

Received: 25 February 2019 Accepted: 7 August 2019

Published online: 22 August 2019

Empathic perspective taking promotes interpersonal coordination through music

Giacomo Novembre^{1,2,3}, Zoe Mitsopoulos³ & Peter E. Keller³

Coordinated behavior promotes collaboration among humans. To shed light upon this relationship, we investigated whether and how interpersonal coordination is promoted by empathic perspective taking (EPT). In a joint music-making task, pairs of participants rotated electronic music-boxes, producing two streams of musical sounds that were meant to be played synchronously. Participants – who were not musically trained – were assigned to high and low EPT groups based on pre-experimental assessments using a standardized personality questionnaire. Results indicated that high EPT pairs were generally more accurate in synchronizing their actions. When instructed to lead the interaction, high and low EPT leaders were equally cooperative with followers, making their performance tempo more regular, presumably in order to increase their predictability and help followers to synchronize. Crucially, however, high EPT followers were better able to use this information to predict leaders' behavior and thus improve interpersonal synchronization. Thus, empathic perspective taking promotes interpersonal coordination by enhancing accuracy in predicting others' behavior while leaving the aptitude for cooperation unaltered. We argue that such predictive capacity relies on a sensorimotor mechanism responsible for simulating others' actions in an anticipatory manner, leading to behavioral advantages that may impact social cognition on a broad scale.

Synchronous behavior is a universal means of communication and cooperation observable in diverse species 1-4. In humans, this kind of behavior can be witnessed during activities such as audiences clapping their hands in unison, military units marching, or groups of athletes or dancers coordinating their movements in space and time⁵⁻⁹. Joint music making is a pervasive example of this phenomenon¹⁰. Even a group of perfect strangers might end up singing together, for example during a competitive sporting game or a religious ritual - more likely so if the individuals support the same team, or believe in the same god, of course.

When multiple individuals coordinate their movements in order to achieve interpersonal synchrony, the group benefits in terms of enhanced interpersonal bonding and social cohesion 11,12. Such pro-social effects of interpersonal synchronization have been reported in numerous laboratory studies using a variety of tasks¹³⁻²³. For instance, dyadic finger tapping in synchrony is more likely to increase feelings of affiliation 18, trust, and likeability 16,24. These effects appear early in ontogenetic development, as evidenced by the finding that 14-month old infants, if moved in synchrony with another individual by an experimenter, are subsequently more likely to engage in cooperative helping behavior with that individual 19,25. Even the mere observation of synchronous group behavior can augment perceived social cohesion^{26,27}.

These previous studies demonstrated that interpersonal synchrony is a sufficient condition to boost interpersonal pro-social processes. However, this is only one part of the story. Complementarily to these observations, some studies have shown that social personality traits can also affect interpersonal coordination skills. For instance, in one study, it was reported that individuals affected by Social Anxiety Disorder are impaired in leading a task requiring interpersonal coordination28. Another study showed that individuals who have high internal Locus of Control (according to a questionnaire assessing to what extent individuals assume life events to be contingent on their personal behavior) are relatively good leaders in the sense that they prioritize stabilizing their own action timing over synchronization with an unreliable virtual partner²⁹. Taken alongside the above evidence, these results suggest that the link between synchrony and prosociality might be bidirectional: increased

¹University College London, Department of Neuroscience, Physiology and Pharmacology, London, UK. ²Neuroscience and Behaviour Laboratory, Istituto Italiano di Tecnologia, Rome, Italy. ³The MARCS Institute for Brain, Behaviour and Development, Western Sydney University, Sydney, Australia. Correspondence and requests for materials should be addressed to G.N. (email: giacomo.novembre@iit.it)

interpersonal coordination can boost social behavior, but also enhanced social behavior can boost interpersonal coordination skills⁶. Yet, the sensorimotor and cognitive mechanisms mediating this bidirectional relationship remain mysterious, as do the personality traits associated with individual variations in the functioning of these putative mechanisms.

Here we hypothesized that a specific social personality trait that might influence interpersonal coordination behavior is empathy, which is generally defined as the human capacity to respond to – and share – experiences of others^{30,31}. Psychological research indicates that human experiences can be shared with others at multiple levels, ranging from sharing others' affective states to the cognitive ability to reason about another's beliefs, thoughts, or intentions by taking their perspective^{31–33}. Thus, empathy can be viewed as a multidimensional construct having distinct components^{34–36}. The component that we investigated here is Empathic Perspective Taking (EPT), which can be assessed using standardized questionnaires^{31,32} that index how spontaneously one individual adopts others' perspectives in everyday life situations. Thus, EPT will hereby be discussed as a proxy of empathic skills relevant to social cognition in general and interpersonal synchrony in particular.

Because interpersonal synchronization requires multiple individuals not only to be precise, but also to anticipate others' behavior^{6,37–40}, we hypothesized that more empathic individuals might perform relatively well on a task requiring interpersonal synchronization due to superior predictive skills. This hypothesis was motivated by a number of observations made in the field of cognitive neuroscience. Specifically, research using neuroimaging and brain stimulation techniques has revealed that more empathic individuals possess an enhanced "motor simulation" mechanism, which is capable of representing another's actions in terms of the neural resources necessary to execute the same action^{41–45}. Further research has shown that motor simulation has a predictive character, i.e. it supports the capacity to anticipate another's upcoming actions in the observer's brain^{45–52}. Taken together, this body of research suggests that more empathic individuals may benefit from enhanced motor simulation, and thereby superior predictive skills when it comes to synchronizing their actions with the actions of others.

To test this hypothesis, we employed a task involving an ecologically valid form of interpersonal synchronization that could also be tightly controlled under laboratory conditions, i.e. a joint music making task ¹⁰. Interpersonal coordination through music is a universal and natural form of social interaction, with widespread examples including ritual and congregational activities or infant-caregiver communication ^{53,54}. Musical coordination is often studied in expert musicians ^{10,55–58}, but it is also advantageous to do so in the general population by exploiting fundamental musical predispositions that have evolved in humans ⁵⁹. The latter approach is well suited to address our goal because it does not confound personality traits related to musicianship with empathic perspective taking. To this end, here we used a custom-built instrument that was developed to allow individuals without musical training to perform music collectively: the E-music box ⁵⁹. The E-music box transforms cyclical rotatory movements into a preprogrammed musical melody whose tempo varies according to the velocity of the rotation (Fig. 1). The tunes can be played with correct rhythm and constant tempo by rotating the handle with constant velocity.

We recruited a group of individuals who had never received formal musical training. We used a standardized questionnaire to assess each individual's empathic score³², and then formed pairs of individuals who scored similarly on the Empathic Perspective Taking (EPT) subscale, indexing an individual's spontaneous tendency to adopt the psychological point of view of others (ranging from 0 to 28). In order to minimize within-pair EPT score variability, participants were paired with partners whose EPT score were within 3 points on the scale (Fig. 1). We then invited these pairs into the lab, and asked them to perform the joint music making task as accurately as possible. To the extent that higher empathic skills are generally associated with higher interpersonal coordination skills, we predicted that those pairs formed by relatively more empathic participants would be more accurate in the interpersonal coordination task. To address this, we computed the average asynchrony between musical tones from the two parts that were meant to be synchronous and compared it across two groups of pairs scoring relatively higher or lower on the EPT assessment (following median split).

