MU SUPPRESSION, MIRROR NEURON ACTIVITY, AND EMPATHY

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Abstract

The ability to understand and interpret the actions and intentions of others is vital to human interaction as well as learning. The purpose of this study was to examine differences in mu suppression to different types of point light stimuli (upright, inverted, and random) and relationships between mu suppression and empathy. Participants (N=7) completed two empathy scales, the Interpersonal Reactivity Index (Davis, 1980) and the Empathy Quotient (Baron-Cohen & Wheelwright, 2004). In addition, EEG data was collected while participants viewed point light stimuli. EEG results indicated significant mu suppression at all central electrode sites for all three stimulus types. Exploratory correlational analyses revealed significant correlations between mu suppression indices and scores on the perspective-taking (PT) subscale of the Interpersonal Reactivity Index. Although future research is necessary, these results provide a basis for future inquiries.

Mu Suppression, Mirror Neuron Activity, and Empathy

Humans are social animals. The ability to understand and interpret the actions and intentions of others is vital to human interaction as well as learning. Premack and Woodruff (1978) used the term *theory of mind* (ToM) to describe this process of attributing mental states to oneself and others. This ability facilitates the development of beneficial relationships through appropriate social interaction. Furthermore, it enables learning through imitation rather than costly trial and error. Mirror neurons are thought to be the neural mechanism underlying this invaluable ability.

Mirror neurons, discovered in area F5 of the rhesus monkey premotor cortex, are visuomotor neurons that discharge in response to the execution or observation of similar actions (Di Pellegrino et al. 1992, Gallese et al. 1996, Rizzolatti et al. 1996). In addition, observation and imitation of facial expressions have been shown to activate mirror neurons (Carr et al., 2003; Leslie, Johnson-Frey & Grafton, 2004). Recent studies have also discovered mirror neurons that respond similarly to sounds associated with an action as they do to the execution or observation of that action (Keysers et al., 2003; Kohler et al., 2002). In addition, the mirror neuron system has been shown to be activated by implied ongoing biological motion (Urgesi et al., 2006). Urgesi et al. define implied motion as the extraction of dynamic information from static images (2006). Studies of the mirror neuron system suggest that its main functions are imitation (Jeannerod, 1994) and understanding the actions of others (Rizzolatti et al., 2001). It is likely, therefore, that the mirror neuron system is vital to imitation learning and appropriate social interactions (Rizzolatti & Craighero, 2004).

Since recordings cannot be taken from single neurons in humans, the only available evidence of a mirror neuron system in humans is indirect. Neurophysiological and brain-imaging studies have produced a great amount of indirect evidence of the existence of a mirror neuron system in humans. The relationship between mirror neuron activity and mu rhythm suppression was initially proposed by Altschuler et al. (1997).

The mu rhythm is generated by sensorimotor cortex, the cortical area involved in voluntary motor control. Mu rhythm oscillation occurs within the 8-12 Hz frequency band and attains maximal amplitude when individuals are at rest (Gastaut & Bert, 1954). Execution, observation, and imagination of movement all result in the suppression of mu amplitudes as a result of desynchronization of groups of neurons in the motor cortex (Gastaut & Bert, 1954; Pineda, Allison & Vankov, 2000).

Mu rhythm suppression, an indirect measure of mirror neuron activity, is recorded over sensorimotor cortex with electroencephalography (EEG) and has been used in numerous studies (Muthukumaraswamy & Johnson, 2004; Oberman et al., 2005; Pineda, Allison & Vankov, 2000; Cochin et al., 1999; Hari, Levanen & Rajj, 2000). EEG is a recording that is obtained through electrodes positioned on the scalp. This recording measures the difference in electrical potential among the various electrode sites and reflects the activity of groups of neurons depolarizing or firing in a desynchronized fashion.

Movement activates the premotor, motor, and sensorimotor areas, indicating the involvement of motor and mirror neurons. During the execution of movement, mu suppression can not be solely attributed to either population of neurons. However, when an individual is at rest and imagines or observes movement, mirror neurons are activated in the premotor, motor, and sensorimotor areas, and motor neurons in these areas are not activated. Mu suppression under these conditions, observed or imagined movement while at rest, should therefore represent an indicator of mirror neuron system functioning (Muthukumaraswamy & Johnson, 2004).

Point-light stimuli (Johansson, 1973) provide a convenient means by which to measure mu suppression during biological movement observation. Point-light walkers, series of lights marking the location of joints and set in motion, are easily recognized as a human form. See Figure 1 for example stills of the point-light stimuli used in this study. Studies have also demonstrated the ability to infer specific characteristics of point-light walkers such as gender and mood (Dittrich et al., 1996; Pollick et al., 2005).

Inversion of the walker significantly reduces individuals' ability to detect biological motion (Bertenthal & Pinto, 1994; Shipley, 2003). This result suggests the necessity of previous experience to perception. Shipley's (2003) study of biological motion used point-light walkers to separate the effects of object and event orientation on recognition. Subjects were asked to determine whether or not a moving biological form was present in displays of point-light walkers with additional visual noise, and detection accuracy was compared across four conditions: upright and inverted displays of a walker walking on feet and upright and inverted displays of a walker walking on hands. While inversion reduced detection accuracy for both walkers, the inverted walking on hands condition revealed the importance of familiar gravity rather than form to perception.

Observation of upright point-light walkers, but not of scrambled biological motion, has been shown to activate the premotor cortex, a region thought to contain mirror neurons, as measured by fMRI (Saygin et al., 2004). Ulloa and Pineda (2007) expanded these results through the use of EEG. Ulloa and Pineda (2007) compared five conditions: two upright point-light biological motion animations (kick and jumping jacks), a matched scrambled variation of each of the two upright animations, and a visual white noise. The two biological motion animations were found to result in significant mu suppression suggesting activation of mirror neurons, while the scrambled animations resulted in marginally significant enhancement. Therefore, observation of an upright point-light walker should result in mu suppression, while inverted and scrambled point-light motion should not result in significant mu suppression.

