self*). A one-way repeated-measures ANOVA with the factor Leadership (Leader, Follower and Joint) was used to analyze the amplitude of *inter* responses, as only the 13.4 Hz response that was significant at the group-level was examined. Note that the factor Leadership for these ANOVAs was different from the experimental conditions (i.e., Follower-Leader, Joint and Leader-Follower) and corresponded to the individual role of the participants – whether they were instructed to lead, follow, or perform jointly. To examine differences in topography, two-way ANOVAs with the factors Leadership (Leader, Follower and Joint) and Electrode (Oz and POz) were conducted on *other*, *self,* and *inter* responses to test the occipital-parietal (inferior-superior) distribution of these responses.

To examine the links between the amplitude of EEG responses and movement synchronization performance, multiple linear regressions analyses were conducted on the dependent variables *mean* and *standard deviation* of the distance and relative phase angles between paired participants' fingers. Absolute mean relative phase values were used in these analyses in order to obtain an actual measure of performance – the amount of deviation from perfect synchrony. Multiple regression analyses (i.e., twelve in total) were conducted separately for each of the four dependent variables and the three experimental conditions with Person 1's *other*, *self*, and *inter,* and Person 2's *other*, *self*, and *inter* amplitudes as independent variables (i.e., six in total) to examine possible interactions between individual roles and EEG responses. Four multiple regression analyses on the same dependent variables were subsequently conducted with the sum of Person 1 and 2 (dual EEG) *other*, *self,* and *inter* responses averaged across conditions as independent variables (i.e., three in total) to examine more general links between EEG responses and movement synchronization performance across dyads.

## 3. Results

Amplitude spectra for EEG responses with baseline subtraction, averaged across the three Leadership conditions and all participants (Person 1 and 2 separately), are presented in Fig. 1. The results indicated significant EEG responses at the targeted frequencies that were, together with dyadic movement synchronization, modulated by the leadership roles assigned to the participants. The results related to movement dynamics, neural dynamics, and the link between the two, are presented in the following sections.

### 3.1. Movement dynamics

Analyses of participants' forearm movements recorded with the 3D motion tracking system as they produced novel movement patterns together, revealed different dynamics depending on leadership instructions. Paired participants' movements were more closely synchronized in the Joint condition, with no assigned leader, compared with the Follower-Leader and Leader-Follower conditions, in which each participant within a dyad was instructed in turn to lead or follow (see Fig. 2).

A one-way repeated-measures ANOVA conducted on the *mean* distance between participants' fingers revealed a statistically significant effect of Leadership, $F(1.95, 52.78) = 9.07$, $MSE = 0.27$, $p = .0005$,

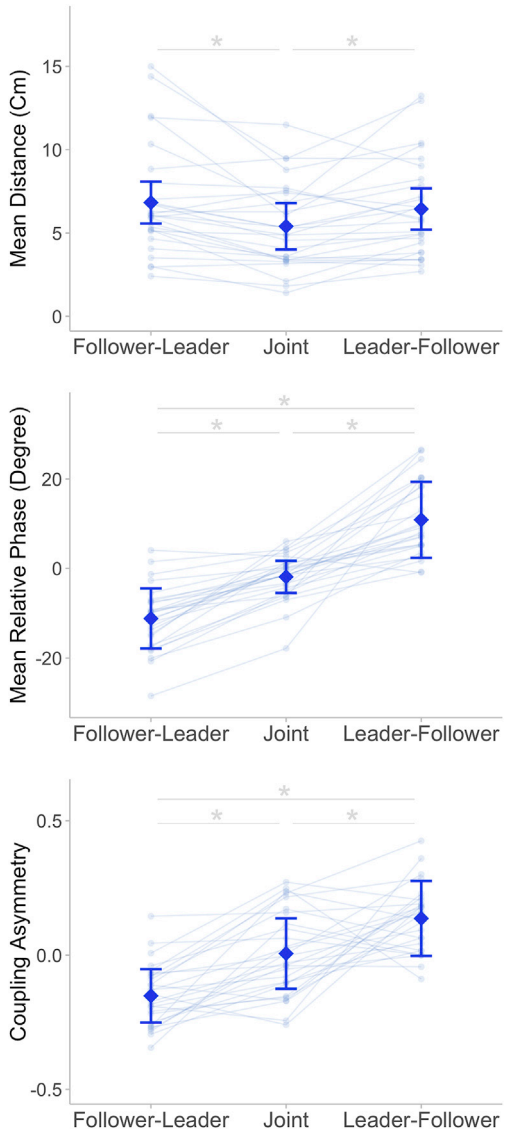


**Fig. 2.** Mean interpersonal finger-finger distance, relative phase, and coupling asymmetry as a function of the different leadership conditions, showing greatest movement synchrony when Person 1 and Person 2 adapt to equivalent degrees in the Joint (no assigned leader) condition. Negative relative phase angles indicate Person 1 lagging behind Person 2, and positive relative phase angles indicate the inverse. Negative coupling asymmetry index values indicate Person 1 adapting more to Person 2 than Person 2 adapting to Person 1, and positive coupling asymmetry index values indicate the inverse. Error bars represent 1 × SD of the mean (computed for within-subject designs (Morey, 2008)), and asterisks represent statistically significant differences ($p < .05$).

$\eta_g^2 = 0.04$. Pairwise comparisons with Bonferroni correction indicated that the interpersonal finger-finger distance was significantly larger in the Follower-Leader condition, $t(54) = 4.12$, $p = .0004$, $d = 0.49$, and Leader-Follower condition, $t(54) = 3.00$, $p = .01$, $d = 0.38$, compared to the Joint condition, and that there was no significant difference between the Follower-Leader and Leader-Follower conditions, $t(54) = -1.21$, $p = .80$, $d = 0.13$ (see Fig. 2). This effect was corroborated by the ANOVA conducted on the *mean* of the relative phase angles between the horizontal displacements of participants' fingers, which also yielded a significant effect of Leadership, $F(1.23, 33.20) = 79.23$, $MSE = 70.27$, $p < .0001$, $\eta_g^2 = 0.64$. Pairwise comparisons indicated that the mean relative phase values exhibited in the three conditions were all significantly different from each other: $t(54) = 12.54$, $p < .0001$, $d = 0.29$, for the difference between Follower-Leader and Leader-Follower; $t(54) = -5.73$, $p < .0001$, $d = 0.15$, for the difference between Follower-Leader and Joint; and $t(54) = 7.25$, $p < .0001$, $d = 0.19$, for the difference between Leader-Follower and Joint. As seen in Fig. 2, a significant negative phase shift occurred in the Follower-Leader condition, $t(27) = -8.35$, $p < .0001$, $d = 1.58$, and a significant positive phase shift occurred in the Leader-Follower condition, $t(27) = 7.03$, $p < .0001$, $d = 1.33$, while the mean relative phase in the Joint condition was not significantly different from 0, $t(27) = -1.98$, $p = .17$, $d = 0.37$. These results indicate that participants were better synchronized in the Joint condition with no assigned leader compared to the other conditions in which the follower lagged behind the leader (Noy et al., 2011).

