Brains "in concert": Frontal oscillatory alpha rhythms and empathy in professional musicians

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ABSTRACT

Playing music in ensemble represents a unique human condition/performance where musicians should rely on empathic relationships. Recent theories attribute to frontal Brodmann areas (BAs) 44/45 and 10/11 a neural basis for "emotional" and "cognitive" empathy. We hypothesized that activity of these structures reflects empathy trait in professional musicians playing in ensemble. Simultaneous electroencephalographic (EEG) alpha rhythms (8–12 Hz) were recorded in three saxophone quartets during music performance in ensemble (EXECUTION), video observation of their own performance (OBSERVATION), a control task (CONTROL), and resting state (RESTING). EEG source estimation was performed. Results showed that the higher the empathy quotient test score, the higher the alpha desynchronization in right BA 44/45 during the OBSERVATION referenced to RESTING condition. Empathy trait score and alpha desynchronization were not correlated in other control areas or in EXECUTION/CONTROL conditions. These results suggest that alpha rhythms in BA 44/45 reflect "emotional" empathy in musicians observing own performance.

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Introduction

Anatomic and functional correlates of music perception/production have been investigated by functional magnetic resonance imaging (fMRI; Koelsch, 2010, 2011; Peretz and Zatorre, 2005). Complex neural systems participate to music perception, encompassing auditory cortex, intra-parietal, temporal sulcus, ventral frontal gyrus (Brodmann's area — BA 44, BA 45, and BA 46), anterior superior insula, and ventral striatum (Koelsch, 2010, 2011; Peretz and Zatorre, 2005). They process pitch and spectral features of musical sounds (Foster and Zatorre, 2010a,b; Schönwiesner and Zatorre, 2008; Zatorre and Belin, 2001), melodic information (Foster and Zatorre, 2010a), music categorization (Klein and Zatorre, 2011; Peretz et al., 2009), and/or music syntax (Sammler et al., 2009, 2011). Emotional content in music perception

also contribute to specific neural activity (Koelsch and Friederici, 2003; Koelsch et al., 2006).

On the other hand, music production and executive monitoring mainly engage prefrontal, premotor and motor systems (Bangert and Altenmüller, 2003; Kamiyama et al., 2010; Katahira et al., 2008; Maidhof et al., 2009), while music imagery involves superior parietal and ventrolateral/dorsolateral frontal areas (Zatorre et al., 2010). Unfortunately, these neuroimaging data do not enlighten the peculiar neural correlates of playing music in ensemble, which is a crucial aspect of music experience.

Simultaneous modifications of background activities in 'target' areas of musicians' brains in concert have never been investigated before, due to obvious intrinsic methodological limitations of fMRI, positron emission tomography, and commercial electroencephalography (EEG)/ magnetoencephalography systems. From a theoretical point of view, it can be hypothesized that playing music in concert is associated to activity of brain networks sub-serving executive, monitoring, and motor control functions, as well as multi-sensory (i.e. somatosensory, auditory, visual) and motor integration. Furthermore, empathic abilities

may play a key role in modulating brain networks sub-serving music processing. Music performance evokes an emotional response through a form of empathy that is based, at least in part, on the perception of the movement and on violations of pulse-based temporal expectancies (Chapin et al., 2010). Expressive music performance evokes emotion and reward-related neural activations, and that affective impact on the brains of listeners is altered by musical training (Chapin et al., 2010). Areas associated with emotions and reward are also involved in emotional responding to music (Blood et al., 1999; Chapin et al., 2010; Phan et al., 2002; Royet et al., 2000). It has been shown that limbic and paralimbic brain areas responded to the expressive dynamics of human music performance (Chapin et al., 2010). Parahippocampus and precuneus activity were found to increase in response to increasing dissonance of short chord sequences (Blood et al., 1999), while increasing consonance was associated with activation of orbitofrontal and frontopolor cortices and subcallosal cingulate (Phan et al., 2002; Royet et al., 2000). Compared to unpleasant music, listening to pleasant music was associated with activation of parahippocampal gyrus, amygdala, temporal poles insula, inferior frontal gyrus (including Brodmann Area 44) and the ventral striatum (Berridge and Robinson, 2003; Knutson et al., 2001; Koelsch et al., 2006). Finally, a relationship between music and body movement is stressed in current theories on embodied cognition where the role of the body is seen as a mediator for music perception (Leman, 2007).

Empathic abilities can be somewhat measured via standardized questionnaires probing the empathy trait, namely how the person emotionally reacts to and understands other people feelings and mental states. There is consensus that the definition of empathy encompasses at least two main dimensions. "Emotional" empathy defined as the immediate affective "contagion" of feelings between the observer and observed person (Shamay-Tsoory, 2011; Shamay-Tsoory et al., 2009). Instead, "cognitive" empathy is based on thinking, and can be defined as the capacity to adopt the psychological point of view of another person thanks to a perspective-taking ability (Frith and Singer, 2008; Shamay-Tsoory, 2011; Shamay-Tsoory et al., 2009). Such distinction of empathic abilities is consistent with phylogenetic/ developmental observations and cognitive models (Decety and Jackson, 2004; Leiberg and Anders, 2006; Preston and de Waal, 2002). In fact, "emotional" empathy/contagion is observed in birds and rodents, whereas "cognitive" empathy/perspective-taking is recognized only in great apes and humans (De Waal, 2008) and starts to manifest itself only during childhood and adolescence maturational processes (Decety and Jackson, 2004; Gallese, 2003; Preston and de Waal, 2002).

It has been hypothesized that two different brain networks subserve "emotional" and "cognitive" empathy (Shamay-Tsoory et al., 2009). "Emotional" empathy would rely upon ventral-lateral frontal areas (i.e. BA 44/45) as suggested by recent studies probing the recognition of other's emotions (Schulte-Ruther et al., 2007), as well as the experience of empathy with people suffering serious threat or harm (Nummenmaa et al., 2008). Furthermore, lesions of ventral-lateral frontal areas are associated to impaired emotional contagion and deficits in the recognition of the emotions expressed by other people (Shamay-Tsoory et al., 2009). Of interest, the BA 44/45 might be part of resonant ventral-lateral frontal and parietal "mirror" systems subserving the understanding of actions and motor intentions performed by others, as well as imitation/observational learning (Gallese et al., 2004; Rizzolatti and Craighero, 2004; Rizzolatti et al., 2006). These frontal areas are active during the observation of musicians playing music as a function of practice (Buccino et al., 2004; Vogt et al., 2007). On the other hand, "cognitive" empathy may rely upon the activation of ventromedial prefrontal areas (BA 10/11) when the evaluation of the similarities and differences between mental states of oneself with respect to those of other individuals is required (Mitchell, 2009). In this line, lesions in the ventromedial prefrontal cortex result in impaired "cognitive" empathy (Shamay-Tsoory et al., 2009). On the whole, it can

be speculated that playing music in ensemble induces remarkable emphatic feelings in musicians due to several inductors including music sounds and observation of own and other body in action, as well as the need for the realization of a common representation and interpretation of the music piece performed.

Summarizing, BA 44/45 and BA 10/11 appear to be involved in "emotional" and "cognitive" empathy, respectively. Here we hypothesized that activity of these areas specifically reflects empathy trait in professional musicians playing in ensemble. Electroencephalographic (EEG) data were recorded in three professional saxophone quartets (i.e. simultaneous recording in any quartet) during music performance in ensemble (EXECUTION), video observation of their own performance (OBSERVATION), video observation of a control task (CONTROL), and resting state condition (RESTING). Cortical activity was indexed by the percentage reduction (i.e. desynchronization) of EEG alpha power (about 8–12 Hz) in the EXECUTION, OBSERVATION, and CONTROL conditions with reference to the RESTING condition as a baseline. EEG source estimation was performed by standardized low resolution electromagnetic brain source tomography (sLORETA; Pascual-Marqui, 2002), in order to model cortical activity in BAs 44/45, 10/11, and control areas. Empathy trait was measured by empathy quotient test (EQT; Lawrence et al., 2004), and EQT score was correlated to the alpha desynchronization. We assumed that if BA 44/45 ("emotional" empathy) or BA 10/11 ("cognitive" empathy) are part of the brain networks sub-serving empathy in musicians playing in ensemble, then the alpha desynchronization of these areas during the EXECUTION and OBSERVATION conditions would be correlated to EQT score. The present EEG experiment on the relationship between empathy traits and brain activity simultaneously recorded in musicians playing in ensemble represents a new experimental model aimed at exploring higher functions in human social communication and cooperation.

Materials and methods

Subjects

Three quartets (12 men) of professional saxophonists with highly international credentials were recruited. Six subjects were right-handed, three were left-handed, and three were ambidextrous as revealed by Edinburgh inventory. They have been practicing several hours/day for more than 12 years at least five times a week. The mean subjects' age was 35.9 years (±3.4 standard error, SE; range: 21 to 50 years). Furthermore, we enrolled 10 age-matched healthy non-musician volunteers whose mean age was 52.2 years (±2.9 SE; range: 34 to 64 years). All subjects gave their informed consent according to the Declaration of Helsinki. They were free to withdraw from the study at any time. The procedure was approved by the local Institutional Ethics Committee.

Design of the system for the simultaneous electrophysiological data recording

The system allows simultaneous recording of electrophysiological data in 4 individuals (Fig. 1A; for details see Babiloni et al., 2011). Briefly, four pre-wired EEG caps are used. Each cap includes 30 electrodes placed on the scalp according to an augmented 10–20 system (Fig. 1B). These electrodes are linked to cephalic reference and ground, and are connected to a single multi-channels amplifier box (Brain Explorer, EB-Neuro©) that also receives the individual bipolar electrooculographic (EOG) and electromyographic (EMG) signals. This box receives audio signals relative to environmental sounds, which are revealed by two dynamic microphones (Shure Beta 57©). A dedicated software managed the simultaneous data collection (GALILEO NT, EB-Neuro©).
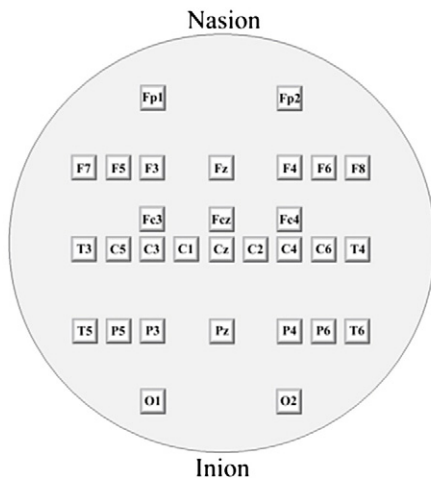
Fig. 1. A: Overview of the four musicians playing in ensemble during simultaneous EEG recordings. B: EEG electrode montage (augmented 10–20 system).

