

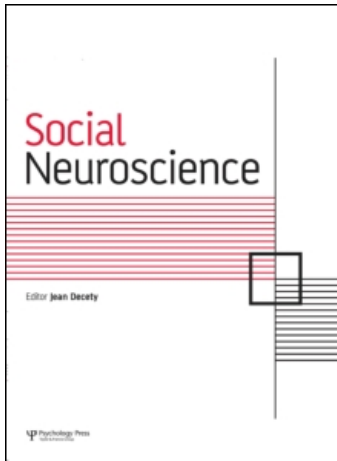
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Access details: Access Details: [subscription number 919316992]

Publisher Psychology Press

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## Social Neuroscience

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title~content=t741771143>

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First published on: 17 February 2010

**To cite this Article** Perry, Anat , Troje, Nikolaus F. and Bentin, Shlomo(2010) 'Exploring motor system contributions to the perception of social information: Evidence from EEG activity in the mu/alpha frequency range', *Social Neuroscience*, 5: 3, 272 – 284, First published on: 17 February 2010 (iFirst)

**To link to this Article:** DOI: 10.1080/17470910903395767

**URL:** <http://dx.doi.org/10.1080/17470910903395767>

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# Exploring motor system contributions to the perception of social information: Evidence from EEG activity in the mu/alpha frequency range

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Putative contributions of a human mirror neuron system (hMNS) to the perception of social information have been assessed by measuring the suppression of EEG oscillations in the mu/alpha (8–12 Hz), beta (15–25 Hz) and low-gamma (25–25 Hz) ranges while participants processed social information revealed by point-light displays of human motion. Identical dynamic displays were presented and participants were instructed to distinguish the intention, the emotion, or the gender of a moving image of a person, while they performed an adapted odd-ball task. Relative to a baseline presenting a nonbiological but meaningful motion display, all three biological motion conditions reduced the EEG amplitude in the mu/alpha and beta ranges, but not in the low-gamma range. Suppression was larger in the intention than in the emotion and gender conditions, with no difference between the latter two. Moreover, the suppression in the intention condition was negatively correlated with an accepted measure of empathy (EQ), revealing that participants high in empathy scores manifested less suppression. For intention and emotion the suppression was larger at occipital than at central sites, suggesting that factors other than motor system were in play while processing social information embedded in the motion of point-light displays.

**Keywords:** Mu rhythms; Alpha; Biological motion; Motor system; Social skills.

## INTRODUCTION

The unparalleled social skills characterizing the human race are based to a large extent on the ability developed (both evolutionarily and ontogenetically) to gain implicit and/or explicit knowledge of our own minds as well as those of others (for a recent discussion and review see Adolphs, 2009; Frith & Frith, 2007). Humans are normally aware of their own mental states such as beliefs, intents, desires,

pretence, knowledge, etc., and are able to understand that others may also have beliefs, desires and intentions that can be similar or different from one's own. The ability to understand the state of mind of others has been labeled "theory of mind" (ToM; Leslie, 1987; Premack & Woodruff, 1978). Although there are numerous studies describing the neural substrates of human social skills in general and ToM in particular (for reviews see Adolphs, 2003; Fiske & Taylor, 2008; Lieberman, 2007; Pfeifer, Lieberman, &

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We thank Dori Bar-On for skillful assistance in running the experiment, NSERC for funding NFT, and the "Hoffman Leadership and Responsibility" fellowship program, at the Hebrew University, for partially funding AP.

Dapretto, 2007), the neural mechanism that enables humans to gain such knowledge and the nature of the information that feeds into it are still under debate.

An interesting view, which stems from the social-cognitive simulation theory (Carruthers & Smith, 1996; Davis & Stone, 1995), is that the information on which ToM skills are based is not sensory but rather motor in nature (e.g. Jackson & Decety, 2004; Rizzolatti, Fogassi, & Gallese, 2001). This idea fits with the ideomotor framework of action (Prinz, 2005) which assumes a common representational format for perception and action emphasizing the intended goals and the motor plans that are necessary to obtain them (e.g. De Vignemont & Haggard, 2008; for a recent review see Iacoboni, 2009). Simulating the actions<sup>1</sup> performed by others and associating the simulated action with motor representations of our own internal states, motivations, and intentions is hypothesized to be a general mechanism whereby we are able to generate knowledge of other minds (Agnew, Bhakoo, & Puri, 2007; Keysers & Perrett, 2004; Niedenthal, Barsalou, Winkielman, Krauth-Gruber, & Ric, 2005).

The most conspicuous evidence for biological feasibility of the simulation theory is the seminal discovery of the mirror neuron system (MNS) in the monkey, a particular class of visuo-motor neurons that discharge both when the monkey does a particular goal-directed action and when it observes another individual (monkey or human) doing a similar action (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996a). The neurophysiological properties of the MNS and its putatively important role in cognition and action raised the question of whether a similar mechanism exists in humans and, assuming that it does, what role this network plays. Not surprisingly, researchers proposed that the MNS may have evolved in humans into a more complex network, expanding its role to form the basis for imitation (Jeannerod, 1994; Rizzolatti et al., 2001), language development (Rizzolatti & Arbib, 1998; Rizzolatti & Craighero, 2004) and even accounting for higher-level social skills such as understanding others' intentions or emotions (Gallese, 2001; Gallese & Goldman, 1998).