A one-way repeated-measures ANOVA conducted on the *standard deviation* (variability) of the distance between paired participants' fingers revealed no significant effect of Leadership, $F(1.89, 50.97) = 2.75$, $MSE = 0.24$, $p = .08$, $\eta_g^2 = 0.02$. The ANOVA conducted on the *standard deviation* of relative phase angles confirmed this result with no significant effect of Leadership, $F(1.83, 49.40) = 0.03$, $MSE = 38.45$, $p = .97$, $\eta_g^2 = 0.0002$, indicating that there was no clear evidence of modulation of the synchrony variability exhibited by dyads depending on leadership instructions.

The movement analyses also revealed that leadership instructions modified the directionality of the coupling between the two participants, that is, the degree of mutual adaptation. A one-way repeated-measures ANOVA performed on coupling asymmetry index values yielded a significant effect of Leadership, $F(1.75, 47.31) = 37.59$, $MSE = 0.02$, $p < .0001$, $\eta_g^2 = 0.45$. Index values in the three leadership conditions all differed significantly from one another: $t(54) = 8.66$, $p < .0001$, $d = 2.44$, for the difference between Follower-Leader and Leader-Follower; $t(54) = -4.73$, $p < .0001$, $d = 1.16$, for the difference between Follower-Leader and Joint; and $t(54) = 3.93$, $p = .0007$, $d = 0.93$, for the difference between Leader-Follower and Joint. The index values were significantly negative in the Follower-Leader condition, $t(27) = -7.05$, $p < .0001$, $d = 1.33$, significantly positive in the Leader-Follower condition, $t(27) = 5.90$, $p < .0001$, $d = 1.11$, and not significantly different from 0 in the Joint condition, $t(27) = 0.19$, $p = 1$, $d = 0.04$. This indicates the occurrence of symmetric coupling – that is, the same degree of mutual adaptation for each participant within a dyad – in the Joint condition and asymmetric coupling in the other conditions, where the follower adapted more to the leader than the inverse.

### 3.2. Neural dynamics

The EEG data revealed neural responses at *other*, *self*, and *inter* (self-other integration) frequencies (Fig. 1) that (i) were present in both participants within dyads, (ii) were selectively modulated depending on leadership instructions (Fig. 3), and (iii) were correlated with dyadic movement synchronization (Fig. 4).

#### 3.2.1. Other responses

Individual's EEG responses specific to their co-performer's forearm movements were observed in the form of large significant peaks (revealed by group-level significance tests conducted on Z-scores) at the *other* fundamental frequency – 7.7 Hz for Person 1 (whose own flicker frequency was 5.7 Hz) and 5.7 Hz for Person 2 (whose own flicker frequency was 7.7 Hz) – and the corresponding harmonics – 15.4, 23.1, 30.8, 38.5, and 46.2 Hz for Person 1 and 11.4, 17.1, 22.8, 28.5, 34.2, 39.9, and 45.6 Hz for Person 2 (see Fig. 1). Reliable peaks at these frequencies were observed in the majority of the participants. Individual-level significance tests indicated significant peaks at the *other* fundamental frequency for all 56 participants, and at the first five harmonics for 52, 38, 36, 21, and 21 participants, respectively.

Comparisons of *other* responses across the leadership conditions revealed selective amplitude modulation depending on whether participants led, followed, or synchronized jointly. A 3 × 6 repeated-measures ANOVA with the factors Leadership (Leader, Follower and Joint) and Harmonic (Fundamental and 1st-5th harmonics) indicated a significant

main effect of Harmonic, $F(2.31, 126.93) = 77.46$, $MSE = 0.005$, $p < .0001$, $\eta_g^2 = 0.40$, showing a large response at the fundamental frequency that decreased with higher harmonics. The analysis also yielded a significant main effect of Leadership, $F(1.68, 92.40) = 25.29$, $MSE = 0.0006$, $p < .0001$, $\eta_g^2 = 0.02$, and a significant interaction between Leadership and Harmonic, $F(2.86, 157.29) = 8.39$, $MSE = 0.0008$, $p < .0001$, $\eta_g^2 = 0.01$. This interaction indicates that the amplitude of *other* responses at the fundamental frequency and first harmonic was larger when following compared to when leading or doing the task jointly without assigned leader, as seen in Fig. 3. Pairwise comparisons conducted for each Harmonic level (18 tests in total) with Bonferroni correction indicated significantly larger *other* responses when participants followed compared to when they led at the fundamental frequency, $t(571.39) = 9.44$, $p < .0001$, $d = 0.44$, and first harmonic, $t(571.39) = 6.86$, $p < .0001$, $d = 0.46$; when they performed jointly compared to when they led at the fundamental frequency, $t(571.39) = -6.28$, $p < .0001$, $d = 0.36$, and first harmonic, $t(571.39) = -6.46$, $p < .0001$, $d = 0.44$, and when they followed compared to when they performed jointly at the fundamental frequency, $t(571.39) = 3.16$, $p = .03$, $d = 0.14$. Pairwise comparisons did not reveal any other significant differences between leadership conditions (all $p$ values $> .05$).

