

Distinguishing Self and Other in Joint Action. Evidence from a Musical Paradigm

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The capacity to distinguish between one’s own and others’ behavior is a cognitive prerequisite for successful joint action. We employed a musical joint action task to investigate how the brain achieves this distinction. Pianists performed the right-hand part of piano pieces, previously learned bimanually, while the complementary left-hand part either was not executed or was (believed to be) played by a co-performer. This experimental setting served to induce a co-representation of the left-hand part reflecting either the self or the co-performer. Single-pulse transcranial magnetic stimulation was applied to the right primary motor cortex and motor-evoked potentials (MEPs) were recorded from the resting left forearm. Results show that corticospinal excitability was modulated by whether the representation of the left hand was associated with the self or the other, with the MEP amplitude being low and high, respectively. This result remained unchanged in a separate session where participants could neither see nor hear the other but still infer his presence by means of contextual information. Furthermore, the amplitude of MEPs associated with co-performer presence increased with pianists’ self-reported empathy. Thus, the sociality of the context modulates action attribution at the level of the motor control system.

Keywords: agency, corticospinal excitability, joint action, music, social context

Introduction

Humans are a social species by nature. The ability to coordinate with others when performing joint actions, such as carrying a bulky object or playing a piano duet, is an integral part of everyday life (Sebanz, Bekkering, et al. 2006) and requires special forms of cognitive representations (Tomasello et al. 2005). The expanding field of cognitive neuroscience has recently identified joint action as a new research challenge and started to investigate the neurocognitive principles underlying coherently coordinated social actions in humans (for a review, see Bekkering et al. 2009).

Numerous studies have shown that, in the perceiver’s brain, one’s own and others’ actions may be co-represented using the same neural resources (Rizzolatti and Sinigaglia 2010; Knoblich et al. 2011). For example, van Schie et al. (2004) have shown that the mere observation of somebody else committing an action error activates the medial frontal cortex as if the error was made by the observer him/herself. Likewise, electrophysiological studies have reported motor activations anticipating others’ actions in the observer’s brain (Kilner et al. 2004; Borroni et al. 2005; Urgesi et al. 2010; Cattaneo et al. 2011). Going a step further, research in joint action has yielded evidence for the integration of a co-actor’s action into one’s

own action planning, even when there is no need to take the other agent into account in order to perform the instructed task (Sebanz et al. 2003, 2005; Sebanz, Knoblich, et al. 2006).

Taken together, these findings suggest that self- and other-related actions are represented within common neural substrates (Prinz 1990). This view is consistent with the “shared representations” hypothesis (Decety and Sommerville 2003; de Vignemont and Haggard 2008). In accordance with this view, it has also been shown that people with stronger tendency to adopt others’ perspective (as defined by psychological tests assessing empathy) rely on these shared representations to a high degree (Gazzola et al. 2006; Kaplan and Iacoboni 2006; Canessa et al. 2009, see also Singer 2006).

The ability to form shared representations may be considered to be a cornerstone of social cognition (Sebanz, Bekkering, et al. 2006). At the same time, however, the notion of shared representations (i.e., representing another’s action in a functionally equivalent way to one’s own) raises the question of how we attribute the action to ourselves or to another agent (action attribution) and, crucially, how we coordinate actions with other individuals.

Let us consider the example of a piano duo. In order to play in synchrony, the pianists must monitor others’ actions and simultaneously integrate them with self-generated actions. How could this be done successfully if monitored and generated actions were functionally equivalent? The equivalence between self and others would result in ambiguity and probably even generate computational problems (Decety and Sommerville 2003; Schütz-Bosbach et al. 2009). From this perspective, a certain degree of agent specificity has to be a prerequisite of successful joint actions. The current research concerns how the brain achieves this.

Recent studies (Schütz-Bosbach et al. 2006, 2009) have found that the observation of identical actions may lead to qualitatively different activations in the motor system depending on whether the action is attributed to the self or to another agent (by means of the rubber-hand illusion; see Botvinick and Cohen 1998). Specifically, inhibition of the activity of the motor system (i.e., corticospinal suppression) was associated with self-representation of actions, whereas other-related actions facilitated motor system activity (i.e., corticospinal facilitation). These findings imply that the motor system may represent other agents as qualitatively different from the self, and as such, it may underpin the distinction (rather than the equality) between self and other that is typically experienced.

In the present study, we aimed at extending the social differentiation hypothesis to a joint action context in which self- and other-related motor representations can be dissociated. To this end, we aimed at showing that when different (but complementary) actions are integrated, thus reflecting

a combination of self- and other-related actions (i.e., joint actions), these representations are agent specific. In doing so, we were particularly concerned with testing whether this distinction is sensitive to the sociality of the context in which one acts and can occur under conditions where an individual merely has the impression (given indirectly by contextual factors) to be interacting with another agent. Thus, the belief of being part of a joint action, and not necessarily direct interpersonal contact, plays a crucial role here.

To address this issue, piano duet playing was chosen as a model task to study complementary actions executed by different agents simultaneously and with precisely coordinated timing. We developed an experimental paradigm that allowed us to dissociate the neural correlates of self- and other-related actions during the execution of a musical joint action task. Amateur pianists were asked to perform the right-hand part of musical pieces—previously learned bimanually—while the left-hand part either was not executed (Self condition) or was ostensibly performed by an experimenter hidden behind a screen (Joint condition) (see Fig. 1, Panel A). The experimenter, however, only feigned playing the piano (i.e., he gently nudged the keyboard in time with the tones of the left-hand part), while the pianists heard a recording. This gave our participants the feeling of acting within a “social context,” while they were in fact part of a “virtual” joint action. As the 2 parts were highly complementary with one other, this experimental setting served to induce a co-representation of the unused hand (Sebanz et al. 2005) in the contralateral motor cortex, reflecting either the self or the co-performer. To

control for the different amount of auditory information between the 2 conditions, we also ran a second session (Mute session), in which the pianists could neither see the experimenter nor hear the other part. In this Mute session, the presence of the experimenter could be inferred by means of the instruction indicating a social, that is, joint action context. For a schematic illustration of the paradigm and the design, see Figure 1.