In the past decade, the alleged human MNS (hMNS) has been extensively investigated through neuroimaging studies (e.g. Buccino et al., 2001; Decety, Chaminade, Grezes, & Meltzoff, 2002; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Grezes,

Armony, Rowe, & Passingham, 2003; Grezes, Costes, & Decety, 1998; Iacoboni & Dapretto, 2006; Iacoboni et al., 1999; Rizzolatti et al., 1996b). Many of these studies suggested that a mirror-like system might, indeed, contribute to the understanding of social behavior (e.g. Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Happe et al., 1996; Leslie, Johnson-Frey, & Grafton, 2004; Singer et al., 2004; Wicker et al., 2003; for a recent review see Carrington & Bailey, 2009). Putative evidence for an hMNS has also been found using electrophysiological measures such as modulating motor evoked potentials elicited by TMS (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995), intracranial single-unit recordings (Mukamel, Iacoboni, & Fried, 2008), magnetoencephalography (MEG; Hari, Salmelin, Makela, Salenius, & Helle, 1997) and electroencephalography (EEG). The latter line of research focused particularly on the modulation of EEG oscillations within the range of 8–12 Hz, although modulations of higher-frequency ranges have also been reported. Given their presumed sources in the somato-motor cortex, these oscillations were labeled Rolandic or “mu” rhythms (for a review see Pineda, 2005).

Like the “alpha block” (Berger, 1929; see also, for example, Goodman, Beatty, & Mulholland, 1980), the suppression of mu rhythms is considered to reflect event-related desynchronization (ERD) of the EEG induced by an enhancement of neural activity in somato-motor regions and prefrontal cortex leading to asynchronous neural firing (Kuhlman, 1978). It should be noted, however, that, although in the same frequency range, the modulation of mu rhythms differs from that of the alpha waves on anatomical and functional dimensions. The modulation of mu is usually seen in more anterior areas (largely recorded over the sensory-motor cortex) compared to the more posterior (parieto-occipital) distribution, which is characteristic to the modulation of alpha (Kuhlman, 1978; Pfurtscheller, 1989). Moreover, in contrast to alpha, mu rhythms are not modulated primarily by visual stimulation, but rather are desynchronized and their power attenuated when engaging in motor activity (Gastaut, 1952), and, crucially, also while *observing actions* executed by someone else (Cochin, Barthelemy, & Martineau, 1998; Cochin, Barthelemy, Roux, & Martineau, 1999; Cohen-Seat, Gastaut, Faure, & Heuyer, 1954; Gastaut & Bert, 1954; Muthukumaraswamy, Johnson, & McNair, 2004). Moreover there are data suggesting that even imagining human actions is sufficient to desynchronize the mu rhythm (Pfurtscheller, Brunner, Schlogl, & Lopes Da Silva, 2006; Pineda, Allison, & Vankov, 2000). Similar findings were shown in MEG (e.g. Cheng et al., 2008), although other MEG studies also

<sup>1</sup>Our definition of “action” in the present context is sufficiently broad to include anything from a particular body posture to the dynamics involved in facial expressions and whole body movements.

report desynchronization in a higher frequency range (“high-mu” or beta) and even higher (15–35 Hz; Hari & Salmelin, 1997; Muthukumaraswamy & Singh, 2008). These characteristics led authors to link the suppression of the mu rhythms amplitude with a human mirror system.

Putative evidence for a direct association between mu rhythms and social skills came initially from mu studies in individuals with autistic spectrum disorders (ASD) who, as a group, have reduced social abilities compared to typically developed individuals. These studies revealed that whereas ASD individuals showed normal mu suppression while self-performing hand movements, in contrast to typically developed individuals they showed no suppression when passively viewing someone else perform the same movements (Martineau, Schmitz, Assaiante, Blanc, & Barthelemy, 2004; Oberman et al., 2005; Oberman, Ramachandran, & Pineda, 2008). Other studies linked mu suppression to social factors in typically developed participants (Oberman, Pineda, & Ramachandran, 2007). More recently, Pineda & Hecht (2009) examined the link between mu rhythms and ToM. They found a positive correlation between the amount of mu suppression and accuracy in tasks that were assumed to tap social skills (assessed in matching isolated eyes by emotion, race, and gender) but not when the task required explicit/declarative reasoning (assessed using cartoon-based scenarios). Whereas, arguably, these data support the simulation theory as a basis for affective ToM skills, they also suggest that additional mechanisms are needed to make mental attributions of beliefs. Moreover, the drastically different stimuli used in that study for testing “social perceptual” as opposed to “social cognitive” skills might have influenced EEG suppression for reasons other than those assumed by the authors.

A pervasive problem in most of the above-cited studies is stimulus control. The complex dynamic stimuli that are used in different experimental conditions usually differ along many dimensions in addition to the one that is studied. One way to control for stimulus differences is to use simplified versions of biological motion such as that induced by point-light displays (Johansson, 1973). Biological motion contains information about all sorts of socially relevant information about an agent. It reveals an agent’s actions and intentions, and it signals sex, emotions, and personality traits (Barclay, Cutting, & Kozlowski, 1978; Blakemore & Decety, 2001; Dittrich, Troscianko, Lea, & Morgan, 1996; Mather & Murdoch, 1994; Pollick, Paterson, Bruderlin, & Sanford, 2001; Runeson, 1994; Troje, 2002a, 2002b). On the other

hand, these stimuli can be controlled in a parametric, principled way, thus manipulating the contents and amount of information they contain (Troje, 2002a, 2002b, 2008).