As shown in Fig. 3, grand-averaged topographies revealed that EEG *other* responses were centered on medial occipital regions, with larger amplitude at Oz compared to POz for all leadership conditions. A two-way ANOVA with the factors Leadership (Leader, Follower and Joint) and Electrode (Oz and POz) on the amplitude of *other* responses (fundamental + first harmonic) indicated a significant main effect of Leadership, $F(1.88, 103.44) = 19.90$, $MSE = 0.04$, $p < .0001$, $\eta_g^2 = 0.03$, of Electrode, $F(1, 55) = 24.12$, $MSE = 0.10$, $p < .0001$, $\eta_g^2 = 0.05$, and a significant Electrode × Leadership interaction, $F(1.91, 104.84) = 14.37$, $MSE = 0.005$, $p < .0001$, $\eta_g^2 = 0.003$. Pairwise comparisons on each Leadership level (3 tests in total) with Bonferroni correction indicated significantly larger *other* response for Oz compared to POz for Follower, $t(64.47) = 5.30$, $p < .0001$, $d = 0.46$, Joint, $t(64.47) = 5.50$, $p < .0001$, $d = 0.53$, and Leader, $t(64.47) = 3.22$, $p = .006$, $d = 0.38$.

### 3.2.2. Self responses

EEG responses associated with participants' own forearm movements were indicated at the group-level by significant peaks at the *self* frequency, that is, at 5.7 Hz for Person 1 and 7.7 Hz for Person 2 – and the first three corresponding harmonics – 11.4, 17.1 and 22.8 Hz for Person 1 and 15.4, 23.1 and 30.8 Hz for Person 2. The majority of the participants exhibited reliable peaks at these frequencies. The fundamental frequency and first three harmonics were significant at the individual-level for 43, 34, 9, and 9 participants out of 56, respectively.

The amplitude of *self* responses was found to be selectively modulated as a function of leadership instructions. A 3 × 4 repeated-measures ANOVA with the factors Leadership (Leader, Follower and Joint) and Harmonic (Fundamental and 1st-3rd harmonics) conducted on *self* responses yielded a significant main effect of Harmonic, $F(1.70, 93.70) = 73.31$, $MSE = 0.0005$, $p < .0001$, $\eta_g^2 = 0.39$, indicating a large response at the fundamental frequency decreasing with higher harmonics (see Fig. 1). No significant main effect of Leadership was found, $F(1.91, 105.29) = 1.63$, $MSE = 0.00008$, $p = .2$, $\eta_g^2 = 0.002$, but the ANOVA indicated a significant interaction between Leadership and Harmonic, $F(3.89, 213.77) = 4.45$, $MSE = 0.00009$, $p = .002$, $\eta_g^2 = 0.01$. These results show that the amplitude of *self* responses was maximal when participants led the improvisation, as seen in Fig. 3. Pairwise comparisons at each Harmonic level (12 tests in total) with Bonferroni correction yielded significantly larger *self* responses when participants led compared to when they followed at the fundamental frequency level, $t(431.98) = -5.03$, $p < .0001$, $d = 0.35$, and a difference between Leader and Joint that was close to significance, $t(431.98) = 2.82$, $p = .06$, $d = 0.19$. No other differences were significant (all $p$ values $> .05$).

As shown in Fig. 3, grand-averaged topographies indicated that *self* responses were in medial occipital regions, as was the case for *other* responses, but with a more superior, parietal localization. A two-way ANOVA with the factors Leadership (Leader, Follower and Joint) and Electrode (Oz and POz) on the amplitude at the fundamental frequency of *self* responses indicated a significant main effect of Leadership, $F(1.76, 96.80) = 5.56$, $MSE = 0.005$, $p = .007$, $\eta_g^2 = 0.02$, but no significant effect of Electrode, $F(1, 55) = 1.08$, $MSE = 0.01$, $p = .3$, $\eta_g^2 = 0.003$, and Electrode × Leadership interaction, $F(1.84, 100.94) = 2.10$, $MSE = 0.0007$, $p = .13$, $\eta_g^2 = 0.001$. Thus, the amplitude of *self* responses measured at POz and Oz did not differ in any of the three leadership conditions in contrast to *other* responses that were larger at Oz.

### 3.2.3. Inter-modulation responses: self-other integration

EEG responses at 13.4 Hz, corresponding to the *inter*-modulation frequency of 5.7 and 7.7 Hz, and thus indexing the occurrence of neural integration of *self* and *other* information, were significant at the group

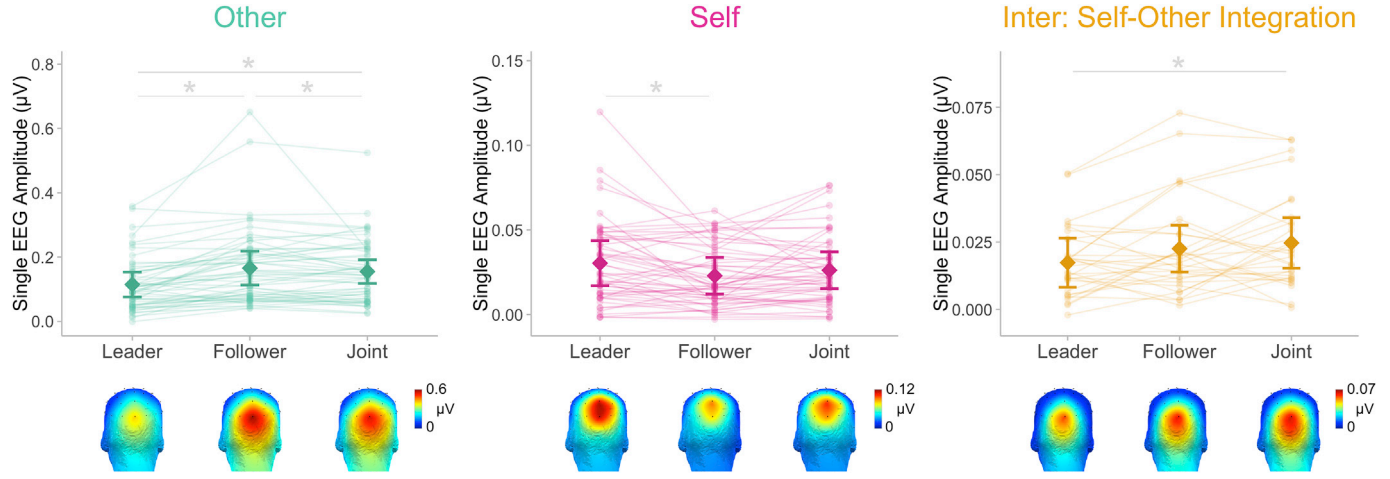


**Fig. 3.** Amplitude of EEG *other*, *self,* and *inter* responses as a function of the different leadership conditions, showing specific selective enhancement depending on whether participants led, followed, or improvised jointly. The data represented correspond to the sum of the fundamental frequency and its first harmonic for *other*, and the fundamentals only for *self* and *inter*, averaged across all channels. All 56 participants are represented for *other* and *self* and only the 31 participants with significant responses at 13.4 Hz are represented for *inter*. Error bars represent 1 × SD of the mean (computed for within-subject designs (Morey, 2008)), and asterisks represent statistically significant differences ($p < .05$). The corresponding grand-averaged topographies are represented with color-scales adjusted to the amplitude of *other*, *self,* and *inter* responses and held constant across the different leadership conditions.

