Connecting minds and sharing emotions through human mimicry

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Chapter 6

Emotional expressions influence trust: modulatory effect of consciousness and mimicry

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All data, code, and materials that are associated with this paper and used to conduct the analyses are accessible on the Leiden University archiving platform DataverseNL.

Abstract

By observing subtle emotional expressions, humans make rapid inferences about others' thoughts and intentions. For instance, when deciding whether to trust someone or not, individuals observe and mimic facial movements and pupil sizes of others, which aids their trust evaluation. Yet, whether spontaneous mimicry depends on visual awareness of the stimulus and which processes underlie the unfolding development of trust in the observer remains unknown. To investigate how visual awareness modulates the relationship between emotional expressions, mimicry, and trust, participants played a series of trust games with different virtual partners whose faces and eyes were in half of the trials rendered invisible using continuous flash suppression (CFS). Participants would either see their partners' face with a neutral, happy, or fearful expression, or partner's eye region in which the pupils were large, medium, or small in size. Subjects' trust investments, facial movements and pupil responses were measured. Results showed that participants' trust declined as visual awareness of the stimuli decayed, which demonstrates that the ability to perceive partners' facial and pupillary expressions of emotion is vital for the establishment of trust. Moreover, we found that facial expressions were mimicked and influenced trust decisions during the control (conscious) but not during the unconscious (suppressed) condition. On the other hand, partners' pupil size influenced trust only when presented unconsciously. These findings imply that while the neurological path linking facial expressions to facial mimicry and trust is predominantly conscious, pupillary expressions of arousal influence trust mainly non-consciously, potentially via subcortical neurophysiological pathways.

Keywords: **consciousness; affect; pupil mimicry; facial mimicry; continuous flash suppression**

Introduction

Humans are able to decide whether to trust a complete stranger in a split of a second (38-ms) (Bar et al., 2006). They do so seamlessly, effortlessly, and often without explicit awareness of how they arrived at such a trivial decision. This implicitly formed intuition resembles a 'gut feeling', which plays an important role in novel situations. Intriguingly, research has shown that people can recognize emotional facial expressions and mimic others even when these signals are not consciously perceived (Skuse, 2003; Tamietto et al., 2009; Tamietto & De Gelder, 2010). This rapid mimicry is thought to reflect the transmission of affect across individuals and potentially serves as a precursor of more complex social abilities such as trust (Carr et al., 2003; Procházková and Kret, 2017). Apart from facial expressions, the mimicry of subtle cues such as pupil size may signal emotional contagion of arousal (Aktar, Raijmakers, & Kret, 2020; Harrison, Singer, Rotshtein, Dolan, & Critchley, 2006; Kret, Tomonaga, & Matsuzawa, 2014). Given the speed with which emotional expressions affect our daily social interactions, the current study investigates whether emotional expressions influence trust decisions without perceivers' conscious awareness. We further test if mimicry is part of the emotional process that contributes to the development of trust on the unconscious level ('gut intuition').

According to the Somatic marker hypothesis, before a decision is made, a parallel somatic/visceral response generates a gut feeling that helps people to tip the decision in one direction or another (Damasio, 1996). One physiologically plausible supposition asserts that during social interactions, emotional information is processed unconsciously, possibly via the retino-collicular-pulvinar-amygdala pathway. This subcortical "low road" is assumed to enable rapid processing of emotional information bypassing the visual cortex, and by doing so, facilitates physiological responses such as pupil dilation and facial mimicry, outside of perceivers' awareness of the visual input (Hassin, 2013; Ledoux, 1996; Morris, Öhman, & Dolan, 1999; Öhman, Flykt, & Esteves, 2001; Skuse, 2003; Tamietto et al., 2009). The clearest evidence for the unconscious processing of emotional facial expressions comes from studies with blindsight patients. Although blindsight patients have a lesion in their primary visual cortex, they are still able to distinguish facial and bodily expressions of emotion without conscious awareness of perceiving them (Anders et al., 2004; Tamietto et al., 2009).