Using fMRI, Saygin, Wilson, Hagler, Bates, & Sereno (2004) were the first to report point-light-associated activation of the premotor cortex (see also Lestou, Pollick, & Kourtzi, 2008). These authors compared the blood-oxygen-level dependent (BOLD) signal elicited by point-light displays revealing biological motion, and nonbiological motion (which was produced by scrambling the pattern of the same point-light stimuli) with stationary point-light displays. These comparisons demonstrated activation of the frontal cortex in response to biological motion but not while the point-light displays were scrambled. Ulloa and Pineda (2007) found a similar pattern by recording EEG. The mu rhythms were suppressed during the observation of point-light induced biological motion but not during observation of motion of scrambled point-light displays. To the extent that mu rhythms reveal the activity of a motor neural network, these findings suggest that the motor system of the observer is recruited “filling in” these simplified displays to recover object information from sparse input and, therefore, may assist in action understanding.

In the present study we used point-light displays of human biological motion to investigate the relationship between mu suppression and the processing of different social aspects revealed by the moving images. Identical stimuli were used while participants were instructed to distinguish the intention, the emotion, or the gender of a moving image. The validity of the stimuli as representing the expected information was examined in a pilot study using behavioral measures. We hypothesized that oscillations in the mu and beta frequency bands would be suppressed during the observation of point-light biological motion images compared to a baseline of a moving circle also represented as a point-light display. Furthermore, we hypothesized that focusing attention on social dimensions that may recruit a simulation process, such as emotions and intentions, would elicit greater mu suppression than when focusing attention on the gender<sup>2</sup> of the moving image.

<sup>2</sup> Although it is conceivable that the gender of an agent has a social value, this value is probably less related to simulation, considering that one has only experienced being either male or female. We did check for an interaction between the gender of the participant and that of the stimuli, but no such interaction was found.

## METHODS

### Participants

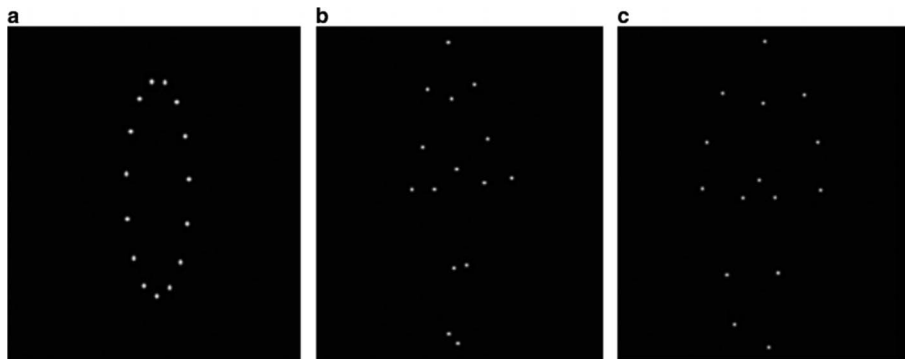
The participants were 26 undergraduates (11 male) from the Hebrew University ranging in age from 19 to 28 (mean age 24.3). They participated in the experiment for payment or course credit. All participants were right-handed; all reported normal or corrected to normal visual acuity and had no history of psychiatric or neurological disorders. They signed an informed consent, which was approved by the Hebrew University ethical committee. Two participants have been excluded for technical reasons. Hence, the reported results are based on 24 participants.

### Stimuli, task, and design

The stimuli used were 5 s long video clips presenting point-light displays of continuous biological motion of a human figure's walk. All stimuli were based on a morphable model spanned by 100 different individual walkers as described in more detail elsewhere (Troje, 2002b, 2008). Walkers used for the current experiment varied along three different dimensions: gender (male or female), expression (sad or happy), and intention (approaching or retreating). The gender dimension was derived in terms of the linear discriminant function that separates the male and female walkers in the data base (Troje, 2002a). Maleness was generated by adding to the average walker a vector pointing in the direction of this discriminant function. The length of this vector corresponded to five *z*-scores with respect to the distribution of the walkers spanning the space and was therefore representing a rather exaggerated male walking style. For a female walker, the same vector was subtracted from the average walker. Happiness and sadness were based on a linear discriminant function based on rankings that naive

observers assigned to the individual walkers (for details, see Troje, 2002b). Again, happiness or sadness was added to a walker by adding or subtracting five *z*-scores of this axis, respectively. This fairly extreme manipulation for the emotion and gender stimuli ensured that these characteristics of the walker were as distinguishable for the observer, as the direction of movement (see "Pilot experiment" below). The impression of approach or retreat was generated using perspective cues. The 3D walkers were rendered by simulating a perspective camera while the walker was translating forward at a natural pace. The distance from the camera changed from 6.5 to 5.3 units of walker height as the walker was approaching the camera at an angle of  $5^\circ$  to the line of sight. The opposite was the case as the walker retreated along a trajectory oriented  $175^\circ$  to the line of sight. Perspective projection thus changed the size of the walker by 122% between the two extreme positions along with other perspective distortions in accordance to the walker's position relative to the camera. All three dimensions were manipulated independently. For example, a point-light display could represent a sad woman walking toward the observer, a happy man walking away, and all other possible combinations (for still pictures of examples, see Figure 1). The clips were presented on a CRT monitor, 70 cm away from the subject's eyes with the point-light displays subtending on average a visual angle of  $11.5^\circ \times 4^\circ$ .

E-Prime (Psychological Software Tools) was used for stimulus presentation and experimental control. In a blocked design each block depicted a different task, requesting the processing of only one dimension (gender, emotion, or intention). Each of the three blocks included two types of trials. Each trial comprised 20 clips keeping constant one of the levels of the relevant dimension (e.g., a male figure in the gender block) and three to six clips presenting the other level (e.g. a female figure in the gender block). The participants were instructed to silently count the occurrence of the



**Figure 1.** Examples of stimuli. (a) The rolling circle presented in the baseline condition. (b) A female image. (c) A male image.

rare event and, at the end of each trial, report this number. The two levels of the other dimensions (emotion and intention in the above example) changed randomly across the 23–26 clips presented in a trial. Hence, although the participants focused on only one of the three dimensions each dynamic point-light display presented all three dimensions. Two types of trials were presented in each block, with the frequent level of the relevant dimension switched, and the order of the trials counterbalanced across participants.

