Increased sensorimotor activity during categorisation of emotionally ambiguous faces

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Abstract

Actions are rarely devoid of emotional content. Thus, a more complete picture of the neural mechanisms underlying mental simulation of observed actions requires more research using emotion information. The present study used high-density electroencephalography to investigate mental simulation associated with facial emotion categorisation. Alpha-mu rhythm modulation was measured at each frequency, from 8 Hz to 13 Hz, to infer the degree of sensorimotor simulation. Results suggest the sensitivity of the sensorimotor activity to emotional information, because (1) categorising static images of neutral faces as happy or sad was associated with stronger suppression in the central region than categorising clearly happy faces, (2) there was preliminary evidence indicating that the strongest suppression in the central region was in response to neutral faces, followed by sad and then happy faces, and (3) in the control task, which required categorising images with the head oriented right, left, or forward as right or left, differences between conditions showed a pattern more indicative of task difficulty rather than sensorimotor engagement. Dissociable processing of emotional information in facial expressions and directionality information in head orientations was further captured in beta band activity (14-20 Hz). Stronger mu suppression to neutral faces indicates that sensorimotor simulation extends beyond crude motor mimicry. We propose that mu rhythm responses to facial expressions may serve as a biomarker for empathy circuit activation. Future research should investigate whether atypical or inconsistent mu rhythm responses to facial expressions indicate difficulties in understanding or sharing emotions.

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Abstract

Actions are rarely devoid of emotional content. Thus, a more complete picture of the neural mechanisms underlying mental simulation of observed actions requires more research using emotion information. The present study used high-density electroencephalography to investigate mental simulation associated with facial emotion categorisation. Alpha-mu rhythm modulation was measured at each frequency, from 8 Hz to 13 Hz, to infer the degree of sensorimotor simulation. Results suggest the sensitivity of the sensorimotor activity to emotional information, because (1) categorising static images of neutral faces as happy or sad was associated with stronger suppression in the central region than categorising clearly happy faces, (2) there was preliminary evidence indicating that the strongest suppression in the central region was in response to neutral faces, followed by sad and then happy faces, and (3) in the control task, which required categorising images with the head oriented right, left, or forward as right or left, differences between conditions showed a pattern more indicative of task difficulty rather than sensorimotor engagement. Dissociable processing of emotional information in facial expressions and directionality information in head orientations was further captured in beta band activity (14-20 Hz). Stronger mu suppression to neutral faces indicates that sensorimotor simulation extends beyond crude motor mimicry. We propose that mu rhythm responses to facial expressions may serve as a biomarker for empathy circuit activation. Future research should investigate whether atypical or inconsistent mu rhythm responses to facial expressions indicate difficulties in understanding or sharing emotions.

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1 INTRODUCTION

Emotions we express through our actions, especially facial gestures, play a crucial role in facilitating the development of a shared cognition with our conspecifics. Shared origins of our perceptions, actions, and emotions have been emphasised in theories of embodied cognition (Decety & Jackson, 2004; Preston & de Waal, 2002). At the core of embodied cognition accounts of social cognition is the concept of mental simulation, which describes the mapping of movements, emotions and sensations of others onto the observer's motor, visceral and somatosensory systems (Decety & Jackson, 2004; Gallese & Sinigaglia, 2011; Preston & de Waal, 2002). Mental simulation theories of action understanding suggest that observed motor acts, defined as a series of goal-related movements, are matched onto the motor system of the observer, thereby allowing an understanding of the intentions behind actions (Gallese et al., 2009). It is this process of external-to-internal mapping that forms the basis of understanding others, including recognising motor actions and inferring their goals, as well as understanding internal states and motivations (Gallese & Sinigaglia, 2011). Successful operationalisation of this mapping process involves reducing any ambiguity present in an observed action to achieve a correct understanding of the intent behind the act being performed. In the context of action perception, ambiguous information can be described as movements that are open to multiple interpretations. Myriads of actions and emotions exhibited in social environments make the skill to resolve ambiguity of social emotion information crucial to understanding others.

Mental simulation that is specifically associated with the activity of the motor system during action observation is called *motor simulation* or *motor resonance* (Gordon et al., 2018). A possible biological basis of motor simulation has been proposed with the discovery of a special category of neurons, called *mirror neurons* , that are active during both action execution and observation in monkeys (Di Pellegrino et al., 1992; Dushanova & Donoghue, 2010; Gallese et al., 1996; Rizzolatti et al., 1996). These motor neurons, mostly selective for a particular movement configuration, such as grasping an object or breaking it, were observed to discharge not only while the monkey executed certain actions, but also while they observed the experimenter perform the same or similar ones (Gallese et al., 1996; Rizzolatti et al., 1996). Due to this response characteristic of mirror neurons, it was argued that they could provide a mechanism for coding the internal motor representations of actions in the motor system which are triggered by perception as well as execution of actions. Through the strengthened connections formed as a result of repeated pairings between the internal motor representations and their consequences, representations of an action activated during its observation would enable access to the knowledge of that action's consequences. Based on this rationale, it was argued that mirror neurons allow understanding actions and their goals (Gallese et al., 1996; Rizzolatti et al., 2001). These types of neurons have also been discovered in humans (Mukamel et al., 2010), and neuroimaging studies have demonstrated that similar patterns of activation in the human brain are generated during action execution and observation (Molenberghs et al., 2012).