In addition, these patients still show emotion recognition capacity accompanied by facial mimicry and pupillary reactions (indicative of autonomic arousal) to unconsciously perceived expressions of fear and happiness (Tamietto et al., 2009). Consistently, numerous studies using blinding methods in healthy subjects imply that salient visual stimuli such as emotional expressions or eye contact evoke physiological and neural responses even when they are not consciously perceived (Carlson and Reinke, 2008; Jiang and He, 2006; Pasley et al., 2004; Stein et al., 2011b; Williams et al., 2004). These studies fostered the view that the unconscious processing of emotional expressions is a general mechanism that helps people to rapidly, effortlessly, and adequately respond. During this process, mimicry potentially provides a feedback mechanism where ones' own visceral changes (e.g. own facial movements in response to facial expressions) contribute to the development of an affective response and social decisions (Preston and Waal, 2002). It is unclear, however, whether mimicry depends on visual awareness and if unconscious processing is shared by healthy individuals and different emotion modalities (for contradicting evidnce see, Hedger, Adams, & Garner, 2015; Stein & Sterzer, 2012; Zhan, Hortensius, & De Gelder, 2015).

Although the majority of studies focus on explicit, prototypical expressions of emotion (e.g. a wide smile signaling happiness; a dropped jaw signaling fear), in real life, people exchange emotional expressions in more subtle ways (Ambadar et al., 2005). For example, several studies have shown that people mimic each other's pupil sizes (Aktar, Raijmakers, & Kret, 2020; Harrison, Singer, Rotshtein, Dolan, & Critchley, 2006; Kret, Tomonaga, & Matsuzawa, 2014), and if partners' pupils synchronously dilate, pupil mimicry promotes trust (Kret, Fischer, & De Dreu, 2015; Procházková et al., 2018; van Breen, De Dreu, & Kret, 2018). These studies reinforce the view that pupil mimicry is an implicit mechanism that contributes to trust decisions. In support of this hypothesis, observed pupil size is often processed unconsciously (Harrison et al., 2006) and increases amygdala activity (K. E. Demos et al., 2008). In contrast to facial expressions that are coordinated by somatic muscles, changes in pupil size are controlled by autonomic nerves that are fully unconscious and uncontrollable (Bradley et al., 2008; Partala and Surakka, 2003). Despite differences in the involvement of the peripheral nervous system, the mimicry of facial expressions and pupil size share common neural mechanisms in social and emotional brain areas (Harrison et al., 2006; Procházková et al., 2018). It is therefore possible that while different types of emotional modalities (e.g. explicit facial expressions or subtle changes in pupil size reflecting arousal) have a similar impact on trust, they may do so via different neurological pathways (Procházková and Kret, 2017). Thus, presenting participants with facial expressions as well as pupil size in the absence of conscious perception would help to disentangle the underlying mechanisms of emotional contagion.

In the present study, we investigated the link between conscious perception, mimicry, and trust in a series of one-person trust games. During these games (Figure 1), subjects were presented with images of faces or eyes of different partners who varied in facial expressions (happy, neutral, fearful) or pupil sizes (large, medium size, small). To manipulate conscious perception, in half of the trials continuous flash suppression was applied (CFS; Tsuchiya & Koch, 2005). CFS is one of the most powerful blinding techniques during which a stimulus is presented to one eye, while a sequence of rapidly changing 'Mondrian' masks is shown to the other. This method allows the presentation of the stimuli to be masked for up to several minutes. After the image was presented, participants were asked to indicate the location of the stimulus, rate their confidence in having seen it, and decide how much money they wanted to invest in their partner, which reflected trust in that partner. Apart from behavioral responses, we tracked participants' muscle activity via electromyography (EMG) and pupil size via a novel method developed by Brascamp and Naber, 2017 (see Figure 1).

We hypothesized that if intuitive trust decisions rely on unconscious affective processing (H1), emotional information conveyed by faces and pupils should modulate trust-related investments during both conscious (control) and unconscious (suppressed) conditions. Specifically, partners with happy facial expressions and large pupils will be trusted more than partners with fearful faces and small pupils. Moreover, if mimicry informs a 'gut feeling' which through somatic markers (Damasio, 1996) implicitly contributes to trust, mimicry should be particularly useful when visual information fades. Thus, (H2) facial/pupil mimicry will occur during both conscious (control) and unconscious (suppressed) conditions. Finally, (H3) mimicry will further modulate trust (mimicry of partners' happy facial expressions/large pupils will increase trust, whilst mimicry of frowning faces/small pupils will decrease trust).