Experimental procedure and EEG recordings

The EEG recordings were performed on each quartet in a different day. A training session of about 10 min was executed before the EEG recordings. The saxophone quartet played a piece taken from their repertoire (i.e. a classical music piece of Domenico Scarlatti: Allegro, from Sonata in A moll L. 223 Kirk. 532, in the arrangement for four saxophones by Salvatore Sciarrino), which was video- and audio-recorded. Afterwards, the EEG data were simultaneously recorded from the 4 saxophonists of each quartet. The EEG data were collected in 4 conditions: eyes-open resting state (4 min; RESTING); observation/listening of the audio–video of own music performance in ensemble (OBSERVATION); observation of a video in which they turned the pages of a score on a lectern (CONTROL), and playing the music piece (EXECUTION). The OBSERVATION and CONTROL videos represented the musicians of the quartet with similar features of luminosity and point of the video camera.

EEG–EOG–EMG data were collected with bandpass of 0.01–100 Hz and sampling rate of 512 Hz (EB-Neuro Be-family©, Firenze, Italy). EMG activity of orbicularis oris, mentalis and bilateral extensor digitorum muscles was recorded by bipolar surface electrodes, in order to monitor movements during music performance. An additional recording channel was used for triggering the reference instants of the event on the on-going EEG–EOG–EMG data of the four musicians, namely the start and stop instants of the music performance. These instants – generally the attacks of musical phrases – could be used for the choice of the same EEG periods in the four musicians.

Testing for empathy

Subjects' empathy as a personality trait was evaluated by empathy quotient test (EQT). This test was developed by Simon Baron-Cohen (Baron-Cohen and Wheelwright, 2004), and measures the person's global level of empathy by means of a questionnaire. EQT comprises 60 items (i.e. 40 empathy-related items and 20 fillers). Table 1 reports the 40 empathy-related items. Basically, this questionnaire probes how the person emotionally reacts to various situations. The score of this test ranges from 0 (minimum) to 80 (maximum) to index the ability of understanding how other people feel and respond appropriately in several circumstances. This test is characterized by high validity, good test-retest reliability, and internal consistency (Lawrence et al., 2004).

Table 1
Items associated to global empathy in Baron-Cohen questionnaire (for details see Baron-Cohen and Wheelwright, 2004).

Empathy related items in empathy quotient test
✔ I can easily tell if someone else wants to enter a conversation.
✔ I find it difficult to explain to others things that I understand easily, when they don't understand it first time.
✔ I really enjoy caring for other people.
✔ I find it hard to know what to do in a social situation.
✔ People often tell me that I went too far in driving my point home in a discussion.
✔ It doesn't bother me too much if I am late meeting a friend.
✔ Friendships and relationships are just too difficult, so I tend not to bother with them.
✔ I often find it difficult to judge if something is rude or polite.
✔ In a conversation, I tend to focus on my own thoughts rather than on what my listener might be thinking.
✔ When I was a child, I enjoyed cutting up worms to see what would happen.
✔ I can pick up quickly if someone says one thing but means another.
✔ It is hard for me to see why some things upset people so much.
✔ I find it easy to put myself in somebody else's shoes.
✔ I am good at predicting how someone will feel.
✔ I am quick to spot when someone in a group is feeling awkward or uncomfortable.
✔ If I say something that someone else is offended by, I think that that's their problem, not mine.
✔ If anyone asked me if I like their haircut, I would reply truthfully, even if I didn't like it.
✔ I can't always see why someone should have felt offended by a remark.
✔ Seeing people cry doesn't really upset me.
✔ I am very blunt, which some people take to be rudeness, even though this is unintentional.
✔ I don't tend to find social situations confusing.
✔ Other people tell me I am good at understanding how they are feeling and what they are thinking.
✔ When I talk to people, I tend to talk about their experiences rather than my own.
✔ It upsets me to see animals in pain.
✔ I am able to make decisions without being influenced by people's feelings.
✔ I can easily tell if someone else is interested or bored with what I am saying.
✔ I get upset if I see people suffering on news programs.
✔ Friends usually talk to me about their problems as they say I am very understanding.
✔ I can sense if I am intruding, even if the other person doesn't tell me.
✔ People sometimes tell me that I have gone too far with teasing.
✔ Other people often say that I am insensitive, though I don't always see why.
✔ If I see a stranger in a group, I think that it is up to them to make an effort to join in.
✔ I usually stay emotionally detached when watching a film.
✔ I can tune into how someone else feels rapidly and intuitively.
✔ I can easily work out what another person might want to talk about.
✔ I can tell if someone is masking their true emotion.
✔ I don't consciously work out the rules of social situations.
✔ I am good at predicting what someone will do.
✔ I tend to get emotionally involved with a friend's problems.
✔ I can usually appreciate the other person's viewpoint, even if I don't agree with it.

Preliminary EEG data analysis

Recorded EEG data were offline segmented in single 2 s epochs; epochs contaminated by ocular, muscular, and other types of artifact were preliminarily identified by a computerized automatic procedure (Moretti et al., 2003) and then corrected by an autoregressive method (Moretti et al., 2003). Finally, two expert electroencephalographists (P.B. and N.M.) manually confirmed this automatic selection and correction, with special attention to residual contaminations of the EEG epochs due to eye movements, blinking, and unwanted hand movements. Therefore, only the EEG epochs extensively free from artifact residuals were accepted for the subsequent post-processing analyses. These EEG epochs were referred to common average reference for further analyses.

Frequency analysis of alpha rhythms

The artifact-free EEG epochs for the experimental conditions were used as an input for EEG power spectrum analysis, which was performed by a standard (Matlab; MathWorks, Natick, Massachusetts USA) FFT algorithm using Welch technique and Hanning windowing function. For the determination of the alpha sub-bands, individual alpha frequency (IAF) peak was identified according to literature guidelines (Klimesch, 1996, 1999; Klimesch et al., 1998). Practically, the IAF was defined as the frequency showing the higher power density at 6–12 Hz range of the individual EEGs. For each subject, we estimated the IAF on the mean power spectrum of all electrodes (Klimesch, 1996, 1999). With reference to the IAF, the alpha sub-bands of interest were as follows: low-frequency alpha band as IAF-2 Hz to IAF and high-frequency alpha band as IAF to IAF + 2 Hz. The mean IAF value was 9.5 Hz (±0.3 SE).

Cortical source analysis of the EEG rhythms by sLORETA

The artifact-free EEG data were given as an input to the original standardized low-resolution brain electromagnetic tomography (sLORETA) software for the EEG source analysis (Pascual-Marqui, 2002; http://www.unizh.ch/keyinst/NewLORETA/LORETA01.htm). sLORETA is a functional imaging technique belonging to a family of standardized linear inverse solution procedures, modeling 3-D distributions of the cortical source patterns generating scalp EEG data (Pascual-Marqui, 2002).

sLORETA computes 3-D linear solutions (sLORETA solutions) for the EEG inverse problem standardized with respect to instrumental and biological noise as mathematically defined in the original paper by Pascual-Marqui (2002). sLORETA solutions are computed within a three-shell spherical head model including scalp, skull, and brain compartments. The brain compartment is restricted to the cortical gray matter/hippocampus of a head model co-registered to the Talairach probability brain atlas, which has been digitized at the Brain Imaging Center of the Montreal Neurological Institute (Talairach and Tournoux, 1988). This compartment includes 6239 voxels (5 mm resolution), each voxel containing an equivalent current dipole.

Computation of task-related decrease/increase (TRPD/TRPI) of alpha sources

Cortical activation/deactivation was indexed as a task-related power decrease/increase (TRPD/TRPI) of EEG alpha rhythms at about 8–12 Hz, respectively. To this aim, alpha TRPD/TRPI was computed for the OBSERVATION, EXECUTION and CONTROL conditions referenced to the RESTING condition taken as a baseline. Specifically, we used the basic formula used for the computation of event-related desynchronization/synchronization (ERD/ERS; Pfurtscheller and Aranibar, 1979; Pfurtscheller and Lopes da Silva, 1999; Pfurtscheller

and Neuper, 1994; Pfurtscheller et al., 1997). This formula is as follows:

$$TRPD/TRPI\% = \left(\frac{event - baseline}{baseline} * 100 \right),$$

where "event" refers to the alpha (LORETA) solutions relative to the OBSERVATION, EXECUTION or CONTROL condition, while "baseline" refers to the alpha (sLORETA) solutions relative to the RESTING condition. The procedure was repeated for low- and high-frequency alpha sub-bands. Percent negative values (i.e. weaker alpha sLORETA solutions during the OBSERVATION, EXECUTION or CONTROL than during the RESTING condition) represented the alpha TRPD as a reflection of cortical activation (Manganotti et al., 1998). On the contrary, percent positive values (i.e. stronger alpha sLORETA solutions during the OBSERVATION, EXECUTION or CONTROL than during the RESTING condition) represented the alpha TRPI as a reflection of cortical deactivation or idling.

Statistical analysis

Since the sLORETA procedure intrinsically provides "low-resolution" EEG source solutions, we did not evaluate sLORETA solutions at the level of single voxels. Rather, we evaluated these solutions at the rough level of large cortical regions of interest (ROIs) probing ventral-lateral and ventromedial frontal areas supposed to subserve empathic abilities (Shamay-Tsoory et al., 2009). For each hemisphere, the ventral-lateral frontal ROI was formed by BAs 44 and 45. The ventromedial frontal ROI was formed by bilateral BAs 10 and 11 as a unique entity. Indeed, we could not disentangle the activation of left and right BA 10 and BA 11, due to the poor spatial resolution of the sLORETA solutions. The sLORETA solution for a given BA was defined as the mean of the sLORETA solutions across all the voxels of that BA. Fig. 2 plots the mentioned cortical regions of interest in the source space of the sLORETA software.