Motor simulation in humans has also been investigated using electroencephalography (EEG) and magnetoencephalography. These studies have identified oscillatory activity in the alpha (8 – 13 Hz) and beta (14 – 25 Hz) frequency bands, originating in motor and somatosensory cortices, as potential neurophysiological markers of action understanding (e.g., Caetano et al., 2007; Simon & Mukamel, 2016; Ulloa & Pineda, 2007). The alpha frequency activity generated by the sensorimotor cortex, also called the *mu rhythm* , is most prominent when the motor system is at rest, and is suppressed by the execution, observation, or imagery of limb and face movements (Cochin et al., 1998; Cochin et al., 1999; Debnath et al., 2019; Lepage & Theoret, 2006; Muthukumaraswamy et al., 2004; Sakihara & Inagaki, 2015). Attenuation of the mu rhythm, known as *mu suppression* , is thought to reflect the desynchronised activity of the sensorimotor cells that is triggered by movement execution or observation (Pfurtscheller et al., 1997). Past mu studies have reported that both execution and observation of grasping hand movements (e.g., Streltsova et al., 2010), pincer movements with thumb and the index finger (e.g., Cochin et al., 1999), and sucking and biting movements (Muthukumaraswamy et al., 2006) induce mu suppression. These findings support the existence of a mirror-neuron network (MNN) in humans that is implicated in action perception (for a review, see Keysers et al., 2018).

Mu rhythm activity has been found to be sensitive to top-down contextual influences. Studies that have investigated the modulatory effect of pain on the mu rhythm have reported greater suppression during visual perception of limbs in painful compared to non-painful situations (Cheng et al., 2014; Hoenen et al., 2015; Yang et al., 2009). For example, Hoenen et al. (2018) demonstrated that viewing actions (e.g., cutting a cucumber) depicting pain (e.g., finger placed between knife and cucumber) evoked stronger mu suppression than their almost visually identical no-pain counterparts (e.g., finger not endangered). Other studies have found that the relevance of the observed action for the observer modulates motor resonance (Dickter et al., 2013; Oberman et al., 2008; Varnum et al., 2016). For example, Dickter et al. (2013) found greater mu suppression in smokers than non-smokers to viewing humans interacting with cigarettes than only cigarette images, whereas both groups showed greater mu suppression while viewing nonsmoking-related stimuli (e.g., toothbrush) in the interaction than the object-only condition. In children, viewing hand movements showed the greatest mu suppression to their own movement, followed by a familiar person's, and least suppression to the stranger's, indicating the sensitivity of the mu rhythm to the actor's familiarity (Oberman et al., 2008). In a study investigating the link between mu suppression, reward value of the stimuli and empathy, Gros et al. (2015) reported stronger mu suppression in the alpha and beta bands while viewing happy expressions that had been conditioned to be associated with a reward compared to those associated with a loss. This finding suggests that empathy towards the actor modulates mu suppression. The sensitivity of the mu rhythm to contextual information indicates that the internal simulation of actions extends beyond crude motor mimicry, which involves merely mirroring the kinematic properties of observed actions and suggests an assessment of the social content of the stimuli.

Recent contributions to our understanding of emotion simulation have come from work exploring mu modulation during observation of different types of facial expressions. In a study in infants, Rayson et al. (2016) found significant bilateral mu suppression for non-emotional expressions (mouth opening), but only right-hemispheric suppression for emotional (happy or sad) facial expressions. An emotion categorisation study from our group reported greater mu suppression while viewing dynamic videos of non-emotional facial movement (mouth opening) compared to non-biological movement (kaleidoscope pattern), but this was not observed for emotional faces (happy or sad) (Karakale et al., 2019). It was proposed that the greater mu suppression in the mouth opening condition may be due to the heavier workload imposed on the sensorimotor system when attempting to extract emotional content from a non-emotional stimulus. This contrasts to the relative ease in inferring happiness/sadness from the very pronounced happy/sad facial expressions. This suggests that the mental simulation system is engaged more by ambiguous social information compared to readily recognisable actions and emotions (Karakale et al., 2019). Several infant studies have also demonstrated that watching actions that do not have readily recognisable meanings (e.g., bringing a cup to the ear, turning on a lamp with head) evoked stronger mu suppression than ordinary actions (bringing a cup to the mouth, turning on a lamp with hand) (Langeloh et al., 2018; Stapel et al., 2010). These findings indicate that the sensorimotor system is involved in deciphering the meaning of unusual actions.