There is developing evidence that empathy, the ability to understand and interpret the actions of others, depends on a properly functioning mirror neuron system. Dysfunctional mu rhythm, specifically reduced mu suppression measured by EEG during action observation, has been reported in individuals with autism spectrum disorders, which are characterized, in part, by deficient empathy (Oberman et al., 2005). Dapretto et al. (2006) used fMRI to measure mirror neuron activity in children with autism spectrum disorders during a task that required observation and imitation of facial expressions. Mirror neuron activity was shown to be reduced in children with autism spectrum disorders and correlated with severity of disease.

The purpose of this study is to examine the connections between mu suppression, mirror neuron activity, and empathy. Mu rhythm suppression, a supposed index of mirror neuron activity, should occur during the observation of upright biological motion but not during the observation of inverted or scrambled biological motion. Since empathy seems to depend on a properly functioning mirror neuron system as demonstrated in studies involving individuals with autism spectrum disorders (Oberman et al., 2005; Dapretto et al., 2006), mu rhythm suppression is expected to be correlated with scores on two measures of empathic ability, Davis' (1980) Interpersonal Reactivity Index and the Empathy Quotient (Baron-Cohen & Wheelwright, 2004).

It is expected that mu rhythm suppression will occur during observation of biological motion in the form of upright point-light walkers. This can be expected, because the mirror neuron system has been shown to be activated by implied ongoing biological motion (Urgesi et al., 2006), and mu suppression during observation of movement while at rest is thought to be an indicator of mirror neuron system functioning (Muthukumaraswamy & Johnson, 2004). Also, point-light stimuli (Johansson, 1973) provide a convenient and reliable means by which to measure mu suppression, suggesting activation of mirror neurons, during observation of biological movement (Ulloa and Pineda, 2007).

In addition, it is expected that little or no mu rhythm suppression will occur during observation of inverted or scrambled motion. Studies have demonstrated a significant reduction in individuals' ability to detect biological motion in animations of inverted point-light walkers (Bertenthal & Pinto, 1994; Shipley, 2003). Activation of the premotor cortex measured by fMRI and mu suppression measured by EEG have both been revealed during the observation of upright point-light walkers but not during the observation of scrambled biological motion (Saygin et al., 2004; Ulloa & Pineda, 2007). Since individuals' ability to detect biological motion is impaired in inverted and scrambled conditions (Bertenthal & Pinto, 1994; Shipley, 2003; Saygin et al., 2004; Ulloa & Pineda, 2007), and the mirror neuron system has been shown to be activated by biological motion (Urgesi et al., 2006), little or no mu rhythm suppression during observation of inverted or scramble motion would support the hypothesis that mu rhythm suppression is an indication of mirror neuron activity.

Furthermore, it is hypothesized that mu suppression will be correlated with empathy scores on Davis' (1980) Interpersonal Reactivity Index (IRI). The IRI is composed of four subscales: fantasy scale (FS), perspective-taking scale (PT), empathic concern scale (EC), and personal distress (PD). Each subscale consists of seven items. The fantasy scale measures the tendency to identify with fictional characters. The perspective-taking scale measures the ability to assume another person's point of view. The empathic concern scale measures the tendency to feel compassion for others. The personal distress scale measures apprehension and discomfort resulting from others' negative experience. It is possible that mu rhythm suppression could be correlated either with the total score of the IRI subscales or only with the scores of certain subscales. Either result would indicate a relationship between mirror neuron system functioning and self-reported empathic ability.

It is hypothesized that scores on Baron-Cohen and Wheelwright's (2004) Empathy Quotient (EQ) should also be correlated with mu suppression. The EQ is comprised of 40 questions that measure empathic ability. On each of the 40 self-report items, level of agreement with the statement is rated (strongly agree, slightly agree, slightly disagree, strongly disagree). Adults diagnosed with autism spectrum disorders have been shown to score significantly lower on the EQ than normal adults (Baron-Cohen & Wheelwright, 2004). A correlation between mu suppression and EQ total score would offer support for a relationship between mirror neuron system functioning and self-reported empathic ability.

Methods

Participants

Participants consisted of 7 right-handed volunteers (2 males, 5 females, aged 20-26 years, average age = 22.57 years) recruited by word of mouth from the undergraduate population at Texas State University. All participants gave written informed consent to take part in this study. The procedures used in this study were approved by the Texas State University Institutional Review Board. Participants had no current psychiatric medication use and had normal or corrected-to-normal vision. The small sample size used in this experiment was chosen for two reasons: first, sample sizes for electroencephalography studies are typically small because of time constraints (i.e., each participant takes approximately 2-3 hours to run) and second, the experiment was a pilot study undertaken to assess the effectiveness of the point light stimuli used in the 3 stimulus conditions (upright, inverted, and random).

Questionnaires

The Interpersonal Reactivity Index (IRI; Davis, 1980) was one of two self-report scales used to assess trait empathy. This index is composed of four seven-item subscales: perspective taking (PT), empathic concern (EC), fantasy (F), and personal distress (PD) (see Appendix A). The alpha coefficients for internal reliability range from .70 to .78 and for test-retest reliability ranges from .61 to .81 for the scale (Davis, 1996). A number of questions were reversed so that participants were not led to answer in one particular direction, and these items were reverse scored prior to analysis. Participants answered 28 questions on a five point Likert scale (one indicating “not like me” and five indicating “very much like me”).

The Empathy Quotient Scale (EQ; Baron-Cohen & Wheelwright, 2004) was also used to assess empathy. The EQ consists of 40 self-report items that ask participants to rate their level of agreement (strongly agree, agree, disagree, strongly disagree) with various statements regarding interpersonal interactions and social perceptions (see Appendix B for the EQ and scoring key).

Stimuli and Task Design

The point light upright walker was obtained with permission from Thomas Shipley at Temple University (Shipley, 2004; http://astro.temple.edu/~tshipley/mocap/dotMovie.html). The upright walker stimulus was a Quicktime movie clip that was 3.0 seconds in duration. The walker was defined by a set of 13 points representing the head, shoulders, elbows, wrists, hips, knees, and ankles. Points were blue dots (approximately 2 mm in diameter) moving against a white background that measured 14.5 cm high and 13.0 cm wide. The inverted walker was created by rotating the upright walker clip by 180 degrees. The random stimulus created by altering the source code of the original clip to change the placement and movement of the dots, such that they appeared in roughly the same configuration as the walker stimuli (+/- 1 cm), but moved in random directions (path length = 1 cm). Each clip was 3.0 seconds long.