For the evaluation of the relationship between subject's empathy trait and EEG modulation, Spearman correlations (two-tailed, N = 12)
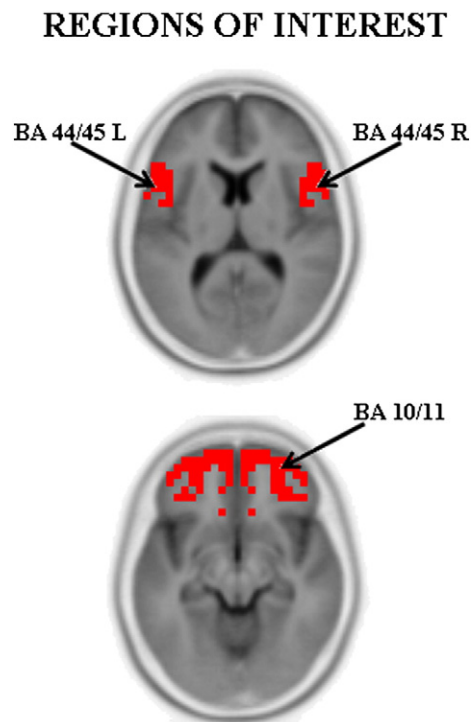
REGIONS OF INTEREST

Fig. 2. Regions of interest for the sLORETA analysis of alpha rhythms; bilateral BA 10 and BA 11 belonging to a ventromedial prefrontal region; BA 44 and BA 45 belonging to inferior prefrontal gyrus of the right and left hemispheres.

were performed between the EQT score and alpha TRPD/TRPI computed in the OBSERVATION, EXECUTION, and CONTROL conditions. This was true for the three ROIs (left and right BA 44/45, bilateral BA 10/11). For each alpha sub-band frequency (low, high), the statistical threshold was set to Bonferroni's correction for 3 repetitions of the test (i.e. the number of BAs), namely $p<0.016$.

Results

EEG power density spectra

For illustrative purpose, Fig. 3 shows the normalized power density spectra (grand average, $N=12$) of artifact-free EEG data for 3
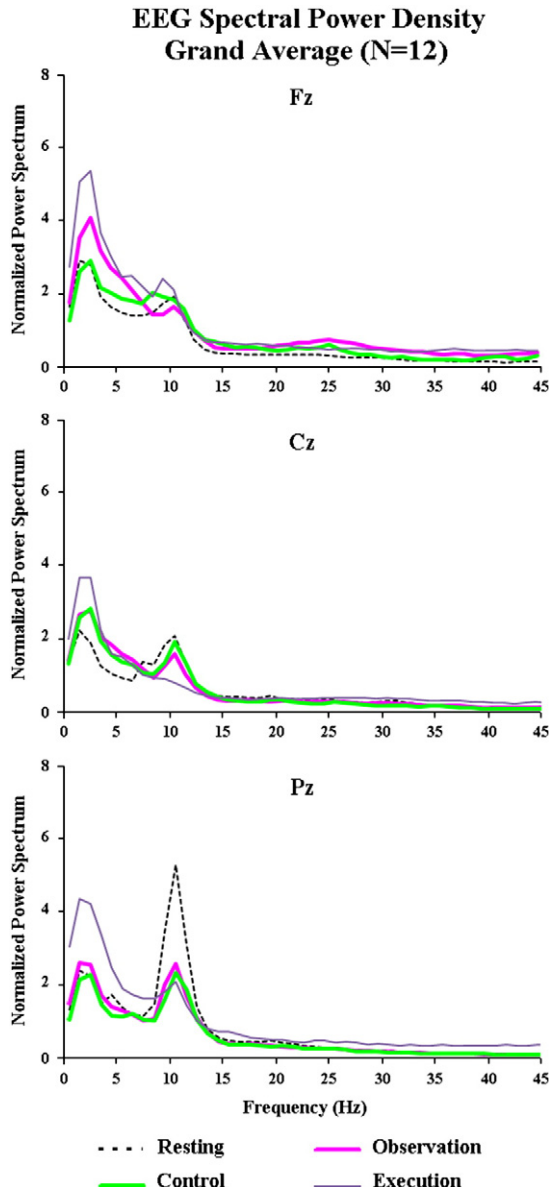

EEG Spectral Power Density
Grand Average (N=12)

Fig. 3. Grand average across the saxophonists of 3 quartet ($N=12$) of the normalized electroencephalographic (EEG) spectral power density values computed for 3 representative electrodes of the midline (Fz, Cz, and Pz of 10–20 electrode montage system). These values refer to the EEG frequencies from 1 to 45 Hz (frequency resolution = 1 Hz) and to 4 experimental conditions: (i) eyes-open resting state condition (RESTING), (ii) observation of an audio–video with own music performance played in ensemble, namely a well-known piece for saxophone quartet (OBSERVATION), (iii) observation of an audio–video showing themselves turning the pages of a score on a lectern (CONTROL), (iv) actual execution in ensemble of the mentioned piece for saxophone quartet (EXECUTION).

representative frontal (Fz), central (Cz), and parietal (Pz) midline electrodes in the RESTING (eyes-open), EXECUTION, OBSERVATION, and CONTROL conditions. The EEG frequencies of interest ranged from 1 to 45 Hz; the normalization of the EEG power density was obtained by normalizing the power density spectra at each electrode with the power density averaged across all frequencies (1–45 Hz) and electrodes. These power spectra revealed the typical features of human cortical EEG oscillatory activity during RESTING (i.e. eyes-open condition) condition and engaging events (EXECUTION, OBSERVATION, and CONTROL conditions). During the RESTING condition, the maximum power density was observed within the alpha band (about 8–12 Hz) at the parietal and occipital electrodes (see Pz electrode in Fig. 1). EEG power density at low frequency bands (delta, 1–4 Hz; theta, 4–8 Hz) was maximum at the frontal electrodes (see Fz electrode in Fig. 3). EEG power density at high frequency bands (beta, 14–30 Hz; gamma, >30 Hz) was globally negligible. Compared to the RESTING (eyes-open) condition, the EXECUTION, OBSERVATION, and CONTROL conditions were characterized by reduced alpha power density at the parietal and occipital electrodes (see Pz electrode in Fig. 1). These results indicate that the current new technology for the simultaneous EEG recording in musicians playing in ensemble is able to record reliable EEG data for subsequent source analysis (Babiloni et al., 2011).

Topography of alpha sLORETA solutions

For illustrative purpose, Fig. 4 shows the sLORETA solutions modeling the distributed EEG sources of low- (about 8–10 Hz) and high-frequency (about 10–12 Hz) alpha power in the musicians experiencing the highest (EQT=64) and the lowest (EQT=34) empathy scores as measured by the EQT questionnaire. For the sake of brevity, task-related alpha power desynchronization or decrement (indicating cortical activation) and synchronization or increment (indicating cortical inhibition) are termed TRPD and TRPI, respectively. The maps refer to the TRPD/TRPI in the OBSERVATION, EXECUTION, and CONTROL conditions referenced to the RESTING condition (representative slices including BA 10/11 and BA 44/45 are illustrated). The musician with the highest empathy score was characterized by an evident and widespread alpha TRPD in the OBSERVATION condition. In contrast, the musician with the lowest empathy score was characterized by an evident and widespread alpha TRPI. For the other two conditions, the maps of the musicians with the lowest and highest empathy score showed no remarkable differences.

Statistical analysis

Figs. 5 and 6 show the scatterplots of the Spearman correlation between EQT score and alpha TRPD/TRPI in OBSERVATION, EXECUTION, and CONTROL conditions. Both low- (about 8–10 Hz) and high- (about 10–12 Hz) frequency bands were considered. The following three BAs of interest were considered: ventral frontal BA 44/45 left, BA 44/45 right and ventromedial BA 10/11 (the relatively low spatial resolution of sLORETA solutions did not allow disentangling the medial aspects of BA 10/11 of the two hemispheres). The r and p values relative to this Spearman correlation analysis are reported in Table 2. In the OBSERVATION condition, there was a statistically significant negative correlation between EQT score and alpha TRPD/TRPI in right ventral-lateral BA 44/45 for both alpha sub-bands (low-frequency alpha: $r=-0.75$, $p=0.004$; high-frequency alpha: $r=-0.67$, $p=0.01$). Furthermore, there was a trend between EQT score values and low-frequency alpha TRPD/TRPI in ventromedial bilateral BA 10/11 ($r=-0.58$; $p=0.05$). The higher the EQT score, the higher the alpha TRPD (cortical activation). These results indicate that in expert musicians observing their music performance in ensemble, the alpha rhythms in the right ventral-lateral frontal regions (BA 44/45) reflect the empathy tract as measured by the EQT score.
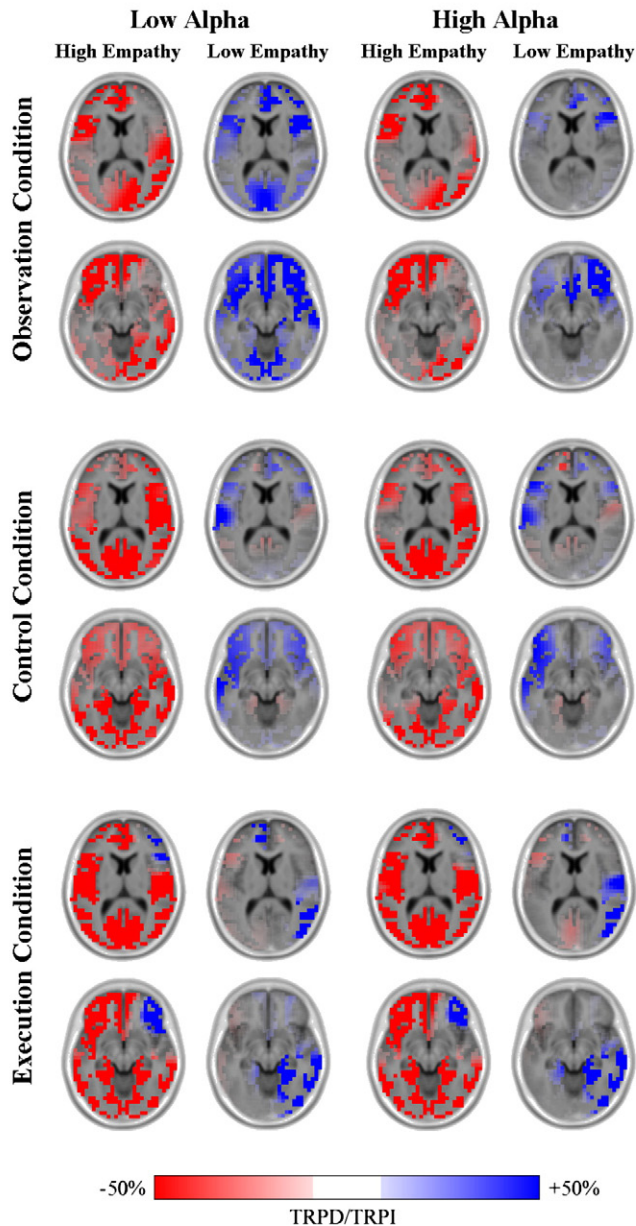
sLORETA MAPS OF ALPHA TRPD/TRPI