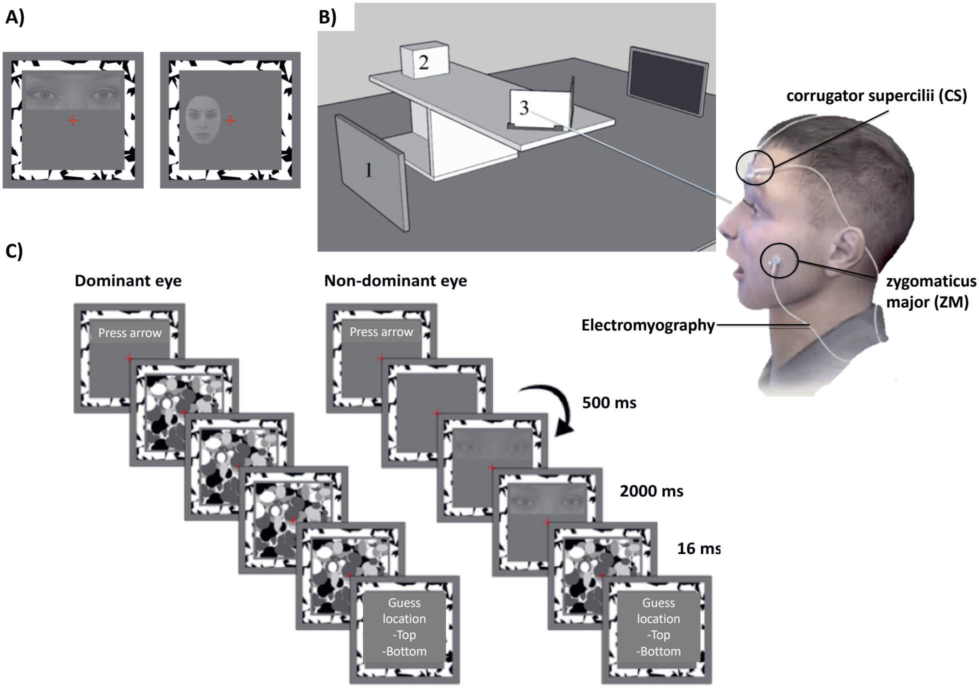


Figure 1. (**A)** Example of neutral facial stimuli on the right, and medium size pupils on the left. All displays were surrounded by a black and white square border to facilitate stable convergence of the images in both eyes. The position was either above or below the fixation cross for the eyes stimuli and left or right of the fixation cross for the faces' stimuli. (**B)** Experimental setup. Screens are numbered 1 the eye tracker is numbered 2 and the mirrors are numbered 3. (**C)** Trial outline for CFS trust game with pupil stimuli as an example. Each trial started with a message indicating the start of a new trial. A red fixation cross was presented during the whole trial. In the dominant eye, the stimulus faded in over a period of 500 ms after which it remained medium size on the screen for 2000 ms, and the trial ended with one Mondrian image presented for 16 ms to mask visual aftereffects. In the non-dominant eye, different Mondrian images were constantly flashed with a frequency of 10 Hz. If no response was given after 2.5 seconds, participants were asked to make a guess for location. After this, they had to indicate confidence in their decision on a 4-point scale (guessing, not confident, quite

confident, very confident). Finally, they were asked to make an investment decision of €0, €2, €4, or €6 in their virtual partner for each trial. After the questions a 5-second inter-trial interval followed. Pictures adapted from (Tamietto & De Gelder, 2010, Figure 3)

Results

Suppression

In our data-set, on average, the suppression broke in 24.3% of the CFS trials (25.9% face trials and in 22.7% eye condition trials). This is in line with earlier work (e.g., Stein, Hebart, & Sterzer, 2011). While many studies use the time until suppression (b-CFS) as the dependent variable (e.g., Stein & Sterzer, 2012; Yang, Zald, & Blake, 2007), for b-CFS results (see Supplementary Table 6-8), the main goal of the current study was to test how conscious awareness of a partner's expression (facial and pupil size) shape (a) trust decisions, (b) mimicry, and (c) the effect of mimicry on trust decisions. This required using awareness as independent variable while keeping a clear-cut separation between conscious and unconscious conditions.