Furthermore, to test the hypothesis that EPT facilitates interpersonal coordination by affecting temporal prediction, we manipulated leader-follower relations via instructions. Specifically, the paired participants were asked to perform the joint music making task across three conditions: one where one participant was instructed to lead and the other to follow, a second condition where these roles switched, and finally a condition during which no leadership was assigned. The assumption behind this manipulation was that prediction demands vary with leadership role: Leaders are primarily responsible for controlling their own actions²⁹ while followers are required to attend to the leader in order to predict his or her action timing, and to adapt to interpersonal timing discrepancies⁵⁹⁻⁶¹. It is therefore optimal for leaders to make their actions as predictable as possible, a strategy that has been previously observed in a variety of joint action contexts^{62,63} and is referred to as a "coordination smoother"⁶⁴. This strategy should facilitate interpersonal coordination accuracy and stability to the extent that the follower can make use of the leader's timing cues. Thus, if EPT increases the use of such cues, then high EPT followers should be better able to predict, and therefore temporally align, their actions with the leaders' actions.

Materials and Methods

Participants. We recruited 58 healthy individuals (39 female, age mean \pm std = 25.64 \pm 8.54 years). All participants were categorized as non-musicians based on a screening questionnaire (the Ollen Musical Sophistication Index, OMSI⁶⁵). All participants reported having normal hearing. All procedures were in accordance with the Declaration of Helsinki and were approved by the human research ethics committee of Western Sydney University (approval number: H10487). Informed consent was obtained from all participants (each being at least 18 years old when the experiment was conducted).

Pre experiment empathy-based assessment. Before taking part in the experiment, empathy was assessed in all participants using the Interpersonal Reactivity Index (IRI)^{31,32}, a questionnaire that was

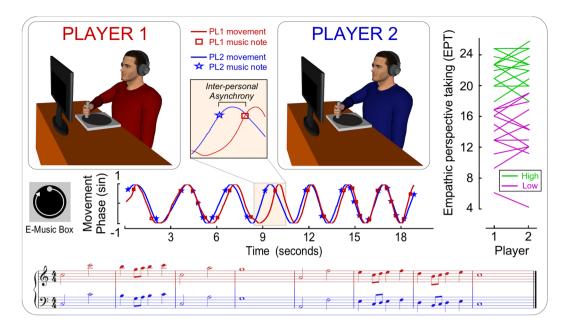


Figure 1. Experimental paradigm. Pairs of musically untrained participants use E-music boxes to perform a musical melody together. The E-music box transforms rotatory movements into a pre-programmed musical melody whose tempo varies according to the rotation velocity. When the E-music box is rotated at constant velocity, the melody is played with correct rhythm and constant tempo (for details see)⁵⁹. Participants are instructed to synchronize their musical outputs as accurately as possible. Their movements are therefore highly controlled and entail continuous rotations of their right arms. The latency of movements and outputted musical tones are used to study interpersonal coordination accuracy, as well as leader-follower relations. Before taking part in the study, each participant is paired with another individual having a similar empathic perspective taking (EPT) score (i.e. their score difference is not larger than 3). Eventually, groups of relatively higher and lower EPT pairs are compared one another following a median split.

administered online. The IRI consists of 28 self-report items measuring empathy as a multidimensional construct. The IRI distinguishes between affective and cognitive empathy as distinct components of the construct. The subscale of interest here was perspective taking (PT), an aspect of cognitive empathy, which refers to one's tendency to adopt another's viewpoint. The PT score ranges between 0 (lowest perspective taking tendency) to a maximum of 28 (highest perspective taking tendency). Following the collection of the above-specified empathic PT scores (EPT), we paired together participants having similar EPT scores (i.e. an absolute score difference not larger than three).

Next, we performed a median split on the sample according to the participants' EPT score (averaged within each pair). This resulted in two groups that are hereafter referred to as Low EPT (n=13 dyads; 1 male-male, 6 female-female, and 6 mixed dyads) and High EPT (n=13 dyads; 2 male-male, 5 female-female, and 6 mixed dyads) groups. Sex ratios were therefore comparable across groups. Yet, we acknowledge that, despite sex being similarly distributed across EPT groups, the sample included more females than males. It would be useful to control this more strictly in future investigations, given that sex and gender can affect both empathy and interpersonal coordination 66,67 .

Three additional pairs falling on the median were excluded in order to form two clearly distinguishable groups. The mean EPT score of each group was 13.73 ± 3.53 for the Low EPT group and 22.35 ± 1.93 for the High PT group. None of the paired participants were friends or romantically involved prior to taking part in the experiment. Low and High EPT groups were comparable in terms of music and dance experience, as assessed using the OMSI scores (t < 2, p > 0.05). Furthermore, the percentage of participants who were born and raised in Australia (16 out of 26 [High EPT] and 15 out of 26 [EPT group]), and the level of education (rated on a 1–8 scale ranging from school certificate to doctoral degree: 3.62 ± 1.49 [High EPT], 3.85 ± 1.75 [Low EPT]), were comparable across groups.

Apparatus and musical material. Participants could control the timing of a pre-programmed melody using the E-Music Box 59 . The E-Music Box is a small disk jockey's turntable with an exterior handle attached, which enables the participant to rotate the turntable in order to produce the pre-programmed melody (Fig. 1; for technical details \sec^{59}). The melody consisted of the first eight bars from the tune *Somewhere over the Rainbow*, originally written for the 1939 movie *The Wizard of Oz.* This tune was chosen for its widespread popularity and familiarity, which was assumed to facilitate the task for the musically untrained participants. Importantly, all participants reported being familiar with this melody and, when asked to rate familiarity on a 1–5 Likert scale, the two EPT groups yielded comparable scores (High EPT: 3.77 ± 1.42 ; Low EPT: 3.46 ± 1.39).

The score of the section of the tune used in the current study is presented in Fig. 1. The part higher in pitch (upper line in the score) and the part lower in pitch (lower line) were separated by two octaves (i.e. the

fundamental frequency of the high pitch tones was four times greater than the fundamental frequency of the low pitch tones). The tone and register for the initial notes were C5 (higher pitch part) and C3 (lower pitch part). Musical Instrument Digital Interface (MIDI) files were created for each note in the score (using the software Max/MSP, with piano as the musical instrument). Each note had equal duration (500 msec) and loudness (which was controlled by applying a constant MIDI velocity of 120).

The outputs from the two E-Music Boxes were fed into a high-performance Dell computer (Dell OptiPlex 960, with dual 3.0 GHz Xenon processors). The computer was programmed to play an eighth note (quaver; i.e. half a beat) following a 45° rotation of the E-Music Box handle. A quarter note (crotchet; i.e. one beat) or a half note (minim; i.e. two beats) were played following 90° or 180° rotations. Hence, as long as the E-Music Box was rotated at constant velocity, the produced music would have the correct rhythmic structure.

Procedure. Participants in the high EPT group and the low EPT group were invited to the lab in pairs and each individual was placed in one of two separate soundproofed rooms. Each room was equipped with a computer monitor (providing instructions to the participants), an E-Music Box and a pair of headphones (providing auditory feedback of their own and their partner's performance). Participants were randomly assigned to play either the low-pitch or the high-pitch musical part.

A trial was structured as follows: First, a fixation cross was presented on the monitor (500 ms). This was followed by a curved arrow (3 s) indicating whether the E-Music Box was supposed to be played through clockwise or anticlockwise rotation of the handle. Subsequently, a metronome was presented (four beats, 750 ms intervals) while a symbol depicting an ear appeared (accompanied by the text "listen"). This was intended to provide a temporal cue helping the participants to establish the correct tempo and to start in synchrony. When the metronome ceased, a "GO" sign appeared on the monitor, at which point participants were instructed to begin producing music through the E-Music Boxes (using the right hand) and synchronizing their music with the music played by the partner. To familiarize participants with the procedure, each pair performed a few training trials before starting the experiment until they felt clear about the task.

All pairs performed 64 trials, which were grouped into 8 blocks of 8 trials. Participants rotated the E-Music Box turntable in the same or in the opposite directions with equal probability. The assignment of directions was counterbalanced across participants. Leadership instructions were provided at the outset of each block, and remained unchanged for the whole block. These instructions were provided by presenting text on the monitor stating either: "you lead" and "you follow" (4 blocks, with alternated instructions across participants) or "No Leadership" (4 blocks, with the same instruction for both participants). The order of the blocks and the trials within each block was randomized.