Fig. 4. Standardized low resolution brain electromagnetic tomography (sLORETA) solutions of the musicians with highest (64) and lowest (34) score of the empathy quotient test (EQT). The maps of sLORETA solutions represent distributed EEG cortical sources of the low- (about 8–10 Hz) and high-frequency (about 10–12 Hz) alpha task-related decrease/increase (TRPD/TRPI) in the OBSERVATION, EXECUTION and CONTROL conditions with reference to the RESTING condition. These maps show the representative slices for ventromedial frontal BAs 10/11 and ventral-lateral frontal BAs 44/45. Color scale: maximum TRPD (i.e. cortical activation) and TRPI are coded in red and blue, respectively. The maximal (%) value of the TRPD/TRPI is reported beneath the maps. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Control analyses

As a main result, we reported a statistically significant correlation between the subject's EQT score (global empathy trait) and alpha TRPD/TRPI in right ventral-lateral frontal areas (i.e. BA 44/45) during the OBSERVATION condition. In this correlation, we used the EQT score developed by Simon Baron-Cohen (Baron-Cohen and Wheelwright, 2004). This test measures the person's global level of empathy by means of a questionnaire (i.e. 40 empathy-related items

and 20 fillers). A first control analysis was performed to evaluate whether the main result of the present study (i.e. a significant correlation between subject's EQT score and alpha TRPD/TRPI in right ventral-lateral frontal areas, BA 44/45 right) assessing emotional and cognitive empathy separately. To address this issue, we divided the 40 empathy items of the EQT in two sub-questionnaires (i.e. one for "emotional empathy" and the other for "cognitive empathy") according to the procedures reported in two previous reference studies (Lawrence et al., 2004; Muncer and Ling, 2006). In particular, Lawrence et al. (2004) reduced the original 40 empathy items to 28 items and subdivided them in three factors: (1) factor 1 was identified as cognitive empathy and consisted of 11 items; (2) factor 2 was identified as emotional reactivity (i.e. emotional empathy) and consisted of 11 items; (3) factor 3 was identified as social skills (i.e. ability to correctly interact with others) and consisted of 6 items. Similarly, Muncer and Ling (2006) identified the same three factors, which consisted each of 5 items. Table 3 reports the items associated to cognitive and emotional empathy in the two mentioned studies (Lawrence et al., 2004; Muncer and Ling, 2006). As a result, we obtained the cognitive and emotional EQT scores for all saxophonists of the four quartets. For the OBSERVATION condition, we computed Spearman correlation (two-tailed, $N = 12$, $p < 0.05$) between the cognitive or emotional EQT scores and low- and high-frequency alpha TRPD/TRPI in right BA 44/45. The r and p values relative to this Spearman correlation analysis are reported in Table 4. The results showed a statistically significant correlation between musicians' emotional EQT score and low-frequency alpha TRPD/TRPI in right BA 44/45 ($p < 0.05$). This was true for the sub-questionnaires formed according to the procedures reported in both Lawrence et al. (2004) and Muncer and Ling (2006). The present control results are in line with previous evidence showing that ventral-lateral frontal areas sub-serve emotional empathy (Shamay-Tsoory et al., 2009).

Since BA 44/45 is typically ascribed to "mirror" system, which is devoted to action understanding/execution, we performed a second control analysis to test whether the alpha TRPD/TRPI did or did not differ in amplitude in the OBSERVATION and EXECUTION conditions ("mirror" areas are expected to show a similar activation during the two conditions). To address this issue, two ANOVAs were performed, namely one for right BA 44/45 and the other for BA 10/11. Alpha TRPD/TRPI was the dependent variable, while Condition (OBSERVATION, EXECUTION) and Band (low-frequency alpha, high-frequency alpha) served as factors. The results showed no statistically significant effect for both right BA 44/45 (Group main effect: $F(1,11) = 0.08$, $p = 0.7$; Band main effect: $F(1,11) = 0.05$, $p = 0.8$; Interaction between Group and Band: $F(1,11) = 0.008$, $p = 0.9$) and BA 10/11 (Group main effect: $F(1,11) = 1.8$, $p = 0.2$; Band main effect: $F(1,11) = 2.7$, $p = 0.1$; Interaction between Group and Band: $F(1,11) = 2.2$, $p = 0.1$), suggesting that the activity of these areas did not differ in the OBSERVATION and EXECUTION conditions.

A third control analysis was performed to test the specificity of the relationship between EQT score (empathy trait) and alpha TRPD/TRPI in the right BA 44/45 during the OBSERVATION condition. To address this issue, Spearman correlation (two-tailed, $N = 12$, $p < 0.05$) was computed between EQT score and alpha TRPD/TRPI in several sensorimotor cortical areas such as BA 41 and BA 42 (acoustic pathway); BA 17, BA 18 and BA 19 (visual pathway); and BA 1, BA 2, BA 3, and BA 4 (somatomotor pathway). No significant correlation was found either for low-frequency or for high-frequency alpha TRPD/TRPI ($p > 0.05$). The r, and p values relative to this Spearman correlation analysis are reported in Table 5

A fourth control analysis was performed to test whether the main results were specific for the musicians, who are especially sensitive to music listening. To address this issue, the same EEG experiment was carried out in a group of 10 age-matched non-musicians. The same procedures of the main experiment were followed. The EEG data were recorded in the OBSERVATION, CONTROL, and RESTING conditions (of course, EXECUTION condition could not be performed by
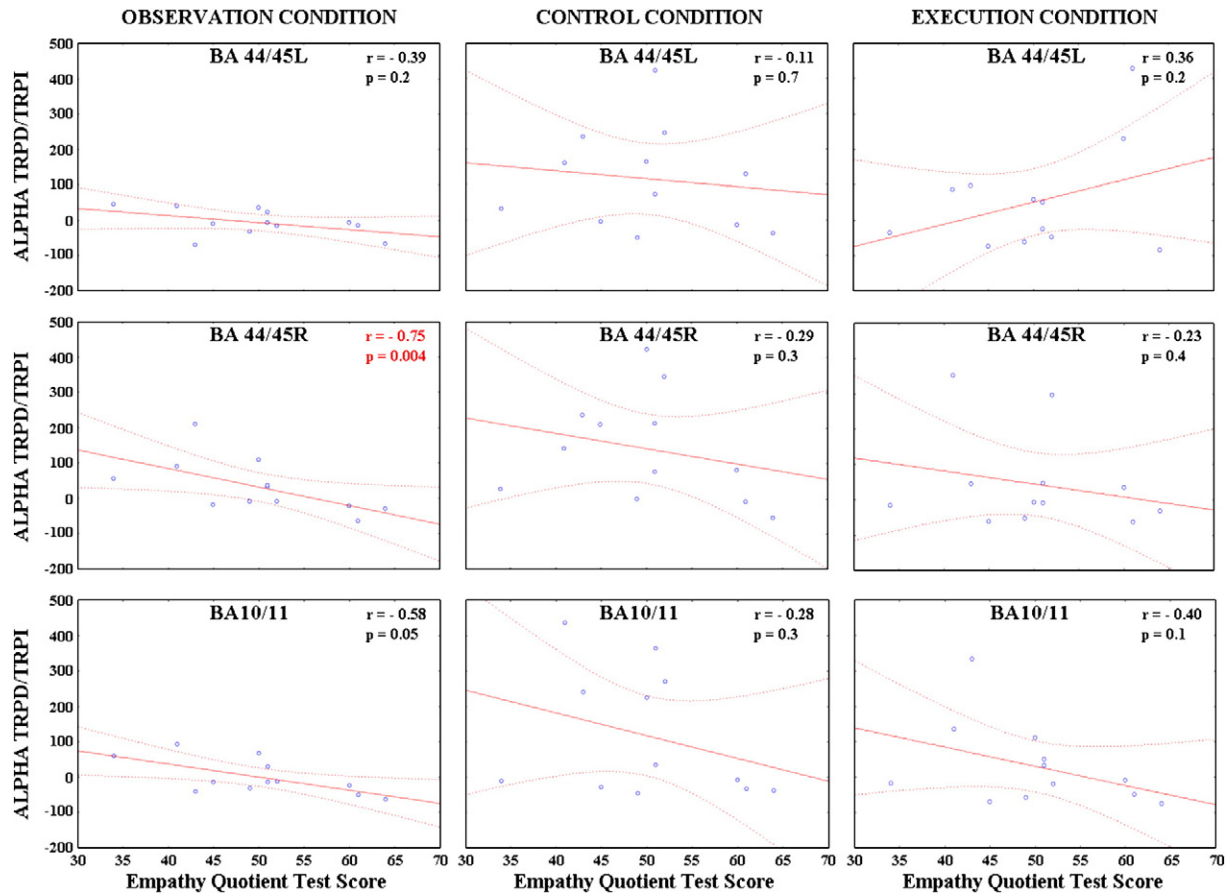
Fig. 5. Scatterplots between the EQT score and low-frequency alpha TRPD/TRPI in the OBSERVATION, EXECUTION and CONTROL conditions. The following 3 cortical regions of interest were considered: BA 44/45 of the left hemisphere, BA 44/45 of the right hemisphere, and bilateral BA 10/11.

the non-musicians). The data analysis showed neither a statistically significant difference of EQT score ($F(1,20) = 0.005$, $p = 0.9$) in the two groups (musicians: 50 ± 2.5 SE; non-musicians: 49.8 ± 2.8 SE) nor a significant correlation (Spearman correlation, two-tailed, $N = 10$, $p < 0.05$) between EQT score and low- and high-frequency alpha TRPD/TRPI in right BA 44/45 and BA 10/11 during the OBSER-VATION and CONTROL conditions ($p > 0.05$). The r and p values relative to Spearman correlation between EQT scores and alpha TRPD/TRPI in right BA 44/45 and BA 10/11 are reported in Table 6.