level and for 31 participants in total at the individual level. Significant responses at the group-level were also found at 21.1 Hz for Person 1 and 19.1 Hz for Person 2, corresponding to the sum of the first harmonic of *other* and the fundamental of *self*. These responses were not included in further analyses because of their small amplitude and the fact that they occurred in only a small number of participants (10 out of 56 participants exhibited significant peaks at these frequencies). No responses were observed at other *inter*-modulation frequencies (i.e., harmonics of 13.4 Hz or lower *inter*-modulation frequency – 2 Hz and corresponding harmonics).

A one-way repeated-measures ANOVA with the factor Leadership (Leader, Follower and Joint) on the 13.4 Hz amplitude revealed an effect of Leadership that was close to significance when conducted on all participants, $F(1.95, 107.40) = 2.88$, $MSE = 0.00006$, $p = .06$, $\eta_g^2 = 0.009$. This effect reached significance when conducted on the 31 participants who exhibited a significant response at 13.4 Hz, $F(1.98, 59.52) = 5.37$, $MSE = 0.00008$, $p = .007$, $\eta_g^2 = 0.04$. Pairwise comparisons with Bonferroni correction revealed significantly larger *inter* responses when participants were instructed to perform the task jointly compared to when they were instructed to lead, $t(60) = -3.19$, $p = .007$, $d = 0.49$. The difference between Follower and Leader did not reach significance, $t(60) = 2.26$, $p = .08$, $d = 0.34$ and the difference between Follower and Joint was likewise not significant, $t(60) = -0.92$, $p = 1$, $d = 0.12$, indicating that self-other integration was maximal when mutual adaptation was required.

As with *other* and *self* responses, *inter* responses were centered on medial occipital regions with grand-averaged topographies most similar to those of the *other* responses for the different leadership conditions (see Fig. 3). A two-way ANOVA with the factors Leadership (Leader, Follower and Joint) and Electrode (Oz and POz) was conducted on the EEG amplitude at 13.4 Hz of the 31 participants who exhibited significant response at this frequency. This analysis indicated a significant main effect of Electrode, $F(1, 55) = 25.25$, $MSE = 0.0035$, $p < .0001$, $\eta_g^2 = 0.05$, and no significant effect of Leadership, $F(1.94, 106.57) = 0.67$, $MSE = 0.0015$, $p = .51$, $\eta_g^2 = 0.001$, and Electrode × Leadership interaction, $F(1.97, 108.48) = 0.48$, $MSE = 0.0003$, $p = .62$, $\eta_g^2 = 0.0002$, showing larger *inter* responses for Oz than POz in the three leadership conditions.

### 3.3. Neural-movement dynamics

Multiple linear regression analyses examining the relationship between EEG responses and dyadic movement synchrony revealed that movement synchronization was high to the extent that the two participants within a dyad exhibited relatively large EEG responses at *other*, *self,* and *inter* frequencies. The separate regression analyses included *mean* distance, *standard deviation* distance, *absolute mean* relative phase, and *standard deviation* relative phase as dependent variables, and dual EEG *other*, *self,* and *inter* responses (sum of the amplitude [fundamental + first harmonic for *other* and fundamentals for *self* and *inter*] of Person 1 and 2) as independent variables. Results are displayed in Fig. 4 for the linear regressions between dual EEG *other*, *self,* and *inter* responses and the *mean* and *standard deviation* of finger-finger distance.

The regression analyses revealed significant (or near-significant) models for *mean* distance, $F(3, 24) = 4.86$, $p = .009$, $R^2 = 0.38$; *standard deviation* of distance, $F(3, 24) = 5.07$, $p = .007$, $R^2 = 0.39$; *mean* relative phase, $F(3, 24) = 2.82$, $p = .06$, $R^2 = 0.26$; and for *standard deviation* of relative phase, $F(3, 24) = 3.28$, $p = .038$, $R^2 = 0.29$, but no significant predictors (all $p$ values > .05). These results indicate that *other*, *self,* and *inter* were correlated with measures of movement synchronization, but were also highly correlated with one another and none explained a uniquely greater amount of variance.

Multiple regressions with the same dependent variables but with Person 1 and 2's *other*, *self,* and *inter* responses as independent variables were conducted separately for each of the three Leadership conditions. These analyses also revealed significant models (all models significant for

