Mental Simulation of Facial Expressions: Mu Suppression to the Viewing of Dynamic Neutral Face Videos

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Abstract

The mirror neuron network (MNN) has been proposed as a neural substrate of action understanding. Electroencephalography (EEG) mu suppression has commonly been studied as an index of MNN activity during execution and observation of hand and finger movements. However, in order to establish its role in higher order processes, such as recognising and sharing emotions, more research using social emotional stimuli is needed. The current study aims to contribute to our understanding of the sensitivity of mu suppression to facial expressions. Modulation of the mu and posterior alpha (8 - 13 Hz) was calculated in 22 participants while they observed dynamic video stimuli, including emotional (happy and sad) and neutral (mouth opening) facial expressions, and non-face stimuli (kaleidoscope pattern). Neutral faces evoked greater mu than alpha suppression, whereas kaleidoscope evoked greater alpha than mu suppression. Source estimation (sLORETA) analysis comparing the neural sources of mu/alpha modulation between neutral face and kaleidoscope showed more suppression in the central regions, including the supplementary motor and somatosensory areas, than the more posterior regions. EEG and source estimation results may indicate that reduced availability of emotional information in the mouth opening condition require more sensorimotor mimicry in deciphering emotion-related information than the full-blown happy or sad expressions, that are more readily recognised.

Keywords

EEG; Mirror neuron; Mu rhythm; Face emotion; Source estimation; sLORETA

1. Introduction

Nonverbal communication is a crucial component of human social behaviour, but its mechanisms are poorly understood. The ability to understand others' mental states from their facial and bodily gestures allows us to respond effectively during social communication. Gallese and Goldman (1998) proposed a simulation theory of action understanding to account for the complexity of this process. Under this model, on observing an action, the observer subconsciously and automatically employs specialised neural circuitry to simulate the action using their own motor system, in turn activating mental states associated with execution of the action, and providing insight into the mental state of the actor. The neural substrate of the simulation theory is proposed to be the *mirror neuron* (Gallese & Goldman, 1998).

Mirror neurons were first discovered in the motor areas of the monkey brain (di Pellegrino et al., 1992). They were observed to fire while the monkey executed a specific action, such as grasping an object, putting it in mouth or breaking it. However, unlike a typical motor neuron, they also fired when the monkey observed another individual performing a similar action. Moreover, the sensory modality by which the action was experienced did not seem to matter for a subset of these neurons: they were triggered by the sound of the action, even when the action was not seen (Kohler et al., 2002). The implication of these findings was that the mirror neurons could be coding the representations of the actions, allowing for recognising the movements involved in an action and inferring the intention behind the action.

The potential role of the mirror neurons in action and intention understanding has ignited an interest in research on the human corollaries of the monkey mirror neuron network (MNN). Evidence for a similar mirroring mechanism in the human brain has come from functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies (Caspers et al., 2010; Molenberghs et al., 2012) as well as single neuron recordings during surgery in humans (Mukamel et al., 2010). In addition to metabolic brain imaging and *in vivo* cellular studies, EEG studies have measured mu rhythm desynchronisation to infer mirroring activity. Mu activity, characterised by 8-13 Hz oscillations detected over the sensorimotor area, has been found to indicate physical inactivity and resting, with movement leading to its suppression (Hari & Salmelin, 1997). The mu rhythm has become implicated in the mirror neuron system as its suppression has been observed during viewing of biological action with or without object interaction, including finger movements (Babiloni et al., 1999; Cochin et al.,

1999) and hand grip movements (Muthukumaraswamy et al., 2004), and while hearing sounds that are linked to actions, such as piano melodies (Wu et al. 2016).

Since the initial discovery of the MNN, research has focused on its potential role in social cognitive processes that rely on an ability to understand actions and intentions, such as empathy. Although the initial research in monkeys found that observation of an action could trigger these neurons only when the action involved an interaction between the actor and an object (Gallese et al., 1996), more recent research with infant monkeys has shown mu suppression in response to observation of facial expressions, indicating that the MNN may be involved in interpreting socially significant behaviour (Ferrari et al., 2012). Consistent with monkey research, some brain imaging studies reported similarity between the activated areas during the imitation of facial expressions and hand movements (Leslie et al., 2004), and the imitation and observation of facial emotions (Carr et al., 2003). Moore et al. (2012) reported mu suppression to the photos of disgusted and happy faces, but not buildings. Similarly, Moore and Franz (2017) found increased mu suppression to the classification of emotions displayed through facial expressions than the emotion words. Another study reported mu suppression in 30-month-old children while they viewed dynamic facial expressions, but not scrambled versions of the same face videos (Rayson et al., 2016).

The involvement of the MNN in face processing has been suggested as a means by which people empathise with others (Carr et al., 2003; Moore et al., 2012). However, as Milston et al. (2013) pointed out, most of the studies that have explored the relation between mu suppression and empathy have used stimuli eliciting pain only (Hoenen et al., 2015; Perry, Bentin et al., 2010; Yang et al., 2009). Hoenen et al. (2013) highlighted that threat inherent in painful stimuli might tap attentional rather than empathic processes, consequently affecting suppression over the central brain areas. Similarly, Perry, Bentin et al. (2010) indicated that the salience of painful stimuli might facilitate sensorimotor reaction to threat. The use of a variety of facial expressions with and without emotional information as the visual stimuli is necessary to investigate the differential sensitivity of the sensorimotor cortex to emotion-related information processing.