Note that repeating the same leadership instruction throughout a given block was meant to induce a stronger and clearer spontaneous lead-lag relationship. This could also be achieved by forming asymmetric pairs from the beginning of the experiment, as done in other studies^{68,69}. Such an approach, however, would have also required additional control measures to determine who (within a pair) should be selected to be the leader or the follower. Thus, for the sake of simplicity, we did not opt for such an alternative approach.

Data analysis. *Interpersonal synchrony.* Synchronization accuracy was measured in terms of absolute asynchronies, here corresponding to the absolute difference between partners' complementary tone onset times (in ms), averaged within each trial. Trials associated with outlying asynchronies, i.e. deviating >3 SDs from the pair's mean asynchrony across all trials, were excluded from further analyses. These constituted 0.96% of all trials.

We also measured how synchronization accuracy changed throughout the course of the musical piece (Fig. 1). To do so, we extracted movement timing, which was indexed by 57 consecutive time points representing when each participant completed a 45° rotation of the E-music box. Note that this is the angle corresponding to the movement necessary to play an eighth-note (half the musical beat interval), which is the shortest note duration in the target melody. Thus, considering that the to-be-played score comprised 7 full bars plus one single note associated with the 8th bar, the total number of these events was 7 (full bars) \times 8 (number of 45° rotations associated with performance of one bar) + 1 (the single note associated with the 8th bar) = 57. The absolute difference between partners' complementary time points provided an index of moment-by-moment synchronization throughout the musical piece.

Individual tempo stability. We computed the variability of each individual's performance tempo in each condition. It was assumed that, in the condition where leadership was assigned, leaders would be relatively more stable in their tempo while followers would be more variable due to adaptation (via temporal error correction) to the leader's timing^{29,70}. Tempo variability was computed separately for each participant by (1) extracting information about movement timing for consecutive 45° rotations of each participant's E-music box (see above), (2) first-order differencing successive time points to yield series of 45° rotation time intervals, and (3) calculating the coefficient of variation (CV) for each participant's performance in each trial by dividing the standard deviation of 45° rotation time intervals by the mean 45° rotation time intervals. When this index was associated with a trial during which no leader was assigned, the average between the two players' CVs was taken.

As with the interpersonal synchrony measure, we also examined how individual tempo stability changed throughout the course of the musical piece. To do so, we conducted a windowed analysis for which the coefficient of variation was computed within a moving window comprising 8 consecutive events (equivalent to 4 beats, or 1 bar) and moving in steps of 1 event. Thus, this analysis yielded timeseries of 50 windowed CVs, with the first windowed CV centered in between the 4th and 5th 45° rotation intervals, and the final centered in between the 52nd and 53rd interval.

Temporal leader-follower relation. To test the hypothesis that empathic followers are better able to predict leaders' performance timing, we computed a continuous index of temporal leader-follower relation in the conditions where one participant was instructed to serve as the leader. This was done by extracting high-resolution phase information indexing continuous movement, i.e. the position of the E-music box handle over time (one sample every 10 ms, i.e. 100 Hz, with phase angles flipped for anticlockwise rotations, so that they were comparable to clockwise rotations). Next, continuous relative phase was computed by subtracting the unwrapped continuous phase of the follower from the unwrapped continuous phase of the leader within each trial⁵⁹. Negative relative phase values indicate that leaders were leading the follower's movements. Values closer to zero suggest that followers' prediction of leaders' performance timing was more accurate. (Note that computing relative phase using the unwrapped phase signals is important in order to guard against effects of phase wrapping, which can produce artificially high measures of synchrony, for example when the performances of two players are separated by a lag of a full cycle. Thus, this measure does not range between 0° and 180°, but between 0° and 360° (one full cycle) * the number of cycles necessary to perform the whole piece).

Note density. In order to assist in interpreting results with respect to factors such as information availability, we computed a descriptive index of note density associated with the musical piece used here. As displayed in Fig. 1, the number of musical notes was not uniform throughout the musical piece. For instance, some bars like the $2^{\rm nd}$, the $6^{\rm th}$ and the $7^{\rm th}$ conveyed a larger number of musical events (a mixture of eight and fourth notes) compared to others such as the $1^{\rm st}$, the $3^{\rm rd}$ and the $5^{\rm th}$ (where only two half notes were presented), or the $4^{\rm th}$ and the $8^{\rm th}$ (where only one full note was presented).

This information is important to consider because it provides an estimate of the amount of information that the two players could exchange during a given interval of the musical piece. This will be used to interpret the timecourses of the statistics illustrated above. To compute note density, we created a 57-elements array – representing all possible note positions available within the duration of our musical piece – and filled it in with either zeros (if no event was associated with a given position) or ones (if one event was present). Next, we computed the sum of these events using a moving window comprising 8 consecutive events and moving in steps of 1 event.

Statistics. Interpersonal synchronization accuracy was averaged across trials, separately for each condition and pair. In the main analysis, these averages were submitted to a single 2×2 mixed design analysis of variance (ANOVA). This ANOVA included a between-subjects factor EMPATHY (low EPT and high EPT) and one within-subjects factor LEADERSHIP (with and without). In a second analysis, we conducted a series of such ANOVAs, one for each of the 57 consecutive time points indexing when each participant completed a 45° rotation of the E-music box. This analysis was intended to reveal the timecourse of the effects yielded by the main analysis, as a function of the musical piece. Because this second analysis involved multiple statistical tests, it was necessary to correct for false positives. This was done using a cluster-based permutation test broadly used for timeseries analyses in neurophysiology⁷¹. The test entailed the following steps. First, neighboring significant time points (p < 0.05) were clustered together, and their cluster significance was computed by summing the F values of all points belonging to each cluster. Next, to assess the significance of each cluster, we permuted the original data by shuffling pairs' averages, i.e. randomly assigning pairs' data to (1) either high or low EPT groups and, within pairs, to (2) leadership conditions. After each permutation (n = 1000 iterations), the clusters with largest significance values were saved. These values were then used to generate a random significance distribution (1000 values). This random distribution was used to define a threshold (p = 0.05) against which the clusters obtained from the original data were compared.

Individual tempo stability (variability of performance tempo indexed by CV of 45° rotations) data were analyzed in a mixed design ANOVA with the between-subjects factor EMPATHY (low EPT and high EPT) and within-subjects factor LEADERSHIP (leader, follower, no leader). Data were averaged across the two individuals within a pair for each level of the LEADRERSHIP factor. As for the previous measure, a series of ANOVAs were also conducted separately for each of the 50 consecutive CVs in order to reveal the timecourse of the effects yielded by the main analysis. The cluster-based permutation test described above was used again to identify significant clusters while correcting for multiple comparisons.

The temporal leader-follower relation index in the leadership assigned condition was averaged and compared between the high EPT group and the low EPT group using a two-sample t-test. Before entering the averages into the statistical test, we normalized these values by subtracting the averaged leader-follower relation index computed for the condition where no leadership was assigned.

Finally, in order to explore the relationship between the timecourse of the effects yielded by the ANOVAs and the structure of the musical piece, we correlated the timecourse of the F values resulting from the ANOVAs conducted for each timepoint with windowed note density. These Pearson's correlations were conducted after transforming the F-values and note density timeseries into z-scores.

