



Research report

EEG mu component responses to viewing emotional faces

Adrienne Moore^{a,*}, Irina Gorodnitsky^a, Jaime Pineda^{a,b}^a University of California, San Diego, Department of Cognitive Science, 9500 Gilman Drive #0515, La Jolla, CA 92093-0515, USA^b University of California, San Diego, Department of Neurosciences, La Jolla, CA 92093-0662, USA

ARTICLE INFO

Article history:

Received 23 May 2011

Received in revised form 22 July 2011

Accepted 26 July 2011

Available online 3 August 2011

Keywords:

Mu rhythm

Facial expression

Simulation

SOBI

EEGLAB

Mirror neuron

ABSTRACT

Simulation theories for the perceptual processing of emotional faces assert that observers recruit the neural circuitry involved in creating their own emotional facial expressions in order to recognize the emotions and infer the feelings of others. The EEG mu rhythm is a sensorimotor oscillation hypothesized to index simulation of some actions during perceptual processing of these actions. The purpose of this research was to extend the study of mu rhythm simulation responses during perceptual tasks to the domain of emotional face perception. Subjects viewed happy and disgusted face photos with empathy and non-empathy task instructions while EEG responses were measured. EEG components were isolated and analyzed using a blind source separation (BSS) method. Mu components were found to respond to the perception of happy and disgusted faces during both empathy and non-empathy tasks with an event-related desynchronization (ERD), activation that is consistent with face simulation. Significant differences were found between responses to happy and to disgusted faces across the right hemisphere mu components beginning about 500 ms after stimulus presentation. These findings support a simulation account of perceptual face processing based on a sensorimotor mirroring mechanism, and are the first report of distinct EEG mu responses to observation of positively and negatively valenced emotional faces.

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1. Introduction

Social interaction relies heavily on nonverbal communication, especially through facial expressions. We make critical inferences about the feelings, motivations, and intentions of others based on observing facial emotion. Simulation theories for the processing of emotional faces assert that observers activate the sensorimotor representations involved in creating their own emotional facial expressions, in order to recognize the emotions and infer the feelings of others [1,2].

Several different forms of facial expression simulation have been identified. One of these is facial mimicry, activation of the facial muscles used to produce a given emotion expression in response to seeing the expression on another face [3,4]. Mimicry has been shown to influence how we feel, for example, to increase liking between interaction partners, and thus to facilitate successful social interactions [5]. A second type of facial simulation is facial mirroring, activation of neural substrates for expression production that is not for the sake of mimicry but rather for producing an “offline” simulation of what is observed [6,7]. Facial mirroring, which refers primarily to the mirroring of the action of generating an emotional facial expression, is believed to be important for making inferences

about how others are feeling [2]. This involves shared premotor representations utilized both for the action of generating or imitating an emotional facial expression oneself and for the perceptual processing of another's face [6,7]. Mimicry and mirroring systems are believed to be distinct, because while viewing the actions of others one's own primary motor cortex (M1) is not usually active [8], and functional magnetic resonance imaging (fMRI) studies of facial mirroring responses have shown premotor but not primary motor cortex activity [6,7]. Some researchers assert that having two distinct systems for mirroring and mimicry may help us distinguish our own actions and sensations from those of others whom we simulate [9].

Another aspect of mirroring in response to faces is the simulation of the emotional feeling conveyed by the face, in addition to the simulation of the facial configuration. Emotion mirroring involves recruiting the cortical activation involved in one's own experiences of an emotion or bodily sensation during the perceptual processing of the same feelings expressed in others [9], and co-occurs with facial mirroring [6]. There is evidence for neural mirroring of an observed feeling state in response to facial expressions across a number of specific feeling states. These include shared neural substrates for feeling and for observing disgust [10], and for feeling and observing pain [11]. Together these simulation processes provide a plausible foundation for the human capacity for inferring and responding to the feelings and experiences of others [12].

* Corresponding author. Tel.: +1 858 373 8705; fax: +1 858 534 1128.

E-mail addresses: armoore@ucsd.edu, adrienne.moore@yahoo.com (A. Moore).

Simulation of observed actions can be investigated by measuring the electroencephalogram (EEG) mu rhythm during action observation [13]. The mu rhythm is a cortical oscillation generated by somatotopically organized sensorimotor cortex near the central sulcus, with distinct oscillations occurring for processing related to different body parts [14]. The neural generators of the mu signal are said to “idle” synchronously when off task, which is typically measured as high 8–13 and 15–25 Hz EEG power at central electrode sites, at rest with eyes open [15]. The mu rhythm is activated, or desynchronized, resulting in suppression of mu spectral power, by movement and movement preparation [16]. The mu rhythm is similarly desynchronized and suppressed by the observation or the imagination of movements of body parts (hands and feet have been primarily studied), linking the mu rhythm to both action and action simulation [13].

Simulation theories of person perception and social cognition were fostered by the study of mirror neurons in monkeys and then of the human mirror neuron system. Individual macaque neurons in premotor region F5 fire to both object-directed hand actions, to ingestive and communicative mouth and lip actions, and to their observation [17]. The human inferior frontal gyrus (IFG), which is believed to be the homolog to macaque F5, has been shown to be similarly activated by perception of actions [18]. This activation appears to facilitate action understanding, inferring goals and intentions when observing people's behavior. For example, premotor mirror neuron regions, active during both execution and observation of an action, are more strongly activated by perception of grasping hands within a meaningful context (drinking or cleaning up) when compared to perception of grasping hands without a contextual scene or to perceiving the context alone [19].