It is crucial to note that findings from some mu suppression studies indicate that mu can easily be confounded with alpha activity, yielding alpha suppression at central electrodes that is similar while viewing biological and non-biological motion. For example, Aleksandrov and Tugin (2012) did not find any systematic differences in mu suppression to the observation of hand movements, non-biological objects or mental counting. The authors argued that

attentional processing was influencing the suppression over the sensorimotor area rather than the modulation of the MNN. Similarly, Perry and Bentin (2010) observed that alpha suppression at the mu and the occipital areas were very similar to the observation of hand movements toward an object, and attributed the decrease in alpha band power to the attentional demands. A recent study conducted by Hobson and Bishop (2016) showed that different types of baseline used to measure mu suppression engage the attention system differently, thus directly impacting the degree of suppression recorded. They found that mu and occipital alpha modulation while viewing hand movements and kaleidoscope movements were consistent with the MNN activity only when the static video of the image that immediately preceded the dynamic video of the image was used as the baseline. Due to the posterior alpha confound associated with attentional processes, the baseline and the control conditions need to be chosen carefully.

The current study aims to contribute to our understanding of the simulation account by investigating the responsiveness of the sensorimotor cortex to emotional and non-emotional facial expressions. To our knowledge, this is the first study to examine the sensitivity of mu rhythm, while controlling for occipital alpha activity, to dynamic neutral and emotional facial expressions not depicting pain. A within-trial baseline method was adopted as per Hobson and Bishop (2016): the 1100 ms static image epoch was used as the baseline for quantifying activity in the subsequent 2050 ms dynamic image epoch. It was hypothesized that mu suppression would be greater in the (1) happy, sad and neutral face conditions than the kaleidoscope condition, and (2) happy and sad conditions than the neutral condition, without a corresponding difference in occipital alpha suppression.

2. Materials and methods

2.1 Participants

Twenty-five participants (16 female) between the ages of 19 and 36 (M = 26.5, SD = ±6) were recruited through flyers placed around the University of Auckland campus. Each participant was compensated with a $20 supermarket voucher. Prior to data collection, a pre-screening questionnaire was emailed to the volunteers to identify whether they met the criteria for participation. Exclusion criteria included self-reported major head injury, psychiatric diagnosis, psychoactive medication use, or sensorimotor problems. All of the participants read

the participant information sheet and signed the consent form prior to data collection. The study protocol was approved by the University of Auckland Human Participants Ethics Committee, and conducted in accordance with the Declaration of Helsinki.

2.2 Stimuli and design

EEG was recorded during a 30-minute computer task, which entailed the viewing of four types of dynamic image videos: happy face, sad face, neutral face (i.e. mouth opening) and kaleidoscope. There were four blocks of 40 trials (160 total). In each block, there were 10 happy, 10 sad, 10 neutral and 10 kaleidoscope videos, in random order. Each video was 6000 ms long. Participants were free to rest between the blocks for as long as they wanted.

Happy and sad face videos were taken from the Amsterdam Dynamic Facial Expression Set (ADFES; van der Schalk et al., 2011). The ADFES is freely available for research from the Psychology Research Unit at the University of Amsterdam. Neutral faces were recorded by OK. Past research has validated mouth opening videos of actors as non-emotional (Rayson et al., 2016). Videos used in the present study were made similar to Rayson et al.'s (2016) and the ADFES stimuli in terms of duration, brightness, size, and contrast. Kaleidoscope images were those used in a previous study (Hobson & Bishop, 2016). All stimuli were greyscaled.

Participants were instructed to minimise movement throughout the experiment, and blinking during trials. As *Figure 1* illustrates, each trial started with a 1000 ms fixation cross against a white background. After the fixation cross, the static image stimulus was presented for 2000 ms, followed by a 2000 ms dynamic image in which the expression changed, and ending with a 2000 ms static image of the last frame of the video. Then, a two-alternative forced-choice response slide showing the correct label alongside one of the other three labels prompted the participant to categorise the stimulus as *happy*, *sad*, *neutral* or *other*. The response slide remained on the screen until the participant gave a response using the keyboard. The participant pressed "d" if the label on the left was correct and "k" if the label on the right was correct. In half of the trials, the correct label was on the right, and in half, on the left. Each trial ended with a 1000 ms feedback slide. The feedback slide displayed the word "Correct" or "Incorrect" depending on the key press.

