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The association between 5-HTTLPR and spontaneous facial mimicry: An investigation using the Facial Action Coding System (FACS)

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Abstract

Facial mimicry has been considered an automatic, spontaneous process. However, recent research suggests that facial mimicry is dependent on the context of the social interaction, with increased mimicry occurring when the understanding of another's emotional states is important. In this study, we examined the social context of facial mimicry of positive and negative facial expressions of emotion, and how mimicry relates to common variants in the serotonin transporter genotype 5-HTTLPR, which has been found to relate to proneness to negativity and to social sensitivity. Overall, the results of this study indicate that the negativity associated with a particular 5-HTTLPR genotype may be due to decreased processing of positive emotion rather than increased processing of negative emotion.

Introduction

In this study, we sought to examine whether a genetic mutation known to increase sensitivity to emotional stimuli would play a role in the extent to which participants spontaneously mimic facial expressions of emotion. We specifically investigated emotional mimicry, which involves the mimicry of facial expressions of emotion and how mimicry conveys emotional intentions within a specific context (Hatfield, Bensman, Thornton, & Rapson, 2014). Recent studies have documented how a number of common genetic mutations known as single-nucleotide polymorphisms (SNPs) relate to cognitive, emotional, and social processes. In psychology in particular, numerous studies have focused on 5-HTTLPR, a degenerate repeat polymorphic region in the serotonin transporter gene 5-HTT, also known as SLC6A4. 5-HTTLPR consists of a combination of two alleles, short and long, and individuals can carry two copies of the low-expressing short allele (s/s), two copies of the long (l/l) allele, or can have a combination of both (s/l).

A great deal of research has associated the s/s variant of 5-HTTLPR with stress sensitivity and negative emotionality (Clarke, Flint, Attwood & Munafò, 2010; Homberg & Lesch, 2011; Sharpley, Palanisamy, Glyde, Dillingham, & Agnew, 2014). Studies show that the s-allele of 5-HTTLPR is associated with increased attention to negative information such as anxious word stimuli (Beevers et al., 2007) negatively valenced emotional expressions (Pergamin-Hight, Bakermans-Kranenburg, van IJzendoorn, & Bar-Haim, 2012; Papousek et al., 2013), and higher cortisol stress reactivity (Miller et al., 2012). Thus, having one or more copies of the s-allele of 5-HTTLPR appears to increase the extent to which people experience and attend to negative emotion.

Facial mimicry: An overview

The tendency for people to mimic those whom they interact with is well documented in scientific research. This mimicry can take the form of the imitation of gestures, body postures, facial expressions, tone of voice, pronunciation patterns, or breathing rates (Bourgeois & Hess, 2008; Oberman, Winkielman, & Ramachandran, 2007). Research on mimicry has evolved over time: early theorists viewed mimicry as a simple by-product of a stimulus response link that had been established between perceiving and performing an action. Contemporary theorists, however, view mimicry as a more complex process, in that the performance of an action, such as mimicry, influences contemporaneous perception of the action (Oberman, Winkielman, & Ramachandran, 2007).

Traditional approaches view facial mimicry as a spontaneous and automatic process. Dimberg, Thunberg, & Elmehed (2000) found that participants would mimic the emotional expressions of masked emotional faces, without even having conscious awareness that they had seen the face. Further research supporting mimicry as an automatic process showed that people with higher levels of empathy, but not people with lower levels of empathy, showed borderline significant mimicry at an automatic processing level, which included both subliminal and very short supraliminal, stimuli (Sonnby–Borgström, 2002). These studies suggest mimicry to be an automatic process, which occurs early in emotional processing.

More recently, research has sought to determine the function of facial mimicry. Currently, mimicry is thought to increase rapport between interaction partners and create social cohesion through affiliation (Bourgeois & Hess, 2008). Emotional facial expressions not only signal emotional states, but also the likelihood of affiliation, as individuals who show happy expressions are perceived as highly affiliative and those who show anger are perceived as non-affiliative (Hess, Blairy, & Kleck, 2000). These two facets interact, as the social signal value of

the emotion interacts with the function of mimicry, creating linkages between individuals (Bourgeois & Hess, 2008). Thus, mimicry aids in the creation of affiliation as it provides a physical connection, showing the interaction partner that the responder is paying attention and relating to them.

Facial mimicry has also been proposed as a method by which individuals come to understand the emotional state of others. The facial feedback theory states that activity of facial muscles can affect a person's emotional experience (Davis, Senghas, Brandt, & Ochsner, 2010; Dzokoto, Wallace, Peters, & Bentsi-Enchill, 2014). More specifically, as facial expressions of emotion are distinct from each other, activation of muscles related to a specific emotion, such as the zygomatic major for happiness or the corrugator for sadness, will cause a person to feel the emotion represented by the muscle activation (Dimberg, Thunberg, & Elmehed, 2000; Ekman, Freisen, & Ancoli, 1980). When participants in a study exaggerate their facial expression, they rate a stimulus as more intense, compared to suppressing their facial expression (Hatfield, Bensman, Thornton, & Rapson, 2014). This pattern has been seen for both positively and negatively valenced stimuli. Furthermore, participants with Botox injections, which reduced the feedback of facial muscles, were found to be less successful at perceiving emotions in other (Neal & Chartrand, 2011). Therefore, following the facial feedback hypothesis, we would expect to see more mimicry when participants are trying to identify emotion, as they will be relying on feedback from their muscles to identify the emotion.