The sensitivity of the mu rhythm to ambiguous social emotion information is a question that remains to be resolved and is key to understanding the role of the sensorimotor system in emotion processing. The aim of this study was to help fill this gap in the literature by investigating the effect of ambiguity in social affective stimuli on mental simulation. For this purpose, we measured EEG power spectra in the alpha (8-13 Hz) frequencies over 128 electrodes during categorisation of happy, sad and neutral facial expressions. As described previously, past research shows that mu modulation likely reflects a higher-order simulation process rather than a simple mirroring of movement kinematics. Thus, although faces with clear, pronounced emotional expressions (unambiguous) possess greater implied facial movement than those with more subdued, subtle expressions (ambiguous), we in fact predict that there would be greater suppression localised to the central areas in response to the ambiguous expressions compared to the unambiguous expressions. This is because the ambiguity inherent to neutral expressions leads to a greater workload being imposed on the sensorimotor system as it attempts to simulate the emotional content. To establish that any effects were specific to evaluating the emotional content of the faces, we included a control task that required participants to judge the direction in which faces were looking. The assumption was that head direction did not require mental simulation; thus, we would not see centrally localised suppression differences across the conditions of the head orientation task. We expected alpha suppression in the occipito-parietal areas in all conditions as posteriorly generated alpha is modulated by a number of non-motor factors, such as visual processing and attention (Hobson & Bishop, 2016). Specifically, we predicted posterior alpha to be suppressed more in the ambiguous conditions of both tasks mainly because categorising ambiguous information would be more difficult.

2 MATERIALS AND METHODS

2.1 Participants

Twenty-three participants with no reported neurological deficits or psychological disorders (12 female, mean age = 24, *SD* = 4.9 years), with normal or corrected-to-normal vision, were recruited through advertisements placed around the University of Auckland campus and online through the School of Psychology website. This sample size was determined by the limited timeframe and resources for this project. Participants were compensated for their time with a $20 supermarket voucher. All participants provided written informed consent, and the experimental protocol was approved by the University of Auckland Human Participants Ethics Committee and conducted in compliance with the Declaration of Helsinki.

2.2 Stimuli

Stimuli were obtained from the Radboud Faces Database (Langner et al., 2010). The stimulus set contained static facial images of 38 actors (19 female) portraying happy, sad and neutral facial expressions for the Emotion task, and left-, right- and forward-oriented faces for the Orientation task. Each image was presented only once in each condition. Images were converted to greyscale and their size corresponded to 7.9° x 8.2deg cm visual angle at a viewing distance of about 57 cm.

2.3 Experimental Tasks and Procedure

Participants completed two 2-alternative-forced-choice tasks which involved categorisation of ambiguous and unambiguous stimuli. In the Emotion task, participants categorised happy, sad, and neutral forward-oriented faces as either happy or sad (i.e., neutral faces had to be categorised as happy or sad). In the Orientation task, they categorised left-oriented (turned 45deg left), right-oriented (turned 45deg right), and forward-oriented neutral face images as either left or right (i.e., forward-oriented faces had to be categorised as left- or right-oriented). Both tasks used an identical protocol (Figure 1). Only one image was presented in each trial. Each trial started with a 2000 ms blank screen, before a fixation cross appeared at the centre of the screen. The duration of this fixation varied randomly between 1050 and 1350 ms. Following the fixation cross, a face stimulus was presented at the same location for 1000 ms. To prevent alpha confound that could arise if participants responded prematurely during the stimulus presentation, a 1000 ms blank screen was presented after the stimulus slide. This ensured that participants waited until the response slide appeared before preparing for or making any early key presses. The response slide which followed the blank screen presented the two possible responses on the left and right of the screen: happy-sad in the Emotion task; or left-right facing arrows in the Orientation task. Participants pressed the "d" key on a keyboard if the emotional expression (Emotion task) or head orientation (Orientation task) more closely matched the label on the left, and the "k" key if it more closely matched the label on the right. The response prompt remained on the screen until a response was made before progressing to the next trial. The two tasks were completed in separate blocks, with the order counterbalanced across participants. Each task contained 38 images in each of their 3 conditions (happy/sad/neutral or left/right/forward), for a total of 114 trials in each block. Participants were allowed a 5- to 10-minute rest period between tasks, and the whole experiment lasted about 30 minutes.

Figure 1

Structure of the Experimental Design

[Figure 1 here]

[Figure 1 legend here]

Happy and sad faces in the Emotion task, and right- and left-oriented head images in the Orientation task were designated unambiguous conditions. These stimuli had a greater degree of implied movement relative to the neutral forward-oriented faces, which were classified as the ambiguous condition and were identical between the two tasks. Participants were only told that some of the expressions/orientations would be easy to categorise whereas others would be more difficult. The fact that some faces contained no emotion or were oriented directly forwards was not made explicit to the participants. During debriefing, some participants expressed finding some images difficult to categorise, but none mentioned that they were neutral or forward-facing.