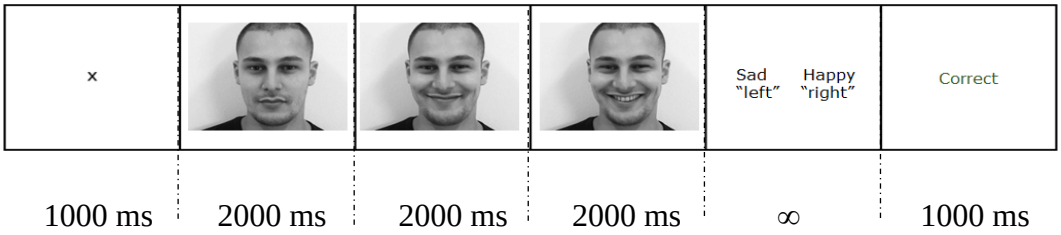

Figure 1. An example of a trial showing the duration of each section in ms. Each condition video was presented for 6000 ms, of which the first 2000 ms was static, the second 2000 ms was dynamic, and the last 2000 ms was static.

Accuracy and reaction time were not analysed. The feedback slide was only used to gauge attention. The highest number of incorrect answers observed for a participant was six (i.e. 4.5%), indicating sustained attention to the stimuli for all participants.

2.3 EEG data recording

EEG recording was conducted in an electrically shielded room (IAC Noise Lock Acoustic - Model 1375, Hampshire, United Kingdom) using 128-channel Ag/AgCl electrode nets (Tucker, 1993) from Electrical Geodesics Inc. (Eugene, Oregon, USA). EEG was recorded continuously (1000 Hz sample rate; 0.1-400 Hz analogue bandpass) with Electrical Geodesics Inc. amplifiers (300-MΩ input impedance). Electrode impedances were kept below 40 kΩ, an acceptable level for this system (Ferree et al., 2001). Common vertex (Cz) was used as a reference. Electrolytic gel was applied before the recording started. Each session consisted of two continuous recordings. After the first two blocks, recording was paused and electrolytic gel was re-applied to ensure the impedance was kept low.

2.4 EEG data preprocessing and analysis

EEG processing was performed using EEGLAB, an open-source MATLAB toolbox (Delorme & Makeig, 2004). For each participant, the continuous data were downsampled to 250 Hz and then high-passed filtered at 0.1 Hz. 6000 ms conditions starting from the stimulus onset at time zero were created to get rid of between-session data. Line noise occurring at the

harmonics of 50 Hz was removed. Bad channels were identified using the EEGLAB pop_rejchan function (absolute threshold or activity probability limit of 5 SD, based on kurtosis) and interpolated. Data were re-referenced to the average of all electrodes. Infomax ICA was run on each of the preprocessed dataset with EEGLAB default settings. Eye movement and large muscle artifact components were visually identified and rejected for each participant. EEG recordings of three participants were identified as very noisy during the cleaning stage and excluded from further processing.

For each condition, from the 6000 ms image video, 800 ms to 1900 ms early epochs corresponding to the static image and 1950 to 4000 ms late epochs corresponding to the dynamic image were extracted. The analysis was conducted for the mu/alpha band of 8 to 13 Hz over two central clusters of electrodes, 6 located around C3 (left hemisphere) and six around C4 (right hemisphere), and over 3 occipital electrodes (O1, Oz and O2). For each of the fifteen electrodes, Fast Fourier Transform (FFT) was used to calculate the power spectral density (PSD) in each trial, separately for early and late epochs. For each trial, mu/alpha suppression at each of the fifteen electrodes was calculated by taking the ratio of the late epoch PSD relative to the early epoch PSD. Ratio values were used as a measure of suppression to control for variability in absolute alpha power due to individual differences in scalp thickness and electrode impedance. Across the central and occipital electrode clusters separately, if a trial PSD ratio had a value greater than 3 scaled median absolute deviations from the median PSD ratio value of the cluster, that trial was excluded as an outlier. For each of the four conditions, the average PSD ratio of the twelve central electrodes was calculated to get a single mu value, and of the three occipital electrodes to get a single alpha value, resulting in eight power scores (i.e. suppression for happy, sad, neutral and kaleidoscope images at central and occipital areas) for each participant.

Since ratio data are non-normal, a log transform was used for statistical analysis. A log ratio value of less than zero indicates suppression, zero indicates no change, and greater than zero indicates facilitation.

2.5 Source estimation

The 128-channel EEG data were analysed using standardised Low Resolution Electromagnetic Tomography method (sLORETA) source localisation (Pascual-Marqui, 2002; free academic software available at http://www.uzh.ch/keyinst/loreta.htm). sLORETA is an

inverse solution that produces images of standardised current density at each of the 6239 cortical voxels (spatial resolution 5 mm) in Montreal Neurological Institute (MNI) space. sLORETA images of the mu/alpha band (8-13 Hz) activity during the late epochs of the neutral and kaleidoscope conditions were computed for each participant, and then the group averages for the two conditions were extracted. Mu/alpha band power associated with late epochs of the neutral and kaleidoscope conditions was compared. A whole-brain analysis was conducted to provide evidence that the reduced mu/alpha band power during the late epoch in the neutral face condition compared to the kaleidoscope condition was localised to the central instead of posterior regions, indicating stimulus-related differences in sensory and motor activity rather than a topographically widespread activity tapping attention. Voxel-wise *t* tests were done on the frequency band-wise normalised and log-transformed sLORETA images. For all *t* tests, the variance of each image was smoothed by combining half the variance at each voxel with half the mean variance for the image. Correction for multiple testing was applied using statistical nonparametric mapping (SnPM) with 5000 permutations.