Results

Interpersonal synchronization accuracy. The ANOVA on mean absolute asynchrony data yielded a statistically significant main effect of EMPATHY, F(1, 24) = 6.76, p = 0.02. This indicated that the high EPT group yielded overall smaller asynchronies (mean \pm SD; 397 \pm 162 ms) compared to the low EPT group (630 \pm 276 ms) (Fig. 2a). Thus, pairs composed of relatively more empathic individuals were more accurate in the interpersonal synchronization task. Both the main effect of LEADERSHIP, F(1, 24) = 1.13, p = 0.30, and the interaction between EMPATHY and LEADERSHIP were not significant, F(1, 24) = 1.02, p = 0.33. (An anonymous reviewer questioned the reliability of median-splitting the data because, in some circumstances, this can lead to artificial subgroups with no practical meaning. To address this issue, we also performed a Pearson correlation analysis between mean absolute asynchrony data from each pair and their EPT scores. The results of this analysis were in

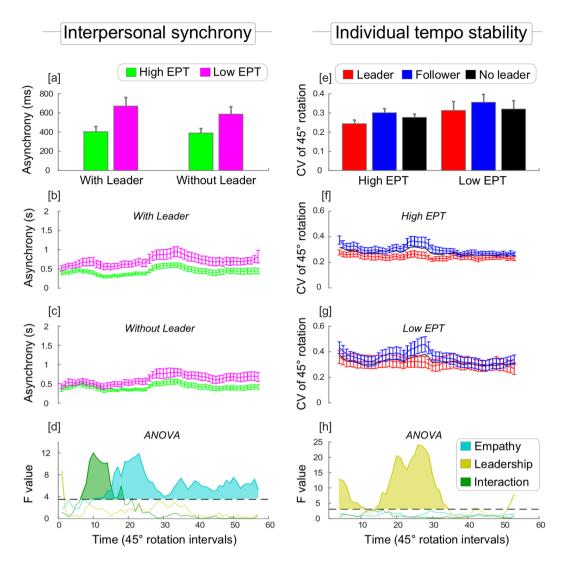


Figure 2. Interpersonal synchrony and individual tempo stability. Left (**a**–**d**): Interpersonal synchronization accuracy expressed in terms of asynchronies (i.e. the smaller the value, the higher the synchronization accuracy). Right (**e**–**h**): Individual tempo stability expressed in terms of the coefficient of variation of participants' movements (i.e. the smaller the value, the more stable and predictable the performed tempo). The top row (**a**,**e**) displays measures averaged across all time points (each indexing 45° rotations of the E-music box). The second and the third rows display measures for each time point. The fourth row display series of F-statistic values obtained after running an ANOVA for each time point (the dashed line indexes significance threshold of each single test, while the shadowed areas indicate significance following correction for multiple comparison using the cluster-based permutation test). The results from the ANOVAs conducted on the averaged measures (displayed in the top row) are reported in the results section. Bars represent 1 standard error of the mean.

line with our conclusions: relatively lower asynchronies (i.e. higher synchronization accuracy) were associated with higher EPT scores (r(24) = -0.43; p = 0.02)).

We next explored how these effects emerged as a function of timepoint during the musical piece. This analysis confirmed that high EPT pairs were generally more accurate than low EPT pairs (Fig. 2d; cluster-corrected significance: p = 0.01). Crucially, however, this analysis also indicated that when a leader was assigned, empathic pairs were relatively faster in establishing synchronization. As displayed in Fig. 2b,c, the enhanced accuracy associated to high EPT pairs had earlier onset when a leader was assigned. This was confirmed by a significant interaction between EMPATHY and LEADERSHIP, which was strongest for the timepoints associated with the second bar of the musical piece (Fig. 2d; cluster-corrected significance: p = 0.04). We noted that this bar corresponded to the first run of relatively short note durations, hence higher note density, suggesting that interactive benefits of empathy and leadership emerged when information about the partner's timing started coming in at a relatively high rate. To confirm this suggestion, we ran a correlation between the timeseries of F values associated with the interaction between EMPATHY and LEADERSHIP (green line in Figs 2d and 3) and note density (Fig. 3). This analysis yielded evidence for a positive significant correlation r(48) = 0.27, p < 0.05.

Relationship of musical note density to interpersonal synchrony and tempo stability

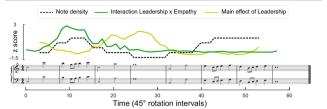


Figure 3. Relationship of musical note density to interpersonal synchrony and tempo stability. Estimated note density (dashed line) is plotted as a function of the musical score, with higher values representing higher density of notes within windows comprising 4 beats. The interaction between EMPATHY and LEADERSHIP associated with interpersonal synchrony (green line, Fig. 2) was stronger when note density was higher. However, the main effect of LEADERSHIP associated with individual tempo stability (yellow line, Fig. 2) was stronger when note density was lower. Statistics are reported in the results section. All timeseries were transformed into z-scores.

In sum, high EPT pairs were more accurate in synchronizing than low EPT pairs. Furthermore, when a leader was assigned, the beneficial effect of empathy emerged earlier, presumably as soon as enough information about the partner's timing was available.

Individual tempo stability. Data for the variability of performance tempo (CV of 45° rotations) with and without leadership assignment are displayed in Fig. 2e. The ANOVA on these data revealed a statistically significant main effect of LEADERSHIP, F(2,48)=11.98, p<0.001, indicating that variability of performance tempo was lower in leaders (0.283 \pm 0.126) than followers (0.329 \pm 0.118) when leadership was assigned, and intermediate when leadership was not assigned (0.304 \pm 0.118). This result indicates that participants, when instructed to act as leaders, maintained more constant timing throughout the task ^{62,64,72}.

Although there is a numerical tendency for lower tempo variability in the high EPT (0.274 \pm 0.065) than the low EPT individuals (0.329 \pm 0.152), the main effect of EMPATHY was not significant, F(1, 24) = 1.32, p = 0.27. Likewise, while the effect of LEADERSHIP is numerically larger for the high EPT group than the low EPT group, the EMPATHY \times LEADERSHIP interaction was not significant, F(2, 48) = 0.99, p = 0.38.

When we explored the timecourse of these effects as a function of the musical piece, it became apparent that the main effect of LEADERSHIP was driven by select sections of the musical piece, namely the 1st, the 3rd and the 4th musical bars (Figs 2f-h and 3). Consistent with this conclusion, the cluster-based permutation test identified two significant clusters. An earlier and relatively small one associated with the 1st musical bar (Fig. 2h; cluster-corrected significance: p < 0.02), and a larger and later one associated with the 3rd and the 4th musical bars (Fig. 2h; cluster-corrected significance: p < 0.001). Looking at the musical score (Fig. 3), these bars contain a relatively low number of notes, and therefore were associated with sections of the musical piece during which less information about the partner's timing was available. To test whether the main effect of LEADERSHIP was indeed stronger when less information about the partner's timing was available, we ran a correlation between the timeseries of F values associated with the main effect of LEADERSHIP (yellow line in Figs 2h and 3) and windowed note density (Fig. 3). This analysis yielded evidence for a significant negative correlation, r(48) = -0.71, p < 0.001.

Thus, when participants were instructed to act as leaders, they maintained more constant timing, presumably in order to increase their predictability and help followers to synchronize^{62,64,72}. This behavior was most evident during sections of the musical piece during which participants could exchange little information and, most importantly, was not different across high and low EPT groups.

Temporal leader-follower relation. Having established that Leaders generally increased their temporal predictability, irrespective of their empathic score, we hypothesized that Followers might be better able to use this information to predict leaders' movement timing and thus improve interpersonal synchronization. To test this hypothesis, we extracted movement information (i.e. phase, indexing movement of the music box with high temporal resolution) and computed a continuous index of relative phase in the conditions where one participant was instructed to serve as the leader.

The mean relative phase for high EPT and low EPT groups is shown in Fig. 4. As should be expected, relative phase was generally negative, indicating that followers' movements generally lagged behind leaders'59,73. Importantly, a statistically significant difference between relative phase in the high and the low EPT group indicated that this tendency was relatively smaller in the high EPT group, t(12) = -2.37, p = 0.03. Thus, high EPT followers lagged behind leaders to a smaller degree ($-15.78^{\circ} \pm 29.11^{\circ}$) than low EPT followers ($-56.85^{\circ} \pm 62.50^{\circ}$). This result is consistent with the hypothesis that high EPT pairs benefitted from superior predictive skills, which allowed followers to synchronize better with the leaders.