2.4 EEG Data Recording

During the experiment, participants sat in a comfortable chair in an electrically- and acoustically-shielded, dimly-lit room. EEG was recorded continuously at 1000 Hz with an analogue band-pass filter of 0.1 - 400 Hz, using a 128-channel Ag/AgCl electrode net (Electrical Geodesics Inc., Eugene, Oregon, USA). Electrode impedances were kept below 40 k, an acceptable level for this system (Ferree et al., 2001). EEG was acquired using a common vertex (Cz) reference and later re-referenced to an average reference offline.

2.5 EEG Data Pre-processing

EEGLAB toolbox (v2023.1; Delorme & Makeig, 2004) was used to pre-process and analyse the EEG data in MATLAB R2023b (Mathworks Inc.). Data cleaning and epoch extraction were done using the RELAX plugin (the Reduction of Electroencephalographic Artifacts; Bailey, Biabani et al., 2023; Bailey, Hill et al. 2023), which provides a fully automated method for EEG data cleaning. First, data were high-pass filtered at 0.5 Hz and low-pass filtered at 40 Hz, and then downsampled to 500 Hz. Bad periods and electrodes were identified and deleted using the default RELAX parameters, which cleaned continuous data using Multi-channel Wiener filtering and wavelet enhanced independent component analysis applied to artifacts (MATLAB scripts modified for this study show default parameter values, accessible at https://osf.io/bx2pe/?view_only=6f65bb5199fd460e861b043ec4b7f223). Then, data were re-referenced to the average of all 128 channels. The continuous recordings were segmented into 3000 ms epochs, extending from 1000 ms before to 2000 ms after stimulus onset. Baseline correction was applied to the pre-stimulus period of 1000 ms to reduce influence of electrode offset. The mean proportion of epochs rejected was .06 in the Emotion task and .07 in the Orientation task, and the mean proportion of channels interpolated was .16 in both tasks.

2.6 EEG Data Analysis

For each task, the STUDY tool in EEGLAB was used to create a study design with the cleaned and epoched datasets. For each participant in each task and condition, trial-averaged event-related (log) spectral perturbation (ERSP) was calculated for 50 log-spaced frequencies from 5 Hz to 30 Hz using Morlet wavelet convolution with a variable number of wavelet cycles. Wavelet cycles increased linearly from 2 cycles at lowest frequency to 6 cycles at highest, in steps of 0.5.

Mean power differences between conditions were investigated separately at each frequency, from 8 Hz to 20 Hz. We used the Fieldtrip software plugin (Oostenveld et al., 2011), available through the STUDY tool, to conduct the analysis using a nonparametric Monte Carlo permutation method. The permutation method does not have any distributional assumptions and provides an exact approximation of the Type I error rate, which make it more robust than traditional parametric tests for small sample sizes (Holt & Sullivan, 2023). For each pairwise comparison, 4000 permutations with cluster-correction statistics were conducted first to control for multiple comparisons. Cluster-based correction was applied by the triangulation method which defined clusters through the selection of neighbouring electrodes, and by calculating the maximum of the cluster-level statistics (Maris & Oostenveld, 2007). For each permutation, significant t -statistics were identified ($p < .05$ corrected). For comparisons which did not survive cluster-correction, a second analysis with 1000 permutations without cluster-correction was conducted ($p < .05$ uncorrected).

2.7 EEG Data Exclusion

Data files of four participants in the Emotion task and one participant in the Orientation task were corrupt. One participant completed only half of the trials in the Orientation task due to an incorrect parameter entry during the data collection process. Recordings from three participants had excessive blink artifacts or drift, and thus did not survive the RELAX cleaning parameters. Finally, accuracy in the unambiguous conditions of both tasks was calculated for each participant to ensure that they had paid attention throughout the task. One participant incorrectly categorised 16% and 26% of the trials in the left and right head orientation conditions, respectively. This differed from the other participants, for whom accuracy was close to 100%. Therefore, these participants were excluded from statistical analysis. The following statistical analyses were conducted on data from 15 participants in the Emotion task and 17 participants in the Orientation task.

3 RESULTS

3.1 Reaction Time and Accuracy

Reaction time (RT; ms) and accuracy data were analysed using R Statistical Software (v.4.3.1; R Core Team 2023). We expected RT to be longer for ambiguous conditions if they were in fact more difficult to categorise than the unambiguous conditions. Plus, if participants paid attention throughout the task, accuracy would be high in the unambiguous conditions.

One-tailed t -tests were conducted to assess the directional predictions for differences in RT. As expected, RT was slower in neutral ($M = 2962$, $SD = 251$) than happy faces ($M = 2839$,$SD = 119$; $t\ (14) = 2.08$, $p = .028$), with a similar trend between neutral versus sad faces ($M = 2868$, $SD = 156$; $t\ (14) = 1.67$, $p = .058$). There was no difference in RT between happy and sad faces ($t\ (14) = 1.34$, $p = .10$). The results were similar in the Orientation task. RT was slower in forward-oriented ($M = 2908$, $SD = 384$) than left-oriented faces ($M = 2715$, $SD = 209$; $t\ (16) = 2.09$, $p = .026$), with a similar trend between forward- versus right-oriented faces ($M = 2753$, $SD = 138$; $t\ (16) = 1.638$, $p = .06$). There was no difference in RT between left- and right-oriented faces ($t\ (16) = 0.91$, $p = .189$).