3. Results

3.1 EEG results

All statistical analyses were performed using *Rstudio* (RStudio Team, 2015; R Core Team, 2018).

Data from 22 participants were included in the analysis. As explained in the methods section, there were four conditions (i.e., happy, sad, neutral, kaleidoscope) and 2 brain regions (i.e. central, occipital) of interest. Before hypothesis testing, a t-test for each condition at each brain region was conducted to ensure that the PSD was significantly reduced during the late compared to the early epoch (all p values < .001). Upon confirming suppression in each condition at both brain regions, a 4 x 2 repeated measures ANOVA was conducted. Mauchly's test indicated that the assumption of sphericity was met for the condition variable. There was a non-significant main effect of condition ($F(3, 63) = 2.74$, $p = .051$, $\eta_p^2 = 0.115$), and a non-significant main effect of region ($F(1, 21) = 1.520$, $p = 0.231$, $\eta_p^2 = 0.067$). However, interpretation of these main effects is complicated by the significant interaction between condition and region ($F(3,63) = 10.734$, $p < 0.001$, $\eta_p^2 = 0.338$) (see *Figure 2*). Among the facial expression conditions, mu suppression was greater than the alpha suppression only for

the neutral face condition (central: M = -.343, sd = 0.1, occipital: M = -.314, sd = 0.097). Kaleidoscope condition showed an opposite pattern (central: M = -.303, sd = 0.086, occipital: M = -.364, sd = 0.08). Based on the mean values, the interaction effect was investigated further with two Bonferroni corrected t-tests ($\alpha_{(0.05)} = 0.025$) to calculate the difference between mu and alpha suppression in the neutral and kaleidoscope conditions. There was significantly greater central than occipital suppression in the neutral condition ($t(21) = -2.735$, $p = .012$), and significantly greater occipital than central suppression in the kaleidoscope condition ($t(21) = 4.409$, $p < .001$). The distribution of the data points can be seen in *Figure 3*. Three participants had at least one ratio score greater than 1.5 times the interquartile range below the 25th or above the 75th quartile. Removing them did not change the pattern of results, so the analyses are reported including these outliers.

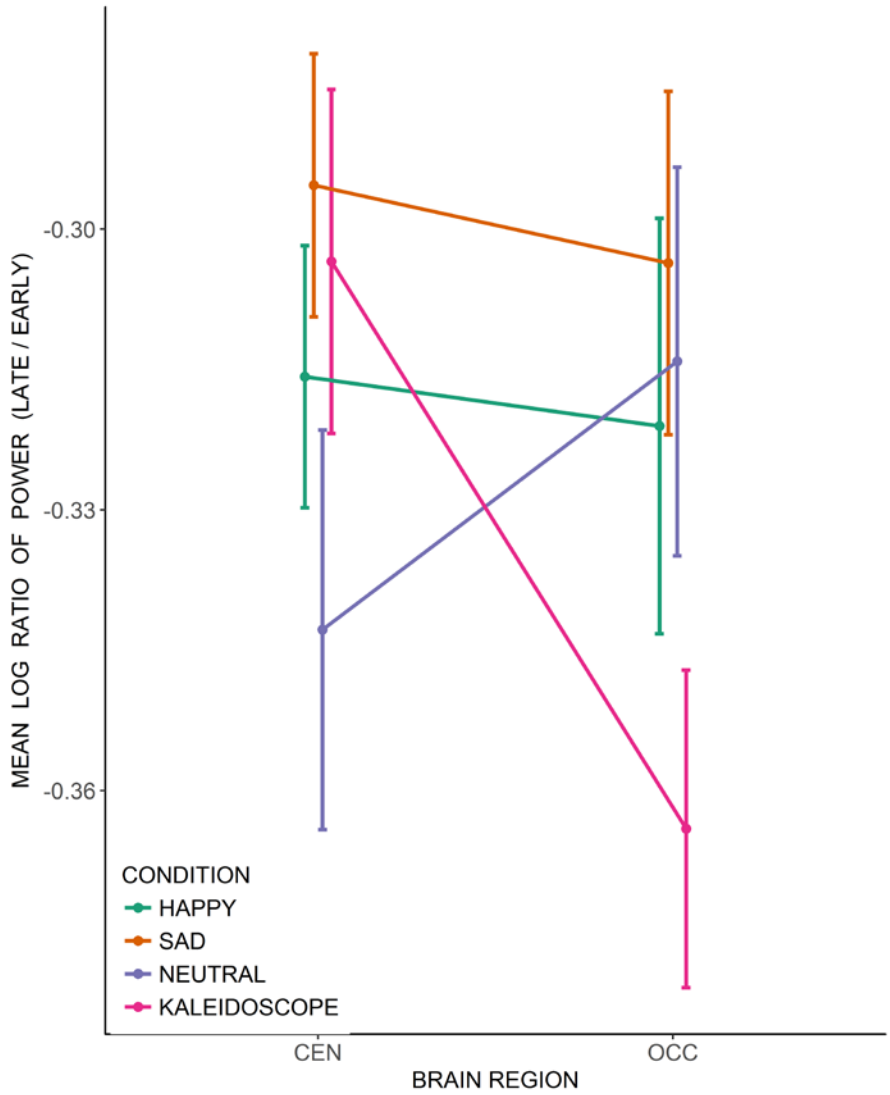

Figure 2. Interaction effect between condition and brain region. Mean suppression and its standard error for each condition are shown by brain region. CEN = Central region, OCC = Occipital region.