In addition to the three experimental task conditions (gender, emotion, intention), a nonbiological movement baseline condition (a right-to-left or left-to-right moving circle composed of the same point-lights) was presented in two separate blocks. In these blocks participants had to report how many times the ball rolled to a predefined (rare) direction (left or right). All possible order permutations of the three experimental and baseline conditions were used, yielding a total of 24 orders, each presented to a different observer.

## Procedure

Participants sat comfortably in an armchair located in an acoustically attenuated and electrically isolated chamber, dimly lighted. They were instructed to refrain from any movement during a trial presentation and their overt behavior was monitored by a video-camera. Each block began with a training session of four point-light displays, which the participant had to rate on the relevant dimension. The training was repeated if needed, although it was rarely used more than once. The clips within each trial were presented continuously without ISI (yielding 100 s of continuous stimulation). A short break separated the trials. During this break, subjects were asked to answer four trivia questions, in order to prevent possible carry-over effects across tasks. At the end of the experiment the participants completed two questionnaires: the Interpersonal Reactivity Index (IRI, Davis, 1980) and the Empathy Quotient (EQ, Baron-Cohen & Wheelwright, 2004). Pearson correlations between mu suppression values and the marks on the different scales were calculated.

## Data acquisition and analysis

### *EEG recording*

The EEG analog signals were recorded continuously (from DC with a low-pass filter set at 100 Hz)

by 64 Ag-AgCl pin-type active electrodes mounted on an elastic cap (Biosemi™, <http://www.biosemi.com/headcap.htm>) according to the extended 10–20 system, and from two additional electrodes placed at the right and left mastoids. All electrodes were referenced during recording to a common-mode signal (CMS) electrode between POz and PO3 and were subsequently re-referenced digitally (see “Data processing” below). Eye movements, as well as blinks, were monitored using bipolar horizontal and vertical electrooculography (EOG) derivations via two pairs of electrodes, one pair attached to the external canthi and the other to the infraorbital and supraorbital regions of the right eye. Both EEG and EOG were digitally amplified and sampled at 1024 Hz using a Biosemi Active II system ([www.biosemi.com](http://www.biosemi.com)).

### *Data processing*

Data were analyzed using Brain Vision Analyzer software (Brain Products; <http://www.brainproducts.com>) and Matlab routines made in-house. Raw EEG data was initially 0.5 Hz high-pass filtered (24 dB) and re-referenced offline to the average of the two mastoids. Eye movements were corrected using an ICA procedure (Jung et al., 2000). Remaining artifacts exceeding  $\pm 100 \mu\text{V}$  in amplitude at the central (C3, Cz, C4) sites were rejected. Because EEG oscillations in the 8–12 Hz frequency are influenced by states of expectancy and awareness (e.g. Laufs et al., 2003), and the mu frequency band overlaps with the posterior alpha band, it is possible that our more anterior recordings might be affected by this posterior activity, which is more related to visual processing. Therefore, as suggested by Pineda and Oberman (2006), the first 10 s of each block was excluded from the analysis to reduce the possibility of attentional transients due to the initiation of the stimulus. For each 5 s stimulus, the first 2 s were segmented, since this was the maximum time needed to extract the information from the stimulus (see pilot data).<sup>3</sup> For each such segment, the integrated power in the 8–12 Hz range was computed using a fast Fourier transform (FFT) performed at 0.5 Hz intervals (based on 2048 points per segment, and using a Hanning window).

A mu suppression index was calculated as the logarithm of the ratio of the power during the experimental conditions relative to the power during the baseline conditions, and used as dependent variable. The ratio (as opposed to a simple subtraction) was used to

<sup>3</sup> The same analysis was also done for the whole 5 s and for the middle 4 s, yielding the same results.

control for the variability in absolute EEG power as a result of individual differences such as scalp thickness and electrode impedance (Pineda & Oberman, 2006). Further, since ratio data are inherently not normally distributed as a result of lower bounding, a log transform was also used for analysis. Hence, a log ratio of less than zero indicates suppression in the EEG amplitude whereas a value of zero indicates no change and values greater than zero indicate enhancement. Consistent with previous studies (e.g. Muthukumaraswamy et al., 2004; Oberman et al., 2007; Pineda & Oberman, 2006) we computed and analyzed the mu-suppression at sites C3, Cz and C4. In addition, we also analyzed mu suppression at the occipital sites, O1, Oz and O2, where alpha modulation is expected. Since some studies reported an upper band of mu (or rather beta) activity, or even at higher frequencies (see "Introduction"), the same analysis was also done for the 15–25 Hz range and for the 25–35 Hz range.

## Pilot experiment

In order to establish the observers' ability to recognize the different dimensions represented by the point-light displays, we assessed performance accuracy and speed in a task in which 24 (naïve) participants categorized the gender or the emotion or the intention expressed in the display, as well as the direction of the rolling circle. As in the EEG, the three experimental conditions and the baseline were blocked. Each block was comprised of 24 5-s clips (3 repetitions of 8 different ones). Each level of each dimension was equally represented (i.e., there were 12 men and 12 women, 6 sad and 6 happy within each gender, and 3 walking towards the observer and 3 away within each emotion). The 24 displays were presented in a quasi-random order, so that two identical clips would not occur one after the other. The baseline block also included 24 clips, 12 showing the circle rolling to the left and 12 showing the circle rolling to the right. The order of the blocks was randomized across participants.