While participants were performing with their right hand, we delivered single-pulse transcranial magnetic stimulations (TMSs) over the right primary motor cortex and examined changes in corticospinal excitability related to action representation (Fadiga et al. 1995; Strafella and Paus 2000). Motor-evoked potentials (MEPs) were recorded from a left forearm muscle (extensor carpi radialis, ECR), which is constantly activated during piano performance (D’Ausilio et al. 2006). We quantified relative corticospinal excitability across our experimental conditions (Self and Joint) by examining the mean MEP peak-to-peak amplitude. A third (Baseline) condition, consisting of the performance of musical pieces for which the left-hand part was unknown, was also tested in order to control for general effects of movement caused by the right playing hand.

Our analysis of action representation focused on the ECR muscle because a previous study (D’Ausilio et al. 2006) has shown that the MEPs recorded from this muscle are modulated by the motor representation of rehearsed piano pieces. However, in order to extend previous findings (D’Ausilio et al. 2006) in terms of the somatotopic specificity of these motor representations, 2 finger muscles associated with the movement of the index finger (first dorsal interosseus, FDI) and the little finger (abductor digiti minimi, ADM) were simultaneously recorded (see Materials and Methods). If the activation of these muscles reflects a somatotopic specific representation of the rehearsed piano piece, then the corticospinal excitability associated with a given finger should increase at around the time when it would strike a key if the left-hand part were to be performed.

In accordance with previous studies (Schütz-Bosbach et al. 2006, 2009), we expected distinct patterns of corticospinal excitability reflecting self- and other-specific representations in the motor system. Moreover, to the extent that these differential activations reflect a difference in the sociality of the context (playing alone vs. playing with a co-performer), this effect should persist even after removal of auditory information (i.e., in the Mute session). In addition, the relative magnitude of other-related motor representation should generally covary with interindividual differences in empathic aptitude (as provided by self-report empathy measures; Davis 1980) in both of the sessions (i.e., with and without auditory information). Thus, analogously to previous findings (Gazzola et al. 2006; Kaplan and Iacoboni 2006; Canessa et al. 2009), pianists with higher self-reported empathy should show relatively high MEP amplitudes while representing other-related actions.

Materials and Methods

Participants

Fifteen right-handed amateur piano players (mean age = 23.6 years; standard deviation [SD] = 2.79, 4 males) participated in the experiment. A questionnaire assessed the weekly amount of practice (mean = 4.01 h; SD = 4.35), years of piano training (mean = 12.50 years; SD = 4.93), and age at which music studies commenced (mean = 8.13 years; SD = 3.11).

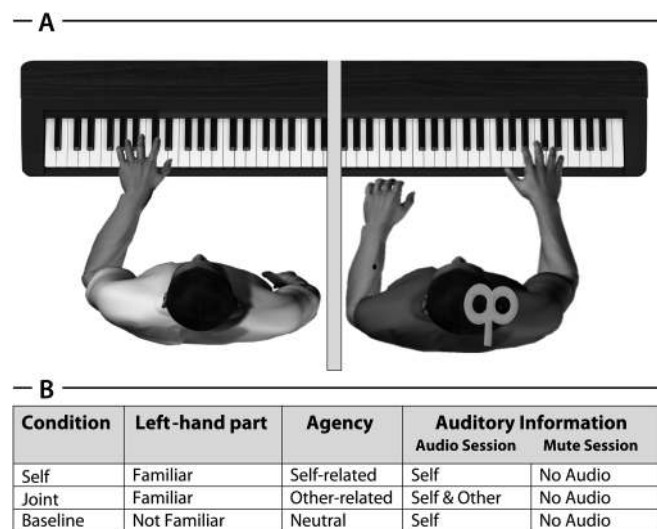


Figure 1. Panel A shows a schematic illustration of the experimental paradigm. The participant (on the right) performed the melody part of the musical pieces using the right hand, while the left forearm rested comfortably on a supportive surface. The experimenter (on the left) was hidden from view behind a screen, where he pretended to perform the complementary bassline part. Participant’s right primary motor cortex was stimulated with TMS. MEPs were measured from the left ECR (indicated with a black dot) using EMG. Panel B gives a summary of the experimental design. The participant was asked to perform the right-hand part of the pieces, while the complementary left-hand part had been previously practiced in both the Self and the Joint conditions but not in the Baseline condition. In a first session (Audio session), participants could hear feedback of their performance and—only in the joint condition—also of the left-hand part ostensibly played by the co-performer. During the second session (Mute session), no auditory information was provided for either part. The label “Agency” refers to whom the motor representation of the left hand was related (the self or the co-performer).

The participants were naïve with regard to the purpose of the study. The experiment was approved by the local ethics committee and informed written consent was obtained from each participant.

Musical Materials

Six chorales by J. S. Bach, which were originally scored for soprano, alto, tenor, and bass voices, were adapted for use in this study. The titles of the chorales (English translations are reported in brackets) are: 1) "Herr, ich habe mißgehandelt" (Lord, I have done wrong), 2) "Meines Lebens letzte Zeit" (Life is well nigh done for me), 3) "So gibst Du nun, mein Jesu, gute Nacht" (So thou givest, my Jesus, good night), 4) "Christus, der ist mein Leben" (Christ is my life), 5) "Die Nacht ist kommen" (The night has come), and 6) "Gottes Sohn ist kommen" (God's son has come). The length of the chorales ranged from 7.5 to 15.5 bars (mean = 12.41 bars; SD = 3.08), their performance duration ranged from 26 to 40 s (mean = 34 s; SD = 5.79). All chorales had a high degree of complementarity between the melody (i.e., the part highest in pitch) and the bassline (the lowest part).