Discussion

Here we compared interpersonal coordination skills across two groups of individuals that were relatively high or low in empathic perspective taking (EPT). We did so in the context of a musical joint action task that required musically untrained pairs of 'non-musician' participants to synchronize the outputs of two E-music boxes, i.e. electromechanical devices that transform rotatory movements into pre-programmed music whose tempo changes as a function of movement rotation speed (Fig. 1)⁵⁹.

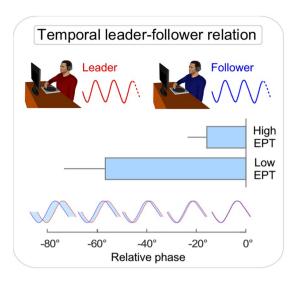


Figure 4. Temporal leader-follower relation. Movement information from both players was codified in terms of phase, indexing the (circular) rotation of the E-music box. Continuous relative phase was computed in order to quantify the extent to which followers' movements lagged behind leaders' movements when leadership roles were assigned. Compared to low EPT followers, high EPT followers lagged behind leaders to a smaller degree. Bars represent 1 standard error of the mean.

We made three primary observations. High EPT individuals were overall (1) more accurate at synchronizing with their partners, as compared to low EPT pairs (Fig. 2a). This result indicated that individuals who possess higher social skills – in this case empathic skills – have higher interpersonal synchronization skills. We also explored leader-follower relations. We observed that (2) when the participants were instructed to act as leaders, they maintained steadier timing throughout the task, and this was irrespective of empathic skills (Fig. 2e). However, (3) high EPT participants instructed to act as followers were better able to pick up such regularities and therefore minimized their temporal lag from leaders, resulting in superior interpersonal coordination (Fig. 4). This result suggested that empathic skills might specifically boost the capacity to predict the timing of others' actions.

A bidirectional relationship between interpersonal coordination and social behavior. A growing number of studies have underlined a relationship between interpersonal coordination and social behavior. In particular, converging evidence suggests that engaging in a collective rhythmic activity entailing interpersonal coordination increases social behavior. Measures of such pro-social effects include affiliation, trust, cooperation, closeness to others, perceived cohesion, and empathy^{13,14,16-23,27}. These studies did not, however, examine the directionality of this relationship, and specifically the possibility that it is bidirectional, i.e. whether it is not only the case that interpersonal synchrony results in pro-social effects, but also that individuals who have stronger social personality traits are generally better at interpersonal coordination tasks. Our study addressed this latter question.

Here we specifically considered one social skill that is broadly regarded as a key ingredient in interpersonal processes: empathy^{74,75}. We specifically considered a sub-scale of this multidimensional construct, i.e. empathic perspective taking^{31,32}. This is the ability of humans to take the perspective of others in everyday life situations. We observed that individuals scoring relatively higher on this scale (high EPT), also own superior interpersonal synchronization skills. This result, taken together with previous research, is consistent with a bidirectional relationship between social skills and interpersonal synchronization. On the one hand, engaging in a coordination task is a sufficient condition to enhance social behavior (as previously shown by others). On the other hand, having a more social personality—high in empathic skills—might generally be linked to being relatively adept at interpersonal coordination.

A mechanism promoting interpersonal coordination in empathic individuals. Our findings point to a strategy and mechanism that are potentially relevant to explaining how empathic individuals achieve superior interpersonal coordination. First, we observed that designated leaders, irrespective of their empathic score, increased the predictability of their actions by making their performance timing more regular (a strategy serving as a "coordination smoother"62,64,72). In other words, leaders attempted to assist followers by increasing the predictability of their performance, similarly so across high and low empathic participants. Remarkably, however, these similar cues were picked up differently by high and low empathic followers, with high EPT followers making better use of this information, and synchronizing more rapidly when their leaders' timing was more predictable. In particular: when high empathic participants acted as followers, their temporal lag with respect to leaders was small (compared to low empathic participants). This suggests that more empathic participants were better at predicting the timing of their partners' actions.

Such a predictive process could be implemented from a psychological and neurophysiological perspective via motor simulation, i.e. the brain's capacity to represent another's actions by means of an internal simulation 49,76-80.

This concept may constitute the neurophysiological instantiation of what is generally referred to as "taking the perspective of another", which is the aspect of empathy we investigated here. In a previous study where we measured a neurophysiological index of motor simulation in participants engaged in a joint musical action task, we provided direct evidence showing that such a simulation process is indeed stronger in more empathic participants⁴³. In a second study, we demonstrated that when motor simulation is temporally impaired by means of "virtual" brain lesions (induced via transcranial magnetic stimulation), participants' ability to coordinate with a co-performer deteriorates, and more so in individuals having higher empathic skills⁴⁵.

This emerging framework linking empathy with predictive motor simulation can potentially unite a number of observations and accounts associated with distinct research areas. In cognitive neuroscience, several studies have underlined the importance of motor simulation processes for both empathy^{41–44,81} and interpersonal coordination tasks^{82–85}. Consistently with these empirical findings, a number of accounts from the fields of psychology and empirical musicology highlight the importance of empathic skills for coordination and collaboration^{86–88}, and how these might emerge through enhanced linkages between perception and action^{80,89,90}. Our work not only links these claims and observations from different fields, but also provides a potential mechanistic explanation of how empathy promotes interpersonal coordination. Specifically, our results indicate that more empathic individuals benefit from enhanced predictive skills when it comes to anticipating others' behavior, and not just an augmented aptitude for cooperation. The notion of "aptitude for cooperation" refers to participants' willingness to cooperate with their partners in order to maximize success in the task, as indexed indirectly by increased individual tempo stability across high and low EPT groups (i.e., a coordination smoother, which was observed in leaders independently of EPT). Our results instead favor an account where predictive skills provide empathic individuals with a behavioral advantage impacting social cognition on a broader scale.

On the relationship between musical interaction and empathy. The relationship between empathy and music is a topic that received considerable recent interest^{91–97}. In this area, several investigations have addressed a specific unidirectional relationship in which musical activities promote empathy. Music students, as compared to non-music students, have been shown to rate higher on empathy scales^{98,99}. Consistently with this, other research has shown that children (without prior musical background) undergoing music programs enhance their empathic skills^{14,100}. Notably, the study by Rabinowitch *et al.* (2013) showed that children engaged in musical group interactions developed higher emotional empathy¹⁴. These results are also supported by other investigations and claims suggesting that musical experience, entailing both sensory and motor musical activities, can promote empathy^{91,101,102}.

None of these studies, however, examined whether individuals with higher empathic scores prior to musical training or related task experience are generally better in the context of a group musical interaction. One reason why this has not been explored could be that such a question is best addressed within musically untrained individuals, especially given that honing musical skills appears to be sufficient to enhance empathy. Here, this limitation was overcome by using the E-music box, a musical instrument that can be played by non-musicians and that can provide rich empirical information concerning the dynamical interaction within a pair⁵⁹.