Emotional contagion, a related concept to facial mimicry, is also thought to help people process and recognize the emotions of others. Emotional contagion is a family of cognitive, psychophysical, behavioral, and social phenomena, best defined as the tendency to mimic the verbal, physiological, and behavioral aspects of another person's experience and to thus

experience the same emotions (Hatfield et al., 2014; Sonnby–Borgström, 2002). Emotional contagion is linked to embodied cognition theory, which states that mimicry of another's experience is a direct simulation into the body, allowing an individual to feel the other's emotions directly (Sonnby–Borgström, 2002). Research by Balconi, Bortolotti, & Gonzaga (2011) showed that when facial mimicry was reduced, the ability of the participants to correctly identify the emotion showed was also reduced, with error rates and response times increasing. Thus, facial mimicry may be one mechanism whereby people discern the emotional state of other via facial feedback.

Biological basis of facial mimicry

A wide body of research has focused on the biological underpinnings of facial mimicry. Research has suggested that the execution of a facial action and the observation of the same action have a shared neural substrate, whereby the activation of facial actions and observation of those actions mutually influence each other (Oberman et al., 2007). This neural substrate was identified with the discovery of mirror neurons, which are activated both when an individual performs an action and when the action is observed (Lee, Josephs, Dolan, & Critchley, 2006; Likowski et al., 2012; Oberman et al., 2007), and researchers have proposed that mirror neurons primarily drive facial mimicry, as people readily catch the emotions of others (Hatfield, Bensman, Thornton, & Rapson, 2014). There are two brain systems which contain mirror neurons, the classical mirror neuron system, consisting of the precentral gyrus, the premotor region, and the supplementary area, and the extended mirror neuron system, which includes, among other regions, the amygdala (Lee et al., 2006; van der Gaag, Minderaa, & Keysers, 2007). In line with the idea that mirror neurons underlie facial mimicry, research has shown that the

amygdala is activated when participants is view facial expressions of emotion (Kircher et al., 2013; Lee et al., 2006; Likowski et al., 2012; van der Gaag et al., 2007).

The amygdala is also highly affected by the genotype for the serotonin transporter gene, the focus of the current study. The serotonin transporter removes released serotonin from the synaptic cleft (Canli & Lesch, 2007). The transporter is coded by two different alleles of 5-HTTLPR, a long allele (l-allele) and a short allele (s-allele), in which the s-allele is a length-variation polymorphism, which manifests as a 43-base pair deletion involving repeat elements 6 to 8 (Canli et al., 2006; Lesch et al., 1996; Pergamin-Hight, Bakermans-Kranenburg, van IJzendoorn, & Bar-Haim, 2012; Wielpuetz, Kuepper, Grant, Munk, & Hennig, 2015). Carriers of at least one s-allele have been found to exhibit heightened amygdala reactivity to threat, altered functional connectivity between the amygdala and the prefrontal cortical structure, a decreased grey matter volume of the amygdala, and higher amygdala activation at rest when compared to l/l individuals (Canli et al., 2006; Canli & Lesch, 2007; Pergamin-Hight et al., 2012).

Research has shown the amygdala to be a processing center for negative emotionality, specifically for fear and threat, with the region also being sensitive to affective salience and the intensity of emotion, discounting the valence of the emotion (Büchel, Morris, Dolan, & Friston, 1998; Hamann & Mao, 2002; Morris, Buchel, & Dolan, 2001; Morris, deBonis, & Dolan, 2002; Winston, O'Doherty, & Dolan, 2003). The s-allele of 5-HTTLPR is directly tied to negative emotionality and has been found to be associated with stress sensitivity, attentional bias toward anxious stimuli, increased vigilance for threat-related information, and overall, enhanced attentional vigilance to negative stimuli (Beevers, Gibb, McGeary, & Miller, 2007; Pergamin-Hight et al., 2012; Schug, Nezlek, & Newman, 2015).

This tendency between the s-allele and negative emotionality has also been captured by personality measures. Carriers of the s-allele show a significant positive association with measures of neuroticism, or associated scales across multiple personality measures, including the NEO-PI-R, Cattell's 16 Personality Factors, and the Tridimensional Personality Questionnaire (Canli & Lesch, 2007; Lesch et al., 1996). Additionally, a significant negative association has been found between the personality trait of agreeableness and the s-allele (Canli & Lesch, 2007).

Other research suggests that the s-allele increases social sensitivity in particular. For instance, s/s individuals have been found to show greater vigilance to social cues (Gyurak et al, 2013) and increased social blushing (Domschke et al., 2009). S-allele carriers also tend to show more sensitivity to the emotional state of their spouses (Schoeby, Way, Karney, & Bradbury, 2012), something that is consistent with the conclusion that the s-allele promotes social sensitivity overall. More recently, Schug, Nezlek, & Newman (2015) examined the impact of social and non-social events on emotions and found that the s-allele only increased negative affect experienced in response to social negative events, but not non-social or positive events. Taken together, these results suggest that, as also theorized by Way & Gurbaxani (2010) and the s-allele of 5-HTTLPR may increase sensitivity to sensitivity to negative stimuli, particularly in social domains.

The current study

In this study we examined whether a common variant of the serotonin transporter gene 5-HTTLPR would be associated with patterns of facial mimicry exhibited by participants in response to stimuli of positive and negative facial expressions of emotion. Specifically, we decided to focus on the mimicry of a positive and negative emotion, or happiness and sadness. We focus on these two emotions specifically for several reasons. First, prior research on mimicry

of facial expressions of happiness has found that people tend to spontaneously mimic happiness regardless of context. Happiness is considered a low cost emotion, as it simply signals wellbeing (Bourgeois & Hess, 2008). Therefore, we expected to see mimicry of happiness, as the expression of happiness is less affected by social context. Furthermore, people who smile more are rated as more affiliative, therefore, we expected to see more mimicry of smiles, as affiliation is one of the functions of mimicry (Hess, Blairy, & Kleck, 2000). While the mimicry of happy expressions is easily affected by muscular noise in the face, our study was not expected to generate extraneous muscular feedback, and therefore will not interfere with the mimicry (Oberman et al., 2007).