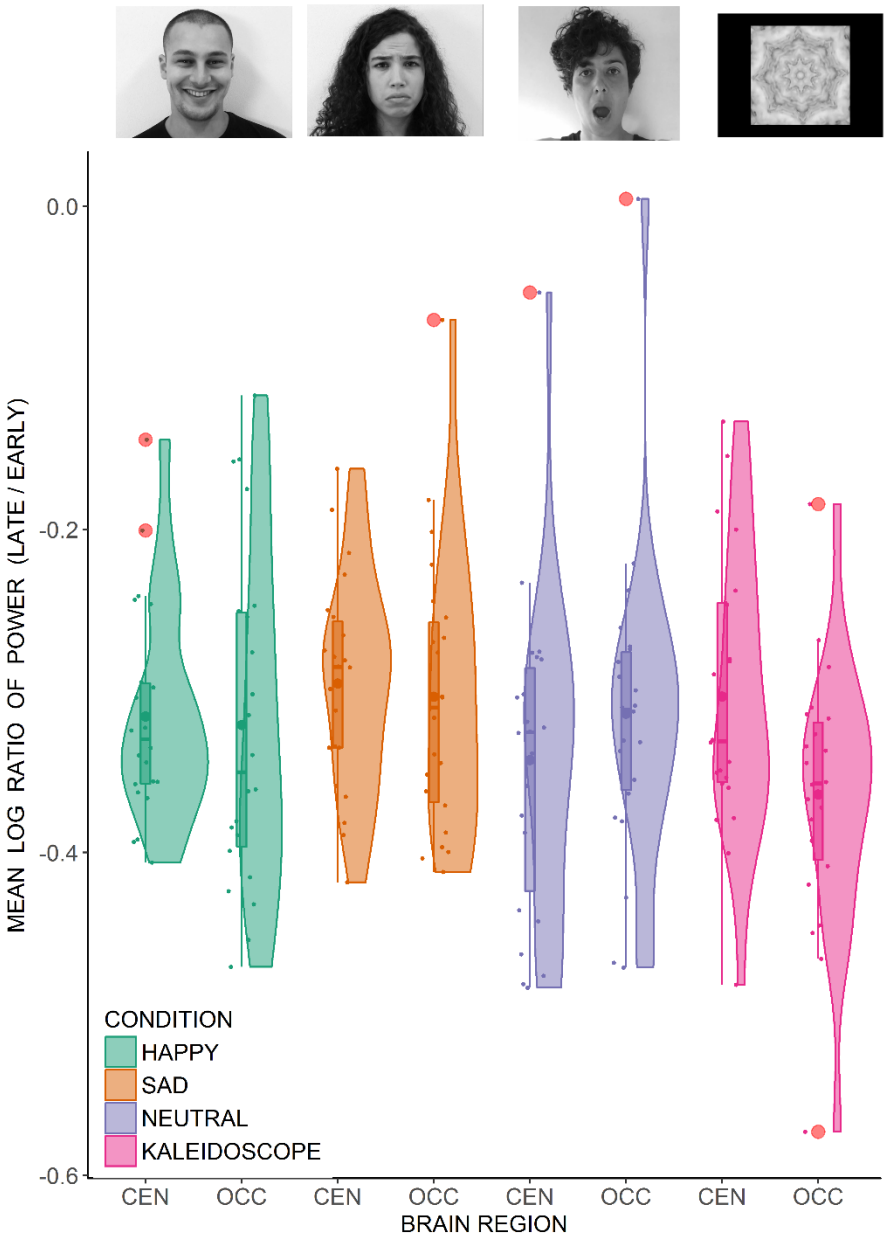

Figure 3. Distribution of the individual mean log ratio scores of twenty-two participants (dots) in the happy, sad, neutral and kaleidoscope conditions at the central and occipital regions. Outliers (>1.5 x interquartile range) are represented by the red disks. Inside the boxplots, dots represent the means and horizontal lines represent the medians. The density plots around the data points represent the kernel probability density of the data at different values. CEN = Central region, OCC = Occipital region.

3.2 Source Estimation Results

The neural sources of the difference in the mu/alpha band current density power between the neutral and kaleidoscope conditions during the late epoch (neutral minus kaleidoscope) were analysed using sLORETA with a one-tailed test (neutral < kaleidoscope). Exceedance proportion test output from sLORETA analysis was used to identify the voxels at which the difference in mu/alpha power between the two conditions was significant ($p < 0.05$). Based on the exceedance proportion test results which showed a threshold of -3.599 for a p-value of 0.0524, differences in alpha power were localised to the fusiform gyrus (BA20) $t = -4.03$ (X= -55 , Y= -40 , Z= -30) (MNI coords), primary somatosensory cortex (BA3) $t = -3.80$ (X= -40 , Y= -25 , Z= 40) , prefrontal cortex (BA9) $t = -5.14$ (X= 10 , Y= 45 , Z= 35), and medial premotor cortex (supplementary motor area; BA6) $t = -3.99$ (X= 10 , Y= -30 , Z= 70) (see *Figure 4*). In the colour scale, blue indicates less alpha power while red indicates the opposite.