Our results indicate that more empathic individuals are predisposed to be more accurate at performing music with others, and that this benefit might originate from superior skill at temporal prediction. Taken together with previous findings^{14,91,100,102,103}, this sheds light upon a bidirectional nature of the relationship between musical interaction and empathy. Such directionality suggests that the capacities to (1) coordinate with others and (2) empathize with others rely on a common mechanism whose functioning is modulated by experience in musical interaction as well as personality traits. As argued above, we claim that such a shared mechanism is motor simulation. We propose that empathic perspective taking might help ensemble musicians to coordinate with others by using information about a partner's past action style (systematic timing variations) to predict their future action timing¹⁰⁴. It should also be noted that this kind of benefit might be harder to observe in the context of simple isochronous tapping tasks (which are often employed) where there is little room for idiosyncratic timing (but mainly random variability), and therefore a critical lack of useful information about action style⁸⁰. In music, by contrast, the challenge of producing a variable rhythm (i.e., different note durations) opens up the possibility for $idiosyncratic\ timing\ patterns^{105,106}\ that, if\ someone\ is\ good\ at\ taking\ another's\ perspective,\ are\ predictable.$ The present study hence suggests a plausible role of empathy in nonverbal communication, which can be conveniently—and with potential universal applicability—studied in the music domain, where there is ample room for individual variation.

Coordination prediction and predictability as a function of information availability. A noteworthy advantage of musical paradigms, compared to standard finger tapping tasks, is that participants are engaged in a rich type of interaction, which can be formally described by a musical score¹⁰. Building on this, and on the fact that the density of notes was not uniform throughout the musical piece, we could compute an index that quantified how much information the two players could exchange throughout performance of the musical piece.

When we used this information to interpret our results, we made two noteworthy observations. Firstly, we observed that the interactive benefit of empathy and leadership began as soon as information about the leader's timing started coming in at a relatively high rate (Fig. 3). This observation is reasonable in light of our interpretation of high EPT followers being better at predicting the leader's action timing. However, the finding provides robust support for our interpretation to the extent that it highlights how the effect occurs selectively when participants begin having access to a sufficient amount of information. Thus, the temporal prediction process strongly depends on the amount of information that is available in a given time within the interpersonal coordination task.

Complementary to this first observation, we also observed that leaders' enhanced predictability – presumably intended to help followers to synchronize – was mostly pronounced when information about the partner was less available (i.e. during segments of the musical piece that entailed lower note density, Fig. 3). This suggested

that leaders took responsibility over keeping the correct tempo for the pair, particularly when less information exchange was available. This observation confirms previous studies suggesting that reducing the variability of one's own actions might indeed be a powerful mechanism for achieving interpersonal coordination in the absence of continuous feedback about a co-actor's actions 63,64.

In sum, these observations strengthen the independence of predictive and cooperative behaviors. Specifically, EPT appears to boost sensorimotor processing in a manner that augments the prediction of others' behavior in followers, but not the aptitude for cooperation in leaders.

Conclusion

The present results provide direct evidence for a tight and bidirectional relationship between coordinated behavior and social cognition. Complementing previous research reporting pro-social effects of interpersonal coordination, we tested whether a social personality trait—empathic perspective taking (EPT)—is sufficient to enhance interpersonal coordination accuracy. We found that EPT promotes interpersonal coordination by specifically enhancing prediction accuracy for others' behavior, while leaving the aptitude for cooperation unaffected. We suggest that such predictive capacity relies on a sensorimotor mechanism responsible for simulating others' actions in an anticipatory manner, leading to behavioral advantages that may impact social cognition more generally.

Data Availability

The data are available from the corresponding author upon request.

References

- Greenfield, M. D. Mechanisms and Evolution of Communal Sexual Displays in Arthropods and Anurans. Adv. Study Behav. 35, 1–62 (2005).
- 2. Merker, B. Synchronous Chorusing and Human Origins. The Origins of Music, https://doi.org/10.1177/10298649000030S105 (2000).
- 3. Merker, B. H., Morley, I. & Zuidema, W. Five fundamental constraints on theories of the origins of music. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 370, 20140095 (2015).
- 4. Ravignani, A., Bowling, D. & Fitch, W. T. Chorusing, synchrony and the evolutionary functions of rhythm. Front. Psychol. 5, 1–15 (2014).
- Coey, C. A., Varlet, M. & Richardson, M. J. Coordination dynamics in a socially situated nervous system. Front. Hum. Neurosci. 6, 164 (2012).
- Keller, P. E., Novembre, G. & Hove, M. J. Rhythm in joint action: psychological and neurophysiological mechanisms for real-time interpersonal coordination. *Philos. Trans. R. Soc. B Biol. Sci.* 369, 20130394–20130394 (2014).
- Marsh, K. L., Richardson, M. J. & Schmidt, R. C. Social Connection Through Joint Action and Interpersonal Coordination. Top. Cogn. Sci. 1, 320–339 (2009).
- 8. Sebanz, N., Bekkering, H. & Knoblich, G. Joint action: bodies and minds moving together. Trends Cogn. Sci. 10, 70-6 (2006).
- 9. Néda, Z., Ravasz, E., Brechet, Y., Vicsek, T. & Barabási, A. L. The sound of many hands clapping. Nature 403, 849-50 (2000).
- D'Ausilio, A., Novembre, G., Fadiga, L. & Keller, P. E. What can music tell us about social interaction? Trends Cogn. Sci. 19, 111–114 (2015).
- 11. McNeill, W. H. Keeping together in time., (Harvard University Press, 1995).
- 12. Mogan, R., Fischer, R. & Bulbulia, J. A. To be in synchrony or not? A meta-analysis of synchrony's effects on behavior, perception, cognition and affect. J. Exp. Soc. Psychol. 72, 13–20 (2017).
- 13. Rabinowitch, T. C. & Knafo-Noam, A. Synchronous rhythmic interaction enhances children's perceived similarity and Closeness towards each other. *PLoS One* **10**, 1–10 (2015).
- 14. Rabinowitch, T.-C., Cross, I. & Burnard, P. Long-term musical group interaction has a positive influence on empathy in children. *Psychol. Music* 41, 484–498 (2013).
- 15. Rabinowitch, T. C. & Meltzoff, A. N. Joint rhythmic movement increases 4-year-old children's prosocial sharing and fairness toward peers. *Front. Psychol.* **8**, 1–9 (2017).
- 16. Launay, J., Dean, R. T. & Bailes, F. Synchronization Can Influence Trust Following Virtual Interaction. Exp. Psychol. 60, 53–63 (2013)
- Kirschner, S. & Tomasello, M. Joint music making promotes prosocial behavior in 4-year-old children. Evol. Hum. Behav. 31, 354-364 (2010).
- 18. Hove, M. J. & Risen, J. L. It's All in the Timing: Interpersonal Synchrony Increases Affiliation. Soc. Cogn. 27, 949-960 (2009).
- Cirelli, L. K., Einarson, K. M. & Trainor, L. J. Interpersonal synchrony increases prosocial behavior in infants. Dev. Sci. 17, 1003–1011 (2014).
- 20. Wiltermuth, S. S. & Heath, C. Synchrony and cooperation. *Psychol. Sci.* **20**, 1–5 (2009).
- 21. Koehne, S., Hatri, A., Cacioppo, J. T. & Dziobek, I. Perceived interpersonal synchrony increases empathy: Insights from autism spectrum disorder. *Cognition* **146**, 8–15 (2016).
- Valdesolo, P., Ouyang, J. & DeSteno, D. The rhythm of joint action: Synchrony promotes cooperative ability. J. Exp. Soc. Psychol. 46, 693–695 (2010).
- 23. Anshel, A. & Kipper, D. A. The influence of group singing on trust and cooperation. J. Music Ther. 25, 145-155 (1988).
- Launay, J., Dean, R. T. & Bailes, F. Synchronising movements with the sounds of a virtual partner enhances partner likeability. Cogn. Process. 15, 491–501 (2014).
- 25. Cirelli, L. K. How interpersonal synchrony facilitates early prosocial behavior. Curr. Opin. Psychol. 20, 35-39 (2018).
- 26. Stupacher, J., Maes, P. J., Witte, M. & Wood, G. Music strengthens prosocial effects of interpersonal synchronization If you move in time with the beat. *J. Exp. Soc. Psychol.* **72**, 39–44 (2017).
- Fessler, D. M. T. & Holbrook, C. Synchronized behavior increases assessments of the formidability and cohesion of coalitions. Evol. Hum. Behav. 37, 502–509 (2016).
- 28. Varlet, M. et al. Difficulty leading interpersonal coordination: towards an embodied signature of social anxiety disorder. Front. Behav. Neurosci. 8, 29 (2014).
- Fairhurst, M. T., Janata, P. & Keller, P. E. Leading the follower: an fMRI investigation of dynamic cooperativity and leader-follower strategies in synchronization with an adaptive virtual partner. Neuroimage 84, 688–97 (2014).
- 30. Preston, S. & de Waal, F. Empathy: Its ultimate and proximate bases. Behav. Brain Sci. 25, 1-20, discussion 20-71 (2001).
- 31. Davis, M. H. Measuring individual differences in empathy: Evidence for a multidimensional approach. *J. Pers. Soc. Psychol.* 44, 113–126 (1983).
- 32. Davis, M. H. A multidimensional approach to individual differences in empathy. JSAS Cat. Sel. Doc. Psychol. 10, 85 (1980).
- 33. Frith, C. D. & Frith, U. The Neural Basis of Mentalizing. Neuron 50, 531-534 (2006).