Other research shows that 5-HTTLPR is related to processing of positive emotions. Research done by Grossmann et al. (2011) on infants has shown that 5-HTTLPR genotype affects the processing of positive emotional expressions. Their results showed that infants with at least one l-allele showed an increased allocation of attention to happy expressions, whereas infants who were homozygous for the s-allele did not. Their research also indicated that the infants homozygous for the s-allele were judged by their parents as smiling less in a variety of contexts and for being less able to focus their attention on one object, compared to how parents of infants with at least one l-allele judged their children. The results of their research suggest that the s/s infants process happiness differently from infants with at least one l-allele, potentially suggesting a decreased sensitivity to positive affect. While this is different from how research has shown adults with an s-allele respond, the impaired processing of positive affect in infancy and childhood may lead to adults who are hypersensitive to negative affect because these adults do not have a foundation of positive affect as a protective factor from their earlier years (Grossmann et al., 2011).

We also examined sadness, as prior research has focused on 5-HTTLPR and negative expressions in particular. In the current study, we were interested in the effects of the 5-HTTLPR genotype on emotional mimicry. We predicted that the genotype of 5-HTTLPR would affect facial mimicry, as particular genotypes have been associated with an increase in sensitivity. Specifically, we predicted that carriers of at least one s-allele would be more likely to mimic the facial expressions of targets. While some researchers consider mimicry of emotional facial expressions an automatic process, other research has found that it is very context dependent. We predicted that there would be more mimicry in our emotion-salient condition than in our control condition. As this is some of the first research looking into the effects of 5-HTTLPR on emotional facial mimicry, all of our hypotheses were exploratory.

Based on literature which suggests that the s-allele of 5-HTTLPR increases sensitivity to emotional stimuli, and in particular negative emotions (e.g., Schug, Nezlek, & Newman, 2015), we predict that individuals with the s-allele, due to their enhanced social sensitivity, would show more facial mimicry overall, particularly of negative expressions. Indeed, enhanced social sensitivity should attune individuals more to the expressions of others, causing more mimicry overall. However, due to the increased attention towards negative stimuli, carriers of the s-allele would also show more mimicry of negative emotions.

We also suspected that s-allele carriers would be more likely to mimic expressions particularly in contexts related to emotion. While a number of researchers have suggested that facial mimicry is an automatic and spontaneous process, more recent research suggests that facial mimicry may be influenced by higher order cognitive processes. For instance, Murata, Schug, Saito, & Kameda (2015) recently conducted two studies showing that facial mimicry only occurred in situations where participants were asked to infer the emotion of a target, but not in

conditions where participants were asked to infer a non-emotional attribute, such as age or body weight from an image. Thus, mimicry may only occur spontaneously when participants are motivated to infer the emotional state of a target, supporting the notion that mimicry can be used as a method to infer the emotional states of others.

Because 5-HTTLPR has been shown to increase susceptibility to negative emotions in social situations but not non-social situations, we suspected that participants would be likely to mimic negative facial expressions of emotion only in conditions where they were motivated to infer the emotional state of the target. We hypothesized that we would see mimicry used as a means to facilitate the processing and recognition of emotional expressions. Therefore we predicted that, as found in previous studies (Murata, Schug, Saito, & Kameda, 2015), facial mimicry would occur more frequently when participants were motivated to infer the emotional state of the target (emotion inference condition), compared to a condition where they were motivated infer a non-emotion related aspect of the target (age-inference condition), as the participant would only need to process and understand emotion in the former condition.

We also made several predictions regarding the relation between 5-HTTLPR and facial mimicry. We predicted we would see the mimicry of happy expressions in all genotypes of 5-HTTLPR, as it is a low cost emotion that is mimicked regardless of context. Due to the increased attention to negative stimuli that has been associated with the s-allele of 5-HTTLPR, we predicted that we would see increased mimicry of sad expressions in s-allele carriers. Finally, because previous studies have suggested that 5-HTTLPR increases sensitivity to negative social stimuli more than to non-social negative stimuli, we suspected that s-allele carriers would show heightened mimicry of negative emotions particularly in the emotion-inference condition relative to the age-inference condition.

Method

Participants

101 participants from the College of William and Mary participant pool took part in this study. Participants received compensation for their participation, either as a monetary compensation or as class credit. Of the 101 participants, 65 were women and 36 were men. Of the women, 23 were homozygous for the l-allele (l/l) and 42 had at least one short allele (s/s or s/l). Ten men were homozygous for the l-allele (l/l) and 26 men had at least one s-allele (s/s or s/l).

Procedure

At the start of the study, participants were seated behind a modified teleprompter box. Behind a wooden monitor, a computer monitor was positioned, with the image facing the top of the box. The ceiling of the box was installed with a mirror at approximately a 45 degree angle, which reflected the image of the computer monitor so that the screen appeared to be in front of the participant, rather than below. A video camera was hidden behind the screen, although participants were informed that they would be filmed during the study and provided their consent. The monitor within the box was connected to another computer, which was controlled by the experimenter. The image was reflected using the UltraMon screen-mirroring program. There was a small shelf attached to the teleprompter box, which had a mouse placed upon it, allowing the participants to navigate the experimental program.