Mean accuracy in the happy face and left- and right-oriented face conditions were 99%, and in the sad face condition 98%, indicating that participants paid attention throughout the experiment. In the ambiguous conditions, 65% of neutral faces were categorised as sad, and 67% of forward-oriented faces were categorised as right

3.2 Time Window Selection Based on Event-Related Spectral Perturbation Results

First, we examined the 5–30 Hz power spectra for neutral, happy and sad faces across all 128 channels

(Figure 2A). In agreement with vast research showing a link between alpha/beta power decreases associated with task engagement (e.g., Griffiths et al., 2019; Vecchio et al., 2022), we observed alpha/beta suppression over the one-second time window of stimulus presentation in all conditions. Then, for each task and for each condition, alpha (8-13 Hz) and lower beta (14-20 Hz) band power spectral densities (PSDs) in five 200 ms-time windows corresponding to the stimulus presentation were assessed (i.e., 0-200 ms, 200-400 ms, 400-600 ms, 600-800 ms, 800-1000 ms). In each task, power across conditions was compared using a nonparametric Monte Carlo permutation test (1000 permutations). Scalp maps in Figure 2B depict electrodes significant at $p < .05$, uncorrected for multiple comparisons. As can be seen in the figure, differences in alpha band suppression in the central areas were observed mainly in the last 200 ms time window (800-1000ms). Thus, we selected this period to investigate any pairwise differences across the conditions of the Emotion task. We also examined alpha and lower beta PSDs across the conditions of the Orientation task (Figure 2C), and observed that the differences were present across the scalp, covering the whole right frontal and left parietal, temporal and occipital areas in the 600-800 and 800-1000 ms time windows (Figure 2D). As in the Emotion task, we selected the 800-1000 ms time window in the Orientation task for further analysis. This helped us compare where the differences in power were localised across the conditions of the two tasks in the same time window.

Figure 2

Temporal Changes in Power in Frequencies of Interest

[Figure 2 here]

[Figure 2 legend here]

3.3 Time-Frequency Analysis

For each task, we examined alpha power differences between all possible pairs in the 800-1000 ms time window (i.e., neutral minus happy, neutral minus sad, happy minus sad; forward- minus left-oriented, forward- minus right-oriented, left- minus right-oriented). If emotion judgment from facial expressions produced sensorimotor activity, we would see significant reductions in the alpha frequency range over central sensors, indicating mu suppression. Furthermore, if ambiguity of the emotion increased the cognitive load on sensorimotor processes, we would see greater suppression to neutral than happy or sad faces. For the control task, the prediction was that head orientation judgment would not require sensorimotor simulation, so there would not be centrally localised suppression distinct from a broader alpha suppression associated with perceptual and attentional processes.

Initially, to have a general idea about whether alpha suppression was present in the majority of the participants, we selected six central and three occipital electrodes and inspected the direction of power changes from baseline in the alpha range in the 800-1000 ms time window for each participant in each condition (see Appendix for the location of the electrodes and individual PSDs). In the Emotion task ($n = 15$), there was decrease in alpha band power in the selected electrodes in 13 participants in the neutral face condition (87%), 11 participants in the happy face (73%) and 12 participants in the sad face condition (80%). In the Orientation task ($n = 17$), power suppression was observed in 12 participants in the forward-oriented faces (71%), 13 participants in the left (76%), and 11 participants in the right-oriented faces (65%). Similarly, in the majority of the participants, there was suppression in the three occipital electrodes in all conditions. This initial scanning of data from several central and occipital electrodes provided a general overview of alpha band activity changes in our sample.

As can be seen in Figure 3A and 3C, there was suppression in the alpha frequencies in all conditions in both tasks across the 128 electrodes. Results of pairwise comparisons are shown in Figure 3B and 3D. From 8 Hz to 13 Hz, neutral faces showed stronger suppression than happy faces in the frontal, central and occipital regions ($p < .05$ corrected). Mid-central suppression appeared localised and thus distinct from frontal and occipital suppression, suggesting a difference between the conditions in sensorimotor processing rather than low-level visual or attentional differences. Stronger suppression to neutral than sad faces over the central sensors was not significant when corrected for multiple comparisons ($p < .05$ uncorrected). Similar to the results from the Emotion task, strongest suppression across the conditions of the Orientation task was in response to forward-oriented faces in all alpha frequencies. Yet, the distribution of suppression showed a different pattern than that observed in the Emotion task. Unlike the Emotion task, differences between forward-oriented and right- or left-oriented faces were localised to the anterior and posterior areas without a clear band of suppression in the central region ($p < .05$ corrected). Finally, there was no difference between left- and right-oriented faces relevant for our investigation of mu suppression ($p < .05$ uncorrected).