- 34. de Vignemont, F. & Singer, T. The empathic brain; how, when and why? Trends Cogn. Sci. 10, 435-441 (2006).
- 35. Decety, J. & Lamm, C. Human empathy through the lens of social neuroscience. Scientific World Journal. 6, 1146-1163 (2006).
- 36. Tusche, A., Bockler, A., Kanske, P., Trautwein, F.-M. & Singer, T. Decoding the Charitable Brain: Empathy, Perspective Taking, and Attention Shifts Differentially Predict Altruistic Giving. *J. Neurosci.* 36, 4719–4732 (2016).
- 37. Keller, P. E. Ensemble performance: Interpersonal alignment of musical expression. *In Expressiveness in music performance: Empirical approaches across styles and cultures* 260–282 (2014).
- 38. Keller, P. E. Joint Action in Music Performance. In Enacting intersubjectivity: A cognitive and social perspective on the study of interactions (eds Morganti, F., Carassa, A. & Riva, G.) 205–221 (IOS Press, 2008).
- 39. Sebanz, N. & Knoblich, G. Prediction in Joint Action: What, When, and Where. Top. Cogn. Sci. 1, 353-367 (2009).
- Konvalinka, I., Vuust, P., Roepstorff, A. & Frith, C. D. Follow you, follow me: continuous mutual prediction and adaptation in joint tapping. Q. J. Exp. Psychol. (Hove). 63, 2220–30 (2010).
- 41. Gallese, V. The 'shared manifold' hypothesis. From mirror neurons to empathy. J. Conscious. Stud. 8, 33-50 (2001).
- Gallese, V. The roots of empathy: The shared manifold hypothesis and the neural basis of intersubjectivity. Psychopathology 36, 171–180 (2003).
- Novembre, G., Ticini, L. F., Schütz-Bosbach, S. & Keller, P. E. Distinguishing self and other in joint action. Evidence from a musical paradigm. Cereb. Cortex 22, 2894–903 (2012).
- Gazzola, V., Aziz-Zadeh, L. & Keysers, C. Empathy and the somatotopic auditory mirror system in humans. Curr. Biol. 16, 1824–9 (2006).
- 45. Novembre, G., Ticini, L. F., Schutz-Bosbach, S. & Keller, P. E. Motor simulation and the coordination of self and other in real-time joint action. Soc. Cogn. Affect. Neurosci. 9, 1062–1068 (2014).
- Aglioti, S. M., Cesari, P., Romani, M. & Urgesi, C. Action anticipation and motor resonance in elite basketball players. Nat. Neurosci. 11, 1109–1116 (2008).
- Pecenka, N., Engel, A. & Keller, P. Neural correlates of auditory temporal predictions during sensorimotor synchronization. Front. Hum. Neurosci. 7, 1–16 (2013).
- Knoblich, G., Seigerschmidt, E., Flach, R. & Prinz, W. Authorship effects in the prediction of handwriting strokes: Evidence for action simulation during action perception. Q. J. Exp. Psychol. 55A, 1027–1046 (2002).
- 49. Keller, P. E., Knoblich, G. & Repp, B. H. Pianists duet better when they play with themselves: on the possible role of action simulation in synchronization. *Conscious. Cogn.* 16, 102–11 (2007).
- Mulligan, D., Lohse, K. R. & Hodges, N. J. An action-incongruent secondary task modulates prediction accuracy in experienced performers: evidence for motor simulation. *Psychol. Res.* 80, 496–509 (2016).
- 51. Kilner, J. M., Friston, K. J. & Frith, C. D. The mirror-neuron system: a Bayesian perspective. Neuroreport 18, 619-23 (2007).
- 52. Wolpert, D. M., Doya, K. & Kawato, M. A unifying computational framework for motor control and social interaction. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **358**, 593–602 (2003).
- 53. Merker, B. H., Madison, G. S. & Eckerdal, P. On the role and origin of isochrony in human rhythmic entrainment. *Cortex* 45, 4–17 (2009).
- 54. Trehub, S. E., Becker, J. & Morley, I. Cross-cultural perspectives on music and musicality. *Philos. Trans. R. Soc. B Biol. Sci.* 370, 20140096–20140096 (2015).
- 55. Glowinski, D., Badino, L., Ausilio, A., Camurri, A., & Fadiga, L. Analysis of leadership in a string quartet. In *Third International Workshop on Social Behaviour in Music at ACM ICMI* 763–774 (2012).
- 56. Volpe, G., D'Ausilio, A., Badino, L., Camurri, A. & Fadiga, L. Measuring social interaction in music ensembles. *Philos. Trans. R. Soc. B Biol. Sci.* 371, (2016).
- 57. Badino, L., D'Ausilio, A., Glowinski, D., Camurri, A. & Fadiga, L. Sensorimotor communication in professional quartets. Neuropsychologia 55, 98–104 (2014).
- 58. Keller, P. E., König, R. & Novembre, G. Simultaneous cooperation and competition in the evolution of musical behavior: Sex-Related modulations of the singer's formant in human chorusing. Front. Psychol. 8, 1–14 (2017).
- 59. Novembre, G., Varlet, M., Muawiyath, S., Stevens, C. J. & Keller, P. E. 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 (2015).
- 60. Gebauer, L. et al. Oxytocin improves synchronisation in leader-follower interaction. Sci. Rep. 6, 1-13 (2016).
- Kawase, S. Assignment of leadership role changes performers' gaze during piano duo performances. Ecol. Psychol. 26, 198–215 (2014).
- 62. Goebl, W. & Palmer, C. Synchronization of timing and motion among performing musicians. Music Percept. 26, 427-438 (2009).
- 63. Vesper, C., van der Wel, R. P. R. D., Knoblich, G. & Sebanz, N. Making oneself predictable: reduced temporal variability facilitates joint action coordination. *Exp. brain Res.* **211**, 517–30 (2011).
- 64. Vesper, C., Butterfill, S., Knoblich, G. & Sebanz, N. A minimal architecture for joint action. Neural Netw. 23, 998-1003 (2010).
- Ollen, J. A criterion-related validity test of selected indicators of musical sophistication using expert ratings. Doctoral Diss. Ohio State Univ. (2006).
- Gaggioli, A. et al. Effects of interpersonal sensorimotor synchronization on dyadic creativity: Gender matters. Front. Psychol. 9, 1–12 (2019).
- 67. Hoffman, M. L. Sex differences in empathy and related behaviors. *Psychol. Bull.*, https://doi.org/10.1037/0033-2909.84.4.712 (1977).
- 68. Sänger, J., Müller, V. & Lindenberger, U. Directionality in hyperbrain networks discriminates between leaders and followers in guitar duets. Front. Hum. Neurosci. 7, 1–14 (2013).
- D'Ausilio, A. et al. Leadership in orchestra emerges from the causal relationships of movement kinematics. PLoS One 7, e35757 (2012).
- 70. Novembre, G., Sammler, D. & Keller, P. E. Neural alpha oscillations index the balance between self-other integration and segregation in real-time joint action. *Neuropsychologia* 89, 414–425 (2016).
- 71. Maris, E. & Oostenveld, R. Nonparametric statistical testing of EEG- and MEG-data. J. Neurosci. Methods 164, 177–90 (2007).
- 72. Glowinski, D. *et al.* The movements made by performers in a skilled quartet: a distinctive pattern, and the function that it serves. *Front. Psychol.* **4**, 841 (2013).
- 73. Keller, P. E. & Appel, M. Individual Differences, Auditory Imagery, and the Coordination of Body Movements and Sounds in Musical Ensembles. *Music Perception* **28**, 27–46 (2010).
- Main, A., Walle, E. A., Kho, C. & Halpern, J. The Interpersonal Functions of Empathy: A Relational Perspective. Emot. Rev. 175407391666944, https://doi.org/10.1177/1754073916669440 (2017).
- 75. Keysers, C. & Gazzola, V. Chapter 21 Towards a unifying neural theory of social cognition. Prog. Brain Res. 156, 379-401 (2006).
- 76. Hurley, S. The shared circuits model (SCM): How control, mirroring, and simulation can enable imitation, deliberation, and mindreading. *Behav. Brain Sci.* 31, 1–22 (2008).
- 77. Gallese, V. & Sinigaglia, C. What is so special about embodied simulation? Trends Cogn. Sci. 15, 512–519 (2011).
- 78. Grush, R. The emulation theory of representation: motor control, imagery, and perception. *Behav. Brain Sci.* 27, 377–96, discussion 396–442 (2004).
- 79. Hove, M. J. Shared circuits, shared time, and interpersonal synchrony. Behav. Brain Sci. 31, 29-30 (2008).