Superlab 4.0.8 (Cedrus Corporation, San Pedro, CA) was used for the presentation of the point light stimuli. Point light clips (upright, inverted, and random) were presented in random order in 4 blocks of 75 trials (25 trials of each stimulus type). Clips were separated by brief intervals of 500, 750, and 1000 ms to allow time for blinks. Still photos of the three point light stimuli are shown in Figure 1.

Electrophysiological Methods

Electroencephalographic (EEG) data was collected in a sound-insulated, radio frequency-shielded recording chamber from an array of 64 scintered Ag-AgCl electrodes (Neuroscan, Compumedics USA, Charlotte, NC). Electrode locations were based on a modification of the 10-20 system (which places electrodes at equal distances – 10% to 20% apart – depending on a person's head size), held in place by an electrode cap. Approximate electrode locations are shown in Figure 2. Eye movements were monitored with additional electrodes placed below the left eye and at the outer canthi of the eyes (to monitor eye movements), and additional electrodes were placed on the left and right mastoids for offline re-referencing (in order to see activity at the top of the head more clearly).To reduce noise in the data, electrode impedances were kept below 5 kΩ. The EEG signal was sampled at a rate of 1000 Hz and amplified with a bandpass of 0.10 to 100 Hz by a Synamps2 amplifier (Neuroscan, Compumedics USA, Charlotte, NC).

Procedure

Upon completion of the informed consent form, some participants filled out the self-report empathy scales using an online data collection utility (Survey Monkey, Menlo Park, CA). Other participants completed the survey after the collection of the electroencephalographic (EEG) data. EEG recording equipment was applied and the participants were moved into the recording chamber, seated in an armchair, and then viewed the 4 blocks of point light stimuli. Each block was approximately 6 minutes long and short breaks were given between blocks. Participants also completed a 5 minute baseline rest period, either before or after the 4 blocks, where they rested quietly with no visual stimulation. After the experiment, participants were asked about their objective experiences regarding the stimuli used in the study.

Data processing

Data were analyzed using SCAN v. 4.3 Analysis software (Neuroscan, Compumedics USA, Charlotte, NC). All data were referenced offline to the average of the left and right mastoids in order to enhance EEG activity over motor cortex at the center of the top of the head (i.e., at the electrode sites of interest). Trials containing eye blinks, eye movement and excessive artifacts (>100 μV at central electrode locations shown in Figure 2) were removed from the data offline to remove activity associated with non-neural events. After artifact rejection, 3000 ms stimulus-locked epochs were used to extract EEG activity associated with each stimulus type.

For the EEG associated each clip type, the integrated power in the 8–12 Hz range was computed for each participant using a Fast Fourier Transform (FFT – a mathematical technique that describes complex waveforms in terms of simpler, constituent frequencies) performed at 1 Hz intervals using a Hanning window (to control for spectral leakage and improve the precision of the FFT).

Mu suppression was defined as the logarithm of the ratio of the power to the different stimulus types, relative to the power during the resting baseline condition, with the assumption that mu synchrony would be highest in the baseline condition because there was no movement or perception of movement, but should be suppressed to different degrees in while watching the moving dots. This index of mu suppression was used as dependent variable in subsequent analyses (Perry, Troje & Bentin, in press; Pineda & Oberman, 2006). Specifically, this ratio was used to control for variability in absolute

EEG power as a result of individual differences (e.g., impedances and scalp thickness), while the data were log transformed in order to meet the assumption of normality for parametric analysis (Pineda & Oberman, 2006). Log ratios of less than zero are indicative of suppression in the EEG frequency range, values of zero are indicative of no change, and values greater than zero are indicative of enhancement (Perry et al., in press).

Results

Mu suppression

Mu suppression was assessed through examination of the relative power of 8-12 Hz activity at central sites (C3, C1, Cz, C2, C4; see Figure 2), in keeping with the research tradition reported in the literature.

Mu suppression indices for each stimulus type relative to baseline (different colored bars) at the different central electrodes sites are shown in Figure 3. First, the suppression indices for each site were examined separately to determine whether mu suppression relative to the baseline rest period at these sites was statistically significant from zero using planned one-sample t-tests, with zero as the critical value. These analyses indicated that for all sites and across all conditions, significant mu suppression was observed $t(6)$'s > 4.40, p's < 0.01.

After determining that significant mu suppression was observed for all electrode sites, to all stimulus types, the effect of stimulus type on mu suppression was assessed with repeated-measures analysis of variance (ANOVA), with mu suppression indices as the dependent variable and stimulus type (upright, inverted, random) and electrode location (C3, C1, Cz, C2, C4) as within-subjects factors. No significant main effect of stimulus type was observed ($F < 1.0$). Similarly, there was no interaction between stimulus type and electrode location ($F < 1.0$). The extremely small sizes of these effects (partial η^2 or effect size for stimulus type = .07, partial η^2 for the interaction = .011) suggests that the lack of significance was not due to the small sample size used in this experiment. There was a main effect of electrode location, $F(4, 24) = 3.04$, $p < .05$. As shown in Figure 3, mu suppression was largest over the vertex electrode (Cz) at the center of the head.

Follow-up correlational analyses: Individual differences in mu suppression

In order to determine whether mu suppression was significantly related to individual differences in empathy, exploratory correlations between mu suppression indices from Cz (where maximal mu suppression was observed) and empathy scale scores were performed. Due to the small number of subjects in the study, only very strong correlations ($r > .60$) and significant correlations ($p < .05$) are reported. In addition, results should be regarded with a measure of caution as they may not generalize to a larger sample.

Mu suppression indices from Cz to the random point light display were significantly correlated with the PT (perspective taking) subscale of the IRI, $r = .79$, $p < .05$. As shown in Figure 4c, higher PT scores were associated with smaller mu suppression indices. In other words, individuals scoring highly on this subscale had less mu suppression to the random walker. Higher PT scores were also marginally related to mu suppression to upright walkers, $r = .69$, $p = .09$ and were highly correlated with mu suppression to the inverted walkers, $r = .62$, $p = .14$. As shown in Figures 4a and 4b, higher PT scores were associated with less mu suppression to the upright and inverted walkers, respectively.