Notated scores comprising only the melody and the bassline of each chorale, or only the melody, were created. Embellishments such as passing notes and fermata (pauses) were omitted in order to reduce the complexity of the material that needed to be learned. The melody part of each chorale was transposed up by one octave so that the participants could perform it comfortably with the right hand while seated at the right-hand side of the keyboard (see Fig. 1, Panel A).

All scores included numerals printed above the melody and the bassline to indicate which finger to use to play each note. (An example of a musical score is provided in Fig. 2.) Pianists learned to perform the pieces using a specific fingering for 2 reasons. First, this served to control for general effects of the right-hand movements, which were thus identical across the participants. Second, this allowed us to deliver TMS pulses at around the times associated with the motor representation of the left-hand index or little finger movement. Three highly experienced pianists provided these fingerings. In doing so, they were asked to maximize the use of the index and little finger in order to allow us to have as many trials as possible (see below). A single version of the fingering was then produced based on consensus among the 3 pianists' suggested fingerings. The resultant musical scores were then submitted to a new group of pianists, who indicated that they found the fingering practicable and comfortable.

Preexperimental Training

One week before the experiment took place; participants received musical scores of the 6 chorales. Three scores depicted the melody and the bassline (these scores were to be used for the experimental conditions), while the other 3 depicted only the melody (these scores were to be used for the Baseline condition). Participants were asked to use their right hand for practicing the melody part and the left hand for the bassline part. Thus, participants learned to play 3 chorales using both the right and the left hands and the other 3 chorales using their right hand only. For the chorales in which only the right-hand melody

part was learned, the participant neither saw the score nor heard the audio versions of the left hand's basslines. To control for differences in the complexity of the chorales, one group of participants (group A, $n = 8$) learned the bassline of chorales 1-3, while another one (group B, $n = 7$) learned the bassline of chorales 4-6.

In addition to the scores, participants were also provided with a Compact Disc that contained audio files of the musical materials, which they were instructed to listen to while practicing. In these files, a metronome (sampled mechanical metronome sound, frequency = 2 Hz) sounded alone for 8 s. Subsequently, the beginning of the part to be practiced (only the melody or both the melody and the bassline) could be heard in piano timbre together with the metronome for 4-6 s (corresponding to the first 2-3 bars of the score). Finally, the metronome continued alone for the entire duration of the chorale (corresponding to a mean of 9.8 bars; SD = 2.97) (see Fig. 2).

Participants were instructed to start playing as soon as the chorale began and, after it stopped, to continue playing the entire piece in time with the metronome, using the fingering indicated in the scores. Two of the 15 participants practiced the pieces in our lab a few days before the experiment (as they had no access to a private piano in the week leading up to the experiment). All the others practiced the pieces at home.

The session on the day of the experiment started with a recording of the participant's performances of the learned materials (right, or right and left hands, depending on the piece). The experiment was carried out only if the participants were able to perform all pieces smoothly without any significant interruptions or mistakes. We also checked that the pianists had learned the correct fingering. Three of the 15 participants had to be dismissed and invited back to the lab a few days later.

Task and Procedure

Participants sat in front of a piano keyboard (Yamaha Clavinova CLP130) on the right side of a polystyrene screen that divided the keyboard into 2 halves (approximately at the position of the key C4). They were asked to play the chorales (with notation visible) with their right hand, while the screen hid the left side of the keyboard, where one of the experimenters sat, hidden from view. The participant's left forearm rested comfortably on a supportive surface fixed to the left arm of their chair, while their right hand was free to move on the keyboard.

A MIDI (Musical Instrument Digital Interface) interface connected the piano keyboard used for performance and the computer running the program that controlled the experiment. This interface converted the MIDI key values received from the piano keyboard into a serial signal that was compatible with Presentation Software (Version 14.2, Neurobehavioral Systems, Inc.), permitting us to record time and codes of the struck keys.

The experiment was run across 2 sessions: one with auditory information (Audio session) and the other without auditory information (Mute session). During the performance of the chorales learned with both hands, participants were either instructed to play with (Joint condition) or without (Self condition) the bassline counterpart "performed" by the

Figure 2. Diagram illustrating the materials for the piano performance task. From top to bottom, the metronome line and the musical score (with fingering) for the initial 10 bars of chorale 6 are displayed. The metronome played alone for 4 bars at a tempo of 120 beats/min (2 Hz). Participants then heard the initial 2 bars of the chorale played by the computer (only the melody in the Self condition, both the melody and the bassline in the Joint condition), which signaled when to start playing. The complete bassline part could be heard in the Joint condition of the Audio session (though it was never performed).

hidden experimenter. The audible counterpart—which was presented only in the Audio session—consisted of a performance recorded earlier by another pianist, and the experimenter was in fact merely feigning to play the piano. To lessen the likelihood that participants would become aware of this subterfuge, the experimenter nudged the keyboard in time with the tones of the bassline (without producing sounds). This caused small perturbations on the keyboard that were similar to those normally experienced when 2 pianists perform on the same piano keyboard and therefore made the context realistic. During the execution of the chorales learned with the right hand only, the bassline was never presented and therefore remained unknown (Baseline condition).

The experiment consisted of 18 blocks of 2 consecutive performances of each chorale. There were 3 different blocks (corresponding to 3 different melodies) for each condition (Baseline condition, Self condition, and Joint condition), with each block being run twice. Interleaved TMS pulses were delivered in relation to the timing performance of the left index or little finger, that is, consistently with the rehearsed fingering of the left hand. The order of the blocks was counterbalanced across participants.

At the beginning of each block during the “Joint condition,” the experimenter verbally informed the participant that they were about to begin a duo performance (even though the experimenter only pretended to play the bassline). Then, the experimenter took his seat behind the screen and was no longer visible throughout the block.

The experimental procedure and the task were analogous to those experienced during the preexperimental training (see above). Specifically, participants heard through headphones (Sony MDR-EX35LP) the same audio files they trained with. They were instructed to synchronize with the audio input and to continue playing the entire piece in time with the metronome using the rehearsed fingering. In the Joint condition, participants were led to believe that they were performing with the experimenter, who was ostensibly playing behind the screen.