Discussion

In the present study, we hypothesized a relationship between individual empathy trait in musicians playing in ensemble and cortical activation modeled in the ventral-lateral and ventromedial frontal areas supposed to sub-serve "emotional" and "cognitive" empathic abilities, respectively (Dziobek et al., 2008; Frith and Singer, 2008; Shamay-Tsoory, 2011; Shamay-Tsoory et al., 2009). To this aim, we used an innovative technology to simultaneously record EEG data in quartets playing in ensemble (Babiloni et al., 2011). The EEG data were recorded while quartets of professional saxophonists played music in ensemble (EXECUTION), observed videos of their own music performance (OBSERVATION) or of a control task (CONTROL), and quietly rested in a relaxed wake state (RESTING). Empathy trait was measured by EQT score (Lawrence et al., 2004), and cortical activation was indexed by the decrement of event-related alpha power ("desynchronization") using the RESTING condition as a baseline. Results showed that OBSERVATION but not EXECUTION or CONTROL

condition induced a statistically significant correlation ($p < 0.05$, corrected) between EQT score and alpha desynchronization in right ventral-lateral frontal gyrus (BA 44/45). The higher the EQT score, the higher the cortical activation as revealed by alpha desynchronization. During the OBSERVATION condition, there was also a slight correlation trend between the EQT score and alpha desynchronization in ventromedial bilateral frontal gyrus (BA 10/11). These results, which were not observed in non-musician control subjects, were quite site and function-specific, since the correlations were found neither in control primary sensory/motor areas nor in the CONTROL conditions. Keeping in mind these data, it can be speculated that in expert musicians observing their music performance in ensemble, empathy trait predicts the cortical activation of a right ventral-lateral frontal region supposed to sub-serve "emotional" empathy (Shamay-Tsoory, 2011; Shamay-Tsoory et al., 2009).

The results of the present study extend previous EEG evidence showing a bilateral frontal-parietal alpha desynchronization during the execution and observation of voluntary movements (Babiloni et al., 1999, 2002; Cochin et al., 1998; Pfurtscheller et al., 1997; Ulloa and Pineda, 2007). They also extend previous EEG evidence showing that alpha desynchronization in bilateral ventral-lateral frontal and parietal areas characterizes professional athletes during the judgment of sporting actions performed by others (Babiloni et al., 2009, 2010), as well as dancers during the recognition of dancing performance (Orgs et al., 2008).

The present EEG results complement the following bulk of previous fMRI evidence about inferior frontal areas and observation of motor actions performed by others. During the observation of music

CORRELATION BETWEEN HIGH-FREQUENCY ALPHA TRPD/TRPI
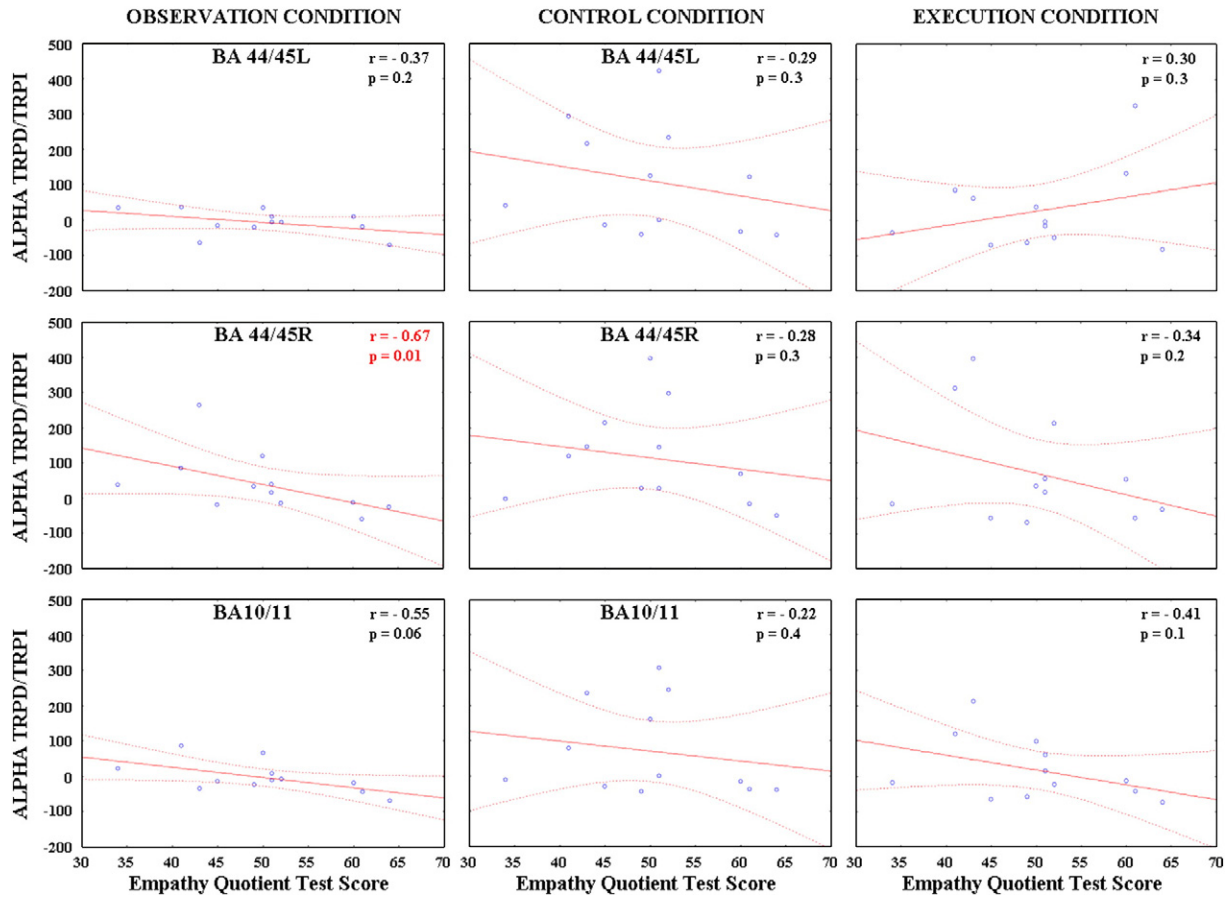## AND EMPATHY QUOTIENT TEST SCORE

Fig. 6. Scatterplots between the EQT score and high-frequency alpha TRPD/TRPI in the OBSERVATION, EXECUTION and CONTROL conditions. The following 3 cortical regions of interest were considered: BA 44/45 of the left hemisphere, BA 44/45 of the right hemisphere, and bilateral BA 10/11.

performance, lateral frontal areas were active when the observed actions were part of the musicians' motor repertoire (Buccino et al., 2004; Vogt et al., 2007). Furthermore, ventral-lateral frontal areas were active when expert dancers recognized movements that they had been trained to perform (Calvo-Merino et al., 2005; Cross et al., 2006). In contrast, the activation of premotor, parietal, and cerebellar areas was found when dancers recognized motor sequences from their own repertoire, compared to those frequently seen but never

Table 2
Spearman correlation values (r and p) between the empathy quotient test (EQT) score and low- (8–10 Hz) and high-frequency (10–12 Hz) alpha task related power decrease/increase (TRPD/TRPI) in the OBSERVATION, EXECUTION, and CONTROL conditions. The following three BAs of interest were considered: BA 44/45 left, BA 44/45 right and BA 10/11. Statistically significant correlations ($p < 0.016$) are indicated in bold.

Spearman correlation values (N = 12)			
	EXECUTION	OBSERVATION	CONTROL
EQT vs low-frequency alpha TRPD in BA 44/45 left	r = 0.36; p = 0.2	r = − 0.39; p = 0.2	r = − 0.11; p = 0.7
EQT vs high-frequency alpha TRPD in BA 44/45 left	r = 0.30; p = 0.3	r = − 0.37; p = 0.2	r = − 0.29; p = 0.3
EQT vs low-frequency alpha TRPD in BA 44/45 right	r = 0.23; p = 0.4	**r = − 0.75; p = 0.004**	r = − 0.29; p = 0.3
EQT vs high-frequency alpha TRPD in BA 44/45 right	r = − 0.24; p = 0.2	r = − 0.67; p = 0.01	r = − 0.28; p = 0.3
EQT vs low-frequency alpha TRPD in BA 10/11	r = − 0.40; p = 0.1	r = − 0.58; p = 0.05	r = − 0.28; p = 0.3
EQT vs high-frequency alpha TRPD in BA 10/11	r = − 0.41; p = 0.1	r = − 0.55; p = 0.06	r = − 0.22; p = 0.4

performed (Calvo-Merino et al., 2006). Finally, ventral-lateral frontal areas in the right hemisphere were active during pleasant music listening (Koelsch and Friederici, 2003; Koelsch et al., 2006). Keeping in mind these data, it can be speculated that BAs 44 and 45 are part of a resonant frontal-parietal "mirror" system engaged not only in the execution of aimed actions and in the understanding of actions performed by others (Gallese et al., 2004; Rizzolatti and Craighero, 2004; Rizzolatti et al., 2006), but also in musicians' "emotional" empathy triggered by the observation/listening of own music performance in concert. Noteworthy, here the observation of music performance in ensemble points to possible differences with respect to the simple "transitive" actions such as reaching, grasping and handling an object. With these simple movements, the attention of the agent or observer is well focused on a short action (i.e. seconds), and the neural correlates of the movement execution and observation can be fruitfully compared. In contrast, execution and observation of music performance in ensemble are complex experiences where the attention focus of the agent or observer can quickly change from a target to another along an event lasting several minutes, with a time-varying degree of individual involvement. Playing music in ensemble requires a constant attention to the general harmony in order not to lose the appropriate timing of entrance/exit of each instrument, as well as the level and type of emotional timber. Furthermore, the attention focus can be substantially different in the execution and observation of music performance in ensemble. In the actual music performance, musician's neural resources are supposed to be mainly focused on fine motor control taking into account multisensory feedback from the action (i.e. somatosensory, auditory, visual)

Table 3
Items associated to cognitive and emotional empathy in sub-questionnaires proposed by Lawrence et al. (2004) and Muncer and Ling (2006).

Lawrence empathy quotient test

Cognitive empathy
- I can pick up quickly if someone says one thing but means another.
- I am good at predicting how someone will feel.
- I am quick to spot when someone in a group is feeling awkward or uncomfortable.
- I can easily tell if someone else is interested or bored with what I am saying.
- I can sense if I am intruding, even if the other person doesn't tell me.
- I can tune into how someone else feels rapidly and intuitively.
- I can easily work out what another person might want to talk about.
- I can tell if someone is masking their true emotion.
- I am good at predicting what someone will do.
- Other people tell me I am good at understanding how they are feeling and what they are thinking.
- I can easily tell if someone else wants to enter a conversation.