Discussion

The mirror neuron system is thought to play an integral role in how primates understand the actions and intentions of other conspecifics and the activity of this system is thought to be reflected in mu suppression in the human electroencephalogram. The purpose of this study was to examine differences in mu suppression to different types of point light stimuli (upright, inverted, and random displays) and relationships between mu suppression and empathy. In addition, this experiment served as a pilot study to determine the effectiveness of various point light stimuli and task instructions.

The primary hypothesis of this study was that mu rhythm suppression over motor cortex would be maximal during the observation of upright biological motion relative to the observation of inverted or random biological motion. This would have indicated mirror neuron activity only during the observation of upright biological motion. Contrary to what was expected, the EEG results indicated significant mu suppression at all central electrode sites for all three stimulus types. Mu suppression was greatest over the center or vertex electrode (Cz). These results suggest that all three stimulus types were seen as representations of biological motion. This interpretation was confirmed by comments made by participants during the debriefing phase after completion of the experiment: all participants reported that all 3 stimuli, including the random walker, were perceived as biologically meaningful stimuli (i.e., bodies in motion).

It was also expected that mu suppression would be correlated with scores on measures of self-reported empathic ability, Davis' (1980) Interpersonal Reactivity Index and its subscales and Baron-Cohen and Wheelwright's (2004) Empathy Quotient. This would have provided further support for the growing body of evidence that indicates dependence of empathic ability on a properly functioning mirror neuron system. Exploratory correlational analyses between mu suppression indices at the site of maximal mu suppression (Cz) and the various empathy scale scores were performed, and the only significant correlations were between mu suppression indices and scores on the perspective-taking (PT) subscale of the Interpersonal Reactivity Index. Mu suppression indices from Cz indicated large correlations ($r > 0.6$) to scores on the PT scale in all three conditions (upright, inverted, and random), such that larger PT scores were associated with attenuated mu suppression indices. Although it was expected that high empathy scores would be correlated with greater mu suppression, higher PT scores were correlated with smaller mu suppression indices in all three conditions. This relationship reached statistical significance for the random point light displays.

One possible explanation for these results may lie in the nature of the perspective-taking component of empathy, which measures the tendency to adopt another's point of view (e.g., "I sometimes try to understand my friends better by imagining how things look from their perspective.") This process is thought represent a more cognitive aspect of empathy that is a self-initiated and controlled process (i.e., a "top-down" process) rather than a stimulus-driven (i.e., "bottom-up") process that engages the mirror neuron system. It is possible that engaging in perspective taking as a means of understanding the actions of others involves the activity of brain regions that are not dependent upon the activity of the mirror neuron system. For example, Decety and Chaminade (2003) suggest that the right inferior parietal cortex may also be involved in self-other distinctions, while other research indicates that the posterior cingulate and precuneus may be involved in perspective-taking (Platek, Mohamed, & Gallup, 2005; Ruby & Decety, 2004). However, given the small sample size, such interpretations should be made with caution. Future studies examining the relationship between mu suppression and perspective taking with larger sample sizes are necessary in order to determine if this result will hold across a larger number of people.

An additional motivation for this experiment was to conduct a pilot study to assess the effectiveness of the point light stimuli used in the three stimulus conditions (upright, inverted, and random). Several limitations were discovered that will be corrected for future studies. First, several participants complained of difficulty focusing on the stimuli for the extended time periods required in this study. This may have been the cause of the great number of artifacts caused by excessive blinking. This can be corrected in future studies by converting the stimuli to a black background with white dots rather than a white background with blue dots. In addition, a frontal view of the point light walkers with larger dots will be used (a front-facing walker represented by 15 dots) in order to amplify the ambiguity produced by inversion.

An unexpected result in this study was significant and equivalent mu suppression for all three stimulus conditions, including the random condition, rather than greater mu suppression for the upright condition. In addition, participants commented during debriefing that all of the stimuli appeared biological, including the random walker. This result could have occurred for two reasons. First, participants were fully briefed prior to the EEG session and were told that they would be observing upright walking, inverted walking and random point light displays and therefore were expecting to observe biological motion. In order to reduce participant expectations, less information regarding the stimuli should be provided to participants prior to data collection. Second, it is possible that the equivalent mu suppression observed in this study was the result of the type of stimuli used. To correct for the type of stimulus used, front views of upright and inverted walkers will be used, in addition to an unambiguously non-biological random condition such as a rolling ball should be used in future studies.

A final future direction that may be taken in order to understand the mu suppression observed during the inverted condition is to analyze its time course after the onset of the point light display. It is possible that there may be a later onset of mu suppression in the inverted condition than in the upright condition which would suggest mental rotation of the stimuli.

Conclusions

Empathy is vital to human interaction. The purpose of this study was to examine differences in mu suppression to different types of point light stimuli (upright, inverted, and random displays) and relationships between mu suppression and empathy. EEG results indicated significant mu suppression at all central electrode sites for all three stimulus types. Although this is contrary to what was expected, it is possible that this result occurred due to ambiguous stimuli and excessive briefing prior to data collection. Exploratory correlation analyses revealed significant correlations between mu suppression indices and scores on the perspective-taking (PT) subscale of the Interpersonal Reactivity Index. This may be explained by the nature of perspective-taking as a cognitive aspect of empathy that may not depend upon the activity of the mirror neuron system. In addition to the main purpose of this study, another important goal was to determine the effectiveness of the point light stimuli and task instructions. This experiment was successful as a pilot study, because it revealed weaknesses of the stimuli and design that can be corrected and implemented with larger sample sizes in future studies. Although there is still much work to be done on this subject, this study provided a good basis for future research.

References

Altschuler, E. L., Vankov, A., Wang, V., Ramachandran, V. S. & Pineda, J. A. (1997). Person see, person do: human cortical electrophysiological correlates of monkey see monkey do cells. Abstract- *Social Neuroscience, 23,* 1848.

Baron-Cohen, S. & Wheelwright, S. (2004). The Empathy Quotient (EQ). An investigation of adults with Asperger Syndrome or High Functioning Autism, and normal sex differences. *Journal of Autism and Developmental Disorders, 34,*163-175.

Bertenthal, B. I. & Pinto, J. (1994). Global processing of biological motions. *Psychological Science, 5,* 221-225.