At the end of the experiment, we quantified participants’ empathy score by using a German questionnaire based on the interpersonal reactivity index (Paulus 2009, based on Davis 1980). This questionnaire allows the assessment of how spontaneously one individual attempts to adopt the perspective of other people, which is indexed by the participant’s score on the “perspective taking” subscale.

Audio Session and Mute Session

To control for the different amount of auditory information received in the Self condition (where only the melody was heard) and the Joint condition (where both the melody and the bassline were heard), the experiment was divided into 2 sessions (Audio session and Mute session), separated by a 15 min break. In the Audio session, participants could hear the metronome, the melody they were playing and the bassline ostensibly played by the experimenter. In the Mute session, only the metronome was heard (as well as the initial 2–3 bars of the rehearsed melody, which signaled to the participant when they should commence playing). In the Audio session, the presence of the experimenter could be inferred from both the sound (reflecting the other part performance) and the social context. In the Mute session, it was the social context instructed beforehand that was indicative of the presence of the other. As we expected that our participants would have been puzzled by starting the experiment with the Mute session (due to inexperience with that particular setting), the Audio session was always performed first.

TMS and Electromyography Recordings

Focal single TMS pulses (Magstim 200, Whitland, UK; 70 mm figure-of-eight stimulation coil) were delivered over the right primary motor cortex to elicit MEPs. The coil was positioned tangentially over the right motor cortex with the handle pointing backward and laterally 45° away from the midline. We recorded TMS-induced MEPs from the ECR muscle of the left forearm using self-adhesive disposable Ag/AgCl electrodes placed in a belly-tendon montage. A ground 1.5 cm metal electrode was placed on the dorsal surface of the wrist. We chose to record MEPs from the ECR because this arm muscle is continuously activated during piano performance (D’Ausilio et al. 2006). Moreover, a previous study has demonstrated that—in piano players—corticospinal

excitability recorded from this muscle is modulated by the motor experience with a given melody (D’Ausilio et al. 2006). Activity from left FDI and left ADM muscles, which are selectively activated for index and little finger movements, respectively, were also recorded. These data served a secondary goal aimed at investigating the somatotopic specificity of the motor representations associated with the self and the other.

The optimal scalp position, at which MEPs with maximal amplitude were elicited, was identified by moving the coil over the right motor cortex while delivering TMS pulses at constant intensity. The TMS intensity was set at 120% of each participant’s resting motor threshold and ranged from 32–62% (mean = 42.25; SD = 8.69) of the maximum stimulator output. Resting motor threshold was defined as the lowest stimulator output that evoked at least 5 of 10 successive MEPs with an amplitude greater than 50 μ V, while the participant’s arm was relaxed. Muscular contraction was constantly visually monitored and full muscular relaxation was obtained. The electromyography (EMG) signal was amplified 1000 times, digitized at 5 kHz, and band-pass filtered (between 10 and 1000 Hz) with a mains hum notch filter at 50 Hz.

TMS pulses were delivered online, with each pulse time locked to critical events, defined as the specific time at which a note should be executed either with the left index or little finger. We chose the critical events by inspecting each chorale and selecting 2–6 notes (mean = 4; SD = 1.20) separated by a time interval that could range from 2.5 to 9.5 s (mean = 4.62; SD = 2.01). The same time intervals were used for the chorales learned using only the right hand (used for the Baseline condition). Pulses were delivered with a randomized jitter locked to the critical event at time 0, –20, or –40 ms. Group A received 52 pulses per condition, while group B received 44 pulses per conditions for each session (this difference is due to the different set of musical materials used between groups).

We stimulated the right primary motor cortex (M1) for 4 reasons. First, TMS stimulation over the right M1 interferes less with the performance of the ipsilateral hand (the right hand, which was supposed to play simultaneously with the pulses) (Chen et al. 1997; Ziemann and Hallett 2001). Second, the amplitude of right hemisphere TMS-induced MEPs is known to be modulated by individuals’ motor experience with a given piano piece (D’Ausilio et al. 2006). Third, stimulation over the right hemisphere meant that participants could perform the melody part (rather than bassline) alone as well as with the accompaniment. This was desirable because the melody parts are musically interesting in their own right, while basslines are less so. Fourth, it has been claimed that a number of brain regions in the right hemisphere—including the right inferior parietal cortex and the right prefrontal cortex—are strongly implicated in agency attribution and self-recognition (Decety and Sommerville 2003; Feinberg and Keenan 2005).

Data Analysis

Analysis of Behavioral Performance

Pianists’ performances were examined offline by analyzing the key codes and the timing of the notes nearest to the TMS pulses. Accuracy was quantified by counting the total number of errors, which were defined as either by an incorrect keystroke (pitch error) or by an absolute asynchrony larger than 250 ms (timing error). Another indication of performance accuracy was obtained by quantifying the timing variability of the keystrokes (as expressed by the SD of the absolute asynchronies), which has been used as an index of “stability” in music performance studies (see Keller et al. 2007). Mean asynchronies were also calculated (i.e., performed note time minus target time, defined by the metronome) in each condition. Mean asynchronies and timing variability were compared across conditions using separate analyses of variances (ANOVAs), each with 3 levels (one for each condition).

Analysis of Corticospinal Excitability (MEP)

Individual peak-to-peak MEP amplitudes were calculated as the absolute distance between the minimum and the maximum values observed within a search window starting 10 ms and ending 80 ms after the TMS pulse. MEPs recorded during performance errors (as defined

above) were excluded from further analyses (1.31% of the total). Trials with detectable background EMG activity preceding the TMS pulse, with MEP amplitudes smaller than 4 times the mean EMG in the 50 ms prior to the TMS pulse, and deviating more than 2 SDs from the mean of each condition and session were discarded (5.09% of the MEPs that were free of performance errors). Following the application of these exclusion criteria, mean values were obtained for an average of 44.94 (SD = 4.33) MEPs per condition from each session and muscle. One participant with outlying data was excluded from further analysis.