A number of studies infer from functional similarities between the mu rhythm and the human mirror neuron system (MNS) that changes in EEG mu (at least the 8–13 Hz component, where this research has focused) reflect “downstream” modulation of sensorimotor cortex neurons by premotor cortex mirror neurons, potentially located in BA 44 [13,20]. Consistent with this, using repetitive transcranial magnetic stimulation (rTMS) to disrupt activity in the left inferior frontal gyrus affects the modulation of mu rhythms over sensorimotor cortex [21]. A canonical mirror neuron triggering stimulus, the observation of an object-directed hand grasping motion, has been shown to decrease mu power relative to simple hand extension and to objectless grasping gestures [22,23]. This shows that the mu rhythm shares the mirror neuron system's preferential activation for goal-directed actions [17]. Further linking mu rhythm simulation to the mirror neuron system, it has been shown that observation of point-light biological motion of full-body gestures (e.g. jumping jacks) both activates premotor MNS areas according to fMRI research [24], and causes EEG mu power suppression [25]. Linking mu power to critical social processes, stimuli varying in degree of sociality (movies of social ball tossing games) have been asserted to suppress the mu rhythm accordingly [26]. Finally, mu suppression has also been correlated with accuracy on social-perceptual tasks, which involve inferring mental states from bodily expressions, but not on social-cognitive tasks, which are linked to language and theory building.

Regarding mu and simulation of faces in particular, very little research has been done. Mental imagery of orofacial movements (tongue movement and lip movement) has been shown to affect the EEG mu rhythm in a manner suggesting simulation in the form of recruitment of motor cortical areas for movement that is imaginary, not actual [27,28]. But mu power changes in response to emotional face observation have not been previously characterized.

This current study predicted that because viewing emotional faces involves simulation of the emotional facial expression, it also elicits a mu rhythm desynchronization. To test this, we compared mu responses to positively and negatively valenced faces,

specifically, to happy and disgusted faces. Because simulation mechanisms are known to differ for different emotion expressions [9,29], we predicted that the mu desynchronization responses to happy and to disgusted faces would be distinct. Because evidence shows that the right hemisphere is preferentially involved in perceptual processing of emotion and emotional faces, we predicted these differences may be right lateralized [30,31]. Finally, we also compared the influence of task conditions that do and do not instruct subjects to attempt to empathize with the perceived emotions. This allowed us to investigate whether the mu face simulation is automatic, or whether deliberate attention to the emotion expressed and an attempt to put oneself “into the shoes” of the observed person influence the mu response.

2. Materials and methods

2.1. Subjects

Thirty undergraduate students were recruited through UCSD courses and compensated for participation with course extra credit. Subjects' vision was normal or corrected to normal. Exclusion criteria included history of neurological disease and current use of psychotropic medications or stimulants other than caffeine. Subjects were also excluded if they scored above 17 (borderline clinical depression) on the Beck Depression Inventory, or if lack of fluency in English interfered with comprehending the instructions. Five subjects were not included in the final study, due to data recording problems. Of the remaining twenty-five subjects, twenty-two (11 females and 11 males) yielded clear mu components as defined in Section 2.4.3. The human study protocol was approved by the Institutional Review Board at UCSD and therefore has been performed in accordance with the ethical standards of the 1964 Declaration of Helsinki. All subjects gave their informed consent prior to the beginning of the experiment.

2.2. Stimuli and experimental design

Subjects viewed six blocks of 40 photos: four blocks of face photos (happy and disgusted, with and without the explicit instruction to empathize), one block of photos of buildings, and one block of static visual noise images. The order in which subjects completed the conditions was pseudo-randomized with all orders approximately equally represented in the final set of subjects, such that the 22 final subjects represented 18 different orders. Finally, at the end of the experiment subjects completed the balanced emotional empathy scale (BEES), a self-report tool for indexing individual differences in dispositional emotional empathy [32].

Face images were greyscaled photos from a validated facial affect stimulus set (the MacArthur Foundation Research Network EEBD NimStim set), which was created by actors coached by a FACS (facial affect coding system) expert [33]. Each block of faces contained 40 unique photos of one emotion (happy or disgusted). The photos depicted both genders and three ethnicities (European-American, African-American, and Asian-American) in random order. Face photos from particular actors and actresses were counterbalanced to appear paired with empathy and non-empathy task instructions with equal frequency.

In the empathy conditions, subjects were instructed to try to experience the emotions felt and expressed by the photographed people, and then to rate how successful they believe they were at empathizing with each on a 1–5 Likert scale. To ascertain whether subjects experienced a change in emotion congruent with the observed faces during the empathy tasks, subjects reported their mood after each block of 40 empathy trials using the PANAS-X (positive and negative affect scale-expanded). The PANAS-X is a well-validated, self-report measure of transient change in mood, consisting of adjectives and short phrases describing potential feelings and emotions in response to which subjects reported to what extent these terms described how they felt at that moment [34]. In the non-empathy conditions, subjects were asked to rate how attractive they found each face on a 1–5 Likert scale, a task, which did not require directly attending to the expressed emotion. In the buildings condition, subjects were asked to rate how well they liked each building on a 1–5 Likert scale. The constraints on order randomization were that two conditions of the same task (empathy or non-empathy) were always adjacent to one another, and the final block of photos viewed was never an empathy condition, to avoid administering the final PANAS-X self-report at the end the experiment when mood is perturbed.

2.3. EEG data acquisition

Comfortably seated in a soundproof and electrically shielded recording booth, subjects were told to fixate gaze at the center of the monitor as much as possible, to minimize movement of facial muscles, to blink only when rating with a button press, and to wait until prompted by a question appearing on the monitor to respond with the button press (see Fig. 1). Care was taken to instruct subjects not to move more than necessary, stressing the potential for motion artifact.

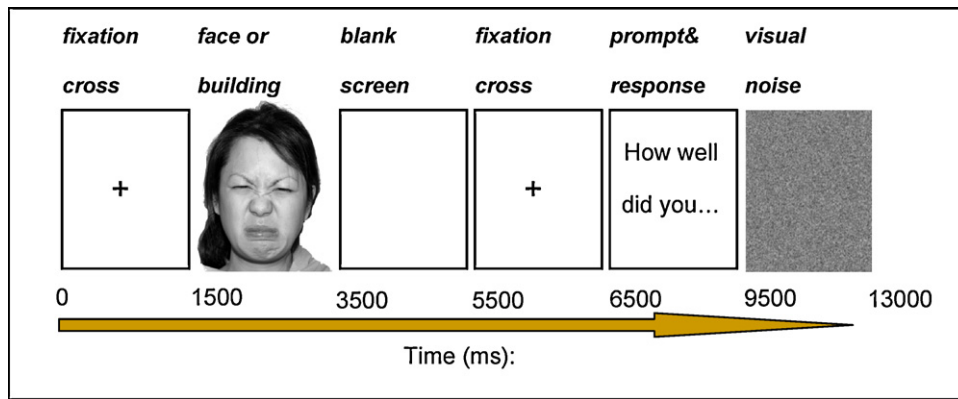


Fig. 1. Timing of individual trials. Stimuli were presented for 2000 ms.