Carr, L., Iacoboni, M., Dubeau, M. C., Mazziotta, J. C. & Lenzi, G. L. (2003). Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proceedings of the National Academy of Sciences, 100,* 5497-5502.

Cochin, S., Barthelemy, C., Roux, S., & Martineau, J. (1999). Observation and execution of movement: similarities demonstrated by quantified electroencephalograpy. *European Journal of Neuroscience, 11,* 1839-1842.

Davis, M. H. (1980). A multidimensional approach to individual differences in empathy. JSAS *Catalog of Selected Documents in Psychology, 10,* 85.

Davis, M. H. (1996). *Empathy: A social psychological approach*. Boulder, CO: Westview Press.

Decety, J., & Chaminade, T. (2003). Neural correlates of feeling sympathy. *Neruopsychologia, 41*, 127-138.

Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: a neurophysiological study. *Experimental Brain Research, 91*,176–80.

Dittrich, W., Troscianko, T., Lea, S., & Morgan, D. (1996). Perception of emotion from dynamic point-light displays represented in dance. *Perception, 25*(6), 727-738.

Gallese, V., Fadiga, L., Fogassi, L. & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain, 119*, 593–609.

Gastaut, H. J. & Bert, J. (1954). EEG changes during cinematographic presentation. *Electroencephalography and Clinical Neurophysiology, 6*, 433–444.

Hari, R., Levanen, S., & Raij, T. (2000). Timing of human cortical functions during cognition: role of MEG. *Trends in Cognitive Science, 4*, 455-462.

Iacoboni, M. & Dapretto, M. (2006). The mirror neuron system and the consequences of its dysfunction. *Nature Reviews Neuroscience*, *7*, 942-951.

Jeannerod, M. (1994). The representing brain: neural correlates of motor intention and imagery. *Behavioral Brain Science, 17*, 187–245.

Johansson, G. (1975). Visual motor perception. *Scientific American, 232*, 76-88.

Keysers, C., Kohler, E., Umiltà, M. A., Nanetti, L., Fogassi, L. & Gallese, V. (2003). Audiovisual mirror neurons and action recognition. *Experimental Brain Research, 153*, 628-636.

Kohler, E., Keysers, C., Umiltà, M. A., Fogassi, L., Gallese, V. & Rizzolatti, G. (2002). Hearingsounds, understanding actions: action representation in mirror neurons. *Science, 297*, 846–848.

Laufs, H., Krakow, K., Sterzer, P., Eger, E., Beyerle, A., Salek-Haddadi, A., et al. (2003). Electroencephalographic signatures of attentional and cognitive default modes in spontaneous brain activity fluctuations at rest. *Proceedings of the National Academy of Sciences of the United States of America, 100*(19), 11053-11058.

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*, 601-607.

Muthukumaraswamy, S. D. & Johnson, B. W. (2004). Changes in rolandic mu rhythm during observation of a precision grip. *Psychophysiology, 41*, 152-156.

Oberman, L. M., Hubbard, E. M., McCleery, J. P., Altschuler, E. L., Ramachandran, V. S. & Pineda, J. A. (2005). EEG evidence for mirror neuron dysfunction in autism spectrum disorders. *Cognitive Brain Research, 2,* 190-198.

Perry, A., Troje, N., & Bentin, S. (in press). Exploring motor system contributions to the perception of social information: Evidence from EEG activity in the mu/alpha frequency range. *Social Neuroscience.* Retrieved March 7, 2010 from http://pissaro.soc.huji.ac.il/Shlomo/publications/pdfs/Perry%20et%20al%20SNS%20in%20press.pdf

Pineda, J. A. (2005). The functional significance of mu rhythms: Translating “seeing” and “hearing” into “doing”. *Brain Research Reviews, 50,* 57-68.

Pineda, J. A., Allison, B. Z. & Vankov, A. (2000). The effects of self-movement, observation, and imagination on mu rhythms and readiness potentials (RP’s): toward a brain-computer interface (BCI). *IEEE Transactions on Rehabilitation Engineering, 8,* 219-222.

Pineda, J.A., & Oberman, L.M. (2006). What goads cigarette smokers to smoke? Neural adaptation and the mirror neuron system. *Brain Research, 1121*(1), 128-135.

Platek, S. M., Mohamed, F. B., & Gallup, G. G. Jr. (2005). Contagious yawning and the brain. *Cognitive Brain Research*, *23*, 448-452.

Pollick, F., Kay, J., Heim, K., & Stringer, R. (2005). Gender Recognition From Point-Light Walkers. *Journal of Experimental Psychology: Human Perception and Performance, 31*(6), 1247-1265.

Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind?. *Behavioral and Brain Sciences*, *1*(4), 515-526.

Rizzolatti, G., Fadiga, L., Fogassi, L. & Gallese, V. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, *3*, 131–141.

Rizzolatti, G., Fogassi, L. & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *National Review of Neuroscience, 2,* 661-670.

Rizzolatti, G. & Craighero, L. (2004). The mirror neuron system. *Annual Review of Neuroscience, 27,* 169-92.

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. *Journal of Cognitive Neuroscience, 16*, 988-999.

Saygin, A. P., Wilson, S. M., Hagler Jr., D. J., Bates, E. & Sereno, M. I. (2004). Point-light biological motion perception activates human premotor cortex. *Journal of Neuroscience, 24,* 6181-6188.

Shipley, T. F. (2003). The effect of object and event orientation on perception of biological movement. *Psychological Science*, *14*, 377-380.

Ulloa, E. R. & Pineda, J. A. (2007). Recognition of point-light biological motion: Mu rhythms and mirror neuron activity. *Behavioural Brain Research*, *183*, 188-194.

Urgesi, C., Moro, V., Candid, M., & Aglioti, S. M. (2006). Mapping implied body actions in the human motor system. *The Journal of Neuroscience*, *26*, 7942-7949.