Raw MEPs recorded from all conditions were normalized by converting them to z -scores separately for each participant and each session. The mean values of the Baseline conditions, which served as a control for effects of 1) motor activity (right-hand piano playing) and 2) time on task (as the Audio session was earlier than the Mute session in the procedure), were subtracted from those of the relative experimental conditions (Self and Joint).

In order to examine the difference between the Self condition and the Joint condition across the 2 sessions (Audio session and Mute session), the baseline-corrected z -transformed MEPs recorded from ECR were entered into a 2×2 repeated measures ANOVA with 2 within-participant factors: Agency (Self, Joint) and Session (Audio, Mute).

The baseline-corrected z -transformed mean values were compared with zero using t -tests. These tests served to examine potential differences between the experimental conditions to the corresponding relative Baseline condition (i.e., if the difference between an experimental condition and its baseline is significant, then the baseline-corrected value should significantly differ from zero; but see below for caveats concerning this analysis).

We also investigated the somatotopic specificity of the motor representations associated with self and other, that is, whether the left-hand part was represented in terms of the specific movements necessary to execute it. For this purpose, the baseline-corrected z -transformed MEPs recorded from FDI and ADM were entered into a repeated measures ANOVA of similar design to that described above, with 2 additional within-participant factors: Finger (Index, Little) and Coincidence (Coincident, Incoincident). The latter factor indicated whether or not the timing of the stimulations was coincident with the time at which the left index or little finger was supposed to hit a key.

Finally, we examined whether the strength of self- and other-related motor representations was influenced by individual differences in empathy, that is, individuals' empathy score (see above). To this end, we estimated the degree of correlation between individual participants' empathy scores (following log transformation) and their mean baseline-corrected z -transformed MEPs recorded from ECR in the Self and Joint conditions (averaged across Audio and Mute sessions).

Results

Behavioral Task Performance

Pianists' performances were generally accurate both in terms of the total number of errors committed (pitch and timing combined, mean averaged across participants = 1.31% of notes nearest to the TMS pulses, SD = 1.96%) and in terms of timing variability (mean = 19.55 ms; SD = 5.87). Both indexes were particularly low, suggesting that musical performance was precise and stable.

The asynchronies produced during the Baseline condition (mean = -25.60 ms; SD = 17.16), the Self condition (mean = -27.53 ms; SD = 15.25), and the Joint condition (mean = -29.72 ms; SD = 14.92) did not differ significantly ($F_{2,26} = 2.020$, $P = 0.153$). Similarly, timing variability did not differ across conditions ($F_{2,26} = 1.451$, $P = 0.253$).

Corticospinal Excitability (MEP) Data

Agency

Figure 3 shows mean baseline-corrected z -scores for each condition and session separately. Uncorrected z -scores from all

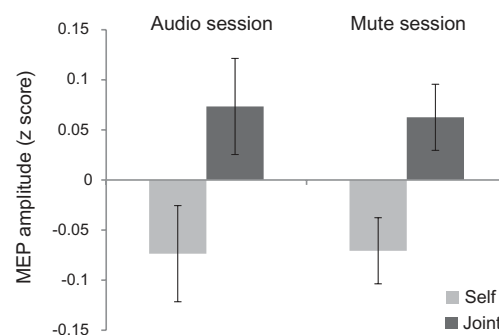


Figure 3. z -Scores representing the baseline-corrected mean MEP amplitudes across conditions (Self and Joint). Zero represents the baseline value. Means recorded from the Audio session (where auditory information was available) are displayed on the left and those recorded from the Mute session (where auditory information was not available) are presented on the right. Error bars represent confidence intervals, which were calculated according to Loftus and Masson (1994).

conditions can be found in Table 1. In Figure 3, it can be seen that, in both sessions, higher MEP amplitudes were elicited in the Joint condition than the Self condition.

The ANOVA on baseline-corrected z -transformed MEPs recorded from the ECR muscle yielded a significant main effect of Agency (Self vs. Joint; $F_{1,13} = 5.709$, $P = 0.033$), indicating that the representation of the self and of the other activated the motor system differently. The 2 conditions elicited very similar MEP amplitudes across the Audio and the Mute session. This was confirmed by the nonsignificant interaction between Agency and Session ($F_{1,13} = 0.023$, $P = 0.882$), suggesting that receiving auditory information was not the source of the variability observed between the experimental conditions. Thus, the effect of Agency can be attributed to the social context present in the Joint condition but not in the Self condition.

A significant effect of Agency was also obtained in an additional ANOVA that included "Group" (A and B) as a between-subjects factor. This ANOVA, furthermore, yielded a significant main effect Group ($F_{1,12} = 16.762$, $P = 0.001$), indicating that the amplitude of the MEPs (relative to the experimental conditions) was generally higher in group A (mean = 0.064; SD = 0.045) than in group B (mean = -0.069; SD = 0.077). This may reflect differences in the difficulty of the pieces encountered by each group, as corticospinal excitability is known to be modulated by task complexity (Haaland et al. 2004; Verstynen et al. 2005). Notably, however, the interaction between Group and Agency ($F_{1,12} = 0.498$, $P = 0.494$) as well as the 3-way interaction between Group, Agency, and Session ($F_{1,12} = 0.427$, $P = 0.526$) were not significant, implying that the effect of Agency, and the combined effects of Agency and Session (which were negligible in the first place), did not differ across groups.

None of the t -tests comparing the baseline-corrected z -transformed mean values against zero was significant (all $P > 0.10$). This implies that none of the individual experimental conditions differed significantly from the corresponding relative Baseline condition. However, note that the Baseline condition should not be seen as an instance of "absence of motor representations" because it is likely that—in the context of our experiment—the musical task led to some representation of the accompanying left-hand part, even if it was not learned previously (cf. Langheim et al. 2002; Meister et al.