Emotional empathy
- I really enjoy caring for other people.
- It is hard for me to see why some things upset people so much.
- If I say something that someone else is offended by, I think that that's their problem, not mine.
- I can't always see why someone should have felt offended by a remark.
- Seeing people cry doesn't really upset me.
- I get upset if I see people suffering on news programs.
- Other people often say that I am insensitive, though I don't always see why.
- I usually stay emotionally detached when watching a film.
- I tend to get emotionally involved with a friend's problems.
- I find it easy to put myself in somebody else's shoes.
- Friends usually talk to me about their problems as they say I am very understanding.

Muncer and Ling empathy quotient test
Cognitive empathy
- I am good at predicting how someone will feel.
- I am quick to spot when someone in a group is feeling awkward or uncomfortable.
- I can sense if I am intruding, even if the other person doesn't tell me.
- I can tune into how someone else feels rapidly and intuitively.
- I can easily work out what another person might want to talk about.

Emotional empathy
- I really enjoy caring for other people.
- If I say something that someone else is offended by, I think that that's their problem, not mine.
- Seeing people cry doesn't really upset me.
- I usually stay emotionally detached when watching a film.
- I tend to get emotionally involved with a friend's problems.

and inputs coming from the other musicians. In the video observation of that music performance, observer's neural resources are supposed to be mainly focused on the quartet performance as a whole, with a dynamic redirection of the attention focus based on the "dialogue" of the individual instruments. Also, there might be less interference

Table 4
Spearman correlation values (r and p) between EQT score and low- (8–10 Hz) and high- (10–12 Hz) frequency alpha TRPD/TRPI in right BA 44/45 in the OBSERVATION condition. Emotional and cognitive EQT score were evaluated using the sub-questionnaires proposed by Lawrence et al. (2004) and Muncer and Ling (2006). Statistically significant correlations (p<0.05) are indicated in bold.

Spearman correlation values (N = 12)		
	Lawrence questionnaires	Muncer and Ling questionnaires
Cognitive EQT vs low-frequency alpha TRPD in BA 44/45 right	r = 0.51; p = 0.08	r = −0.42; p = 0.17
Cognitive EQT vs high-frequency alpha TRPD in BA 44/45 right	r = −0.48; p = 0.12	r = 0.51; p = 0.08
Emotional EQT vs low-frequency alpha TRPD in BA 44/45 right	**r = −0.63; p = 0.02**	**r = −0.65; p = 0.019**
Emotional EQT vs high-frequency alpha TRPD in BA 44/45 right	r = 0.51; p = 0.08	r = 0.56; p = 0.06

Table 5
Spearman correlation values (r and p) between the EQT score and low- and high-alpha TRPD/TRPI in the OBSERVATION condition. The following BAs of interest were considered: BA 41 and BA 42 (acoustic pathway); BA 17, BA 18 and BA 19 (visual pathway); and BA 1, BA 2, BA 3, and BA 4 (somatomotor pathway).

Spearman correlation values (N = 12)	
EQT vs low-frequency alpha TRPD in BA 41	r = −0.42; p = 0.17
EQT vs high-frequency alpha TRPD in BA 41	r = −0.26; p = 0.41
EQT vs low-frequency alpha TRPD in BA 42	r = −0.42; p = 0.17
EQT vs high-frequency alpha TRPD in BA 42	r = −0.31; p = 0.31
EQT vs low-frequency alpha TRPD in BA 17	r = −0.51; p = 0.09
EQT vs high-frequency alpha TRPD in BA 17	r = −0.38; p = 0.21
EQT vs low-frequency alpha TRPD in BA 18	r = −0.47; p = 0.11
EQT vs high-frequency alpha TRPD in BA 18	r = −0.32; p = 0.30
EQT vs low-frequency alpha TRPD in BA 19	r = −0.33; p = 0.27
EQT vs high-frequency alpha TRPD in BA 19	r = −0.32; p = 0.30
EQT vs low-frequency alpha TRPD in BA 1	r = −0.54; p = 0.06
EQT vs high-frequency alpha TRPD in BA 1	r = −0.55; p = 0.06
EQT vs low-frequency alpha TRPD in BA 2	r = −0.54; p = 0.06
EQT vs high-frequency alpha TRPD in BA 2	r = −0.45; p = 0.13
EQT vs low-frequency alpha TRPD in BA 3	r = −0.52; p = 0.08
EQT vs high-frequency alpha TRPD in BA 3	r = −0.47; p = 0.11
EQT vs low-frequency alpha TRPD in BA 4	r = −0.50; p = 0.09
EQT vs high-frequency alpha TRPD in BA 4	r = −0.41; p = 0.18

among the brain networks sub-serving empathy and executive functions/sensorimotor control in the (passive) observation than in the execution condition.

The present results hint that ventral-lateral frontal areas of right hemisphere may sub-serve "emotional" empathy in expert musicians playing in ensemble (Shamay-Tsoory et al., 2003, 2004). A bulk of previous studies suggest that human right hemisphere is dominant for the recognition and expression of emotions as well as related empathic abilities (Leslie et al., 2004; Perry et al., 2001; Rankin et al., 2006; Ruby and Decety, 2003, 2004; Shamay-Tsoory et al., 2003, 2004). Brain activity increased in right frontal areas during the observation of movements having higher group-average esthetic ratings (Calvo-Merino et al., 2008). Furthermore, right frontal and parietal areas were markedly active during tasks implying the recognition of emotional face expressions (Etcoff, 1984; Gur et al., 1994; Leslie et al., 2004; Rueckert and Pawlak, 2000). On the other hand, patients with right hemisphere atrophy were characterized by remarkable deficits in empathy when compared to those with left hemisphere atrophy (Perry et al., 2001; Shamay-Tsoory et al., 2003, 2004). In this vein, the degree of empathy deficits correlated to the volume of the atrophy in the right hemisphere (Rankin et al., 2006). Furthermore, patients with focal lesions in the right hemisphere presented deficits in the recognition of emotions from facial expressions (Adolphs, 2001; Adolphs et al., 2000), as well as in the expression of intense emotions (Borod et al., 1996). Moreover, converging evidence in individuals with congenital amusia from lesion (Stewart et al., 2006) and modern structural MRI (Hyde et al., 2006, 2007; Mandell et al., 2007) studies

Table 6
Spearman correlation values (r and p) between EQT score and low- and high-frequency alpha TRPD/TRPI in non-musician control group for the OBSERVATION and CONTROL conditions. The following BAs of interest were considered: BA 44/45 right and BA 10/11.

Spearman correlation values (N = 10)		
	OBSERVATION	CONTROL
EQT vs low-frequency alpha TRPD in BA 44/45 right	r = −0.34; p = 0.33	r = −0.31; p = 0.38
EQT vs high-frequency alpha TRPD in BA 44/45 right	r = 0.03; p = 0.93	r = −0.48; p = 0.20
EQT vs low-frequency alpha TRPD in BA 10/11	r = −0.45; p = 0.18	r = −0.32; p = 0.38
EQT vs high-frequency alpha TRPD in BA 10/11	r = −0.53; p = 0.11	r = −0.54; p = 0.10

points to a network of temporal and frontal lobe areas, especially in the right hemisphere, as the critical brain substrate of amusia. There is also evidence showing more severe amusia and alteration of magnetic mismatch negativity in patients with focal lesions in the right than left hemisphere (Särkämö et al., 2010), Finally, fMRI evidence shows that individuals with congenital amusia are characterized by a reduced activity in the right inferior frontal gyrus to small pitch changes, whereas the activity in their left and right auditory cortex is comparable to control subjects (Binder et al., 2004). Of note, it has been proposed that the human "mirror" system is specialized to the left hemisphere as a neural basis for language evolution (Corballis, 2002; Iacoboni, 2005; Rizzolatti and Arbib, 1998). This idea is essentially based on the "mirror" features of Broca's area, namely a predominant speech area in left BAs 44/45. However, this claim has not been confirmed when properly tested by fMRI (Aziz-Zadeh et al., 2006). In this theoretical framework, the present findings suggest that during the observation of own music performance played in ensemble, ventral frontal regions especially of right hemisphere may be related to musicians' empathy trait.

In the present study, just a statistical correlation trend was found between the trait of empathy and activation of bilateral BA 10/11 during the OBSERVATION condition. Noteworthy, we could not disentangle the sources of alpha rhythms in right (maybe dominant for "perspective-taking" empathy; Ruby and Decety, 2003, 2004) and left BA 10/11, due to the low spatial resolution of the EEG techniques used (i.e. centimeters). Therefore, a definitive conclusion about the role of BA 10/11 needs the implementation of new psychometric tests able to disentangle the measurement of "emotional" and "cognitive" empathic abilities, as well as the use of high-resolution EEG or magnetoencephalographic techniques to better disentangle alpha desynchronization in the medial aspects of the left and right ventral frontal areas.

The present results hint that the modulation of ventral-lateral frontal alpha rhythms (about 8–12 Hz) represents one of the physiological mechanisms at the basis of "emotional" empathic abilities in musicians playing in ensemble. These rhythms reflect the functional modes of thalamo-cortical and cortico-cortical loops that facilitate/inhibit the transmission and retrieval of both sensorimotor and cognitive information into the brain (Brunia, 1999; Pfurtscheller and Lopes da Silva, 1999; Steriade and Llinas, 1988). Specifically, low-frequency alpha rhythms (about 8–10 Hz) would sub-serve subject's global attentive readiness, whereas high-frequency alpha rhythms (about 10–12 Hz) would reflect the task-related oscillation of specific neural systems for the elaboration of task-specific information (Klimesch, 1996, 1999; Klimesch et al., 1998). Based on this theoretical framework, it can be speculated that desynchronization of ventral-lateral frontal alpha rhythms underlines global attention and "emotional" empathic processes in musicians observing their own performance in ensemble.