The stimuli-presenting program was created in OpenSesame version 2.8.1 (Mathôt, Schreii, and Theeuwes, 2012), which is an open-source, Python-based program for designing psychology experiments. There were four versions of the program created, so as to counterbalance for order effects. Before the program was started, the experimenter would turn on

the obscured video camera, so as to record the facial expressions of the participant. While participants were unable to see the camera during the study through the teleprompter monitor, they consented to the filming of their facial expressions and the camera and tripod were visible to participants before they were seated in front of the teleprompter. The format of the program had two parts: explicit facial expression elicitation, as well as spontaneous facial mimicry elicitation.

For the explicit facial expression elicitation portion, instructions were given to make a facial expression for a specific emotion. The emotions that were asked to be produced were anger, happiness, and sadness. The order of presentation was randomized. Participants were shown a simple line drawing of the expression being requested. Participants were told to hold the expression for five seconds. This task was included for a separate study, but also served to allow participants to become accustomed to the filming of their facial expressions.

After completing the explicit facial expression elicitation portion of the program, participants alerted the experimenter. The experimenter then adjusted the video camera to ensure that the participant's face was in the frame and visible. The experimenter would then press a key on their computer, allowing the participant to move on to the next portion of the study.

In the second portion of the study, participants were told that they would be shown a series of videos of people. Participants were also told that they would be asked to either guess the age of the person in the video or what they were feeling in the video. We chose to use morphed dynamic images of facial expressions, over a single static image, as previous research has indicated that dynamic presentations of emotional facial expressions increase facial mimicry (Fujimura, Sato, & Suzuki, 2010; Sato, Fujimura, & Suzuki, 2008). The videos were a morph from a neutral expression to an emotional expression. The morphs were created using the Popims Animator (Guigan, Vinther, Scarbroug, & Guigan, 2010). Each morph was 20 frames long and

lasted 3.9 seconds. The neutral frame lasted 2000ms, each of the 18 frames in the morph lasted 50ms, and the fully morphed expression lasted 1000ms. This was consistent with an earlier study (Murata, Schug, Saito & Kameda, 2015). Four counterbalanced versions of the program were created, with the order of the videos varying. The counterbalancing additionally included which videos were primed with the age inference or the emotion inference.

There were a total of 24 stimuli videos, with 12 women and 12 men. The faces were taken from the Japanese and Caucasian Facial Expression of Emotion (JACFEE) database (Matsumoto & Ekman, 1988) and the Advanced Telecommunication Research International (ATR) database (Kamachi et al., 2001). The facial expressions in both databases were certified by EMFACS to be representative of the appropriate emotions. Within each gender/ethnicity combination, there were two stimuli videos created for each expression, angry, sad, and happy. These three emotions were chosen because they were mimicked most frequently in a prior study conducted in Japan (Murata, Schug, Saito, & Kameda, 2015).

Before each video was displayed, participants would be primed with the question they would be answering. The question was either, “How does this person feel?” or “How old is this person?” Next, a fixation cross would be presented for 500ms and was accompanied by a beep to signal the start of the video. A 500ms blank screen was shown at the end of the video and another beep sounded. This was followed by a multiple-choice question, which asked either “How does this person feel?” or “How old is this person?” For the emotion condition, the answer choices were sad, happy, angry, fearful, surprised, and disgusted, or Ekman’s six universal emotions (Ekman, 1971). Participants were given unlimited time to answer. Selecting an answer automatically sounded a third beep, of a different frequency to the previous two, followed by a 500ms blank screen and the next prime-fixation-video-blank-question sequence.

Following the facial mimicry task, participants were asked to provide a saliva sample. DNA was collected and extracted using the DNA Genotek Oragene kits. Every sample was given an anonymous code and processed by an external laboratory (ACGT, Inc.). For each of the DNA samples, the sample was PCR amplified for the 5-HTT repeat region target using primers. One of the primers was labeled with a fluorescent probe (5-HTT, locus symbol SCL6A4). By examining 10% of randomly chosen STR reactions with agarose gel electrophoresis, the quantity and quality of STR was evaluated. These products were then formulated with foramide and reference standard and then heat denatures in 96-well plates, which were loaded and run on the 3730xl Genetic Analyzer. GeneMapper ID Software determined the size of the STR products for each sample, based on STR peak size.

Analysis of Facial Mimicry

Facial mimicry was analyzed using the Facial Action Coding System (FACS) developed by Paul Ekman. Following the method of a prior study (Murata, Schug, Saito, & Kameda, 2015), we isolated specific action units (AUs) that have been found to correlate with emotional expressions, such as AU 12 with happiness and AUs 1 and 4 with sadness (Ekman et al., 1980). A certified FACS coder went through the videos of each participant and coded for any AUs visible on the face. The participant was assessed at the start of the stimulus presentation, the end of the stimulus presentation, and after they selected an answer to the prompt for the stimulus. For the purposes of this thesis, we focused the analysis on mimicry observed in response to facial expressions of happiness and sadness.

Results

First, we examined differences in action units observed in response to facial expressions of happiness and sadness in the emotion inference and age inference conditions. The results for all action units coded are shown in Figure 1 (happiness) and Figure 2 (sadness).

Overall, supporting the results of a previous study examining facial mimicry in conditions where participants were motivated to infer the emotion of the target vs. a non-emotional physical attribute of a target (Murata, Schug, Saito, & Kameda, 2015), facial mimicry was observed more strongly in the emotion inference condition than the age inference condition. That is, when viewing facial expressions of happiness, the action unit particularly relevant to expressions of happiness (AU12) was observed more frequently in the emotion inference condition than in the age inference condition, although the effect was only marginally significant $t(106)=1.87$, $p=.068$. For action units observed in response to facial expressions of sadness, more mimicry for action units related to sadness (AU1 and AU4) were observed in the emotion inference condition, although the effect was not statistically significant for any action units.