Figure 3

Power Spectral Density at Each Alpha Frequency in the 800-1000 ms Time Window

[Figure 3 here]

[Figure 3 legend here]

3.4 Exploratory Analysis

Upon observing topographic changes across the alpha band (from 8 Hz to 13 Hz), we wanted to see how the activity unfolded through the low beta frequencies. Siqi-Liu et al. (2018) have investigated the modulation of alpha as well as lower beta activity in response to point-light displays of emotional versus neutral body movements. The observation was stronger suppression in response to emotional point-light displays in frequencies from 9 Hz to 19 Hz. Another influential paper pointing to the potential role of beta suppression in mirror neuron research was a meta-analysis by Fox et al. (2016). The authors suggested that future research investigates the sensitivity of beta activity to sensorimotor simulation since beta-mu could be less confounded by posterior alpha suppression associated with low-level visual and attentional processes (see for a review Fox et al., 2016).

To address the gap in the literature in beta-mu activity, we conducted further analysis for the same time window (800-1000 ms) after stimulus onset in the lower beta band (14-20 Hz). The analysis revealed both similarities and differences across conditions in the distribution of alpha-mu and beta-mu power. As shown in Figure 4, from 14 Hz to 17 Hz, differences between neutral and happy faces continued to show a pattern similar to that observed in the alpha band, and then got localised to the more posterior areas ($p < .05$ corrected). Activity differences between neutral and sad faces were similar to that observed between neutral and happy faces when not corrected for multiple comparisons, and any differences between happy and sad faces disappeared with increasing frequencies ($p < .05$ uncorrected). In the Orientation task, there was a very similar suppression pattern in the alpha and beta band activity, with widespread differences between forward and left- or right-oriented faces becoming more pronounced in the beta band ($p < .05$ corrected). Finally, as in the alpha range, there was no difference between left- and right-oriented faces that demanded our attention.

Figure 4

Power Differences Between Conditions at Each Beta Frequency in the 800-1000 ms Time Window

[Figure 4 here]

[Figure 4 legend here]

4 DISCUSSION

The goal of this study was to investigate the sensitivity of sensorimotor simulation to ambiguous facial expressions. To do this, we measured EEG mu suppression as participants viewed unambiguous (happy/sad) and ambiguous (neutral) facial expressions. The categorisation of neutral faces as happy or sad is a more difficult task than categorising easy-to-recognise happy or sad faces, which could inflate overall alpha suppression in the neutral face condition. Thus, to control for task difficulty effect on alpha activity, we also measured alpha power in a second task which involved categorising left-oriented, right-oriented and forward-oriented faces as left- or right-oriented. The same face stimuli were used in the neutral face and forward-oriented face conditions. Slower response time, inconsistent binary categorisation of faces, and greater widespread alpha and beta suppression in ambiguous conditions in both tasks suggest that the task was in fact more difficult for the ambiguous than the unambiguous stimuli. Although it is difficult to completely dissociate the effects of visual processing and task difficulty from emotion understanding, we saw centrally localised alpha-mu band differences more clearly together with less pronounced beta suppression in the Emotion task. Thus, our findings suggest that alpha-mu rhythm is sensitive to emotion understanding from faces.

There were different patterns of brain activity in the two tasks. Emotion judgment affected central areas differently for ambiguous and unambiguous emotions from 8 Hz to 17 Hz, suggesting stronger engagement of the sensorimotor cortex when emotion was difficult to understand. Specifically, there was stronger suppression to neutral than happy faces. Nevertheless, stronger suppression to neutral than sad faces did not survive multiple comparisons and is reported here as a preliminary finding which needs to be investigated in future research. Similarly, greater mu suppression to sad than happy faces was observed in the alpha range only when not corrected for multiple comparisons, so this finding should also be interpreted with appropriate caution until replicated in future work. In contrast to the differences across the conditions of the Emotion task, differences between forward and left- or right-oriented faces were not centrally localised, were more widespread and became even more pronounced in the beta band. Analysis of the changes in the mu-alpha and mu-beta rhythms reveals the differences in the processing of ambiguity in different contexts. Given the link between mental simulation and mu suppression, greater suppression to neutral faces showing minimal expression compared to easy-to-recognise happy faces suggests the involvement of the MNN in the emotion evaluation process.

Similar findings suggesting a link between mu suppression and ambiguity have recently been reported. In a study which investigated facial expression-related mu modulation, Krivan et al. (2020) used face images depicting happy and sad emotional expressions as well as more ambiguous ones, specifically, neutral, happy tearful and sad tear-free expressions. They observed stronger mu suppression in response to the more unusual/ambiguous facial expressions than the unambiguous expressions. In another recent study, Gulbetekin et al. (2023) investigated whether tactile stimulation on one's face would influence mu rhythm activity during observation of neutral faces. They measured alpha range power changes in the central and occipital areas associated with observation of neutral faces and non-face visual stimuli, and found stronger mu and alpha suppression in the touch condition compared to the no-touch condition only in response to faces. The authors interpreted stronger occipital alpha suppression as indicating increased attention to the face stimuli triggered by tactile stimulation. More interestingly, mu suppression to faces in the touch condition suggested that the somatosensory cortex plays an important role in shared mental representations of one's own body and the bodies of others. Taken together, these findings highlight the involvement of the sensorimotor processes in processing of others' faces.