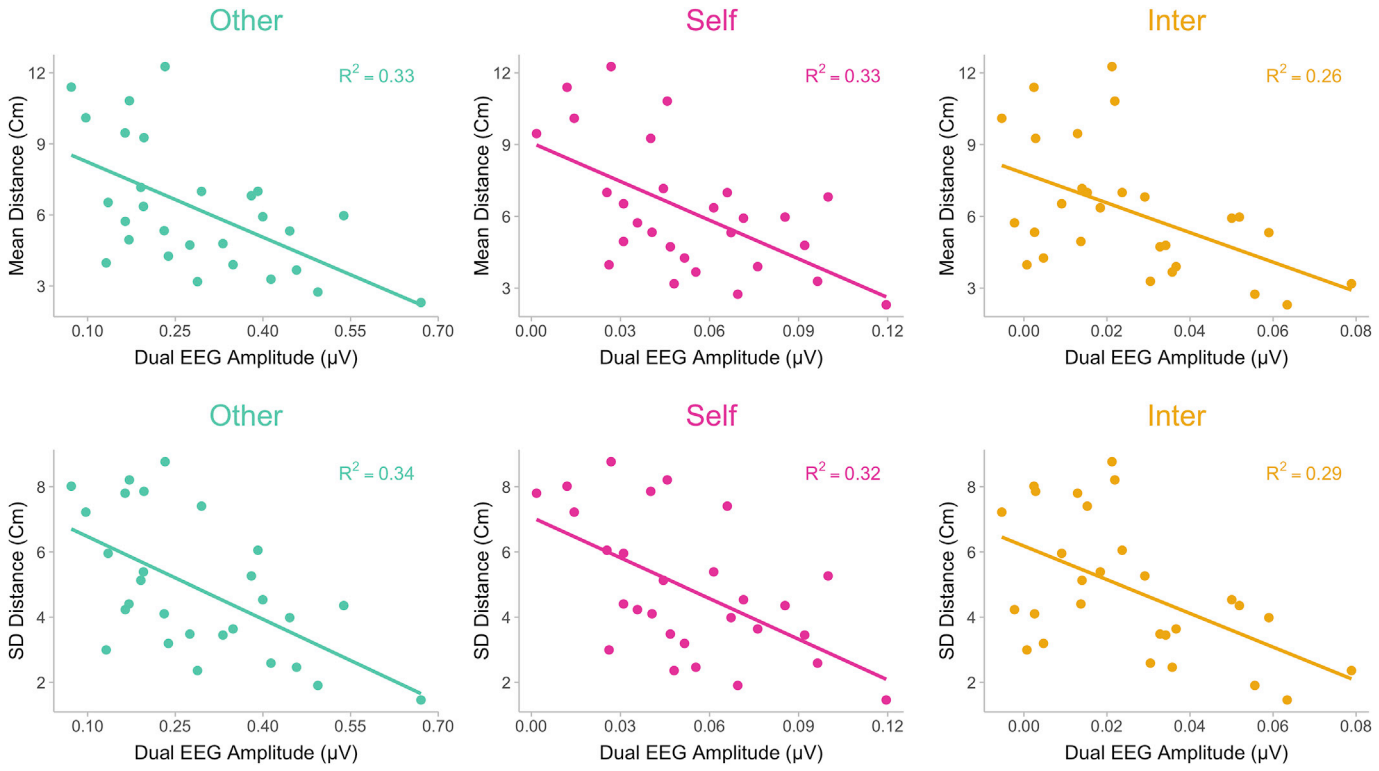


**Fig. 4.** Relationship between the amplitude of EEG *other*, *self*, and *inter* responses, and the *mean* and *standard deviation* of the finger-finger distance for all dyads, showing that larger dual EEG responses correlate with better synchronization performance. Dual EEG responses correspond to the sum of the EEG responses (fundamental and first harmonic for *other* and fundamentals for *self* and *inter*, averaged across all channels) of Person 1 and 2. The diagonals represent the lines of best fit with the corresponding R-squared values.

the *mean* and *standard deviation* of the distance [all $p$ values $< .05$] and 2/6 models significant [$p$ values $< .05$] for the *mean* and *standard deviation* of the relative phase angles) but no significant predictors (all $p$ values $> .05$). This confirms that it was the global EEG response in general and not the specific *other*, *self*, or *inter* responses in particular that predicted dyads' movement synchronization performance, independently of leadership instructions.

## 4. Discussion

This study employed dual-EEG and frequency-tagging techniques to investigate the neural mechanisms underlying the capacity of humans to synchronize their movements with one another accurately in time and space. EEG recordings of dyads producing novel forearm movements in synchrony revealed the neural tracking and integration of self- and other-generated information, and showed that the magnitude of these brain responses predicted dyads' behavioral synchronization performance.

The results revealed that, consistent with previous behavioral work (Noy et al., 2011), dyadic movement synchronization during joint improvisation was superior when no leader was assigned than when one individual within a pair served as leader. Going beyond behavior, however, we show that this superior interpersonal coordination is associated with enhanced neural integration of self- and other-generated movements. This advance was made possible by EEG frequency-tagging techniques allowing us to identify a neural marker of self-other integration in the form of a 13.4 Hz response corresponding to the result of a nonlinear integration of unique *self* and *other* frequencies (i.e., 5.7 and 7.7 Hz) (Boremanse et al., 2013, 2014; Norcia et al., 2015; Alp et al., 2017, 2018). This *inter*-modulation frequency response was observed in medial-occipital areas, suggesting that information related to self- and other-generated movements is integrated at early stage in visual regions, possibly in the primary visual cortex. The maximal amplitude of this response observed in the joint condition when no leader was assigned supports the hypothesis that self-other integration is key for successful joint improvisation, supporting mutual adaption and anticipation (Keller et al., 2016; Novembre et al., 2016). Self-other integration captured here in the form of enhanced EEG amplitude at the *inter*-modulation frequency might also underlie the subjective state of 'togetherness' often experienced by expert improvisers (e.g., actors and musicians, Noy et al., 2011).

The results also revealed that *self*, *other,* and *inter* responses were largest under different leadership conditions, showing that these responses exhibit independent amplitude modulations, and thus, might have specific functions in establishing and maintaining joint movement synchronization. *Other* responses were larger when participants followed compared to when they performed jointly or when they led, and next largest when they performed jointly compared to when they led. This demonstrates that the neural tracking of a partner's movement is strong to the extent that adaptation to the other's movement is required, which is in line with recent magneto-encephalography results reported with hand-opening and closing actions (Zhou et al., 2016).

*Self* responses were also selectively modulated depending on leadership instructions. The neural tracking of *self*-generated movements was strongest when participants led, which is consistent with leaders exhibiting enhanced attention to their own movements in the context of joint action. Importantly, *self* responses showed a more superior, parietal distribution compared to the *other* responses, compatible with activity originating from the primary visual cortex, where the lower position of an individual's own finger in the visual field under our task setup projects to the superior lip of the calcarine sulcus (Clark et al., 1994; Wandell et al., 2007). The difference in the amplitude of *self* responses observed in the different leadership conditions, together with their more superior distribution, suggests that the neural tracking of an individual's own movements is modulated at the earliest visual cortical stage and relatively independently of eye movements. This finding is noteworthy because it suggests that the selective modulation of *self* responses based on leadership instructions is functional and not simply the consequence of greater eye fixations or smoother pursuit of one's own movements when leading, as such processes would have led to changes in topographies across conditions. Instead, our result shows that participants use visual feedback of their own movement when coordinating with others, especially when leading, which is remarkable given that it could be argued that somatosensory feedback should be sufficient for efficient motor control on a simple horizontal arm movement task (Proteau, 1992; Vidoni and Boyd, 2008).