At the present early stage of the research, we can just speculate that the present results on alpha desynchronization and empathy specifically reflect social communication and cooperation in playing music in ensemble. Indeed, empathy intrinsically emerges as a brain function to represent the intentions, feelings, and emotions of the others as a basis for sharing the perception of the social context and for framing the social communication and interaction. Playing music in ensemble is grounded upon parallel individual feelings, emotions and actions that refer to a common representation of the music piece and of the specific actual contribution of the other musicians in the general plan of the music performance. In this framework, empathy would contribute to the update on the feelings, emotions and intentions of the other musicians. However, it cannot be excluded that a similar relationship between alpha desynchronization and empathy would be found in saxophonists observing themselves playing solo music. Future studies should include a control condition with a solo performance for comparison.

In conclusion, we used a new EEG technology (Babiloni et al., 2011) to explore the relationship between individual empathy trait and musicians' brains in concert, with a focus on prefrontal areas supposed to sub-serve empathic abilities. Results showed a significant correlation between empathy trait score and alpha desynchronization (indexing cortical activation) modelled in right ventral-lateral frontal gyrus (BA 44/45) during the observation of music performance played in ensemble. The higher the empathy trait score, the higher the alpha desynchronization. These results suggest that alpha rhythms of right ventral-lateral frontal regions (BA 44/45) reflect "emotional" empathy in musicians observing own music performance in concert. Since we cannot exclude a similar relationship between alpha desynchronization and empathy in saxophonists observing themselves playing solo music, a safe conclusion is that the present results refer to observing music performance.

References

Adolphs, R., 2001. The neurobiology of social cognition. Curr. Opin. Neurobiol. 11 (2), 231–239.

Adolphs, R., Damasio, H., Tranel, D., Cooper, G., Damasio, A.R., 2000. A role for somatosensory cortices in the visual recognition of emotion as revealed by three-dimensional lesion mapping. J. Neurosci. 20 (7), 2683–2690.

Aziz-Zadeh, L., Koski, L., Zaidel, E., Mazziotta, J., Iacoboni, M., 2006. Lateralization of the human mirror neuron system. J. Neurosci. 26 (11), 2964–2970.

Babiloni, C., Carducci, F., Cincotti, F., Rossini, P.M., Neuper, C., Pfurtscheller, G., Babiloni, F., 1999. Human movement-related potentials vs desynchronization of EEG alpha rhythm: a high-resolution EEG study. Neuroimage 10 (6), 658–665.

Babiloni, C., Babiloni, F., Carducci, F., Cincotti, F., Cocozza, G., Del Percio, C., Moretti, D.V., Rossini, P.M., 2002. Human cortical electroencephalography (EEG) rhythms during the observation of simple aimless movements: a high-resolution EEG study. Neuroimage 17 (2), 559–572.

Babiloni, C., Del Percio, C., Rossini, P.M., Marzano, N., Iacoboni, M., Infarinato, F., Lizio, R., Piazza, M., Pirritano, M., Berlutti, G., Cibelli, G., Eusebi, F., 2009. Judgment of actions in experts: a high-resolution EEG study in elite athletes. Neuroimage 45 (2), 512–521.

Babiloni, C., Marzano, N., Infarinato, F., Iacoboni, M., Rizza, G., Aschieri, P., Cibelli, G., Soricelli, A., Eusebi, F., Del Percio, C., 2010. "Neural efficiency" of experts' brain during judgment of actions: a high-resolution EEG study in elite and amateur karate athletes. Behav. Brain Res. 207 (2), 466–475.

Babiloni, C., Vecchio, F., Infarinato, F., Buffo, P., Marzano, N., Spada, D., Rossi, S., Bruni, I., Rossini, P.M., Perani, D., 2011. Simultaneous recording of electroencephalographic data in musicians playing in ensemble. Cortex 47 (9), 1082–1090 Epub 2011 May 19.

Bangert, M., Altenmüller, E.O., 2003. Mapping perception to action in piano practice: a longitudinal DC-EEG study. BMC Neurosci. 4, 26.

Baron-Cohen, S., Wheelwright, S., 2004. The empathy quotient: an investigation of adults with Asperger syndrome or high functioning autism and normal sex differences. J. Autism Dev. Disord. 34, 163–175.

Berridge, K.C., Robinson, T.E., 2003. Parsing reward. Trends Neurosci. 26, 507–513.

Binder, J.R., Liebenthal, E., Possing, E.T., Medler, D.A., Ward, B.D., 2004. Neural correlates of sensory and decision processes in auditory object identification. Nat. Neurosci. 7, 295–301.

Blood, A.J., Zatorre, R.J., Bermudez, P., Evans, A.C., 1999. Emotional responses to pleasant and unpleasant music correlate with activity in paralimbic brain regions. Nat. Neurosci. 2, 382–387.

Borod, J.C., Rorie, K.D., Haywood, C.S., Andelman, F., Obler, L.K., Welkowitz, J., Bloom, R.L., Tweedy, J.R., 1996. Hemispheric specialization for discourse reports of emotional experiences: relationships to demographic, neurological, and perceptual variables. Neuropsychologia 34 (5), 351–359.

Brunia, C.H., 1999. Neural aspects of anticipatory behavior. Acta Psychol. (Amst) 101 (2–3), 213–242.

Buccino, G., Vogt, S., Ritzl, A., Fink, G.R., Zilles, K., Freund, H.J., Rizzolatti, G., 2004. Neural circuits underlying imitation learning of hand actions: an event-related fMRI study. Neuron 42 (2), 323–334.

Calvo-Merino, B., Glaser, D.E., Grèzes, J., Passingham, R.E., Haggard, P., 2005. Action observation and acquired motor skills: an fMRI study with expert dancers. Cereb. Cortex 15 (8), 1243–1249.

Calvo-Merino, B., Grèzes, J., Glaser, D.E., Passingham, R.E., Haggard, P., 2006. Seeing or doing? Influence of visual and motor familiarity in action observation. Curr. Biol. 16 (19), 1905–1910.

Calvo-Merino, B., Jola, C., Glaser, D.E., Haggard, P., 2008. Towards a sensorimotor aesthetics of performing art. Conscious. Cogn. 17 (3), 911–922 Epub 2008 Jan 22.

Chapin, H., Jantzen, K., Kelso, J.A., Steinberg, F., Large, E., 2010. Dynamic emotional and neural responses to music depend on performance expression and listener experience. PLoS One 5 (12), e13812.

Cochin, S., Barthelemy, C., Lejeune, B., Roux, S., Martineau, J., 1998. Perception of motion and qEEG activity in human adults. Electroencephalogr. Clin. Neurophysiol. 107 (4), 287–295.

Corballis, M.C., 2002. From Hand to Mouth: The Origins of Language. Princeton UP, New Jersey.

Cross, E.S., Hamilton, A.F., Grafton, S.T., 2006. Building a motor simulation de novo: observation of dance by dancers. Neuroimage 31 (3), 1257–1267.

de Waal, F.B., 2008. Putting the altruism back into altruism: the evolution of empathy. Annu. Rev. Psychol. 59, 279–300.

Decety, J., Jackson, P.L., 2004. The functional architecture of human empathy. Behav. Cogn. Neurosci. Rev. 3 (2), 71–100.

Dziobek, I., Rogers, K., Fleck, S., Bahnemann, M., Heekeren, H.R., Wolf, O.T., et al., 2008. Dissociation of cognitive and emotional empathy in adults with Asperger syndrome using the Multifaceted Empathy Test (MET). J. Autism Dev. Disord. 38, 464–473.

Etcoff, N.L., 1984. Selective attention to facial identity and facial emotion. Neuropsychologia 22 (3), 281–295.

Foster, N.E., Zatorre, R.J., 2010a. Cortical structure predicts success in performing musical transformation judgments. Neuroimage 53 (1), 26–36.

Foster, N.E., Zatorre, R.J., 2010b. A role for the intraparietal sulcus in transforming musical pitch information. Cereb. Cortex 20 (6), 1350–1359.

Frith, C.D., Singer, T., 2008. The role of social cognition in decision making. Philos. R. Soc. Lond. B Biol. Sci. 363, 3875–3886.

Gallese, V., 2003. The roots of empathy: the shared manifold hypothesis and the neural basis of intersubjectivity. Psychopathology 36 (4), 171–180.

Gallese, V., Keysers, C., Rizzolatti, G., 2004. A unifying view of the basis of social cognition. Trends Cogn. Sci. 8 (9), 396–403.

Gur, R.C., Skolnick, B.E., Gur, R.E., 1994. Effects of emotional discrimination tasks on cerebral blood flow: regional activation and its relation to performance. Brain Cogn. 25 (2), 271–286.

Hyde, K.L., Zatorre, R.J., Griffiths, T.D., Lerch, J.P., Peretz, I., 2006. Morphometry of the amusic brain: a two-site study. Brain 129, 2562–2570.

Hyde, K.L., Lerch, J.P., Zatorre, R.J., Griffiths, T.D., Evans, A.C., Peretz, I., 2007. Cortical thickness in congenital amusia: when less is better than more. J. Neurosci. 27, 13028–13032.

Iacoboni, M., 2005. Understanding others: imitation, language, empathy. In: Hurley, S., Chater, N. (Eds.), Perspectives on Imitation: Imitation in Animals. MIT, Cambridge, MA.

Kamiyama, K., Katahira, K., Abla, D., Hori, K., Okanoya, K., 2010. Music playing and memory trace: evidence from event-related potentials. Neurosci. Res. 67 (4), 334–340 Epub 2010 Apr 18.

Katahira, K., Abla, D., Masuda, S., Okanoya, K., 2008. Feedback-based error monitoring processes during musical performance: an ERP study. Neurosci. Res. 61 (1), 120–128 Epub 2008 Feb 14.

Klein, M.E., Zatorre, R.J., 2011. A role for the right superior temporal sulcus in categorical representation of musical chords. Neuropsychologia 49 (5), 878–887.

Klimesch, W., 1996. Memory processes, brain oscillations and EEG synchronization. Int. J. Psychophysiol. 24 (1–2), 61–100.

Klimesch, W., 1999. EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. Brain Res. Brain Res. Rev. 29 (2–3), 169–195.

Klimesch, W., Doppelmayr, M., Russegger, H., Pachinger, T., Schwaiger, J., 1998. Induced alpha band power changes in the human EEG and attention. Neurosci. Lett. 244 (2), 73–76.

Knutson, B., Adams, C.M., Fong, G.W., Hommer, D., 2001. Anticipation of increasing monetary reward selectively recruits nucleus accumbens. J. Neurosci. 21, 159.

Koelsch, S., 2010. Towards a neural basis of music-evoked emotions. Trends Cogn. Sci. 14 (3), 131–137.