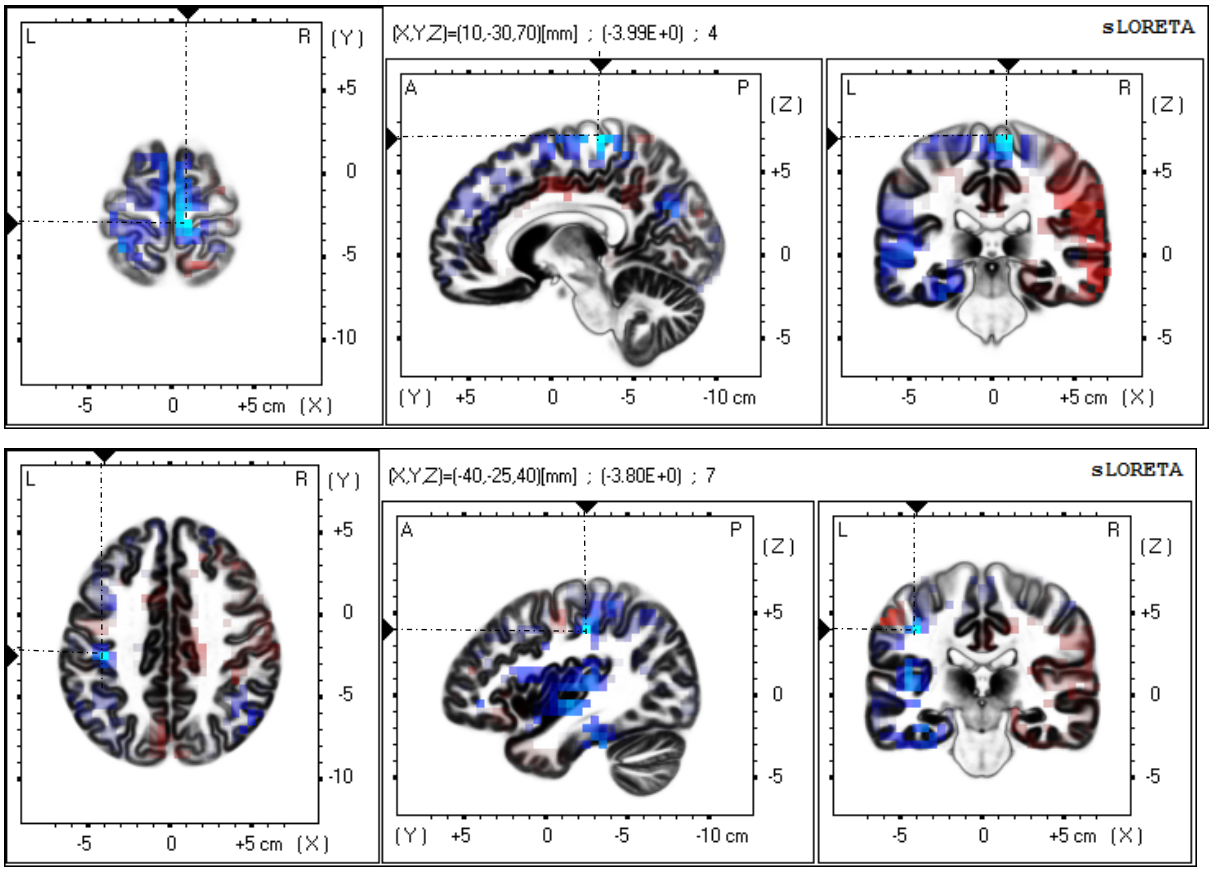

Figure 4. Current density power analysis in the mu/alpha band (8 - 13 Hz), averaged across twenty-two participants, between the neutral face and kaleidoscope conditions during the late epoch found significant voxels ($p < 0.05$) best matched to the supplementary motor area (top) and the primary somatosensory area (bottom). Horizontal (left), sagittal (middle), and coronal (right) sections through the voxel with the maximal *t*-statistic (local maximum) are displayed. Blue indicates less power in the alpha band in the neutral face than the kaleidoscope condition.