2004). Moreover, note that the outcome of these comparisons cannot be interpreted as straightforwardly as the difference between Self and Joint conditions. This is because the Self versus Joint contrasts compare identical performances (i.e., same motor task but different agency attribution), while the Self versus baseline and Joint versus baseline contrasts include additional variance related to differences in the motor tasks (i.e., performance of different chorales and differing agency attribution).

Somatotopic Specificity (of Motor Representations)

This analysis investigated 1) whether the modulation of the MEPs recorded from ECR in response to rehearsed music (as observed above and in D'Ausilio et al. 2006) was also present in muscles involved in striking the keys (FDI, associated with index movements, and ADM, associated with little finger movements) and 2) whether this modulation is related to the time at which a specific finger is supposed to strike a key.

The z -transformed MEP amplitudes for FDI and ADM are reported in Table 2. The ANOVA on these data indicated that the main effect of Coincidence was not significant ($F_{1,13} = 0.27$, $P = 0.871$), as was the case for the difference between agency conditions ($F_{1,13} = 0.349$, $P = 0.565$) across fingers and sessions (all $P > 0.1$). Separate ANOVAs (one for each muscle) also yielded null effects (i.e., all $P > 0.1$). These results suggest that the main effect of Agency observed for ECR 1) was unlikely to reflect a representation of the specific movements necessary to perform the left-hand part and 2) was not associated to a modulation of other (more specific) muscles involved in piano performance.

Individual Differences Related to Empathy

A final set of analyses investigated the relationship between the empathy scores of individual participants (following log transformation) and the motor representation of self or of another agent (as indexed by the baseline-corrected z -transformed MEPs in the Self and Joint conditions, respectively, averaged across Audio and Mute sessions). This analysis revealed a significant positive correlation between the empathy scores

and the MEPs recorded during the Joint condition: $r_{12} = 0.619$, $P = 0.018$ (see Fig. 4). This result indicates that MEP amplitude reflecting the other increased with increasing empathy scores. No significant correlations were observed between MEPs recorded in the Self condition and empathy scores: $r_{12} = 0.318$, $P = 0.267$. Thus, the empathy scores and the MEPs significantly correlated only when the context was social (i.e., in the Joint condition). This corroborated the hypothesis that the motor facilitation effect observed in the Joint condition depended on the social context: More empathic participants were more sensitive to social contextual information.

Discussion

The present study investigated the distinction between self- and other-related motor representations in the context of a musical joint action task. Simultaneous self- and other-related motor representations were examined by means of a novel paradigm that required pianists to perform the right-hand part of chorales—previously learned bimanually—while the complementary left-hand part was either not performed (Self condition) or was believed to be performed by a co-performer (Joint condition). Results show that the representation of identical actions—either linked to the self or to another

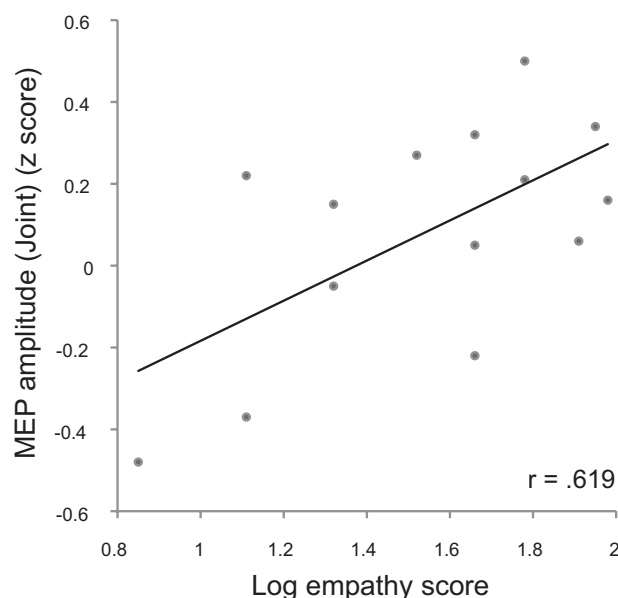


Figure 4. Scatter Plot showing the positive linear relationship between individual log-transformed empathy scores (on the x-axis) and MEP amplitudes recorded from ECR (average of Audio and Mute sessions for the Joint condition) reflecting motor representations of the co-performer (on the y-axis). Each data point represents an individual pianist. The diagonal indicates the line of best fit.

Table 1

Mean MEP amplitudes (z-scores) recorded across agency (Baseline, Self, and Joint) and sessions (Audio and Mute) from left ECR

	MEP (z-scores) from ECR	
	Audio session	Mute session
Baseline	-0.012 (± 0.291)	-0.013 (± 0.172)
Self	-0.061 (± 0.209)	-0.052 (± 0.141)
Joint	0.076 (± 0.254)	0.066 (± 0.166)

Note: SDs are shown in parentheses.

Table 2

Mean MEP amplitudes (z-scores) recorded across agency (Baseline, Self, and Joint), sessions (Audio and Mute), and pulse time conditions (Coincident and Incoincident) from left FDI and left ADM

	MEP (z-scores) from FDI				MEP (z-scores) from ADM			
	Audio session		Mute session		Audio session		Mute session	
	Coincident	Incoincident	Coincident	Incoincident	Coincident	Incoincident	Coincident	Incoincident
Baseline	0.092 (± 0.300)	0.062 (± 0.248)	0.062 (± 0.300)	-0.029 (± 0.218)	-0.002 (± 0.257)	0.048 (± 0.413)	0.066 (± 0.294)	0.140 (± 0.227)
Self	0.073 (± 0.280)	-0.080 (± 0.341)	-0.049 (± 0.291)	-0.049 (± 0.324)	-0.023 (± 0.376)	-0.011 (± 0.348)	-0.152 (± 0.259)	-0.005 (± 0.279)
Joint	-0.033 (± 0.231)	-0.058 (± 0.320)	0.039 (± 0.308)	0.020 (± 0.298)	0.017 (± 0.307)	0.017 (± 0.250)	-0.073 (± 0.272)	0.041 (± 0.257)

Note: SDs are shown in parentheses.

person—differed from each other as indexed by TMS-induced corticospinal excitability. Specifically, MEP amplitudes associated with the self were lower than MEP amplitudes associated with the other's performance.