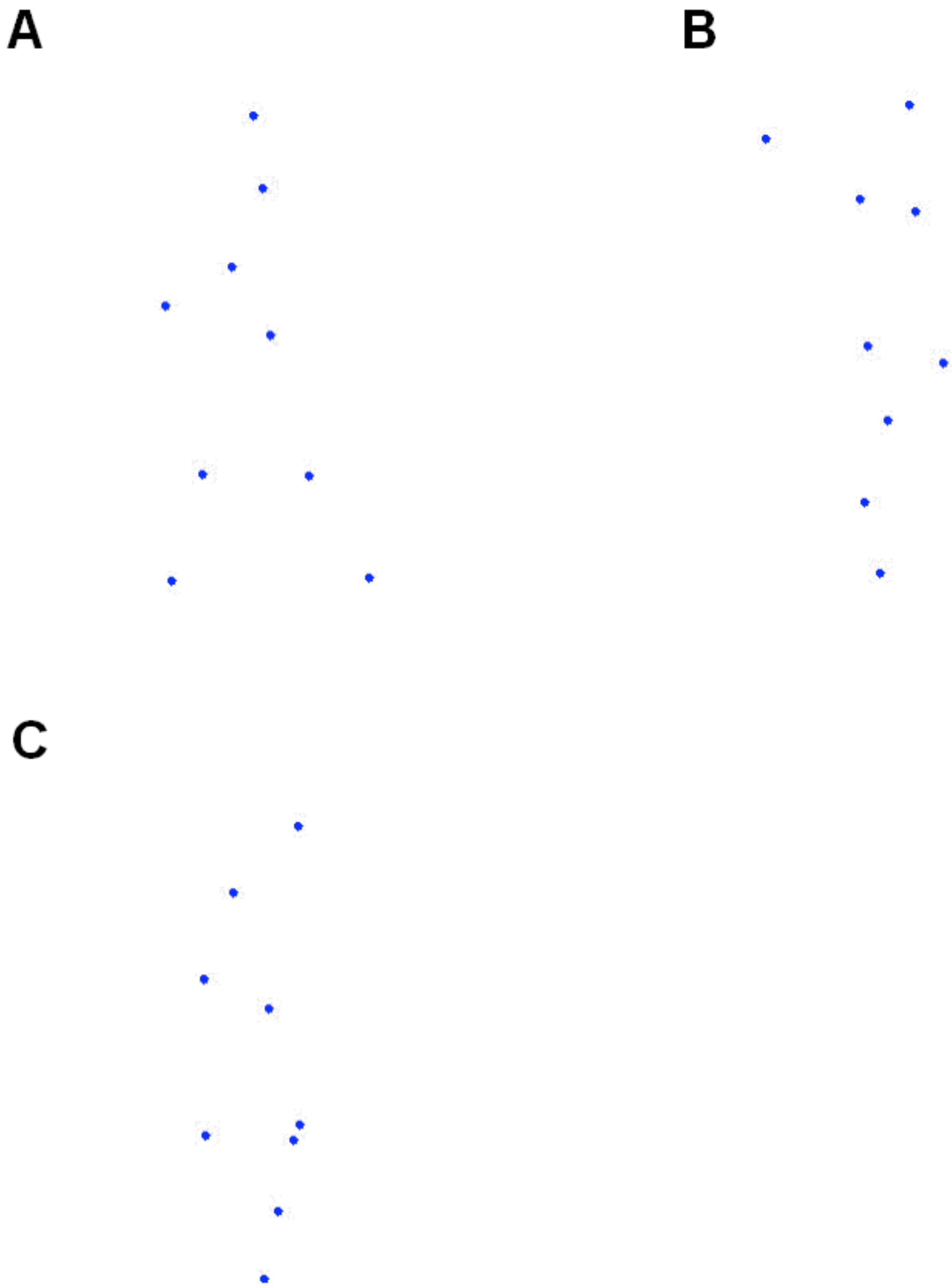
Figure Captions

Figure 1. Example stills of the point light stimuli used in the study: A) upright walker, B) inverted walker and C) random dot display.

Figure 2. Approximate electrode placements for the 64 channel QuikCap. Locations of interest over motor cortex (from left to right: C3, C1, Cz, C2, C4) are shown within the rectangle.

Figure 3. Indices of mu suppression for the three stimulus types at central electrode sites over motor cortex. For all stimulus types, significant mu suppression was observed.

Figure 4. Scatterplots depicting the relationship between PT scores and mu suppression indices to: A) upright, B) inverted, and C) random dot displays.



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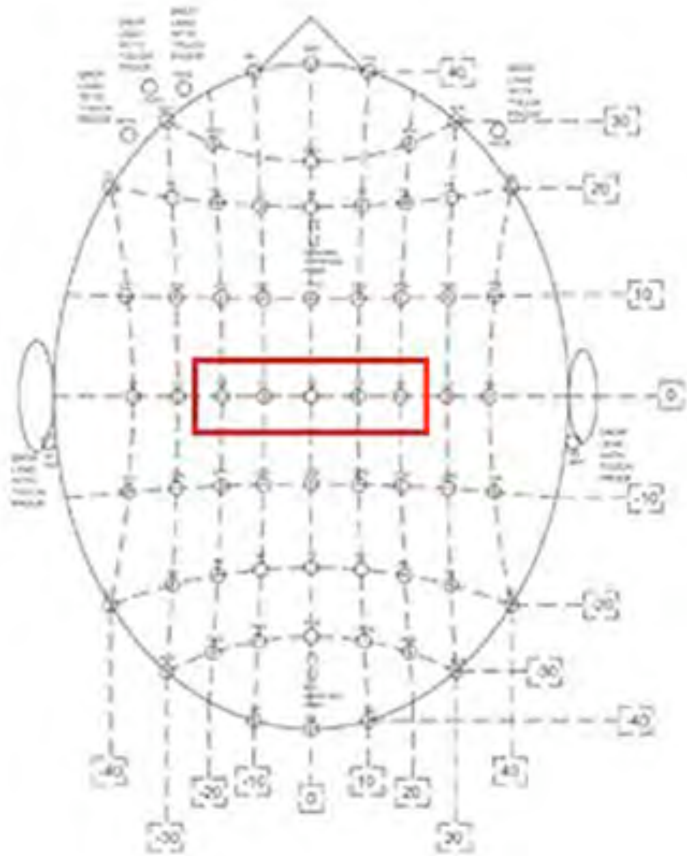