Continuous EEG was recorded using a NeuroScan system (NeuroScan, Inc., Herndon, VA) from 13 electrodes placed according to the International 10–20 System (O1, O2, T5, T6, P3, PZ, P4, C3, CZ, C4, F3, FZ, and F4) referenced to electronically linked mastoid electrodes. Additionally, bipolar electrooculogram (EOG) was recorded from four electrodes to monitor blinks and eye movements (positioned vertically at the supraorbital ridge and lower outer canthus of the left eye, and horizontally at the middle outer canthi of left and right eyes). Impedances were set below 10 kΩ (usually below 5 kΩ) for HEOG and VEOG, and below 5 kΩ for mastoids and cap electrodes. Data were sampled at 500 Hz and filtered to the .05–30 Hz band by the NeuroScan acquisition software.

2.4. EEG data analysis

The EEGLAB Matlab Toolbox [35] was used as the platform for data analysis, with some integrated customized routines, including eSOBI,

the second-order blind identification (SOBI) algorithm for epoched data [http://sites.google.com/site/bioanalyze/]. We used blind-source separation (BSS) to reduce noise and artifacts in the EEG data and to extract the mu rhythm components.

2.4.1. Preprocessing

Data records from each subject were highpass filtered above 4 Hz, yielding 4–30 Hz bandpassed data. Data epochs time-locked to the presentation of a single photo were extracted from 1500 ms before stimulus presentation to 2000 ms after stimulus presentation. Mean baseline values were removed from each epoch. Trials containing button presses incorrectly made during the epoched time period were deleted (resulting in 191–200 total epochs per subject). Data epochs from the visual noise condition were removed and the remaining epochs for each subject were concatenated. The reason visual noise was excluded was that it elicited strong, occipital

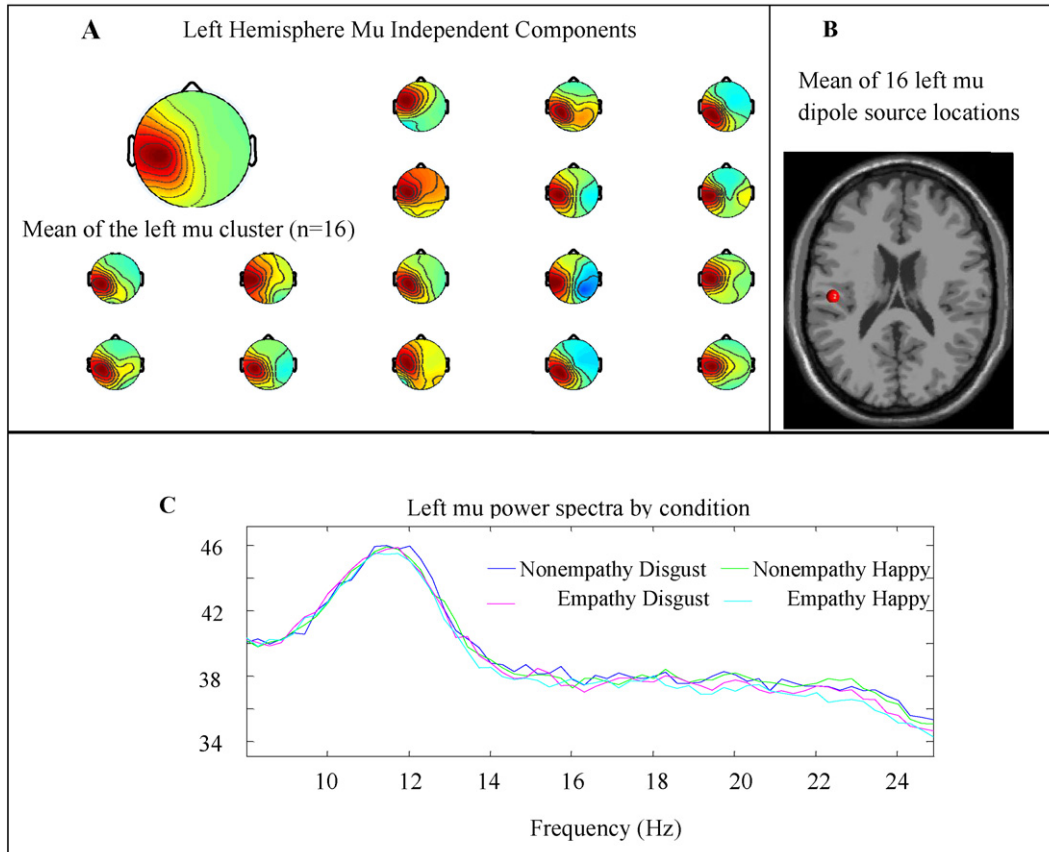


Fig. 2. Left mu cluster: (A) Mean and individual topographic scalp maps, (B) Cluster mean DIPFIT dipole location, (C) Cluster mean power spectrum, $10 \times \log_{10} (\mu V^2/Hz)$, for each condition.