This result is strikingly similar to those of 2 previous TMS studies that investigated self- and other-related motor representations by means of a purely perceptual task (Schütz-Bosbach et al. 2006, 2009) and linked them to cortical inhibition and facilitation, respectively. Although our data cannot be interpreted in terms of cortical inhibition, as MEP amplitude is not a direct measure of it, both interpretations indicate that self- and other-related motor representations are not equivalent. (However, it is worth noticing that the difference between Self and Joint is consistent with the possibility that inhibitory mechanisms are involved here. For example, it is possible that the participants were generally inhibiting any movements of the left hand in order to avoid errors [as the left-hand part had been learned but was not supposed to be executed] and that a similar process did not occur [or was reduced] when the left-hand part was believed to be played by the co-performer. Also note that this hypothesis could be tested in future work using direct measures of cortical inhibition [such as the duration of the TMS-induced silent period analyzed by Schütz-Bosbach et al. 2009].)

Importantly, our finding extends the previous ones by showing that processes underlying self-other distinction are also involved in motor tasks where participants believe that they are acting with another individual or alone. This implies that the neural mechanisms underlying action attribution are intrinsically social. Furthermore, we were able to replicate this result in a separate session during which the participants received neither visual nor auditory information from the co-performer but could still infer the presence of the other by means of contextual information. This finding is particularly important as it highlights that the origins of these agent-specific motor representations are strongly related to the sociality of the context in which one acts (but might still rely on perceptual processes, see below).

Considerable evidence supports the notion that representations of other agents' actions are processed by the same neural resources that would be used to perform the actions (for a review, see Rizzolatti and Sinigaglia 2010). Along the same lines, research in the emerging field of joint action has introduced the concept of "shared task representation" (for a review, see Knoblich et al. 2011), which postulates that when 2 or more agents perform a task together, each individual tends to form a task representation that refers to not only their own part but also to the part of the task that is performed by the co-performer (Sebanz et al. 2003; Atmaca et al. 2008). The latter view is also supported by electrophysiological evidence suggesting that people mentally perform the partner's task (Sebanz, Knoblich et al. 2006; Tsai et al. 2008).

How can our results be reconciled with the notion of shared representations? Our results are consistent with this concept to the extent that self- and other-related actions share resources at the neuroanatomical level. We found that the representation of the other led to an increase of cortical excitability in the neural circuits supporting execution of the same actions. However, our data do not support the conclusion that the 2 specific neurophysiological representations are equivalent in the context of joint action but rather that agent-specific motor representations are reflected in the amount of corticospinal excitability. We argue that a certain degree of agent specificity

is necessary in order to integrate co-represented and self-generated actions successfully in the interacting brain. This distinction may be critical in joint actions during which each individual constantly needs to adapt (or correct) his or her behavior in response to others' actions. Otherwise, functional equivalence of simultaneous self- and other-related motor representations would result in ambiguity and the generation of computational errors (Decety and Sommerville 2003; Schütz-Bosbach et al. 2009). Our conclusion may inform other studies and the literature on joint action, where co-performers are often assumed to be represented in an agent-neutral way (see, e.g., Vesper et al. 2010).

It has been argued that other-related actions automatically trigger imitative behavior (Brass 2001; for a review, see Hurley 2005), which according to some authors should be suppressed rather than facilitated, if one does not intend to act (Brass et al. 2001; Tsai et al. 2006; de Bruijn et al. 2008). However, it should be noted that our task consisted of the performance of complementary actions, which—compared with imitative actions—are known to lead to different responses in the brain and behavior (Newman-Norlund et al. 2007; van Schie et al. 2008) and have been suggested to override the automatic tendency to imitate (Knoblich et al. 2011). As recently argued by Bekkering et al. (2009), action selection is strongly influenced by the social environment and—very often—complementary rather than imitative movements are the most appropriate ones when people cooperate toward a common goal. From this perspective, our findings are in line with Newman-Norlund et al. (2007), who report that areas in the mirror neuron system (such as the right inferior frontal gyrus and bilateral inferior parietal lobes) are more active when observing complementary rather than imitative actions.

One important novel finding of our study is that the self-other distinction seems to be strongly related to the context in which one acts, implying that the neural mechanisms underpinning this distinction are influenced by implicit contextual factors (perhaps in conjunction with top-down processes, such as participants' expectations and beliefs, see Teufel et al. 2010; Obhi et al. 2011). Two pieces of evidence support this notion. First, our results remained unchanged after removal of auditory information, that is, in the Mute session, where participants could neither see nor hear the other player. This indicates that neither visual nor acoustic perception of the co-performer (which is commonly experienced during live musical ensemble performance) is necessary for associating action representations with specific agents. This conclusion does not imply that the observed effects were entirely independent of perceptual input (or processes) as 1) the subject could feel the perturbations (produced by the experimenter) on the keyboard and 2) results in the Mute session might reflect auditory imagery processes related to the (preceding) Audio session. Nevertheless, our findings demonstrate that direct interpersonal contact is not necessary for action attribution because the same effects were obtained independently of whether audio feedback was provided to the subject. Along these lines, previous behavioral evidence has suggested that motor representations can be modulated by an individual's beliefs, such as whether they are perceiving a human or a wooden hand covered by a glove (Liepelt and Brass 2010; Vlainic et al. 2010). Moreover, other studies have provided evidence for shared task representations even when participants merely believed that they were performing a task

with a partner (Tsai et al. 2008; Ruys and Aarts 2010; but for caveats, see Welsh et al. 2007).