Effects of emotional actions on mu suppression were investigated in two other important studies. In Weiblen et al. (2023), participants observed pictures of hands and feet in painful and neutral situations and rated the painfulness of the situation for themselves, and for the actor who was told to have either normal or heightened pain sensitivity. They measured somatosensory mu suppression in response to painful and neutral images in people with Tourette syndrome and matched controls, and found stronger mu suppression in response to painful than neutral stimuli in the control group. This finding provides support for the idea that the sensorimotor simulation system is modulated by emotional content. The authors attributed less pain-related mu suppression in the Tourette syndrome group to an altered processing of others' emotional states in brain regions associated with the MNN. Similarly, Siqi-Liu et al. (2018) observed that the mu rhythm was modulated by the availability of emotional information in body movements. In their time-frequency analysis, which has inspired our own, they examined high-density EEG data collected while participants viewed dynamic videos of point-light displays showing emotional or neutral body movements in biologically plausible and scrambled configurations. Within the time widow of 1.3-1.5 seconds after stimulus onset, there was stronger mu-alpha suppression in the centroparietal/occipital electrodes and stronger beta suppression in the frontocentral sites in response to emotional compared to neutral movement. This observation indicates that action simulation processes originating from the sensorimotor areas are more active when there is emotion-related information in the movement. Even though this finding appears to be in contrast with ours which suggests stronger suppression to neutral than happy faces, this divergence may be explained by differences in cognitive processes engaged by different task instructions. Specifically, Siqi-Liu et al. (2018) used a one-back task in which participants monitored for the immediate repetition of each movement. Thus, they captured more automatic sensorimotor responses associated with emotional stimuli. Unlike this task, in our study, participants were explicitly asked to pay attention to the emotion in each face and make a judgment about its valence. Thus, even though we observed the strongest suppression to neutral facial expressions than the other way around, we arrive at a similar conclusion: emotion understanding engages sensorimotor processes, with stronger engagement in response to ambiguous emotions.

Sensitivity of the mu rhythm to subtle movement which does not provide readily-recognisable emotional expression may be due to the heightened social importance it gains when its social signal is ambiguous. According to the social-relevance hypothesis of the MNN (Kilner et al., 2006), the MNN is activated only when the observed information is deemed socially relevant (Kilner et al., 2006; Menoret et al., 2015). For example, Kilner et al. (2006) reported greater mu suppression during observation of arm movements when the actor was facing towards the participant rather than facing away from them. They interpreted this result as indicating the role of visuospatial attention as a gating mechanism for the mirroring system, leaving only the socially-relevant information for further processing. In the current study, high social significance of emotion information may have activated the sensorimotor cortex differentially in response to easy-to-recognise happy faces versus more ambiguous ones. From this perspective, the mirroring system is likely to be engaged more by social stimulus that demands attention, because resolving ambiguity is crucial for social interaction. In line with this reasoning, sad facial expressions would also be more likely to additionally engage sensorimotor processes than happy expressions. First, more generally, negative facial expressions tend to draw our attention as they communicate potential negative outcomes or need for assistance, and thus are particularly effective at attracting our attention (Eastwood et al., 2001). In fact, the evolutionary importance of detecting threats may explain our tendency to label neutral faces as displaying negative emotions (Albohn et al., 2019). This tendency, evident in our sample as a "sad bias", resulted in the majority of neutral faces being categorised as sad. Second, in the context of our study, the posed facial expressions made the sad face stimuli less familiar for the observer than the more common and natural happy face stimuli. Based on the literature reviewed above, greater social relevance or less familiarity of the sad faces would be expected to engage the sensorimotor system possibly at a level comparable to neutral faces, and more than the familiar easy-to-recognise happy faces. Our data provide preliminary evidence suggesting these differences, which need to be replicated in larger samples.

Similar to the "sad bias" observed in the Emotion task, we also noted a "right-oriented" bias in the Orientation task. One possible explanation for this observation is drawn from the well-documented left gaze bias during face exploration, which refers to our tendency to look at the left side of a face (from the observer's point of view; see for a review Samson et al., 2014). It may be that when we focus on the left side of a forward-oriented face directly in front of us, we expect it to be looking towards us, and thus perceive the head as being slightly oriented to our right. Another explanation could be that participants more frequently used their dominant right hand when the stimulus orientation was ambiguous. These speculations need to be verified by eye tracking and handedness data.