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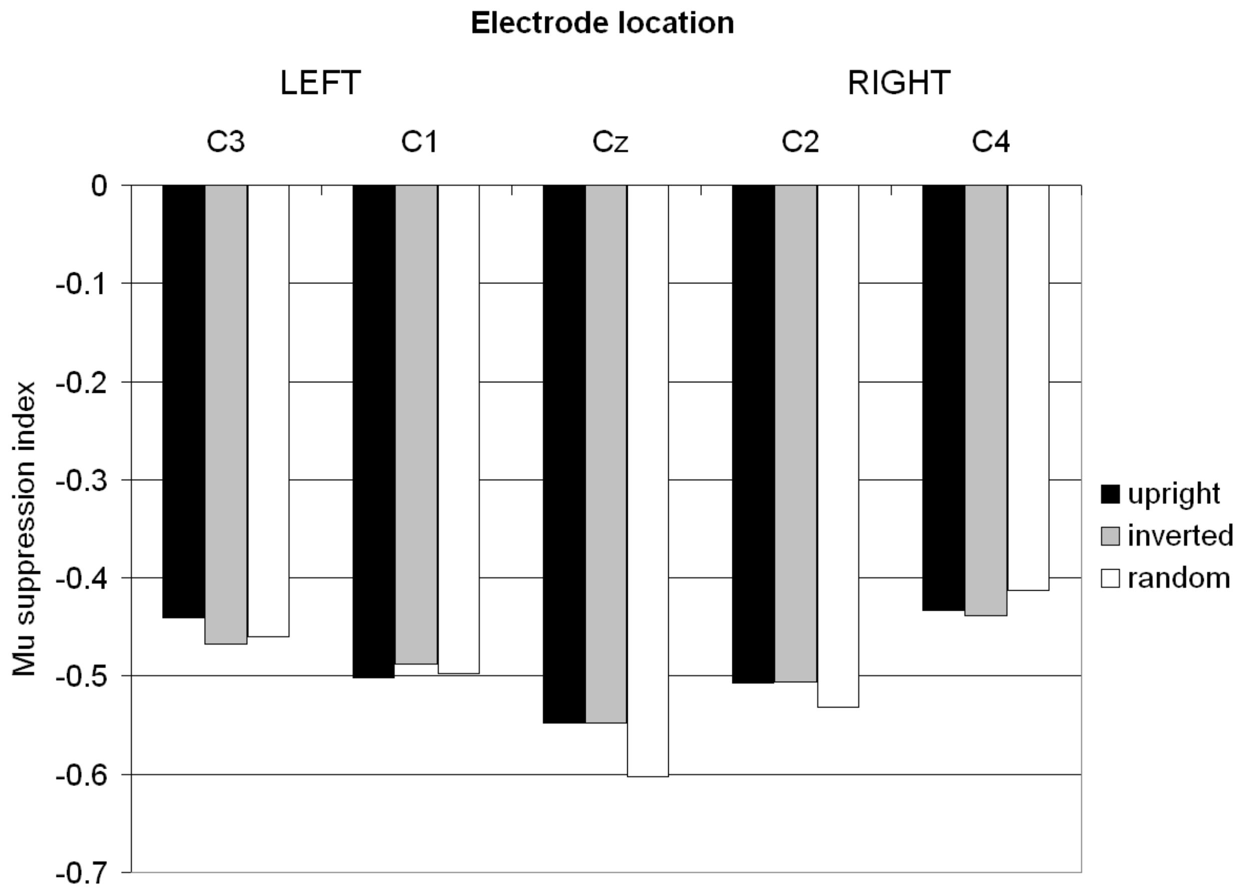

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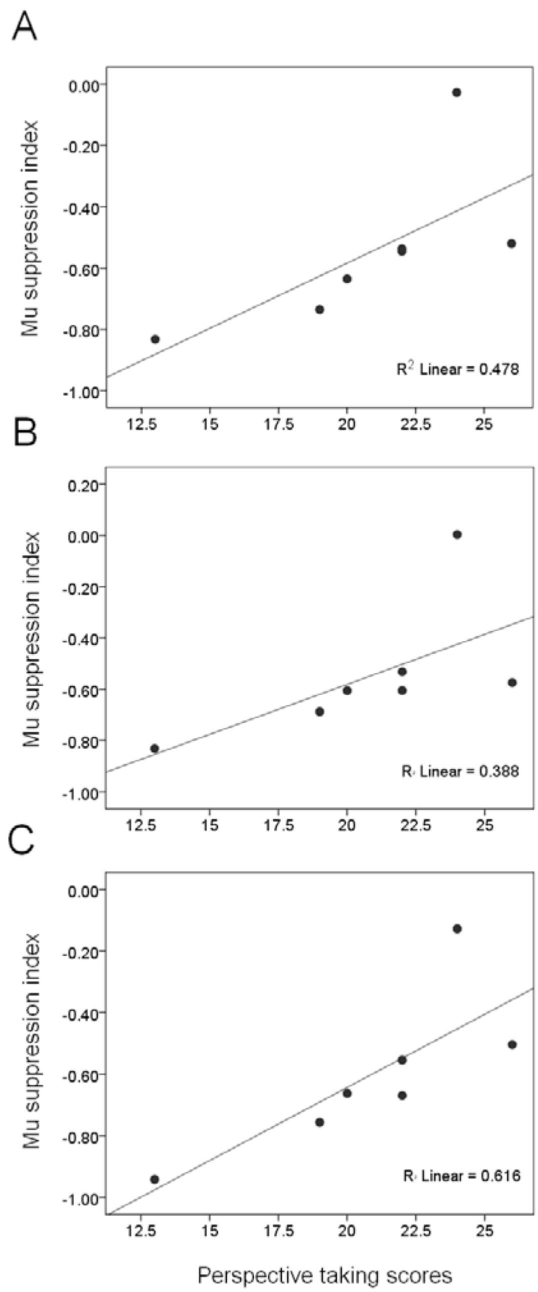

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APPENDIX A

Interpersonal Reactivity Index (Davis, 1980)

Please rate the following items on a scale of 1 (not at all like you) to 5 (very much like you)

1. I daydream and fantasize, with some regularity about things that might happen to me.
   1 2 3 4 5
   Not like me Very much like me

2. I often have tender, concerned feelings for people less fortunate than me.
   1 2 3 4 5
   Not like me Very much like me

3. I sometimes find it difficult to see things from the "other guy's" point of view.
   1 2 3 4 5
   Not like me Very much like me