The participants were instructed to categorize as quickly and as accurately as possible each display according to the dimension relevant in each block. They responded by pressing either the "1" or the "2" key on the keypad using the dominant hand.

## RESULTS

### Pilot data

The RTs and accuracy in the pilot experiment were analyzed by a one-way ANOVA with Condition (gender,

**TABLE 1**

Response times (SDs) and percentage of accuracy (SDs) in detecting the relevant information provided by point-light displays in the pilot task

	<i>Gender</i>	<i>Emotion</i>	<i>Intention</i>	<i>Baseline</i>
Response time	952 (291)	1252 (356)	1766 (670)	742 (249)
Accuracy	98.3 (0.9)	88.2 (3.8)	89.9 (2.1)	96.5 (3.1)

emotion, intention, baseline) as a within-subject factor (Table 1). The degrees of freedom were corrected using the Greenhouse-Geisser epsilon (G-GE).

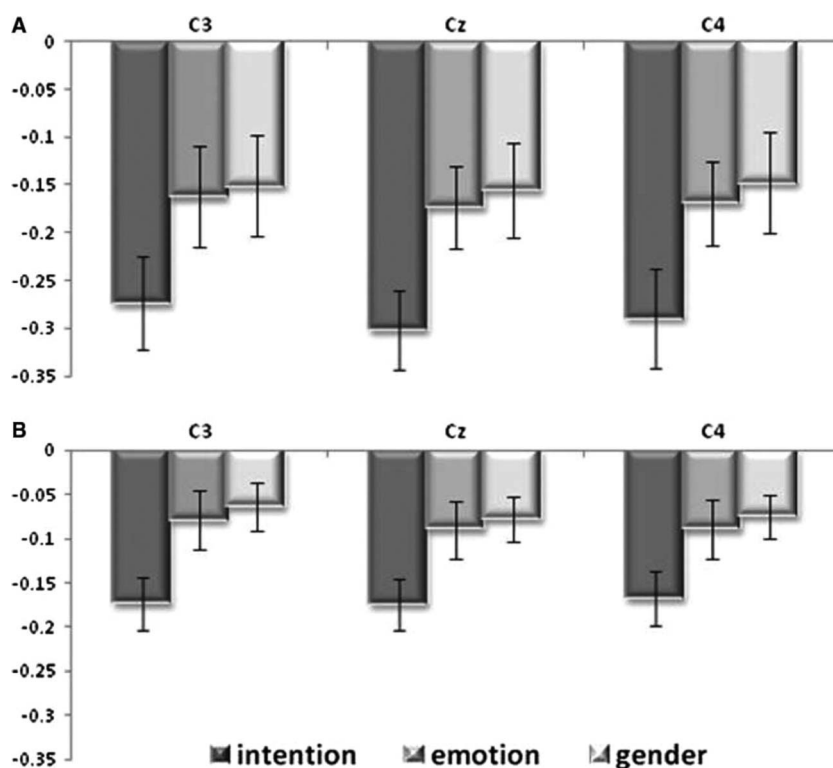
The analyses showed that the effect of Condition was significant for both accuracy and RT,  $F(1, 23) = 3.6$ , mean squared error (MSe) = 2.7,  $p < .05$ ; G-GE = 0.6 and  $F(1, 23) = 30.0$ , MSe = 263088,  $p < .0001$ ; G-GE = 0.6, respectively. Pairwise comparisons revealed that accuracy was lower for intention relative to gender ( $p < .01$ , Bonferroni corrected) and no other significant differences. For RTs, the pairwise comparisons revealed that the response to the rolling circle direction decision was the fastest, followed by the gender decision and the emotion decision, while the intention decision was the slowest ( $p < .05$  in all pairwise comparisons, Bonferroni corrected).

### EEG data

The mu suppression (as defined above) was analyzed initially at central sites, conforming to the research tradition in this domain. Then we continued with the analysis of the EEG modulation at occipital sites, in order to compare the mu suppression with alpha.

As a first step we examined whether the suppression index (collapsed across the central sites, C3, Cz, and C4) was statistically significant by comparing each condition to zero using planned  $t$ -tests. These analyses showed that in all three experimental conditions the suppression was significant,  $t(23) = 2.98$ ,  $p < .01$ ;  $t(23) = 3.67$ ,  $p < .01$ ;  $t(23) = 6.18$ ,  $p < .01$ , for gender, emotion, and intention, respectively.

Finding that the observation of biological motion reduced the mu-rhythms' amplitude relative to the non-biological movement condition, we examined the effect of the experimental condition (i.e., the type of task-relevant information extracted from the point-light displays) and site using a two-way repeated measure ANOVA design with degrees of freedom corrected by G-GE procedure. The factors were Site (C3, Cz, C4), and Social information type (gender, emotion, intention). Since initial analysis showed that there was no difference between the two levels in



**Figure 2.** Mu suppression for the different conditions at central electrodes, (A) in the mu (alpha) range 8–12 Hz, and (B) in the upper mu (beta) range 15–25 Hz. The Y-axis indicates mu suppression index (log ratio of the power in the experimental conditions over baseline; a value of zero means no suppression, see text).