Next we examined whether, overall, whether the valence of the target facial expression or the condition played a role in determining facial mimicry. Following the method of Murata, Schug, Saito & Kameda (2015), we defined facial mimicry as the occurrence of one matched AU per expression (AU1 for sadness and AU12 for happiness). We performed a 2 (target valence: happiness or sadness) x 2 (condition: emotion inference vs. age inference) ANOVA on the proportion of trials in which mimicry was observed. The results indicated a significant effect of target valence $F(1,101)=9.76$, $p=.0023$, and a marginal effect of condition $F(1,101)=9.76$, $p=.07$, indicating that participants were more likely to show mimicry in the emotion inference vs. the age inference condition. The valence x condition interaction was not significant.

5-HTTLPR and Facial Mimicry

Next we examined whether the facial mimicry in each condition was impacted by 5-HTTLPR genotype. Note that because not all samples from participants in this study have been genotyped, the sample size differs in the following analyses. Following previous studies examining 5-HTTLPR, we created a dummy variable indicating whether the participant had one or more copies of the s-allele (i.e., s/s and s/l variants, coded as 1) or were homozygous for the L allele (l/l), coded as 2. We performed a 2 (target valence: happiness or sadness) x 2 (condition: emotion inference vs. age inference) x 2 (5-HTTLPR: s/s and s/l vs. l/l) mixed model ANOVA with target valence and condition as within subjects factors and 5-HTTLPR as a between subjects factor. Overall, there were significant main effect observed for 5-HTTLPR $F(1,88)=4.86$, $p=.03$, valence $F(1,88)=11.10$, $p=.0013$, and condition $F(1,88)=4.27$, $p=.021$. These effects were qualified by a significant condition x 5-HTTLPR interaction $F(1,88)=4.27$, $p=.021$ and a marginally significant valence x condition interaction $F(1,88)=2.97$, $p=.089$. The valence x 5-HTTLPR and valence x condition x 5-HTTLPR interactions did not meet significance criteria ($F(1,88)=2.43$, $p=.12$ and $F(1,88)=2.10$, $p=.15$, respectively). Overall, the results indicated that, as shown in Figure 3, contrary to our hypothesis participants with one or more copies of the s-allele were less likely than individuals homozygous for the l allele to show facial mimicry in the emotion condition relative to the age condition.

Discussion

In this study, we examined the influence of the serotonin transporter gene 5-HTTLPR on facial mimicry in response to positive and negative facial expressions of emotion, in situations where participants were motivated to infer the emotional state, or a non-emotional aspect of the target. Overall, our hypothesis that there would be more mimicry in the emotion inference

condition was supported. This finding gives weight to previous research that indicates emotional facial mimicry is not automatic. If this mimicry were truly automatic, we would expect to see no difference between the emotion inference condition and the age inference condition. This finding supports the idea of facial mimicry as a strategy to determine the emotion of the expresser. As we see a significant increase in mimicry in the emotion inference condition, it is clear mimicry is being used as a process in regards to understanding the emotional expressions of the other. Additionally, since we found that participants were more likely to display the action unit relevant to the emotion being displayed, particularly in regards to AU 12 in response to happy emotions, which further supports mimicry as a process to recognize emotion.

For action units observed in response to sad facial expressions, we found a non-significant increase in the mimicry of action units related to sadness, namely AU1 and AU4. As sadness is associated with more subtle and localized expression changes of the face, this result is not entirely unexpected (Oberman, Winkielman, & Ramachandran, 2007). Furthermore, as discussed in the same study, sadness is generally associated with an overall reduction in muscle tone, making the observation of AUs less relevant to the emotion and thus its mimicry. It is additionally hypothesized that the positioning of the physical body and posture might be a better indication of sadness. Additionally, sadness is a high-cost emotion to recognize, as the observer might then be compelled to act upon it and try to reassure the interaction partner, therefore, studies have found that sadness is typically only mimicked by ingroup members (Bourgeois & Hess, 2008). As the faces in our study were taken from a database and were not anyone the participants knew, we might not have been able to access to full potential extent of the mimicry of sad faces, as the expressers were not part of a social ingroup.

Contrary to our hypothesis, participants with at least one s-allele were found to be less likely to show facial mimicry, particularly in the emotion condition. This finding contradicts our hypothesis that participants with one or more s-alleles would show more mimicry due to increased sensitivity. However, it may be in line with findings from previous research. Grossmann et al. (2011) found that infants with at least one s-allele dedicated less attention to happy expressions and were also judged by their parents to be less likely to smile and laugh. This research suggests that the effects of 5-HTTLPR is associated with a lessened processing of happy expressions, similar to the results we found with decreased mimicry of happy expressions in participants with at least one s-allele.

While the valence x condition x 5-HTTLPR was not significant, the pattern suggests that the mimicry we observed was driven by positive emotional expressions, as participants were more likely to mimic a happy facial expression. One explanation for this is that it has been found that facial mimicry may be especially important in recognizing happiness, but less important for sadness (Oberman et al., 2007). However, research conducted by Grossmann et al., (2011) showed that infants with one or more l-allele increased their allocation of attention to happy expressions, whereas infants homozygous for the s-allele did not. While most of the previous research has tied 5-HTTLPR functioning to negative, particularly fearful, affect, the results of Grossmann et al., (2011) showed that 5-HTTLPR variation might also be tied to the processing of positive, especially happy, affect. This is also what we found in our study. While in general, positive affect is mimicked more due to it being a low-cost and low-risk action, we see that participants who are homozygous for the l-allele showing greater mimicry of happy facial expressions than the s-allele carriers, when we would expect both to show increases mimicry of

facial expressions of happiness relative to facial expressions of sadness (Bourgeois & Hess, 2008).