4. Sometimes I don't feel very sorry for other people when they are having problems.
   1 2 3 4 5
   Not like me Very much like me

5. I really get involved with the feelings of the characters in a novel.
   1 2 3 4 5
   Not like me Very much like me

6. In emergency situations, I feel apprehensive and ill-at-ease.
   1 2 3 4 5
   Not like me Very much like me

7. I am usually objective when I watch a movie or a play, and I don't often get completely caught up in it.
   1 2 3 4 5
   Not like me Very much like me

8. I try to look at everybody's side of a disagreement before I make a decision.
   1 2 3 4 5
   Not like me Very much like me

9. When I see someone being taken advantage of, I feel kind of protective towards them.
   1 2 3 4 5
   Not like me Very much like me

10. I sometimes feel helpless when I am in the middle of a very emotional situation.
1 2 3 4 5
Not like me Very much like me

11. I sometimes try to understand my friends better when I am in the middle of a very emotional situation.
1 2 3 4 5
Not like me Very much like me

12. Becoming extremely involved in a good book or movie is somewhat rare for me.
1 2 3 4 5
Not like me Very much like me

13. When I see someone get hurt, I tend to remain calm.
1 2 3 4 5
Not like me Very much like me

14. Other people's misfortunes do not usually disturb me a great deal.
1 2 3 4 5
Not like me Very much like me

15. If I'm sure I'm right about something, I don't waste much time listening to other people's arguments.
1 2 3 4 5
Not like me Very much like me

16. After seeing a play or a movie, I have felt as though I were one of the characters.
1 2 3 4 5
Not like me Very much like me

17. Being in a tense emotional situation scares me.
1 2 3 4 5
Not like me Very much like me

18. When I see someone being treated unfairly, I sometimes don't feel very much pity for them.
1 2 3 4 5
Not like me Very much like me

19. I am usually pretty effective at dealing with emergencies.
1 2 3 4 5
Not like me Very much like me

20. I am often quite touched by things that I see happen.
1 2 3 4 5
Not like me Very much like me

21. I believe that there are two sides to every question and try to look at them both.
1 2 3 4 5
Not like me Very much like me

22. I would describe myself as a pretty soft-hearted person.
1 2 3 4 5
Not like me Very much like me

23. When I watch a good movie, I can very easily put myself in the place of a leading actor.
1 2 3 4 5
Not like me Very much like me

24. I tend to lose control during emergencies.
1 2 3 4 5
Not like me Very much like me

25. When I'm upset at someone, I usually try to "put myself in his shoes" for a while.
1 2 3 4 5
Not like me Very much like me

26. When I am reading an interesting story, I imagine how *I* would feel if the events in the story were happening to me.
1 2 3 4 5
Not like me Very much like me

27. When I see someone who badly needs help in an emergency, I go to pieces.
1 2 3 4 5
Not like me Very much like me

28. Before criticizing somebody, I try to imagine how I would feel if *I* were in their place.
1 2 3 4 5
Not like me Very much like me

APPENDIX B

Empathy Quotient Scale and Scoring Key (Baron Cohen & Wheelwright, 2004)

Responses that score 1 or 2 points are marked. Other responses score 0. For total score, sum all items.

		strongly agree	slightly agree	slightly disagree	strongly disagree
1.	I can easily tell if someone else wants to enter a conversation.	2	1		
2.	I find it difficult to explain to others things that I understand easily, when they don't understand it first time.			1	2
3.	I really enjoy caring for other people.	2	1		
4.	I find it hard to know what to do in a social situation.			1	2
5.	People often tell me that I went too far in driving my point home in a discussion.			1	2
6.	It doesn't bother me too much if I am late meeting a friend.			1	2
7.	Friendships and relationships are just too difficult, so I tend not to bother with them.			1	2
8.	I often find it difficult to judge if something is rude or polite.			1	2
9.	In a conversation, I tend to focus on my own thoughts rather than on what my listener might be thinking.			1	2
10.	When I was a child, I enjoyed cutting up worms to see what would happen.			1	2
11.	I can pick up quickly if someone says one thing but means another.	2	1		
12.	It is hard for me to see why some things upset people so much.			1	2

13.	I find it easy to put myself in somebody else's shoes.	2	1		
14.	I am good at predicting how someone will feel.	2	1		
15.	I am quick to spot when someone in a group is feeling awkward or uncomfortable.	2	1		
16.	If I say something that someone else is offended by, I think that that's their problem, not mine.			1	2
17.	If anyone asked me if I like their haricut, I would reply truthfully, even if I didn't like it.			1	2
18.	I can't always see why someone should have felt offended by a remark.			1	2
19.	Seeing people cry doesn't really upset me.			1	2
20.	I am very blunt, which some people take to be rudeness, even though this is unintentional.			1	2
21.	I don't tend to find social situations confusing	2	1		
22.	Other people tell me I am good at understanding how they are feeling and what they are thinking.	2	1		
23.	When I talk to people, I tend to talk about their experiences rather than my own.	2	1		
24.	It upsets me to see animals in pain.	2	1		
25.	I am able to make decisions without being influenced by people's feelings.			1	2
26.	I can easily tell if someone else is interested or bored with what I am saying.	2	1		

27.	I get upset if I see people suffering on news programmes.	2	1		
28.	Friends usually talk to me about their problems as they say I am very understanding.	2	1		
29.	I can sense if I am intruding, even if the other person doesn’t tell me.	2	1		
30.	People sometimes tell me that I have gone too far with teasing.			1	2
31.	Other people often say that I am insensitive, though I don’t always see why.			1	2
32.	If I see a stranger in a group, I think that it is up to them to make an effort to join in.			1	2
33.	I usually stay emotionally detached when watching a film.			1	2
34.	I can tune into how someone else feels rapidly and intuitively.	2	1		
35.	I can easily work out what another person might want to talk about.	2	1		
36.	I can tell if someone is masking their true emotion.	2	1		
37.	I don’t consciously work out the rules of social situations.	2	1		
38.	I am good at predicting what someone will do.	2	1		
39.	I tend to get emotionally involved with a friend’s problems.	2	1		
40.	I can usually appreciate the other person’s viewpoint, even if I don’t agree with it.	2	1		