4. Discussion

The current study investigated the modulation of mu rhythm while participants observed videos of emotional and neutral facial expressions and kaleidoscope patterns. Mu suppression, but not occipital alpha suppression, was predicted to be greater in the face conditions than the kaleidoscope condition, with greater suppression in the emotional face than the neutral face condition. In contrast to our prediction, only the neutral faces were associated with stronger mu activity than that for the kaleidoscope condition. In the happy and sad face conditions, a lack of

difference in alpha band power between the central and occipital regions made it difficult to distinguish mu from posterior alpha modulation. Greater mu than alpha suppression in the neutral face condition, accompanied with less mu than alpha suppression in the kaleidoscope condition suggests that mu rhythm modulation associated with neutral face processing is distinct from the attenuation of the overall alpha activity power associated with information processing and attention. Similar opposing trends of alpha and mu suppression between biological and non-biological movement was observed by Hobson and Bishop (2016). Greater occipital alpha suppression in the kaleidoscope than the neutral face condition may be explained by low-level visual differences between the two conditions, such as the contrast and the frequency domain information in the stimuli, and/or disparate demands on attention. In addition to the results from the scalp-recorded EEG activity, source analysis data provide further support for a more localised than an overall difference in alpha band power between neutral face and kaleidoscope conditions, suggesting different levels of activity between conditions in the face-related (i.e., fusiform gyrus) and MNN areas, specifically, the primary somatosensory cortex, prefrontal cortex and supplementary motor area.

We offer a number of possible explanations for the results. Firstly, the results may be attributed to the sensitivity of the sensorimotor cortex to human-object interaction. Most research that has investigated the role of MNN in action observation involves hand and finger movements that almost always suggest some sort of interaction with an object, such as pincer movement with the thumb and the index finger (e.g., Cochin et al., 1999), manipulating objects (e.g., Gazzola & Keysers, 2009), or bringing food to mouth (Ferrari et al., 2003). In the present study, mouth opening gesture may have been perceived as an action associated with eating. In that case, the sensorimotor cortex could be engaged by an action that implies interaction with an object (i.e., food), thereby supporting intention understanding (i.e., eating). Secondly, the MNN may be involved in the recognition of deliberate, voluntary gestures rather than involuntary communicative actions. Yet, mu suppression is reported to be modulated by contextual information, such as the familiarity of the observed person (Oberman et al., 2008) or gaming context in which the hand gestures are viewed (Perry et al., 2011). In addition, viewing emotional facial gestures that do not suggest object interaction or deliberate action also seems to modulate mu rhythm (Moore et al., 2012; Moore & Franz, 2017; Rayson et al., 2016). Thus, explanations which restrict mu suppression to voluntary or object-related actions are unlikely.

A third explanation is that the amount of emotional information available for the emotion recognition process may modulate the MNN, with higher ambiguity evoking stronger activity

across the network to support recognition. According to the simulation theory of mirror neurons proposed by Gallese et al. (2004), action and emotion understanding depends on the activity of the motor and visceromotor brain regions while viewing others. More recent evidence, as reviewed by Wood et al. (2016), demonstrates the role of sensory simulation in addition to motor simulation in emotion recognition, pointing to a large overlap between brain areas involved in production and observation of facial expressions. Our third explanation provides further support to the simulation account of face processing (Moore et al., 2012; Oberman et al. 2008). Greater mu suppression while viewing a facial expression, though emotionally neutral or ambiguous, than a kaleidoscope is in line with Moore et al.'s (2012) findings, which showed that viewing happy and disgusted faces evoke significantly more mu suppression than buildings. However, greater mu suppression to neutral face than a kaleidoscope, along with a lack of difference in mu suppression to happy face, sad face and kaleidoscope deviate from the findings of previous studies which would predict greater mu suppression to emotional than non-emotional facial gestures. This finding may be either due to emotional and neutral facial movements tapping different MNN areas, or an overall increase in the MNN activity driven by greater ambiguity of emotional information. An fMRI experiment conducted by van der Gaag et al. (2007) found bilateral inferior frontal operculum activation to viewing emotional facial expressions but somatosensory activation to neutral movements (i.e. blowing up the cheeks). The authors attributed their findings to distinct processing pathways, more visceral in the former and more proprioceptive in the latter. A similar differential pathway may explain the current findings. Another possibility is that the greater ambiguity of the emotion in the neutral image requires the MNN more than the full-blown, easy to recognise emotional expressions. In other words, when the emotion information is presented in high intensity, the cognitive task of recognition may not be demanding enough to activate the MNN, thereby bypassing the system.

Our last explanation is that the ambiguity of emotional information may modulate the signalling within the mirroring network. Current EEG results may indicate that more ambiguous facial expressions are associated with greater sensorimotor input than full-blown facial expressions. One possible reason for increased sensorimotor activity during viewing ambiguous facial expressions may be the reduced activity of some neurons in the premotor areas. Modulation of the excitatory input to the sensorimotor cortex during action observation has been offered as an explanation by Woodruff et al. (2011) for the positive relationship they observed between perspective-taking ability and the size of the difference between execution

and observation-related mu suppression. The rationale for this account is based on the findings of a study which provided evidence for the existence of a subgroup of neurons in the human supplementary motor area that are excited by execution, but inhibited by observation of hand grasping actions and facial emotional expressions (Mukamel et al., 2010). As proposed by Mukamel et al. (2010) and Woodruff et al. (2011), these observation-inhibited neurons may be the mechanism for self-other discrimination, which may explain reduced input to the sensorimotor cortex during observation.