The best explanation for the higher levels of positive facial mimicry from the l/l participants comes from Grossmann et al.'s (2011) study, which found that s/s infants process happy expressions differently compared to l/l infants. Additionally, parents of infants homozygous for the s-allele reported that their children smiled less frequently and were less able to devote their attention to a single object for a period of time than the parents of l-allele carrying infants. They hypothesized that variations in 5-HTTLPR critically altered the processing of positive emotion, which will affect the response to negative emotions later in development. As the infants with at least one l-allele are responding with increased sensitivity to positive emotion from birth, they build up a positive default, against which negative emotions stand out. As the s/s infants do not develop this positive background, the increased sensitivity to the processing of negative emotions in adulthood would be due to the reduced acquisition of a positive affect foundation during childhood.

While our study results did not show the increased sensitivity to negative emotions in the form of increased mimicry, we did observe the differential response to positive emotions. If the s-allele is associated with a lower response to processing positive emotions, this could provide a gene x environment interaction. As the infants smile less, their parents provide less positive feedback. This begins a cycle of how the infant, and then growing child and adult, interact with the world and how the world responds, creating a feedback loop biased towards negativity. Further investigations into this potential gene x environment interaction are recommended.

Limitations

This study is not without limitations. One of the largest limitations of the current study is the small sample size, which limits the power of our analyses. Further studies should have a larger sample size to allow them to draw stronger conclusions about the interactions of emotional facial mimicry and 5-HTTLPR variations.

Further, this study did not examine the impact of gender, either for the participant or the target stimuli. Additionally, our study had more women represented than found in the population. Further work should aim for a more equal ratio of genders, in case there is an effect of gender upon facial mimicry. This is important, as previous research has found differences between men and women due to differential processing of positively and negatively valenced emotions. Positive emotions are also recognized faster on the faces of women, whereas negative expressions are recognized faster on the faces of men (Stel & Knippenberg, 2008).

Further research might also want to consider using different modalities to investigate this reaction. We chose to use FACS, as emotional facial mimicry is tied to social signaling and FACS captures what would be seen in interactions. However, many studies on facial mimicry use electromyography (EMG), which on the one hand can pick up much subtler reactions of facial muscle movements, but on the other hand is much more likely to generate noisy data, and typically cannot differentiate between subtle differences in facial expressions.

Future research should also have a brain activation component, to see if the link between how the amygdala functions in regards to mimicry and 5-HTTLPR can be detected. Furthermore, brain activation methods have an increased sensitivity compared to EMG or FACS, with the effect size of a given genotype increasing up to an order of magnitude when measured in terms of brain activation instead of tradition behavioral methods (Lesch et al., 1996). As sadness is

associated with a reduction in muscle tone, EMG may detect the changes in facial muscles in response to sad faces at an increased rate that FACS (Oberman et al., 2007).

Links between stressful life events and proneness to negative stimuli are another avenue for future research. While some researchers have disputed the gene x environment interactions, the majority of findings point to an interaction between the s-allele of 5-HTTLPR and stressful life events (Gillespie, Whitfield, Williams, Heath, & Martin, 2005). Carriers of the s-allele are more likely to develop depression as they experience more stressful life events, whereas the risk of depression does not increase as stressful life events increase for l/l individuals (Munafò, Durrant, Lewis, & Flint, 2009). The interaction between stressful life events on depression is stronger for carriers of the s-allele as compared to those homozygous for the l-allele (Caspi et al., 2003). Lastly, lower levels of long term contextual threat of the stressful life events was found to be associated with increased risk of depression for s/s individuals (Kendler, Kuhn, Vittum, Prescott, & Riley, 2005). Therefore, looking at the links between stressful life events and proneness to negative stimuli as a moderator of the risk for depression could reveal important mechanisms behind this gene x environment interaction. Furthermore, if facial mimicry is used to try to elucidate these connections, the results will indicate if the s-allele of 5-HTTLPR is associated with differential processing of positive emotions or increased attention to negative stimuli.

Other studies in the future may wish to examine how individual differences in the tendency to engage in facial mimicry relate to other aspects of psychological functioning and behavior. For instance, the expression of positive facial expressions of emotion, and emotional expressivity in general, has been linked in prior research to pro-social preferences. Research has shown that altruists, or people often open to helping others and affiliation, are more likely to

express various facial expressions, such as smiles and head nods, which aids in the detection of altruists from non-altruists, indicating that expressions do function for affiliative purposes (Brown, 2003; Mehu, Grammer, & Dunbar, 2007). Behavioral studies have also shown that people who default to cooperation expressed happiness more than those who did not cooperate, showing that happy expressions and affiliation are intertwined (Schug, Matsumoto, Horita, Yamagishi, & Bonnet, 2010). Thus, future research should examine the link between social preferences for cooperation and facial mimicry.

In conclusion, our research confirmed some of our predictions, while failing to support others. We found that our overarching hypothesis was supported, with more mimicry occurring in situations in which context demanded understanding of emotions. Our prediction that we would see mimicry of happy expressions in all genotypes of 5-HTTLPR was not supported, as carriers of the s-allele mimicked happy expressions less than l/l individuals. However, we did find that l/l individuals tended to show more mimicry particularly in response to positive stimuli. Thus, while most research has focused on the impact of the s allele, future research may seek to examine the impact of the l allele of 5-HTTLPR on the processing and experience of emotion. The results of our study, while preliminary, pointing towards the proneness to negativity shown by s-allele carriers in prior studies may be caused by decreased attention towards positive stimuli, rather than increased attention to positive stimuli. We hope that future research will help to shed more light on this association.