To check for the level of awareness, we used subjective and objective measures (as in Yang, Brascamp, Kang, & Blake, 2014). During CFS, as an objective measure, participants were asked to indicate the location of the stimuli (up/down for eyes, left/right for faces). As a subjective measure, subjects were asked to rate their confidence in seeing the stimuli from 1 (guess) to 4 (very confident) (Oliver et al., 2015; Raio et al., 2012). As expected, the CFS objective measure (the location detection performance) significantly correlated with participant's confidence ratings ($r = 0.825$, $p < 0.0001$, $N = 50$), which confirmed the validity of subjective awareness measures. Moreover, subjective measures showed that during CFS, participants were "guessing" the stimulus location in 43.0% of CFS trials (confidence level = 1) and during these trials, the average detection performance was 54%, which was significantly above chance level: (binomial test: $p < 0.001$). In the rest of the CFS trials (57% of the total number of CFS trials), participant's mean confidence level ranged between 2 and 4 ($M = 2.1$) on a 4-point scale (2 = not confident (15.5% trials), 3 = quite confident (19.6% trials) and 3 = very confident (22.1% trials), after excluding trials where the suppression broke (b-CFS), participants' detection performance reached 84% (above

6

chance level: $p < 0.001$ by binomial test). Finally, in the control condition, participants were correct about the stimulus location in 97.3% of the trials.

The level of awareness varied during CFS, in half of the CFS trials participants were not consciously aware of the stimuli at all, while in the other half of the trials subjects sustained some residual vision. To evaluate the evidence for unconscious affective processing, we split the data into different awareness categories: (*1) The conscious condition* represents the control trials where participants perceived the stimuli without suppression and were confident in seeing it (confidence level = 4). *(2) The semi-conscious condition* represents CFS trials where participants reported to be 'somewhat confident' in spotting the location of the stimuli (confidence level = 2 - 4). Finally, *(3) The unconscious condition* represents the trials where stimuli were shown under suppression and subjects reported that they were guessing the stimulus location (confidence level = 1).

(H1) Does emotional information influence trust during control and suppressed (CFS) conditions?

To test the first hypothesis evaluating the effect of experimental condition on trust, we used a Generalized linear model with a two-level structure defined by trials (level 1) nested in subjects (level 2). In this model, participants' trust (investment level) was subjected to a 2 x 3 x 3 factorial design with expression modality (pupils, face), emotion (Faces: happy, neutral, fearful; Pupils: large, medium, small), and awareness level (conscious, semi-conscious, unconscious) as within-subject factors. As a stimulus, for the pupil and face conditions we used different pictures of four males and four females. We further included the interaction terms between all the above variables (no random effects were included in the final model).

Facial expressions of emotion

The results of a Generalized linear model with the conditions: expression modality (pupils, face), emotion (Faces: happy, neutral, fearful; Pupils: large, medium, small), and awareness levels (conscious, semi-conscious, unconscious) showed a main effect of partner's expression on trust [F (1, 17808,00) = 80619,00, $p < 0.0001$] whereas partners with happy facial expressions were trusted more than partners with neutral ($p < .0001$) or fearful expressions ($p < .0001$, Figure 2). Importantly, in support of the first hypothesis, we show that facial expression can influence participants' trust even under suppressed (CFS) condition. Nevertheless, a significant three-way interaction between suppression, expression modality and emotion [F (2, 17808) = 24.019, $p < 0.0001$] demonstrated that facial expressions modulated trust only when participants had some confidence in having seen the stimuli. Specifically, facial expression modulated trust during both conscious and semi-conscious conditions (happy > neutral > fearful: all ps < 0.05), but not when participants were fully unaware of the stimuli (all $ps > 0.05$).

Pupillary expressions of arousal

Partners' pupil size also modulated trust. Post-hoc pairwise comparisons of the significant three-way interaction between suppression, expression modality, and emotion revealed that although during conscious control trials, participants' investments did not differ between partners' pupil sizes (all ps > 0.05, Figure 2), partners' pupil size moderated trust decisions during suppressed (CFS) trials. Specifically, in the semi-conscious condition partners with large pupils were trusted more than partners with medium ($p < .0001$) and small pupils ($p < .0001$). Further, a similar pattern emerged during the unconscious (fully suppressed) condition where partners with large pupils were trusted more than partners with small pupils ($p < 0.05$). We additionally found a significant effect of emotional modality, whereas subjects trusted partners more when they saw their eye-regions as compared to partners' whole faces [F (1, 17808) = 19.87, $p < 0.0001$], (Supplementary Table 1). A main effect of awareness levels [F (1, 17808) = 770.61, $p < 0.0001$] indicated that participants trusted their partner more during control trials compared to suppressed (CFS) semi-conscious trials and unconscious trials.