Of particular interest is the finding that dyadic synchronization performance was correlated with the amplitude of *self*, *other,* and *inter* responses exhibited by the paired participants. The larger the *self*, *other,* and *inter* EEG responses of the dyads, the more synchronized their behavioral performance. This result demonstrates the robustness of the frequency-tagging approach used here in providing a direct measure of the strength of the perceptual coupling within the dyads and their capacity to synchronize, regardless of the numerous sources of variability inherent to EEG measurements (e.g., anatomical, noise, and artifact differences) (Nunez and Srinivasan, 2006). EEG in this study captured individual differences in neural tracking capacity of human movements in general, including self- and other-generated movements. This observation paves the way for a new avenue of research to determine the degree to which individual differences specific to the neural tracking capacity of either self- or other-generated movements explain differences in synchronization performance across leadership conditions. The significant correlations between frequency-tagged EEG responses and both mean and standard deviation synchronization measures also encourage future examination of whether these neural responses are linked to specific mechanisms that support movement synchronization, such as global period matching and local error correction mechanisms (Schulze and Vorberg, 2002; Repp and Keller, 2008; Varlet et al., 2012, 2014).

Previous dual EEG studies examining the role of neural oscillations in joint action have demonstrated that the amplitude of oscillations in the alpha (8–12 Hz) frequency band was linked to the form and stability of interpersonal coordination displayed by co-actors (Tognoli et al., 2007; Dumas et al., 2010; Naeem et al., 2012; Konvalinka et al., 2014; Novembre et al., 2016; Goldstein et al., 2018). This suggests that alpha-band oscillations play a role in establishing and maintaining coordinated movements with others, which may be part of the broader capacity for alpha oscillations to function generally in facilitating cognitive, perceptual, and motor processes in a wide variety of tasks (Klimesch, 1999; Jensen and Mazaheri, 2010; Hanslmayr et al., 2011). With regard to functions specifically related to interpersonal coordination, previous dual-EEG studies have found evidence for inter-brain synchrony, especially in the alpha-frequency band, when participants interact together (Dumas et al., 2010; Goldstein et al., 2018). However, the precise nature of links between the coordination exhibited at the behavioral level and the alpha modulation occurring at intra-brain level remain unclear (Burgess, 2013). Moreover, measures of alpha-band neural oscillations alone do not allow neural activity specific to the perceptual tracking of self- and other-generated movements to be dissociated, thus stopping short of clarifying their functional relevance to dyadic coordination. Here, we extend this previous work by identifying robust markers of the neural tracking and integration of self- and other-generated movements, and by showing how these markers are modulated according to leadership conditions and how they correlate with coordination performance.

It could be particularly fruitful in future research to investigate the links between the neural markers revealed in the current study and those revealed in the alpha-frequency band literature. Amplitude modulation of frequency-tagged responses might be selectively associated with specific features in activity pattern and response magnitude in the alpha-frequency band. For instance, differences in intrinsic alpha neural activity (e.g., mean, amplitude) could explain inter-individual differences, especially in the occurrence of 13.4 Hz self-other integration responses that we observed in most, but not all participants. Indeed, finding that only a subgroup of our participants exhibited significant responses at this

frequency could be related to differences in intrinsic alpha activity such as higher frequency and/or larger amplitude (Tognoli et al., 2007; Konvalinka et al., 2014; Novembre et al., 2016). Exploring links with other frequency ranges, such as beta (13–30 Hz) and gamma (30–70 Hz), could also be a promising avenue, as there is evidence showing the relevance of neural activity in these ranges in the context of self- and other-generated actions (Press et al., 2011; Dumas et al., 2012). Therefore, combining frequency-tagging techniques with measures used in previous dual-EEG studies could help the field in advancing toward a broader and deeper understanding of the neural mechanisms underlying interpersonal coordination.

To conclude, this study revealed evidence for the neural tracking of self- and other-generated movements and their integration during joint performance on a task requiring improvised motion. The magnitude of the neural tracking responses and the integration of information related to the movements of *self* and *other* were found to be selectively modulated depending on leader-follower relations, and also to provide a robust marker of individual differences in the capacity to synchronize with others. Neural self-other integration was reflected in participants' EEG with maximal amplitude under conditions where no leader was designated for the joint task, suggesting that self-other integration occurring at early stages in the visual system might be key in supporting enhanced mutual adaption and anticipation, and the subjective state of 'togetherness' often experienced by expert improvisers. Finally, our findings provide proof-of-concept for the combined use of dual-EEG and frequency-tagging techniques for the investigation of the perceptual-motor processes underlying joint performance in humans in ecologically-valid contexts. Extending the technique to naturalistic everyday scenarios could be a promising strategy to further understanding of how these processes develop and change along the life span.

## Declaration of competing interest

The authors declare no competing interests.

## Author contributions

MV, SN and PK designed the experiment, analyzed the data and wrote the paper. MV and PN collected the data. All authors approved the final version of the manuscript.

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## References

Ales, J.M., Farzin, F., Rossion, B., Norcia, A.M., 2012. An objective method for measuring face detection thresholds using the sweep steady-state visual evoked response. J. Vis. 12, 18.

Alp, N., Kohler, P.J., Kogo, N., Wagemans, J., Norcia, A.M., 2018. Measuring integration processes in visual symmetry with frequency-tagged EEG. Sci. Rep. 8, 6969.

Alp, N., Nikolaev, A.R., Wagemans, J., Kogo, N., 2017. EEG frequency tagging dissociates between neural processing of motion synchrony and human quality of multiple point-light dancers. Sci. Rep. 7, 44012.

Batschelet, E., 1981. Circular Statistics in Biology. Acad Press.

Boremanse, A., Norcia, A.M., Rossion, B., 2013. An objective signature for visual binding of face parts in the human brain. J. Vis. 13, 6.