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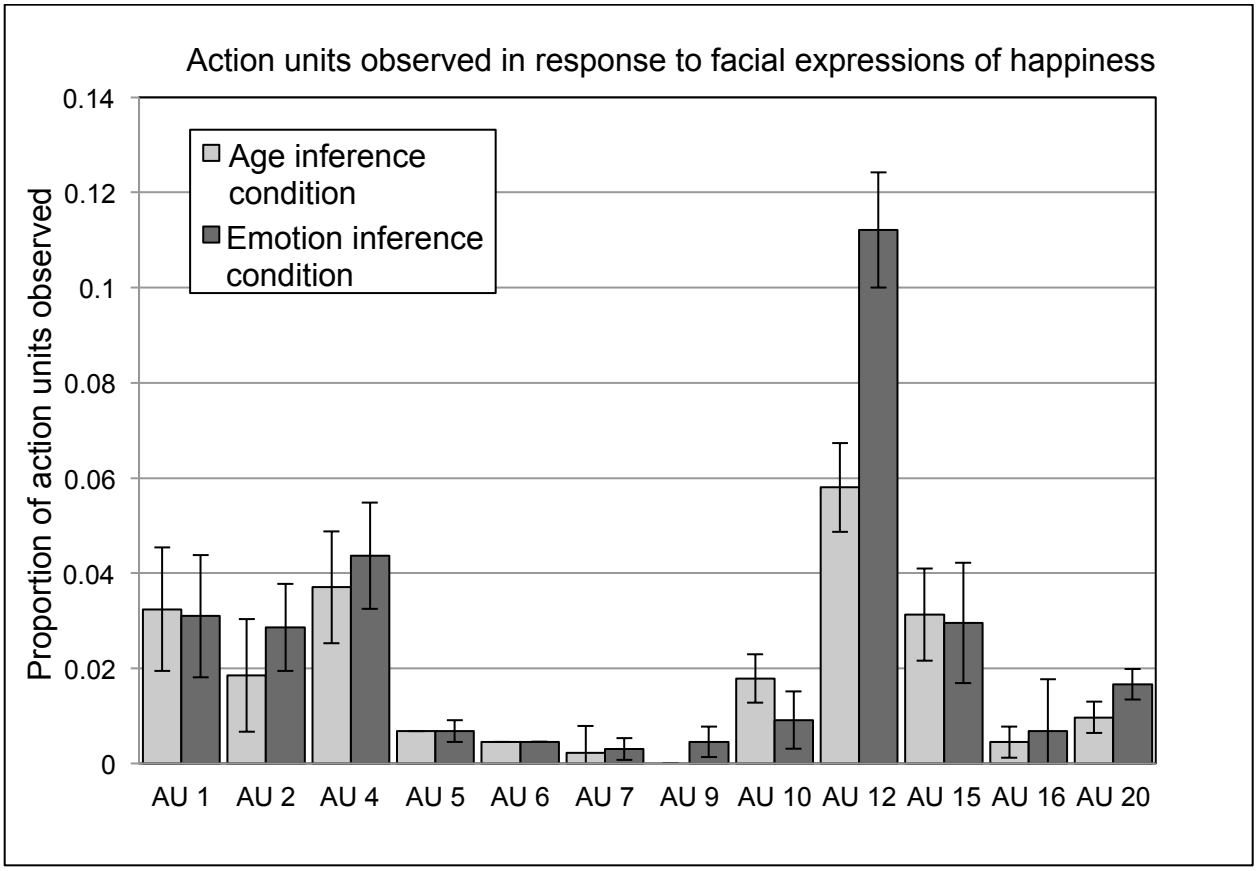

Figure 1. Proportion of trials in which each action unit was observed in response to facial expressions of happiness in the Age and Emotion Inference Conditions.