- 80. Novembre, G. & Keller, P. E. A conceptual review on action-perception coupling in the musicians' brain: what is it good for? *Front. Hum. Neurosci.* 8, 1–11 (2014).
- 81. Pecenka, N. & Keller, P. E. The role of temporal prediction abilities in interpersonal sensorimotor synchronization. *Exp. Brain Res.* 211, 505–15 (2011).
- 82. Cacioppo, S. et al. You are in sync with me: Neural correlates of interpersonal synchrony with a partner. Neuroscience 277, 842–858 (2014).
- 83. Fairhurst, M. T., Janata, P. & Keller, P. E. Being and feeling in sync with an adaptive virtual partner: brain mechanisms underlying dynamic cooperativity. *Cereb. Cortex* 23, 2592–600 (2013).
- 84. Hadley, L. V., Novembre, G., Keller, P. E. & Pickering, M. J. Causal Role of Motor Simulation in Turn-Taking Behavior. *J. Neurosci.* 35, 16516–16520 (2015).
- 85. Vanzella, P. et al. fNIRS Responses in Professional Violinists While Playing Duets: Evidence for Distinct Leader and Follower Roles at the Brain Level. Front. Psychol. 10, 164 (2019).
- 86. Baimel, A., Severson, R. L., Baron, A. S. & Birch, S. A. J. Enhancing "theory of mind" through behavioral synchrony. Front. Psychol. 6, 1–6 (2015).
- 87. Haddon, E. & Hutchinson, M. Empathy in piano duet rehearsal and performance. Empir. Musicol. Rev. 10, 140-153 (2015).
- 88. Yokozuka, T., Ono, E., Inoue, Y., Ogawa, K. I. & Miyake, Y. The relationship between head motion synchronization and empathy in unidirectional face-to-face communication. *Front. Psychol.* **9**, 1–10 (2018).
- 89. Vuoskoski, J. K. Music, Empathy, and Affiliation: Commentary on Greenberg, Rentfrow, and Baron-Cohen. *Empir. Musicol. Rev.* 10, 99–102 (2015).
- 90. Wöllner, C. Is empathy related to the perception of emotional expression in music? A multimodal time-series analysis. *Psychol. Aesthetics, Creat. Arts* 6, 214–223 (2012).
- 91. Clarke, E., DeNora, T. & Vuoskoski, J. Music, empathy and cultural understanding. Phys. Life Rev. 15, 61-88 (2015).
- Miu, A. C. & Baltes, F. R. Empathy manipulation impacts music-induced emotions: A psychophysiological study on opera. PLoS One 7 (2012).
- 93. Kawase, S. Associations among music majors' personality traits, empathy, and aptitude for ensemble performance. *Psychol. Music* 44, 293–302 (2016).
- 94. Eerola, T., Vuoskoski, J. K. & Kautiainen, H. Being moved by unfamiliar sad music is associated with high empathy. Front. Psychol. 7, 1–12 (2016).
- 95. Egermann, H. & McAdams, S. Empathy and Emotional Contagion as a Link Between Recognized and Felt Emotions in Music Listening. Music Percept. *An Interdiscip. J.* **31**, 139–156 (2013).
- 96. King, E. & Waddington, C. Music and empathy., (Routledge), https://doi.org/10.4324/9781315596587 (2017).
- Walton, A. E., Washburn, A., Richardson, M. J. & Chemero, A. Empathy and groove in musical movement. In Proceedings of A Body of Knowledge - Embodied Cognition and the Arts conference (2018).
- 98. Hietolahti-ansten, M. & Kalliopuska, M. Self-Esteem and Empathy among children actively involved in music. *Percept. Mot. Learn.* 72, 1364–1366 (1991).
- 99. Kalliopuska, M. Empathy Among Children in Music Class. Percept. Mot. Skills 72, 382-382 (1991).
- Kalliopuska, M. & Ruokonen, I. A study with a follow-up of the effects of music education on holistic development of empathy. Percept. Mot. Skills 76, 131–7 (1993).
- 101. Greenberg, D. M., Rentfrow, P. J. & Baron-Cohen, S. Can Music Increase Empathy? Interpreting Musical Experience Through the Empathizing-Systemizing (E-S) Theory: Implications for Autism. *Empir. Musicol. Rev.* 10, 80–95 (2015).
- 102. Laird, L. Empathy in the Classroom. Music Educ. J. 101, 56-61 (2015).
- 103. Greenberg, D. M., Rentfrow, P. J. & Baron-cohen, S. Can Music Increase Empathy? Interpreting Musical Experience Through The Empathizing – Systemizing (E-S) Theory: Implications For Autism. Empir. Musicol. Rev. 10, 79–94 (2015).
- 104. Novembre, G., Knoblich, G., Dunne, L. & Keller, P. E. Interpersonal synchrony enhanced through 20 Hz phase-coupled dual brain stimulation. Soc. Cogn. Affect. Neurosci. 12, 662–670 (2017).
- 105. Colley, I. D., Keller, P. E. & Halpern, A. R. Working Memory and Auditory Imagery Predict Sensorimotor Synchronization with Expressively Timed Music. Q. J. Exp. Psychol. 0, 1–49 (2017).
- 106. Repp, B. H. & Keller, P. E. Self versus other in piano performance: detectability of timing perturbations depends on personal playing style. *Exp. Brain Res.* **202**, 101–10 (2010).

Acknowledgements

P.K. is supported by a Future Fellowship grant from the Australian Research Council (FT140101162).

Author Contributions

All authors conceptualized the study and the experimental design. Z.M. collected the data under the supervision of G.N. All authors analyzed the data. G.N. drafted the manuscript and prepared all figures. All authors edited and approved the final version of the manuscript.

Additional Information

Competing Interests: The authors declare no competing interests.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit https://creativecommons.org/licenses/by/4.0/.

© The Author(s) 2019