Although the findings of this study expand the literature on the involvement of the mu rhythm in emotion understanding from faces, behavioural correlates of this neural activity in people with or without emotion processing difficulties remain to be elucidated in future studies. We speculate that hypo-, hyper- or inconsistent reactivity of the mu rhythm associated with facial expression processing signals difficulties with emotion understanding from faces, and thus may represent a biomarker of the activation of empathy circuits. A balanced activation of these circuits would be necessary for interpreting emotion cues accurately and responding to them empathically, enabling effective social communication. In various psychological disorders and conditions, including mood and anxiety disorders and alexithymia, individuals commonly experience difficulties in interpreting facial expressions (Bourke et al., 2010; Cook et al., 2013). In these populations, reading emotions from subtle facial expressions may be evident in their pattern and intensity of mu rhythm activity during social situations. Furthermore, the mu rhythm may be a neural marker not only of emotion*understanding* but also emotion *sharing* , facilitated by the transmission of information from the motor representations to the limbic areas (Nummenmaa et al., 2008). Future clinical studies can investigate the relationship of the mu rhythm with social communication and empathic skills. This knowledge could help fill the gap in the literature around the biological indicators that reflect difficulties in emotion regulation, processing and expression.

In conclusion, the present findings suggest that the sensorimotor processing might become more intense as it attempts to resolve the ambiguity in facial expressions. Future work should further test this idea by addressing some of the limitations of our study. First, we used static images instead of dynamic ones to minimise artifactual data and confounds associated with perceptual differences that could arise from using dynamic facial expressions in the Emotion task and head movements in the Orientation task. This approach ensured that any observed effects were due to the experimental conditions rather than differences in the dynamic properties of the stimuli. Despite this advantage, dynamic video stimuli with longer epochs would more closely mimic real-world experiences and be more engaging for participants, enhancing ecological validity and participant engagement. Furthermore, observing real movement would engage the mirroring network more strongly, which in turn would enhance the mu signal. Future studies could use both static and dynamic stimuli to compare their effects on mu suppression. A second improvement to the experimental design would be to consistently use either text or image on the response slides of both tasks to ensure that the perceptual and attentional loads are as similar as possible across the tasks. Third, the short duration of the stimulus presentation of 1000 ms limited our analysis to the first second after the stimulus onset. Longer stimulus presentation would help understand how the neural activity unfolds over a longer time period. Finally, due to the small sample size and the number of analyses conducted without correcting for multiple comparisons, results must be interpreted with caution. The findings warrant future research with larger samples in order to provide further support for the claim that there is stronger mu suppression associated with socially relevant ambiguous emotional expressions compared to easily recognisable actions.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author, OK. The data is not publicly available as consent was not obtained from the participants for its dissemination.

AUTHOR CONTRIBUTIONS

OK conceived the experiment, performed data acquisition, analysis, interpretation of the data, and wrote and revised the manuscript. NM contributed substantially to the critical revision of the manuscript. MM contributed substantially to the study design. IK supervised the study and contributed to the design of the experiment. All authors approved the final draft of the manuscript for publication (OK, NM, MM, IK).

DECLARATION OF INTEREST

None.

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ABBREVIATIONS

EEG: electroencephalography

MNN: mirror-neuron network

Power Spectral Densities: PSDs

Reaction time: RT

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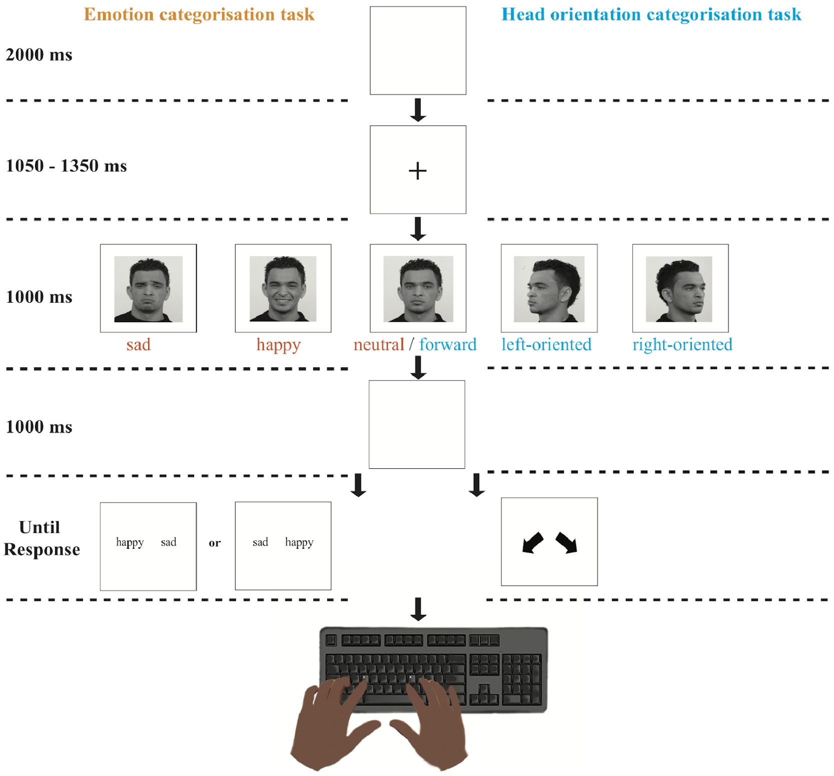

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