Boremanse, A., Norcia, A.M., Rossion, B., 2014. Dissociation of part-based and integrated neural responses to faces by means of electroencephalographic frequency tagging. Eur. J. Neurosci. 40, 2987–2997.

Burgess, A.P., 2013. On the interpretation of synchronization in EEG hyperscanning studies: a cautionary note. Front. Hum. Neurosci. 7, 881.

Chang, A., Livingstone, S.R., Bosnyak, D.J., Trainor, L.J., 2017. Body sway reflects leadership in joint music performance. Proc. Natl. Acad. Sci. 114, E4134–E4141, 201617657.

Charman, T., Swettenham, J., Baron-Cohen, S., Cox, A., Baird, G., Drew, A., 1997. Infants with autism: an investigation of empathy, pretend play, joint attention, and imitation. Dev. Psychol. 33, 781.

Cirelli, L.K., Einarson, K.M., Trainor, L.J., 2014. Interpersonal synchrony increases prosocial behavior in infants. Dev. Sci. 17, 1003–1011.

Clark, V.P., Fan, S., Hillyard, S.A., 1994. Identification of early visual evoked potential generators by retinotopic and topographic analyses. Hum. Brain Mapp. 2, 170–187.

Coey, C.A., Varlet, M., Richardson, M.J., 2012. Coordination dynamics in a socially situated nervous system. Front. Hum. Neurosci. 6, 164.

D'Ausilio, A., Novembre, G., Fadiga, L., Keller, P.E., 2015. What can music tell us about social interaction? Trends Cogn. Sci. 19, 111–114.

Di Russo, F., Pitzalis, S., Aprile, T., Spitoni, G., Patria, F., Stella, A., Spinelli, D., Hillyard, S.A., 2007. Spatiotemporal analysis of the cortical sources of the steady-state visual evoked potential. Hum. Brain Mapp. 28, 323–334.

Dumas, G., Martinerie, J., Soussignan, R., Nadel, J., 2012. Does the brain know who is at the origin of what in an imitative interaction? Front. Hum. Neurosci. 6, 128.

Dumas, G., Nadel, J., Soussignan, R., Martinerie, J., Garnero, L., 2010. Inter-brain synchronization during social interaction. PLoS One 5 e12166.

Goldstein, P., Weissman-Fogel, I., Dumas, G., Shamay-Tsoory, S.G., 2018. Brain-to-brain coupling during handholding is associated with pain reduction. Proc. Natl. Acad. Sci. 115, E2528–E2537, 201703643.

Hanslmayr, S., Gross, J., Klimesch, W., Shapiro, K.L., 2011. The role of alpha oscillations in temporal attention. Brain Res. Rev. 67, 331–343.

Hove, M.J., Risen, J.L., 2009. It's all in the timing: interpersonal synchrony increases affiliation. Soc. Cogn. 27, 949–960.

Jacques, C., Retter, T.L., Rossion, B., 2016. A single glance at natural face images generate larger and qualitatively different category-selective spatio-temporal signatures than other ecologically-relevant categories in the human brain. Neuroimage 137, 21–33.

Jensen, O., Mazaheri, A., 2010. Shaping functional architecture by oscillatory alpha activity: gating by inhibition. Front. Hum. Neurosci. 4, 186.

Keller, P.E., Novembre, G., Hove, M.J., 2014. Rhythm in joint action: psychological and neurophysiological mechanisms for real-time interpersonal coordination. Phil Trans R Soc B 369, 20130394.

Keller, P.E., Novembre, G., Loehr, J., 2016. 14 musical ensemble performance: representing self, other and joint action outcomes. In: Shared Representations: Sensorimotor Foundations of Social Life, p. 280.

Kelso, J.A., 1995. Dynamic Patterns: the Self Organization of Brain and Behaviour. The MIT Press.

Klimesch, W., 1999. EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. Brain Res. Rev. 29, 169–195.

Knoblich, G., Butterfill, S., Sebanz, N., 2011. Psychological research on joint action: theory and data. In: Psychology of Learning and Motivation. Elsevier, pp. 59–101.

Konvalinka, I., Bauer, M., Stahlhut, C., Hansen, L.K., Roepstorff, A., Frith, C.D., 2014. Frontal alpha oscillations distinguish leaders from followers: multivariate decoding of mutually interacting brains. Neuroimage 94, 79–88.

Lenc, T., Keller, P.E., Varlet, M., Nozaradan, S., 2018. Neural tracking of the musical beat is enhanced by low-frequency sounds. Proc. Natl. Acad. Sci. 115, 8221–8226.

MacRitchie, J., Varlet, M., Keller, P.E., 2017. Embodied expression through entrainment and co-representation in musical ensemble performance. In: The Routledge Companion to Embodied Music Interaction. Routledge, pp. 150–159.

Marsh, K.L., Isenhower, R.W., Richardson, M.J., Helt, M., Verbalis, A.D., Schmidt, R.C., Fein, D., 2013. Autism and social disconnection in interpersonal rocking. Front. Integr. Neurosci. 7, 4.

Marsh, K.L., Richardson, M.J., Schmidt, R.C., 2009. Social connection through joint action and interpersonal coordination. Top Cogn Sci 1, 320–339.

Morey, R.D., 2008. Confidence Intervals from Normalized Data: A Correction to Cousineau (2005). Reason, vol. 4, pp. 61–64.

Mouraux, A., Iannetti, G.D., 2008. Across-trial averaging of event-related EEG responses and beyond. Magn. Reson. Imaging 26, 1041–1054.

Naeem, M., Prasad, G., Watson, D.R., Kelso, J.S., 2012. Electrophysiological signatures of intentional social coordination in the 10–12 Hz range. Neuroimage 59, 1795–1803.

Norcia, A.M., Appelbaum, L.G., Ales, J.M., Cottereau, B.R., Rossion, B., 2015. The steady-state visual evoked potential in vision research: a review. J. Vis. 15, 4.

Novembre, G., Sammler, D., Keller, P.E., 2016. Neural alpha oscillations index the balance between self-other integration and segregation in real-time joint action. Neuropsychologia 89, 414–425.