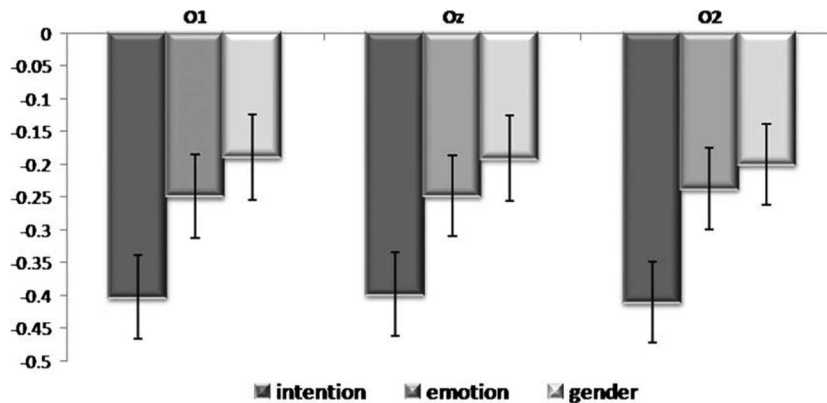
each condition (e.g., men versus women in the gender condition), they were collapsed and analyzed together. There was a significant effect for Social information type,  $F(2, 46) = 3.7$ ,  $MSe = 0.117$ ,  $p < .05$ ; G-GE = 0.93, no effect of Site,  $F(2, 46) < 1.0$ , and no interaction,  $F(4, 92) < 1.0$ . Post-hoc contrasts showed that the suppression in the gender and emotion conditions was similar ( $F < 1.0$ ) and together smaller than the magnitude of suppression in the intention condition,  $F(1, 23) = 5.7$ ,  $MSe = 0.208$ ,  $p < .05$  (Figure 2A). None of the effects interacted with the gender of the participants.

Similar analyses for higher frequency ranges showed a similar pattern for the upper mu/beta range (15–25 Hz). The initial comparisons showed that although the suppression was smaller than in the mu range (Figure 2B), it was still significant,  $t(23) = 2.898$ ,  $p < .05$ ;  $t(23) = 2.662$ ,  $p < .05$ ;  $t(23) = 5.840$ ,  $p < .01$ ; for gender, emotion, and intention, respectively. The ANOVA showed a significant effect of Social information type,  $F(2, 46) = 4.4$ ,  $MSe = 0.063$ ,  $p < .05$ ; G-GE = 0.76, no effect of Site,  $F(2, 46) < 1.0$ , and no interaction,  $F(4, 92) < 1.0$ . As in the mu range, post-hoc contrasts showed that this effect reflected a higher suppression in the intention condition vs. the emotion and gender conditions,  $F(1, 23)$

$= 5.6$ ,  $MSe = 0.111$ ,  $p < .05$ , with no difference between the latter two,  $F(1, 23) < 1.0$  (see Figure 2B). The 25–35 Hz showed a different pattern altogether. Suppression was evident only for gender,  $t(23) = -3.941$ ,  $p < .01$ , approached significance for intention,  $t(23) = -2.016$ ,  $p = .056$ , and was not significant for emotion,  $t(23) = -1.148$ ,  $p = .26$ . No further significant effects were revealed by the ANOVA,  $F(2, 46) < 1.0$  for Site, Social information type and their interaction.

Finally, the analysis of the EEG suppression at occipital sites (O1, Oz, and O2) in the 8–12 Hz range, which presumably reflects the modulation of alpha, showed that across sites the suppression was significant in all three conditions,  $t(23) = -6.621$ ,  $p < .01$ ;  $t(23) = -3.931$ ,  $p < .1$ ;  $t(23) = -3.070$ ,  $p < .01$ , for intention, emotion, and gender, respectively. The ANOVA resulted in a pattern similar to that found at the central sites. The effect of Social information type was significant,  $F(2, 46) = 6.0$ ,  $MSe = 0.170$ ,  $p < .01$ ; G-GE = 0.85, reflecting larger suppression in the intention relative to both other conditions,  $p < 0.5$  and  $p < .01$  for emotion and gender, respectively, with no difference between the latter two,  $p = .313$  (see Figure 3). There was no effect of Site,  $F(2, 46) < 1.0$ , and no interaction,  $F(4, 92) < 1.0$ . A direct comparison between the suppression of the occipital and

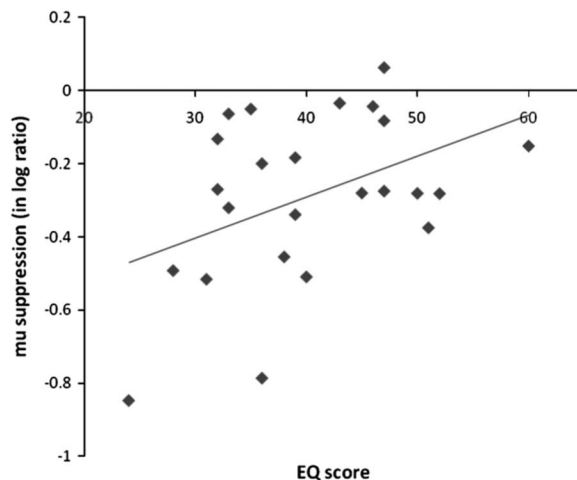




**Figure 3.** Suppression for the different conditions at occipital electrodes, at the 8–12 alpha range. The Y-axis indicates mu suppression index (log ratio of the power in the experimental conditions over baseline; a value of zero means no suppression, see text).

central sites (collapsed over electrode sites) showed that the suppression at the occipital sites was overall larger than at the central sites,  $F(1, 23) = 11.7$ ,  $MSe = 0.019$ ,  $p < .01$ , and was modulated by condition,  $F(2, 46) = 5.1$ ,  $MSe = 0.03$ ,  $p < .01$ ;  $G-GE = 0.95$ . Pairwise comparisons showed that whereas the suppression at the occipital sites was larger than at the central sites for the intention,  $t(23) = 4.286$ ,  $p < .01$ , and emotion condition,  $t(23) = 2.954$ ,  $p < .01$ , there was no site difference in the gender condition,  $t(23) = 1.576$ ,  $p = 0.13$ .