Woodruff et al. (2011) argued that understanding actions and intentions while maintaining the idea that these belong to the observed person, as indicated by lower sensorimotor activity, may allow the observer to empathise with the actor without executing their action. This mechanism may explain some of the findings which indicate either a lack of or a negative relationship between mu suppression and empathy scores (Milston et al., 2013; Moore et al., 2012; Perry, Troje et al., 2010; Silas et al., 2010). Non-MNN and MNN areas involved in emotion processing except the sensorimotor cortex may be activated more in highly empathic individuals than others. If high empathy does not need the engagement of the sensorimotor mirroring, less mu suppression would be expected while viewing emotion information. On the basis of previous work, we propose that emotion-related information may activate the observation-inhibited mirror neurons in the premotor and the somatosensory cortices, leading to less excitatory input to the sensorimotor cortex. Reduced or lack of socially relevant information, as in mouth opening, may activate these inhibitory neurons less, leading to increased excitatory input to the sensorimotor cortex. This increased sensorimotor activity may aid action and emotion recognition in the face of subtle expressions.

Source estimation imaging of alpha generators provided further support for the last explanation which suggests the differential involvement of the MNN areas during face simulation. The difference in alpha band power between neutral face and kaleidoscope conditions was localised to the fusiform gyrus, medial prefrontal cortex, supplementary motor area and primary somatosensory cortex. Greater activity in the fusiform gyrus in response to faces than kaleidoscope was expected as this area responds more to faces than objects (Haxby et al. 2000). The premotor areas, including the supplementary motor area, and the primary somatosensory cortex are the key regions implicated in sensorimotor simulation during action observation (Wood et al. 2016) and motor imagery (Burianová et al. 2013). The premotor cortex has been a primary region investigated in studies of action observation (Buccino et al., 2001; Johnson-Frey et al., 2003; Raos et al., 2004, 2007). One of the proposed functions of

mirror neurons that are located in the premotor cortex is supporting action recognition via internally representing the motor properties of observed actions (Gallese et al., 1996; Wild et al., 2003). When considered from this execution/observation matching system perspective, motor information available in the observed face may be coded onto the premotor mirror neurons, allowing for understanding of the mental state associated with the observed action.

While the motor representations of actions are stored in the premotor areas, the somatosensory areas may be involved in storing tactile and proprioceptive representations of these actions (Gazzola & Keysers, 2009). Research indicates that, along with the primary motor cortex, the primary somatosensory cortex may be involved in the mental rehearsal of observed grasping actions in monkeys (Raos et al., 2004) and prediction of sensory consequences of the observed hand actions in humans (Avikainen et al., 2002). In addition to hand actions, there is evidence for the involvement of somatosensory representations in our ability to simulate basic emotions while observing facial expressions (Adolphs et al., 2000). As discussed in Gazzola and Keysers (2009), sensory representations of actions may be allowing the system to detect the mismatch between what an action is predicted to feel like and what it actually feels like during execution, and correct motor errors. According to this perspective, signalling from the somatosensory cortex to the premotor cortex may be a necessary step for action understanding and imitation. This signalling may explain the increased activity we observed in these two brain areas associated with viewing a neutral facial movement. More work is needed to investigate the differential modulation of the motor and sensory cortices by low vs. high intensity emotion information.

There are some limitations of the current study. Low-level visual properties, such as the contrast and the frequency domain composition of the images, in the face and the kaleidoscope conditions were not matched. Future studies should aim to match contrast and frequency components of stimuli across conditions in order to mitigate the effect of these non-task related factors on alpha activity. Furthermore, in the face videos, every actor performed only one facial expression. This might have led the participants to learn the movement that followed each static image, leading to habituation across the blocks. Using the same actors for different facial expressions might help avoid habituation-driven mu and alpha activity changes.

In conclusion, ambiguity or complexity of emotional information may result in greater activity in the sensorimotor areas if difficulty of the emotion recognition task requires a stronger engagement of the simulation system. Present findings provide support for the involvement of the MNN in face simulation, and indicate a complex relationship between

sensorimotor activity and facial expression processing. Current data call for further research on the observation-related activity within and between the key brain areas involved in mimicry and social information processing. The explanations offered above which attribute the observed effect to the ambiguity of emotion may be addressed in future studies by comparing the level of activity in the premotor, motor and somatosensory areas in response to social stimuli depicting different intensities of various emotions. In an attempt to extend the present findings, we are currently engaged in a further emotion recognition study using high and low intensity facial expressions as stimuli, collecting EEG data from adults with an autism spectrum disorder and control participants. Future research may also examine the coordinated activity of the involved brain regions by connectivity analyses to quantify the differences in their associations or dependencies under different conditions. High spatial resolution neuroimaging techniques, such as fMRI, can be employed to investigate the involvement of the main MNN areas as well as deeper brain regions in the simulation of ambiguous motor and emotion information.

Declaration of interest: None.

Author contributions: OK performed data acquisition, analysis, interpretation of the data and wrote the first draft of the manuscript. IK contributed substantially to the design of the experiment and critical revision of the manuscript. MM contributed substantially to data analysis and critical revision of the manuscript. All authors approved the final draft of the manuscript for publication.

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