Novembre, G., Varlet, M., Muawiyath, S., Stevens, C.J., Keller, P.E., 2015. The E-music box: an empirical method for exploring the universal capacity for musical production and for social interaction through music. R Soc Open Sci 2, 150286.

Noy, L., Dekel, E., Alon, U., 2011. The mirror game as a paradigm for studying the dynamics of two people improvising motion together. Proc. Natl. Acad. Sci. 108, 20947–20952.

Nozaradan, S., Peretz, I., Missal, M., Mouraux, A., 2011. Tagging the neuronal entrainment to beat and meter. J. Neurosci. 31, 10234–10240.

Nunez, P.L., Srinivasan, R., 2006. Electric Fields of the Brain: the Neurophysics of EEG. Oxford University Press, USA.

Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.-M., 2011. FieldTrip: open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. Comput. Intell. Neurosci. 2011, 156869.

Painter, D.R., Dux, P.E., Travis, S.L., Mattingley, J.B., 2014. Neural responses to target features outside a search array are enhanced during conjunction but not unique-feature search. J. Neurosci. 34, 3390–3401.

Phillips-Silver, J., Keller, P., 2012. Searching for roots of entrainment and joint action in early musical interactions. Front. Hum. Neurosci. 6, 26.
Pikovsky, A., Rosenblum, M., Kurths, J., Kurths, J., 2003. Synchronization: a Universal Concept in Nonlinear Sciences. Cambridge university press.
Press, C., Cook, J., Blakemore, S.-J., Kilner, J., 2011. Dynamic modulation of human motor activity when observing actions. J. Neurosci. 31, 2792–2800.
Proteau, L., 1992. On the specificity of learning and the role of visual information for movement control. In: Advances in Psychology. Elsevier, pp. 67–103.
Quek, G., Nemrodov, D., Rossion, B., Liu-Shuang, J., 2018. Selective attention to faces in a rapid visual stream: hemispheric differences in enhancement and suppression of category-selective neural activity. J. Cogn. Neurosci. 30, 393–410.
Regan, M.P., Regan, D., 1988. A frequency domain technique for characterizing nonlinearities in biological systems. J. Theor. Biol. 133, 293–317.
Renton, A.I., Painter, D.R., Mattingley, J.B., 2018. Differential deployment of visual attention during interactive approach and avoidance behavior. Cerebr. Cortex 29, 2366–2383.
Repp, B.H., Keller, P.E., 2008. Sensorimotor synchronization with adaptively timed sequences. Hum. Mov. Sci. 27, 423–456.
Richardson, D.C., Dale, R., Kirkham, N.Z., 2007a. The art of conversation is coordination. Psychol. Sci. 18, 407–413.
Richardson, M.J., Harrison, S.J., Kallen, R.W., Walton, A., Eiler, B.A., Saltzman, E., Schmidt, R.C., 2015. Self-organized complementary joint action: behavioral dynamics of an interpersonal collision-avoidance task. J. Exp. Psychol. Hum. Percept. Perform. 41, 665.
Richardson, M.J., Schmidt, R.C., Kay, B.A., 2007b. Distinguishing the noise and attractor strength of coordinated limb movements using recurrence analysis. Biol. Cybern. 96, 59–78.
Rosenblum, M.G., Cimponeriu, L., Bezerianos, A., Patzak, A., Mrowka, R., 2002. Identification of coupling direction: application to cardiorespiratory interaction. Phys Rev E 65, 041909.
Rosenblum, M.G., Pikovsky, A.S., 2001. Detecting direction of coupling in interacting oscillators. Phys Rev E 64, 045202.
Schmidt, R.C., Richardson, M.J., 2008. Dynamics of interpersonal coordination. In: Coordination: Neural, Behavioral and Social Dynamics. Springer, pp. 281–308.
Schulze, H.-H., Vorberg, D., 2002. Linear phase correction models for synchronization: parameter identification and estimation of parameters. Brain Cogn. 48, 80–97.
Sebanz, N., Bekkering, H., Knoblich, G., 2006. Joint action: bodies and minds moving together. Trends Cogn. Sci. 10, 70–76.
Singmann, H., Bolker, B., Westfall, J., Aust, F., 2015. Afex: Analysis of Factorial Experiments. R Package Version, 013–145.
Team, R.C., 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, 2016.
Tognoli, E., Lagarde, J., DeGuzman, G.C., Kelso, J.S., 2007. The phi complex as a neuromarker of human social coordination. Proc. Natl. Acad. Sci. 104, 8190–8195.
Valdesolo, P., Ouyang, J., DeSteno, D., 2010. The rhythm of joint action: synchrony promotes cooperative ability. J. Exp. Soc. Psychol. 46, 693–695.
Varlet, M., Marin, L., Capdevielle, D., Del-Monte, J., Schmidt, R., Salesse, R., Boulenger, J.-P., Bardy, B.G., Raffard, S., 2014. Difficulty leading interpersonal coordination: towards an embodied signature of social anxiety disorder. Front. Behav. Neurosci. 8, 29.
Varlet, M., Marin, L., Raffard, S., Schmidt, R.C., Capdevielle, D., Boulenger, J.-P., Del-Monte, J., Bardy, B.G., 2012. Impairments of social motor coordination in schizophrenia. PLoS One 7 e29772.
Vidoni, E.D., Boyd, L.A., 2008. Motor sequence learning occurs despite disrupted visual and proprioceptive feedback. Behav. Brain Funct. 4, 32.
Wandell, B.A., Dumoulin, S.O., Brewer, A.A., 2007. Visual field maps in human cortex. Neuron 56, 366–383.
Wickham, H., 2016. Ggplot2: Elegant Graphics for Data Analysis. Springer.
Wiltermuth, S.S., Heath, C., 2009. Synchrony and cooperation. Psychol. Sci. 20, 1–5.
Zemon, V., Ratliff, F., 1982. Visual evoked potentials: evidence for lateral interactions. Proc. Natl. Acad. Sci. 79, 5723–5726.
Zemon, V., Ratliff, F., 1984. Intermodulation components of the visual evoked potential: responses to lateral and superimposed stimuli. Biol. Cybern. 50, 401–408.
Zhou, G., Bourguignon, M., Parkkonen, L., Hari, R., 2016. Neural signatures of hand kinematics in leaders vs. followers: a dual-MEG study. Neuroimage 125, 731–738.