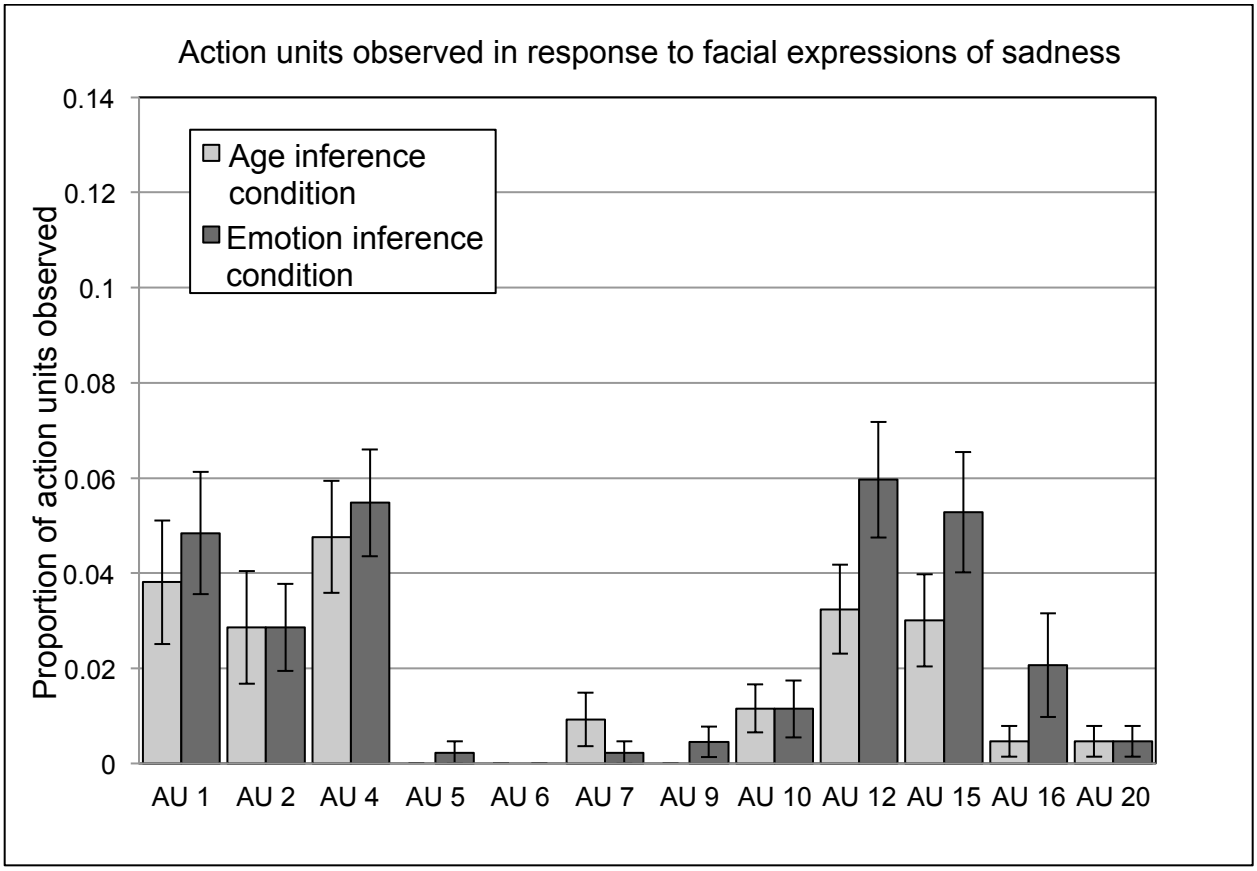

Figure 2. Proportion of trials in which each action unit was observed in response to facial expressions of sadness in the Age and Emotion Inference Conditions.

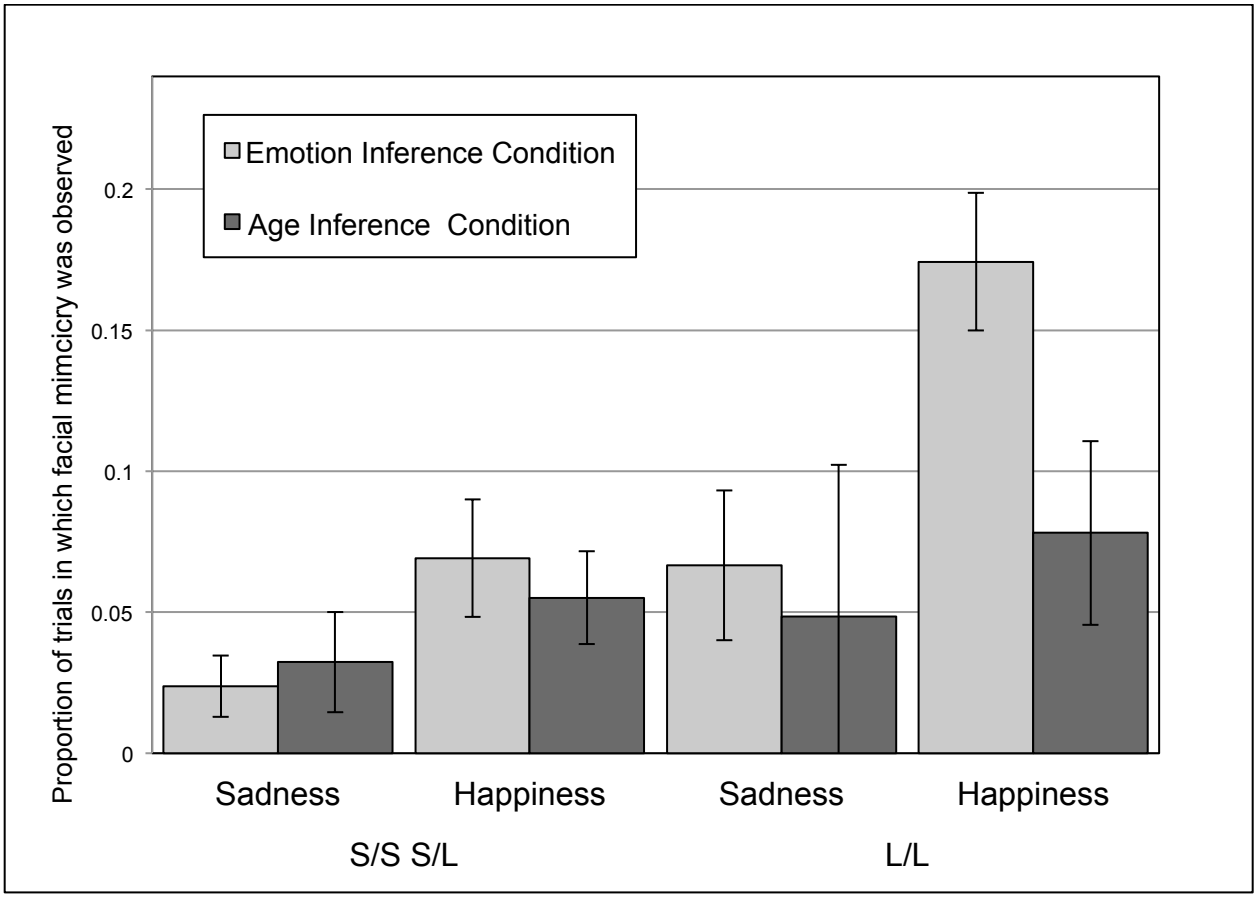

Figure 3. Facial Mimicry observed in response to facial expressions of sadness and happiness, by genotype and experimental condition.