A significant positive correlation was found between suppression index for intention in the 8–12 Hz range and the EQ score both for the central ( $r = 0.43$ ,  $p < .05$ ) and for the occipital sites,  $r = 0.48$ ,  $p < .05$ . Figure 4 shows this correlation at the central sites. In other words, the amount of suppression was



**Figure 4.** Correlation between EQ and suppression in the intention discrimination condition in the mu range in central electrodes;  $r = 0.428$ ,  $p < 0.05$ .

*smaller* in participants with higher EQ scores. No correlation was found between suppression indices and the IRI score ( $r = 0.210$ ,  $p = .325$ ), and no correlations were found when focusing on the beta band (15–25 Hz).

## DISCUSSION

The immediate goal of this study was to explore how the social value of the task-relevant information extracted from point-light displays of biological motion affects the pattern of mu suppression. Since previous studies suggested that this electro-physiological manifestation might engage a human analog of the mirror neuron system, the farther-reaching goal of this study was to explore to what extent a mirror mechanism in humans would be differentially activated by symbolized acts that differ in social relevance. To this end, we compared the mu suppression induced by identical point-light displays when the task-imposed classification criteria were the gender of the symbolized image, or its alluded emotion (happy or sad), or its implied intention (defined as moving toward or away from the observer). Consistent with a previous report (Ulloa & Pineda, 2007) the amplitude of the mu rhythms recorded during the observation of biological motion was significantly lower than that recorded during the observation of nonbiological motion in all three experimental conditions, indicating mu suppression. A similar pattern was found in a higher (beta) EEG range (15–25 Hz) but not in an even higher, (low-gamma) range (25–35 Hz). In concert with an fMRI study, which showed that point-light biological motion activates regions in the inferior prefrontal cortex that are putatively part of the hMNS (Saygin, et al., 2004), the present EEG modulations might suggest

that point-light biological motion engages a mirror neuron system. Evidence for the sensitivity of this EEG modulation to the task-determined social relevance of different informational aspects extracted from motion might suggest that this putative manifestation of the mirror neuron system in humans is sensitive to the social significance of the observed motion.

However, the pattern of differences in mu suppression across conditions did not entirely confirm our predictions. Although, as expected, the suppression in the gender discrimination condition was numerically the smallest, it was not significantly different from the suppression in the emotion discrimination, and the suppression in the intention condition was the highest. Since the stimuli did not vary systematically across tasks, the difference between conditions must have been related to the task: in other words, to the informational dimension that was relevant and presumably captured the participants' attention. Hence, it is intriguing that the mu suppression in the emotion condition was similar to that in the gender condition and significantly smaller than in the intention condition. The relatively small level of suppression in the current emotion condition might reflect, at least in part, the higher ambiguity in extracting the emotion from the motion of the displayed stimuli. Notwithstanding the highly accurate performance (indeed similar for the intention and the emotion conditions), the discrimination between two types of motion does not imply that the emotion has been, necessarily, the basis for the distinction. For example, the happy motion is, by definition "more bouncy" and somewhat faster than the sad motion. In fact, some participants noted that, although understanding the task after the practice stage, the happy and sad figures looked to them mostly as walking fast or slow, maybe a bit tilted or erect, but not really depicting an emotion. It should also be noted that the more extreme manipulations chosen to render gender and emotion characteristics in movement as distinguishable as those of intention may have been at the cost of their "naturalness" while the intention condition was not manipulated in any sense that made it extreme. So, it is possible that despite being sufficient to induce suppression in the 8–12 Hz EEG range, point-light displays of biological motion are not optimal for exploring motor mechanisms involved in the perception of affective states. Yet, it is interesting to notice that a similar pattern of mu suppression was reported by Pineda and Hecht (2009), who used photographs of expressive natural eyes to assess different social perception skills. While matching the eyes by emotion, race, or gender, the mu suppression was similar for the gender and emotion conditions, both significantly smaller than in the race matching condition.

It should also be noted that no differences were found between the two levels of each condition. It would have been interesting to find, for example, differences between approach and retreat (considering the different evolutionary value of each) or an interaction between the gender of the participants and that of the figures presented (gender differences have been found in other mu studies, e.g. Cheng et al., 2008). Again, it may be the case that point-light biological figures, with their advantage of stimulus control, are disadvantageous for more subtle comparisons.

Other factors could also account for the particular pattern of the condition effects in the present study. The behavioral evidence in the pilot task raises the possibility that task difficulty *per se* could, at least partly, account for the pattern of EEG suppression. The participants were slowest in the intention discrimination task and fastest in the gender task. Moreover, accuracy was highest in the gender discrimination task. Yet task difficulty cannot be the only account because the pattern of suppression did not completely mirror the pattern of behavior. First, accuracy was similar for the discrimination of emotion and intention, yet suppression was significantly higher in the latter condition. Second, whereas neither intention nor emotion could have been discerned in the absence of movement, the gender of the "agent" could have been determined (albeit less accurately) even in stationary point-light displays.