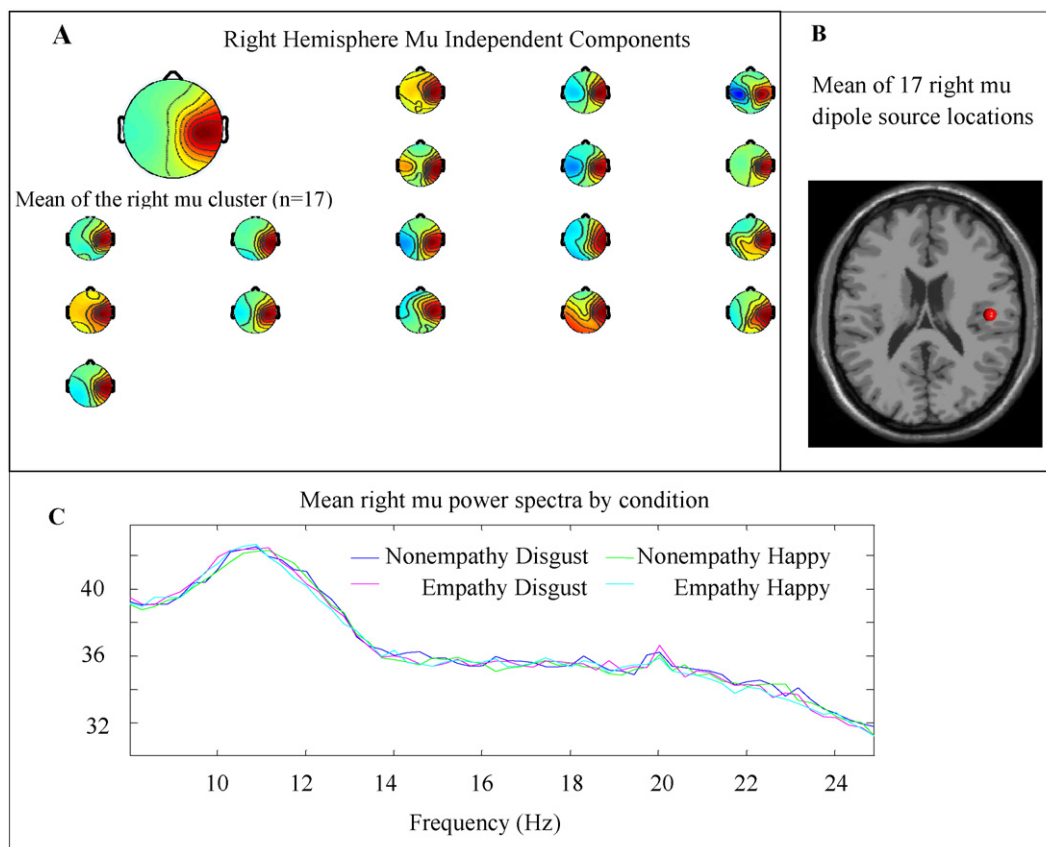


Fig. 3. Right mu cluster: (A) Mean and individual topographic scalp maps, (B) Cluster mean DIPFIT dipole location, (C) Cluster mean power spectrum, $10 \times \log_{10}(\mu V^2/Hz)$, for each condition.

8–13 Hz alpha activity apparent in the raw EEG record, which can occasionally alter the robustness of source separation of other, weaker cerebral sources.

2.4.2. Component separation

SOBI, a well-validated BSS method, was used to separate the preprocessed EEG signals into independent components. BSS attempts to separate linearly mixed signals without information about the mixing process. The SOBI algorithm, introduced by Belouchrani et al. [36], attempts to perform the joint approximate diagonalization of a set of time-lagged covariance matrices obtained from the data. SOBI has been found to be effective in removing EOG and EMG artifacts, noise, and also for separating EEG cerebral sources, including mu components [37–40]. SOBI is also computationally fast and can work well on short data records.

The eSOBI algorithm is a modification of SOBI for processing epoched data.

The eSOBI algorithm was applied three times as follows. In the first step, eSOBI was used similarly to the procedures described by Ng and Raveendran [38] to extract and remove components that contained a large portion of noise and artifacts, including ocular artifacts. Next, “cleaned” EEG data were reconstructed from the remaining non-artifactual components. In the second step, eSOBI was applied to the cleaned EEG data to identify trials in which subject motion distorted EEG components. After rejecting those trials, cleaned EEG data were once again reconstructed and eSOBI was applied a third time. The mu rhythm components were identified from the third decomposition. Sequential application of eSOBI yielded data with improved signal to noise ratio, by unmixing and removing standard EEG artifacts from the brain activity data. This overall approach was found to yield the most robust results for our data.

2.4.3. Identifying mu components

To identify mu rhythm components, we first used individual topographic scalp maps (Figs. 2A and 3A) to identify all centrally located generators, with dipolar structure, and with the focus lateralized left or right of the midline. However, topographic projections depend on the orientation of the electric field, so sources from other parts of the cortex may occasionally appear as emanating from the sensorimotor region in a topographic map. One solution is to localize the cortical generators of selected components to verify their foci. Therefore, as our second validation step we performed such localization using the equivalent dipole DIPFIT function

and standard Boundary Element Model (MNI) head model, with the warp montage function to co-register the electrode locations with the head model, followed by coarse and fine fitting [35] (Figs. 2B and 3B). The localization identified one left lateralized component, which was located outside the central cortical region, and it was excluded from further analysis. In the third validation step, spectral analysis was performed on the remaining components. All of the components that passed the second validation step had peak power in the alpha (8–13 Hz) range (Figs. 2C and 3C), as is characteristic of mu. This analysis identified 22 subjects with at least one clear mu component. Of those 22, 11 had both left and right hemisphere mu components. No subjects had more than one mu component per hemisphere, indicating that the identified components captured the entire left or right mu rhythm responses extracted for each subject. The final mu clusters contained 17 right lateralized and 16 left lateralized mu components (Figs. 2A and 3A).

2.4.4. Spectral and statistical analyses

Event related spectral perturbations (ERSPs), deviations in spectral power relative to a baseline, were calculated for each component in the left and right mu clusters using built-in EEGLAB procedures [35] as follows. A time-frequency decomposition was computed for each individual condition using wavelets with Morlet tapers, and the deviations in log spectral power in each time-frequency bin were then computed, relative to the mean of the log spectral power of the 1500 ms pre-stimulus baseline. To compare responses for specific experimental conditions, the common baseline was calculated across those test conditions using EEGLAB, and the component ERSP values were adjusted for the common baseline for each test.

To assess statistical differences, nonparametric resampling methods available in EEGLAB were used [41]. A bootstrap resampling methods was used to test whether ERSP deviations in spectral power in the post-stimulus interval were significantly larger relative to the pre-stimulus period for each subject and each separate condition. The statistical differences across the four face conditions were analyzed for the right and the left clusters by comparing ERSP values in each time-frequency bin for that cluster using repeated measures permutation comparison of the 2X2 (empathy/non-empathy X happy/disgusted) design. To address the increased probability of false discoveries in multiple hypotheses testing, all ERSP results were corrected using Benjamini and Hochberg [42] false discovery rate correction with an alpha value of .05.