A second result suggests that self-other distinction is related to social-contextual factors: corticospinal excitability associated with the representation of the co-performer increased with increasing empathy scores. This positive correlation is possibly attributable to highly empathic individuals being more sensitive to the sociality of the context and thus prone to forming a more salient representation of the co-performer (Gazzola et al. 2006; Kaplan and Iacoboni 2006; see also Singer 2006 for a review and similar conclusions). This finding is in line with previous research showing that motor activation during action observation can be modulated by social factors such as the relationship between 2 agents (for a review, see Frith and Frith 2010) and that interactive partners are favored over noninteractive “loner” partners (Kourtis et al. 2010). Concerning the latter point, it can be mentioned that our “Self” and “Joint” conditions might also be conceptualized in terms of “solo” and “ensemble” playing, as the self (i.e., the participant performing the right-hand part) was present in both conditions.

It should be noted that joint music making is an extraordinarily powerful means of social cohesion (Wiltermuth and Heath 2009; Kirschner and Tomasello 2010) and, not surprisingly, has been used for the therapeutic treatment of autism in children (Kim et al. 2008) and affective disorders (Koelsch et al. 2010). In this regard, experimental approaches such as ours might prove fruitful for understanding the neural mechanisms underpinning the social functions of joint music production.

We now turn to a discussion of the presumed neurophysiological processes underpinning the observed effects. We consider 2 interpretations that differ in terms of the specificity of the observed motor representations. The first view assumes that the observed modulation of corticospinal excitability reflects a representation of the specific movements necessary to perform the left-hand part (either associated with the self or the other). This view would imply that our experimental paradigm induced the formation of specific motor (or auditory) images of the left-hand part, which could either match (Self) or not (Joint) each individual pianist’s internal models (Wolpert et al. 1995; Wolpert and Ghahramani 2000). This interpretation would fit well with the possibility that self-related and other-related motor representations are associated with corticospinal suppression and facilitation, respectively (see Schütz-Bosbach et al. 2006, 2009). Indeed, computational models and neuroscientific work has linked motor prediction and sensorimotor suppression by showing that motor areas may predict the sensory consequences of movements in order to cancel the sensory reafferences (Blakemore et al. 1998; Haggard and Whitford 2004; see also Poulet and Hedwig 2007). Analogously, if the pianists were mentally imagining the sound of the complementary part (either their sound or the sound of the co-performer), the different auditory imagery processes (associated with self and other) might have been either suppressed or facilitated just as a real efferent copy of the action effect (see Brass et al. 2009; Spengler et al. 2009).

Thus, this view would implicate potential auditory imagery processes in the task and would still hold true if the outcome of the Mute session was attributed to a transfer effect related to the (preceding) Audio session, as the 2 sessions differed only in terms of auditory information. It should also be noted that,

given the strong evidence for body-specific auditory-motor coupling in musicians’ brains (Haueisen and Knösche 2001; Bangert et al. 2006; Lahav et al. 2007; see also Gazzola et al. 2006 and D’Ausilio et al. 2009 for comparable evidence outside the music domain), this account would predict a specific somatotopic mapping of the represented actions. However, this prediction did not receive support in our analysis of FDI and ADM muscles.

The second interpretation of the Self/Other MEP difference would suggest that, instead of forming a task-specific representation of the co-performer (i.e., in the Joint condition), participants developed a more complex action plan that took into account the other as a potential co-actor. Thus, the facilitation effect observed in the Joint condition would not reflect a “copy” of the movements associated with the left-hand part but rather a social modulation of the motor system reflecting the increasing task complexity that emerge in “joint action” compared with “solo action” (i.e., as playing in an ensemble involves demands over and above those encountered when playing alone; see Keller 2008).

This interpretation takes into consideration the increasing behavioral possibilities that emerge when 2 people coordinate their actions, which would be taken into account (by the motor control system) even when an agent merely believes that he or she is acting in a social environment. This view fits well with the finding that corticospinal excitability associated with the representation of the co-performer was higher in participants with higher empathy scores, as more empathic participants (i.e., with higher perspective taking score) are more likely to consider others as potential co-actors. Moreover, it does not predict a specific somatotopic mapping of the represented actions but rather a more general modulation of the motor control system (perhaps implying more flexibility), which is consistent with our results. It can also be noted that the specific effectors used to perform an action (i.e., the identity of the fingers employed) are often uninformative when it comes to understanding (or predicting) its goal because the same goal can be achieved in different manners (Bekkering et al. 2000; Novembre and Keller 2011; Ticini et al. 2011; see also Grafton and Hamilton 2007). Therefore, highly specific motor representations would not necessarily facilitate successful joint actions.

Both the accounts discussed above support the view that—in the context of a joint action—the motor control system is particularly sensitive to the identity of the agent (self or other) of a represented action and that (social) contextual information is one means for achieving this distinction. Moreover, both views would support the idea that the modulation of corticospinal excitability observed here reflects prediction mechanisms shared between action perception and execution (Kilner et al. 2007; Overy and Molnar-Szakacs 2009). Future studies could explore to what extent these mechanisms support successful coordination with others. In the case of music, for instance, it would be fruitful to investigate whether these mechanisms are the means by which musicians playing in ensemble maintain synchrony with one another (Keller et al. 2007; Keller 2008).

In conclusion, the present investigation used a novel approach in order to examine the distinction between self and other in a context that was social. Using a musical joint action task involving virtual duet piano performance, we showed that the representation of identical actions—either

linked to the self or to another—led to a difference of corticospinal excitability. This implies that, although self and other share neuroanatomical resources within the motor system, their neurophysiological representations are not necessarily equivalent in the interactive brain. Remarkably, we also showed that the same distinction can be observed in a situation in which the social context could be only inferred indirectly by contextual factors rather than direct interpersonal contact. Hence, in some cases, “believing” to be part of a joint action may be sufficient for the motor control system to be recruited as if one is sharing a task with a potential co-actor.

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