Another caveat that needs to be considered while interpreting the current results is the scalp distribution of the suppression effects, which were higher over occipital than over central (sensory-motor) areas. This pattern is in line with recent MEG findings, which show both occipital and central activation in response to modulations of the hMNS (defined as regions activated both during observation and execution tasks; Muthukumaraswamy & Singh, 2008). Since the baseline condition was identical across tasks and in all experimental conditions, participants were visually stimulated to the same extent (roughly similar to the extent of visual stimulation in the baseline condition), and the occipital suppression cannot reflect a visually induced alpha-ERD. Nevertheless, the observed distribution reduces our ability to interpret the current task-induced EEG modulations in the 8–12 Hz as manifesting motor activity. The literature associating EEG oscillations in the alpha (8–12 Hz) range with different aspects of cognitive activity is vast, and a discussion of this literature is beyond the scope of the current paper. But it is notable that, notwithstanding the visual alpha-block phenomenon, an overall decrease in alpha power has been linked to increasing demands of attention, alertness, episodic memory, and

task-load in general (for reviews see Klimesch, 1999; Sauseng & Klimesch, 2008; Ward, 2003). Interestingly, in addition to its occipital focus, alpha desynchronization has also been found in our laboratory (Zion-Golombic, Kutas, & Bentin, in press) as well as reported by others in more anterior, parietal and prefrontal regions in the absence of any executed or observed movement. This suggests that suppression of alpha rhythms in the visual cortex might be related to a dorsal frontoparietal network controlling for visuospatial attention (Capotosto, Babiloni, Romani, & Corbetta, 2009). Even more relevant to our present findings is a recent study showing that the magnitude of motor cortical excitability (as indexed by TMS-elicited motor evoked potentials), is modulated by the amount of alpha power in the motor cortical areas (Sauseng, Klimesch, Gerloff, & Hummel, 2009). Based on these data we should not be surprised to find that alpha rhythms in the occipital cortex are desynchronized in parallel to the more anterior desynchronization of the so-called mu rhythms. Yet it is not clear why this attentional system would yield greater suppression for intention than for gender or emotion. It might be possible, in fact, that depicting whether someone is walking toward you or away could have a higher ecological value and, consequently, attract more attention. This hypothesis is post hoc and requires additional validation.

The present data, however, are not evidence that the EEG desynchronization in the alpha range recorded either at central or occipital sites reflect only a nonspecific attention mechanism. First, we should recognize that in the majority of studies associating alpha with cognitive processing the modulation occurred in *anticipation* of the stimulus, which was not the case in our present study. Moreover, as we mentioned above, the influence of the task condition on the amount of suppression cannot be solely accounted by task difficulty, and it is unlikely that the participants were more engaged in one condition than in another. Finally, additional (albeit indirect) corroboration of the involvement of social factors in the amount of EEG suppression is provided by the correlation between the magnitude of suppression in the intention condition and the EQ score, which is an index of the participant's empathic ability. Moreover, although not significant, the IRI score (another index of empathy) and suppression for intention were correlated in the same direction.

Although there are no previous reports of correlations between mu (or alpha) suppression and empathy, the hMNS has already been implicated with empathic abilities both at a theoretical level (Gallese, 2003; Preston & De Waal, 2002) and by empirical

(mostly imaging) studies (e.g. Danziger, Failenot, & Peyron, 2009; Gazzola, Aziz-Zadeh, & Keysers, 2006; Warren et al., 2006; for a review see Gallese, Keysers, & Rizzolatti, 2004). Moreover, individual variation in the mirror activation has been correlated with the level of empathy indexed by standard questionnaires. For example, Schulte-Rüther, Markowitsch, Fink, & Piefke (2007) showed that subjects with higher empathy scores exhibited stronger activations in the left and right inferior frontal cortices, as well as in the left STS: areas considered to comprise the hMNS. Similarly, Singer and colleagues (2004) showed that subjects high in empathy exhibited stronger activations in brain areas related to the perception and experience of pain while watching their partners in pain, in comparison to those lower in empathy. However, in contrast to the above studies, the correlation that we found in the presents study between empathy and mu suppression was negative; that is, participants with higher empathy scores showed less mu suppression. It is difficult to interpret this correlation in the context of the opposite pattern found in fMRI studies, particularly in light of Sauseng and colleagues' (2009) study in which they found increased motor responses were anticipated by *reduced* alpha amplitude. However, tentatively we may suggest that people higher in empathy *do not need* to simulate the other's motor acts for such tasks (which may be trivial for them), and instead have some ready heuristics or rules to perform such tasks (cf. "theory theory"; Churchland, 1988; Gopnik, 1993; Gopnik & Wellman, 1992; Wellman, 1990). A detailed distinction between the simulation theory and the theory theory is far beyond the scope of this paper. However, it is important to note that although they were originally viewed as mutually exclusive, many authors now argue for a hybrid account in which both play a role in enabling social abilities (e.g. Carruthers & Smith, 1996; Currie & Ravenscroft, 2002; Gallagher, 2007; Nichols & Stich, 2003). Our interpretation has recently been corroborated in a behavioral study (Sivan & Shamay-Tsoory, personal communication) in which low- and high-empathy groups were asked to judge biological motion figures, while participants either stood freely or with interruption in spontaneous body movement (thus creating "muscular noise"; for similar designs see Niedenthal, Brauer, Halberstadt & Innes-Ker, 2001; Oberman, Winkielman & Ramachandran, 2007). This study showed that only within the low-empathy group was recognition accuracy lower when the tasks were performed with the body manipulation, while within the high empathy group the manipulations did not degrade performance. Evidently, more research is needed in order to better understand the

relationship between empathy and different accounts of the human MNS.

Manuscript received 17 August 2009  
 Manuscript accepted 6 October 2009  
 First published online 17 February 2010

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