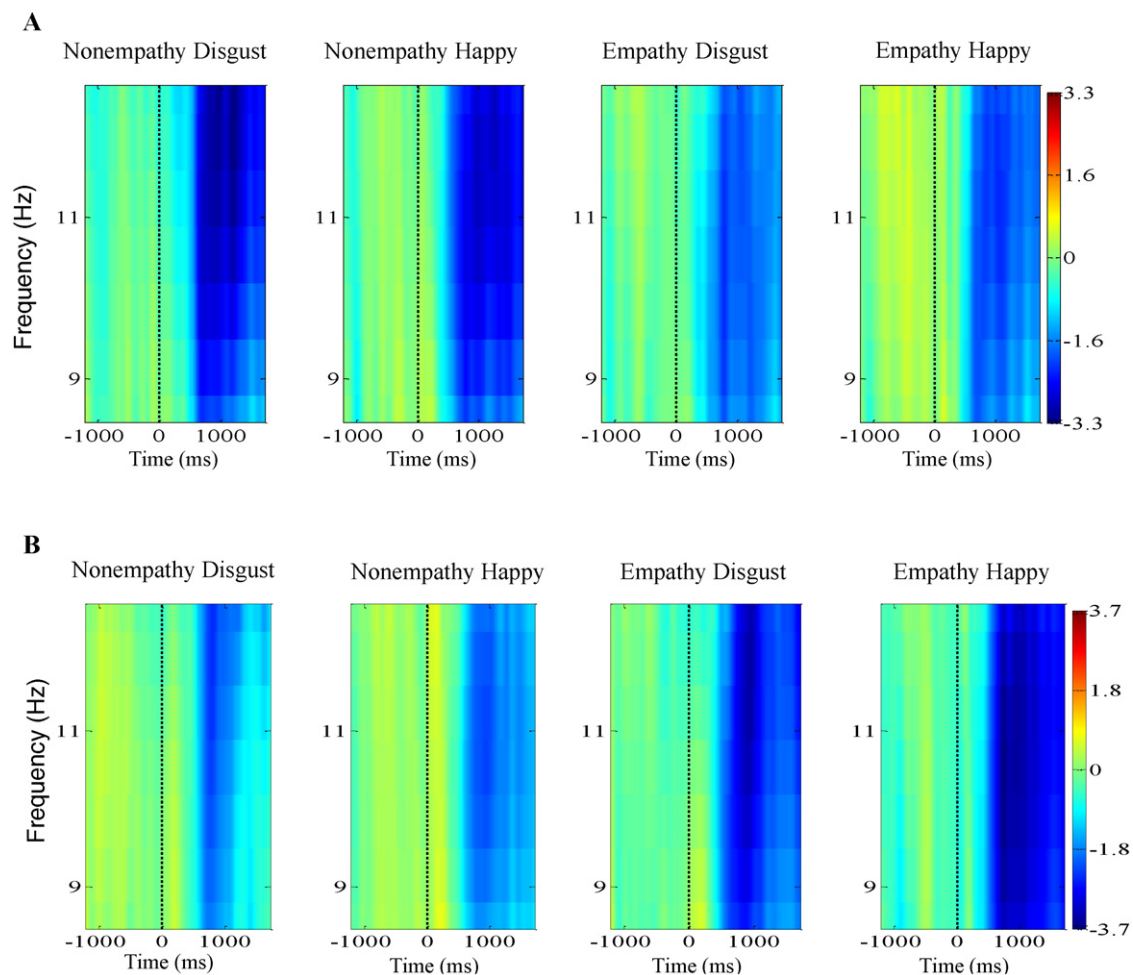


Fig. 4. (A) Left mu cluster, event related spectral perturbations (8–13 Hz power, dB), (B) Right mu cluster, event related spectral perturbations (8–13 Hz power, dB).

3. Results and discussion

3.1. Emotion and empathy self-report results

Mood measurement (the PANAS-X) was administered two times to each subject, following the two empathy tasks. The differences (first score minus second score) between mood change for subjects who would be predicted to have a mood score drop if empathizing (empathized with happy first, then with disgust) and subjects who would be predicted to have a mood score increase if empathizing (empathized with disgust first and then with happy) were compared. 90% of the subjects who empathized with happy faces first and then disgusted faces experienced a drop in mood, with a mean drop of 8.6 points. 62.5% of the subjects who empathized with disgusted faces first and then happy faces experienced an improvement in mood, with a mean increase of 2.75 points. This difference was statistically significant (2 tailed, unequal variance t -test, $t(15.7) = -3.59$, $p < .003$, after confirming data does not differ from Gaussian, Kolmogorov-Smirnov $z = 355$, $p = \sim 1.0$), confirming that the empathy task successfully modulated subject mood. Though mood responses were not measured following the non-empathy conditions, it is possible that subjects also experienced an empathetic mood convergence during the non-empathy conditions due to observing emotional faces.

Individual differences in trait emotional empathy reported through the BEES questionnaire were calculated as well, with the prediction that the trait empathy measure may be correlated with how much self-reported mood was perturbed in the empathy

conditions and/or with the magnitude of the mu face response ERSPs. However, no significant correlations were found between individual differences in trait empathy and amount of mood change due to observing emotional faces or magnitude of mu EEG response.

3.2. EEG component separation results

To cluster mu components together we used mu power spectra, topographic maps, and equivalent dipole source localizations as criteria for inclusion of a component in the mu clusters. Mu components were found in the left and/or the right hemispheres of most subjects (22 of 25). In Figs. 2A and 3A it can be observed that the centers of the topographic projections of components vary slightly more for the left than the right cluster. The underlying cause may be poorer performance for source separation of left mu responses due to weaker responses in the left than the right hemisphere during emotional face perception [30].