Koelsch, S., 2011. Toward a neural basis of music perception — a review and updated model. Front. Psychol. 2, 110.

Koelsch, S., Friederici, A.D., 2003. Toward the neural basis of processing structure in music. Comparative results of different neurophysiological investigation methods. Ann. N. Y. Acad. Sci. 999, 15–28.

Koelsch, S., Fritz, T.V., Cramon, D.Y., Müller, K., Friederici, A.D., 2006. Investigating emotion with music: an fMRI study. Hum. Brain Mapp. 27 (3), 239–250.

Lawrence, E.J., Shaw, P., Baker, D., Baron-Cohen, S., David, A.S., 2004. Measuring empathy: reliability and validity of the empathy quotient. Psychol. Med. 34 (5), 911–919.

Leiberg, S., Anders, S., 2006. The multiple facets of empathy: a survey of theory and evidence. Prog. Brain Res. 156, 419–440.

Leman, M., 2007. Embodied Music Cognition and Mediation Technology. The MIT-Press, Cambridge, MA.

Leslie, K.R., Johnson-Frey, S.H., Grafton, S.T., 2004. Functional imaging of face and hand imitation: towards a motor theory of empathy. Neuroimage 21 (2), 601–607.

Maidhof, C., Rieger, M., Prinz, W., Koelsch, S., 2009. Nobody is perfect: ERP effects prior to performance errors in musicians indicate fast monitoring processes. PLoS One 4 (4), e5032.

Mandell, J., Schulze, K., Schlaug, G., 2007. Congenital amusia: an auditory-motor feedback disorder? Restor. Neurol. Neurosci. 25, 323–334.

Manganotti, P., Gerloff, C., Toro, C., Katsuta, H., Sadato, N., Zhuang, P., Leocani, L., Hallett, M., 1998. Task-related coherence and task-related spectral power changes during sequential finger movements. Electroencephalogr. Clin. Neurophysiol. 109 (1), 50–62.

Mitchell, J.P., 2009. Inferences about mental states. Philos. Trans. R. Soc. Lond. B Biol. Sci. 364, 1309–1316.

Moretti, D.V., Babiloni, F., Carducci, F., Cincotti, F., Remondini, E., Rossini, P.M., Salinari, S., Babiloni, C., 2003. Computerized processing of EEG–EOG–EMG artifacts for multi-centric studies in EEG oscillations and event-related potentials. Int. J. Psychophysiol. 47 (3), 199–216.

Muncer, S.J., Ling, J., 2006. Psychometric analysis of the Empathy Quotient (EQ) scale. Pers. Individ. Differ. 40, 1111–1119.

Nummenmaa, L., Hirvonen, J., Parkkola, R., Hietanen, J.K., 2008. Is emotional contagion special? An fMRI study on neural systems for affective and cognitive empathy. Neuroimage 43, 571–580.

Orgs, G., Dombrowski, J.H., Heil, M., Jansen-Osmann, P., 2008. Expertise in dance modulates alpha/beta event-related desynchronization during action observation. Eur. J. Neurosci. 27 (12), 3380–3384.

Pascual-Marqui, R.D., 2002. Standardized low-resolution brain electromagnetic tomography (sLORETA): technical details. Methods Find. Exp. Clin. Pharmacol. 24 (Suppl. D), 5–12.

Peretz, I., Zatorre, R.J., 2005. Brain organization for music processing. Annu. Rev. Psychol. 56, 89–114 Review.

Peretz, I., Gosselin, N., Belin, P., Zatorre, R.J., Plailly, J., Tillmann, B., 2009. Music lexical networks: the cortical organization of music recognition. Ann. N. Y. Acad. Sci. 1169, 256–265.

Perry, R.J., Rosen, H.R., Kramer, J.H., Beer, J.S., Levenson, R.L., Miller, B.L., 2001. Hemispheric dominance for emotions, empathy and social behaviour: evidence from right and left handers with frontotemporal dementia. Neurocase 7 (2), 145–160.

Pfurtscheller, G., Aranibar, A., 1979. Evaluation of event-related desynchronization (ERD) preceding and following voluntary self-paced movement. Electroencephalogr. Clin. Neurophysiol. 46 (2), 138–146.

Pfurtscheller, G., Lopes da Silva, F.H., 1999. Event-related EEG/MEG synchronization and desynchronization: basic principles. Clin. Neurophysiol. 110 (11), 1842–1857.

Pfurtscheller, G., Neuper, C., 1994. Event-related synchronization of mu rhythm in the EEG over the cortical hand area in man. Neurosci. Lett. 174 (1), 93–96.

Pfurtscheller, G., Neuper, C., Flotzinger, D., Pregenzer, M., 1997. EEG-based discrimination between imagination of right and left hand movement. Electroencephalogr. Clin. Neurophysiol. 103 (6), 642–651.

Phan, K.L., Wager, T., Taylor, S.F., Liberzon, I., 2002. Functional neuroanatomy of emotion: a meta-analysis of emotion activation studies in PET and fMRI. Neuroimage 16, 331–348.

Preston, S.D., de Waal, F.B., 2002. Empathy: its ultimate and proximate bases. Behav. Brain Sci. 25 (1), 1–20 discussion 20–71.

Rankin, K.P., Gorno-Tempini, M.L., Allison, S.C., Stanley, C.M., Glenn, S., Weiner, M.W., Miller, B.L., 2006. Structural anatomy of empathy in neurodegenerative disease. Brain 129 (Pt 11), 2945–2956.

Rizzolatti, G., Arbib, M.A., 1998. Language within our grasp. Trends Neurosci. 21, 188–194.

Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. Annu. Rev. Neurosci. 27, 169–192 Review.

Rizzolatti, G., Fogassi, L., Gallese, V., 2006. Mirrors of the mind. Sci. Am. 295 (5), 54–61 (Nov).

Royet, J.P., Zald, D., Versace, R., Costes, N., Lavenne, F., et al., 2000. Emotional responses to pleasant and unpleasant olfactory, visual, and auditory stimuli: a positron emission tomography study. J. Neurosci. 20, 7752–7759.

Ruby, P., Decety, J., 2003. What you believe versus what you think they believe: a neuroimaging study of conceptual perspective-taking. Eur. J. Neurosci. 17 (11), 2475–2480.

Ruby, P., Decety, J., 2004. How would you feel versus how do you think she would feel? A neuroimaging study of perspective-taking with social emotions. J. Cogn. Neurosci. 16 (6), 988–999.

Rueckert, L., Pawlak, T., 2000. Individual differences in cognitive performance due to right hemisphere arousal. Laterality 5 (1), 77–89.

Sammler, D., Koelsch, S., Ball, T., Brandt, A., Elger, C.E., Friederici, A.D., Grigutsch, M., Huppertz, H.J., Knösche, T.R., Wellmer, J., Widman, G., Schulze-Bonhage, A., 2009. Overlap of musical and linguistic syntax processing: intracranial ERP evidence. Ann. N. Y. Acad. Sci. 1169, 494–498.

Sammler, D., Koelsch, S., Friederici, A.D., 2011. Are left fronto-temporal brain areas a prerequisite for normal music-syntactic processing? Cortex 47 (6), 659–673 Epub 2010 Jun 8.

Särkämö, T., Tervaniemi, M., Soinila, S., Autti, T., Silvennoinen, H.M., Laine, M., Hietanen, M., Pihko, E., 2010. Auditory and cognitive deficits associated with acquired amusia after stroke: a magnetoencephalography and neuropsychological follow-up study. PLoS One 5 (12), e15157.

Schönwiesner, M., Zatorre, R.J., 2008. Depth electrode recordings show double dissociation between pitch processing in lateral Heschl's gyrus and sound onset processing in medial Heschl's gyrus. Exp. Brain Res. 187 (1), 97–105.

Schulte-Ruther, M., Markowitsch, H.J., Fink, G.R., Piefke, M., 2007. Mirror neuron and theory of mind mechanisms involved in face-to-face interactions: a functional magnetic resonance imaging approach to empathy. J. Cogn. Neurosci. 19, 1354–1372.

Shamay-Tsoory, S.G., 2011. The neural bases for empathy. Neuroscientist 17 (1), 18–24.

Shamay-Tsoory, S.G., Tomer, R., Berger, B.D., Aharon-Peretz, J., 2003. Characterization of empathy deficits following prefrontal brain damage: the role of the right ventromedial prefrontal cortex. J. Cogn. Neurosci. 15 (3), 324–337.

Shamay-Tsoory, S.G., Tomer, R., Goldsher, D., Berger, B.D., Aharon-Peretz, J., 2004. Impairment in cognitive and affective empathy in patients with brain lesions: anatomical and cognitive correlates. J. Clin. Exp. Neuropsychol. 26 (8), 1113–1127.

Shamay-Tsoory, S.G., Aharon-Peretz, J., Perry, D., 2009. Two systems for empathy: a double dissociation between emotional and cognitive empathy in inferior frontal gyrus versus ventromedial prefrontal lesions. Brain 132 (Pt 3), 617–627.

Steriade, M., Llinas, R.R., 1988. The functional states of the thalamus and the associated neuronal interplay. Physiol. Rev. 68 (3), 649–742.

Stewart, L., von Kriegstein, K., Warren, J.D., Griffiths, T.D., 2006. Music and the brain: disorders of musical listening. Brain 129, 2533–2553.

Talairach, J., Tournoux, P., 1988. Co-Planar Stereotaxic Atlas of the Human Brain: 3-Dimensional Proportional System — An Approach to Cerebral Imaging. Thieme Medical Publishers, New York.

Ulloa, E.R., Pineda, J.A., 2007. Recognition of point-light biological motion: mu rhythms and mirror neuron activity. Behav. Brain Res. 183 (2), 188–194.

Vogt, S., Buccino, G., Wohlschläger, A.M., Canessa, N., Shah, N.J., Zilles, K., Eickhoff, S.B., Freund, H.J., Rizzolatti, G., Fink, G.R., 2007. Prefrontal involvement in imitation learning of hand actions: effects of practice and expertise. Neuroimage 37 (4), 1371–1383.

Zatorre, R.J., Belin, P., 2001. Spectral and temporal processing in human auditory cortex. Cereb. Cortex 11 (10), 946–953.

Zatorre, R.J., Halpern, A.R., Bouffard, M., 2010. Mental reversal of imagined melodies: a role for the posterior parietal cortex. J. Cogn. Neurosci. 22 (4), 775–789.