3.3. EEG spectral and statistical results

Event-related perturbations in spectral power time-locked to stimulus presentation for the left and right mu component clusters were used to compare experimental conditions as described in Section 2.4.4. ERSPs are referred to as event-related desynchronizations (ERDs) if the direction of post-stimulus change in power is decreasing, and as event-related synchronizations (ERSs) if the direction of post-stimulus change in power is increasing. The ERD corresponds with mu power suppression, which has been reported

in response to movement and movement simulation, while the ERS corresponds to mu power enhancement. All significant mean ERSPs from all subjects and all face viewing conditions in both clusters except for one mean response were ERDs, not ERSs, consistent with the face simulation hypothesis.

3.3.1. Buildings to faces ERSP comparison

To compare mu ERSP responses to viewing emotional faces with mu ERSP responses to the control viewing buildings, for each subject we calculated the mean response for each condition across 40 trials. Observing faces elicited more statistically significant ERD responses than observing buildings in both the left and right mu clusters, consistent with a face simulation mechanism indexed by mu suppression. In the left mu cluster, buildings elicited a statistically significant ($p < .05$) ERD response in 50% of subjects, while faces elicited a significant ERD response in 81.3%. On the right, buildings elicited a significant ERD response in 47.1% of subjects, while face elicited a significant ERD in 76.5%. We confirmed that the difference between percentage of subjects who responded to faces and percentage of subjects who responded to buildings in each cluster was significant with a Wilcoxon signed ranks test ($z = -2.236$, $p = .025$, both clusters). While this confirmed significant mu suppression to viewing emotional faces relative to the control condition, further studies are needed to understand the nature of the mu response to observing buildings. Future research should determine whether the mu response to buildings indicates a baseline responsivity of sensorimotor EEG components to any complex visual stimuli observed for the sake of a rating task. Following this confirmation that faces elicited significantly greater mu suppression than the control buildings, we then compared in detail differences between the responses to the four face observation conditions.

3.3.2. Face conditions ERSP comparison

The mean ERSP values computed as described in Section 2.4.4 above are displayed in Fig. 4. ERDs were observed beginning approximately 500 ms after stimulus presentation in both the left and the right mu clusters in the 8–13 Hz range in response to observing both happy and disgusted faces, with and without the explicit instruction to empathize with the faces. As ERD responses indicate activation of the mu rhythm and are characteristic of real and imagined bodily movement, this suggests simulation of the action of producing a facial expression in response to observing both positively and negatively valenced faces.

Though faces elicited essentially the same number of significant ERDs from the left and right hemispheres (from 81% of subjects on the left and from 77% of subjects on the right), there were significant differences between the four face processing condition ERDs only on the right. The results from non-parametric, permutation-based statistical comparison of the right hemisphere ERSP responses to the four face processing conditions are shown in Fig. 5. A main effect of facial emotion observed (happy vs. disgusted) was found in the right mu clusters ($p < .05$). This lateralization of effects is consistent with many reports of different roles for the left and right hemispheres in processing emotional faces, and with many reports of right hemisphere dominance for face processing and emotion processing [1,30,31]. The time course of the post-stimulus response main effect of facial emotion observed involves a significantly greater ERD to disgusted faces than to happy faces at around 500 ms post-stimulus presentation, followed by a larger, significantly greater ERD to happy faces than to disgusted faces at around 600 ms, 1000 ms and 1500 ms (see Fig. 5A and B). The time course of these differences indicates more rapid face simulation for negatively valenced, disgust faces, but an overall more extensive simulation response for positively valenced, happy faces.

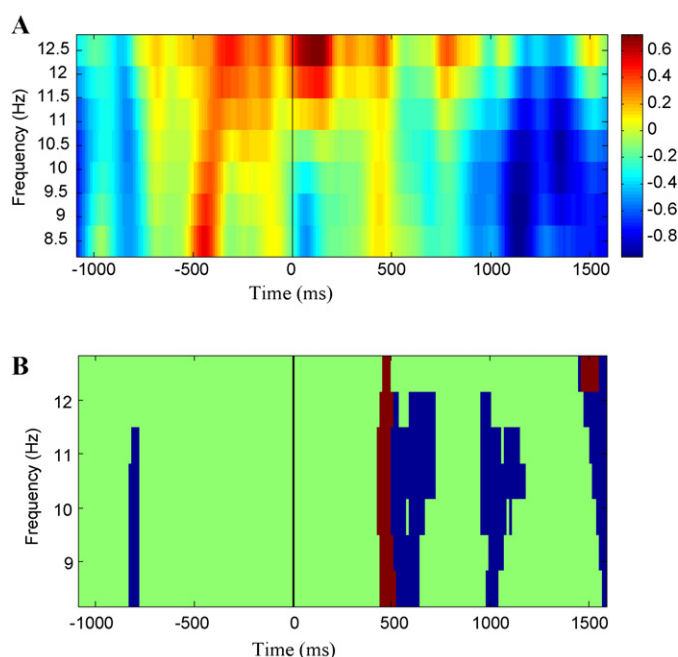


Fig. 5. (A) Main effect of emotional facial expression, right hemisphere mu ERSP power. Response to happy faces minus response to disgusted faces, right mu cluster power, in dB (8–13 Hz). Shows the mean ERSP power collapsed across the empathy and non-empathy conditions $((EH-ED + NH-ND)/2)$. Redder regions indicate ERSP power to happy > ERSP power to disgust, therefore, post-stimulus ERD to disgust > ERD to happy. Bluer regions indicate that ERSP to happy < ERSP to disgust, therefore, ERD to happy > ERD to disgust. (B) Significant differences by emotional facial expression, right hemisphere mu ERSP. Shows the regions where ERSP differences between happy and disgust are statistically significant. In red regions the ERD to disgusted faces is significantly greater than the ERD to happy. In blue regions the ERD to happy faces is significantly greater than the ERD to disgusted faces. $p < .05$ after FDR correction at all red and blue data points.

At around –800 ms pre-stimulus, the right hemisphere power briefly differs significantly between happy and disgusted face conditions, with higher power in the happy face conditions ($p < .05$). Because the stimuli were presented in blocks to facilitate mood convergence in one direction across blocked trials, subjects were able to anticipate the upcoming facial expression. These pre-stimulus differences by face type are attributed to anticipatory simulation of facial expressions, as mental imagery is another class of simulation known to be reflected in mu power changes [27,28].

After FDR correction for multiple comparisons across time and frequency bins, no significant differences were found in the mu component responses when comparing empathy and non-empathy conditions ($p > .05$). Absence of differences between the mu responses in empathy and non-empathy conditions in this study may indicate that the mu ERD reflects an automatic simulation process which is not influenced by the deliberate attempt to empathize. Alternately, it is possible that this analysis was not sensitive enough to detect significant differences by task, in part due to the correction for multiple comparisons across a large number of time and frequency bins (1400), which increases the probability of false negatives. Future research could address these alternatives.

3.4. Mirroring and mimicry

Viewing emotional faces has been shown to elicit a facial mimicry response measured by EMG recording from electrodes placed above the facial muscles responsible for generating a particular expression [3] [43]. This mimicry occurs both within 500–1000 ms [44], and also at slower time scales [45,46]. Facial

mimicry responses could contribute to the mu suppression effects reported here.

However, evidence also exists indicating that mu power changes while observing face stimuli do not necessarily reflect this covert muscle movement. An MEG study of observation of faces producing speech and non-speech lip forms while EMG was collected reported activity in BA 44 and in sensorimotor areas, indicating simulation, but found no significant facial EMG activity [47]. This is consistent with other studies of mu simulation responses and EMG. For example, in a study wherein subjects imagined hand movements in order to move a cursor by means of a brain-computer interface, hand EMG activity was reported to be very low. Further, the correlation between cursor target position and EMG was reported to be much lower than that between target position and mu EEG [48]. This supports the idea that mu reflects a simulation process that is distinct from motor processes that produce mimicry's movement. Future research on mu suppression in response to emotional face perception should attempt to distinguish between mu ERD effects due to facial mimicry and mu ERD effects due only to neural mirroring. Simultaneous measurement of facial EMG and EEG responses while subjects observe emotional faces may accomplish this.

4. Conclusion

This study extends EEG mu mirroring research to the domain of emotional face perception by identifying the mu responses to viewing happy and disgusted facial expressions. Mu component event-related desynchronization responses occurred to observation of both disgusted and happy faces with and without the deliberate attempt to empathize with the emotion viewed. This event-related decrease in mu component power is believed to indicate simulation of the action of producing an observed facial expression, consistent with previous accounts of mu power suppression responses to both action execution and action perception in other domains [23,25]. In the right hemisphere, the mu component responses to observation of these positively and negatively valenced emotional faces were distinct. Specifically, at around 500 ms disgusted faces elicited a more robust ERD, with a stronger ERD to happy faces subsequently. The findings reported here support a simulation theory of face processing based on a sensorimotor mirroring mechanism, wherein first-person action execution and third-person action perception share common neural substrates.

Acknowledgements

Special thanks to Dr. Andrea Chiba and the Temporal Dynamics of Learning Center for mentoring and support.

Development of the MacBrain Face Stimulus Set was overseen by Nim Tottenham and supported by the John D. and Catherine T. MacArthur Foundation Research Network on Early Experience and Brain Development. Please contact Nim Tottenham at tott0006@tc.umn.edu for more information concerning the stimulus set.

References

- [1] Adolphs R. Recognizing emotion from facial expressions: psychological and neurological mechanisms. *Behav Cogn Neurosci Rev* 2002;1:21–62.
- [2] Adolphs R. How do we know the minds of others? Domain-specificity, simulation, and enactive social cognition. *Brain Res* 2006;1079:25–35.
- [3] Dimberg U. Facial reactions to facial expressions. *Psychophysiology* 1982;19:643–7.
- [4] Hess U, Blairy S. Facial mimicry and emotional contagion to dynamic emotional facial expressions and their influence on decoding accuracy. *Int J Psychophysiol* 2001;40:129–41.
- [5] Chartrand TL, Bargh JA. The chameleon effect: the perception-behavior link and social interaction. *J Pers Soc Psychol* 1999;76:893–910.
- [6] Carr L, Iacoboni M, Dubeau MC, Mazziotta JC, Lenzi GL. Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proc Natl Acad Sci USA* 2003;100:5497–502.
- [7] Leslie KR, Johnson-Frey SH, Grafton ST. Functional imaging of face and hand imitation: towards a motor theory of empathy. *Neuroimage* 2004;21:601–7.
- [8] Gazzola V, Keysers C. The observation and execution of actions share motor and somatosensory voxels in all tested subjects: single-subject analyses of unsmoothed fMRI data. *Cereb Cortex* 2009;19:1239–55.
- [9] Bastiaansen JA, Thioux M, Keysers C. Evidence for mirror systems in emotions. *Philos Trans R Soc Lond B: Biol Sci* 2009;364:2391–404.
- [10] Wicker B, Keysers C, Plailly J, Royet JP, Gallese V, Rizzolatti G. Both of us disgusted in My insula: the common neural basis of seeing and feeling disgust. *Neuron* 2003;40:655–64.
- [11] Saarela MV, Hlushchuk Y, Williams AC, Schurmann M, Kalso E, Hari R. The compassionate brain: humans detect intensity of pain from another's face. *Cereb Cortex* 2007;17:230–7.
- [12] Gallese V, Keysers C, Rizzolatti G. A unifying view of the basis of social cognition. *Trends Cogn Sci* 2004;8:396–403.
- [13] Pineda JA. The functional significance of mu rhythms: translating seeing and hearing into doing. *Brain Res Brain Res Rev* 2005;50:57–68.
- [14] Pfurtscheller G, Neuper C, Andrew C, Edlinger G. Foot and hand area mu rhythms. *Int J Psychophysiol* 1997;26:121–35.
- [15] Pfurtscheller G, Stancak Jr A, Neuper C. Event-related synchronization (ERS) in the alpha band—an electrophysiological correlate of cortical idling: a review. *Int J Psychophysiol* 1996;24:39–46.
- [16] Neuper C, Wortz M, Pfurtscheller G. ERD/ERS patterns reflecting sensorimotor activation and deactivation. *Prog Brain Res* 2006;159:211–22.
- [17] Rizzolatti G, Craighero L. The mirror-neuron system. *Annu Rev Neurosci* 2004;27:169–92.
- [18] Kilner JM, Neal A, Weiskopf N, Friston KJ, Frith CD. Evidence of mirror neurons in human inferior frontal gyrus. *J Neurosci* 2009;29:10153–9.
- [19] Iacoboni M, Molnar-Szakacs I, Gallese V, Buccino G, Mazziotta JC, Rizzolatti G. Grasping the intentions of others with one's own mirror neuron system. *PLoS Biol* 2005;3:e79.
- [20] Oberman LM, Hubbard EM, McCleery JP, Altschuler EL, Ramachandran VS, Pineda JA. EEG evidence for mirror neuron dysfunction in autism spectrum disorders. *Brain Res Cogn Brain Res* 2005;24:190–8.
- [21] Keuken MC, Hardie A, Dorn BT, Dev S, Paulus MP, Jonas KJ, et al. The role of the left inferior frontal gyrus in social perception: an rTMS study. *Brain Res* 2011;1383:196–205.
- [22] Muthukumaraswamy SD, Johnson BW. Changes in rolandic mu rhythm during observation of a precision grip. *Psychophysiology* 2004;41:152–6.
- [23] Muthukumaraswamy SD, Johnson BW, McNair NA. Mu rhythm modulation during observation of an object-directed grasp. *Brain Res Cogn Brain Res* 2004;19:195–201.
- [24] Saygin AP, Wilson SM, Hagler Jr DJ, Bates E, Sereno MI. Point-light biological motion perception activates human premotor cortex. *J Neurosci* 2004;24:6181–8.
- [25] Ulloa ER, Pineda JA. Recognition of point-light biological motion: mu rhythms and mirror neuron activity. *Behav Brain Res* 2007;183:188–94.
- [26] Oberman LM, Pineda JA, Ramachandran VS. The human mirror neuron system: a link between action observation and social skills. *Soc Cogn Affect Neurosci* 2007;2:62–6.
- [27] Spiegler A, Graitmann B, Pfurtscheller G. Phase coupling between different motor areas during tongue-movement imagery. *Neurosci Lett* 2004;369:50–4.
- [28] Pfurtscheller G, Brunner C, Schlogl A, Lopes da Silva FH. Mu rhythm (de)synchronization and EEG single-trial classification of different motor imagery tasks. *Neuroimage* 2006;31:153–9.
- [29] Lee TW, Josephs O, Dolan RJ, Critchley HD. Imitating expressions: emotion-specific neural substrates in facial mimicry. *Soc Cogn Affect Neurosci* 2006;1:122–35.
- [30] Borod JC, Cicero BA, Obler LK, Welkowitz J, Erhan HM, Santschi C, et al. Right hemisphere emotional perception: evidence across multiple channels. *Neuropsychology* 1998;12:446–58.
- [31] Killgore WD, Yurgelun-Todd DA. The right-hemisphere and valence hypotheses: could they both be right (and sometimes left)? *Soc Cogn Affect Neurosci* 2007;2:240–50.
- [32] Mehrabian A, Epstein N. A measure of emotional empathy. *J Pers* 1972;40:525–43.
- [33] Tottenham N, Tanaka JW, Leon AC, McCarry T, Nurse M, Hare TA, et al. The Nim-Stim set of facial expressions: judgments from untrained research participants. *Psychiatry Res* 2009;168:242–9.
- [34] Watson D, Clark LA, Tellegen A. Development and validation of brief measures of positive and negative affect: the PANAS scales. *J Pers Soc Psychol* 1988;54:1063–70.
- [35] Delorme A, Makeig S. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J Neurosci Methods* 2004;134:9–21.
- [36] Belouchrani A, AbedMeraim K, Cardoso JF, Moulines E. A blind source separation technique using second-order statistics. *IEEE Trans Signal Process* 1997;45:434–44.
- [37] Romero S, Mananas MA, Barbanjo MJ. A comparative study of automatic techniques for ocular artifact reduction in spontaneous EEG signals based on clinical target variables: a simulation case. *Comput Biol Med* 2008;38:348–60.
- [38] Ng SC, Raveendran P. Enhanced mu rhythm extraction using blind source separation and wavelet transform. *IEEE Trans Biomed Eng* 2009;56:2024–34.

- [39] Shoker L, Sanei S, Chambers J. Artifact removal from electroencephalograms using a hybrid BSS–SVM algorithm. *IEEE Signal Process Lett* 2005;12:721–4.
- [40] Gómez-Herrero G, De Clercq W, Anwar H, Kara O, Egiazarian K, Van Huffel S, et al. Automatic removal of ocular artifacts in the EEG without a reference EOG channel. In: *Proc 7th Nordic Signal Process Symp (NORSIG)*. 2006. p. 130–3.
- [41] Manly BFJ. *Randomization, bootstrap, and Monte Carlo methods in biology*. 3rd ed. Boca Raton, FL: Chapman & Hall/CRC; 2007.
- [42] Benjamini Y, Hochberg Y. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J R Stat Soc* 1995;289–300.
- [43] Lundqvist LO. Facial EMG reactions to facial expressions: a case of facial emotional contagion? *Scand J Psychol* 1995;36:130–41.
- [44] Dimberg U, Thunberg M. Rapid facial reactions to emotional facial expressions. *Scand J Psychol* 1998;39:39–45.
- [45] Sonnby-Borgstrom M, Jonsson P. Models-of-self and models-of-others as related to facial muscle reactions at different levels of cognitive control. *Scand J Psychol* 2003;44:141–51.
- [46] Sonnby-Borgstrom M, Jonsson P, Svensson O. Gender differences in facial imitation and verbally reported emotional contagion from spontaneous to emotionally regulated processing levels. *Scand J Psychol* 2008;49:111–22.
- [47] Nishitani N, Hari R. Viewing lip forms: cortical dynamics. *Neuron* 2002;36:1211–20.
- [48] Vaughan TM, Miner LA, McFarland DJ, Wolpaw JR. EEG-based communication: analysis of concurrent EMG activity. *Electroencephalogr Clin Neurophysiol* 1998;107:428–33.