Together, these data imply that people tend to withhold trust when they cannot see their partners' eyes or face properly. Crucially, in line with the first hypothesis, we show that emotional cues can influence participants' trust even under visual suppression. Nevertheless, after controlling for subjective awareness scores, our data demonstrate that some level of visual percept is necessary for emotional facial expressions to influence trust evaluation. On the other hand, partner's pupil size seems to impact trust unconsciously.

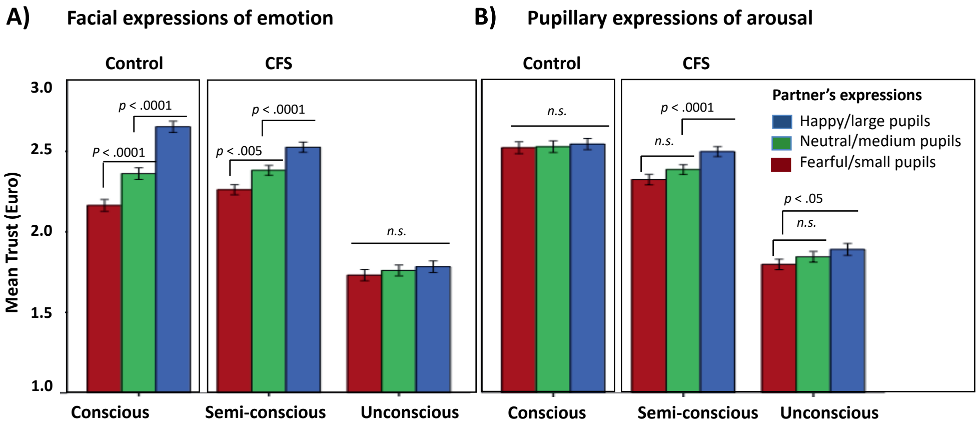


Figure 2: (A) Bar plots display investment level (mean +/- standard error) split by subjects' level of awareness. On average, participants trusted their partner more during un-suppressed control trials compared to suppressed semi-conscious trials [β = - 0.069, SE = 0.013, CI (0.044, 0.095), $p < .0001$] and unconscious trials [β = 0.588, SE = 0.014, CI (0.560, 0.616), $p < .0001$]. In the facial expression condition, expression affected trust in both the control and CFS conditions: Partners with happy facial expressions were trusted more than partners with neutral [β = 0.113, SE = 0.014, CI (0.086, 0.140), $p < .0001$] or fearful expressions [β = 0.182, SE = 0.014, CI (0.155, 0.209, $p < .0001$]. However, this effect was modulated by the level of awareness. When subjects reported some level of awareness, in the semi-conscious condition partners with large pupils were trusted more than partners with medium [β = 0.113, SE = 0.033, CI (0.062, 0.192), $p < .0001$] and small pupils [β = 0.181, SE = 0.035, CI (0.112, 0.249), $p < .0001$]. (B) In the pupillary expression condition, partners' pupil size affected trust only in the two CFS conditions but not in the conscious condition. A similar pattern emerged during the unconscious (fully suppressed) condition where partners with large pupils were trusted more than partners with small pupils [β = 0.082, SE = 0.041, CI (0.003, 0.162), $p < 0.05$].

(H2) Will facial/pupil mimicry occur during the control and suppressed (CFS) conditions?

Facial Mimicry

To test for facial muscle mimicry, we selected trials where participants observed their partners' faces. We then used two separate Generalized linear models to predict changes in the two EMG amplitudes of the corrugator supercilii (CS) and the zygomaticus major (ZM) muscles. As predictors, we used partner expression in the 3 conditions (happy, neutral, fearful) and awareness levels (conscious, semi-conscious, unconscious). The interactions between the two predictors were included as well. Furthermore, we added three orthogonal polynomials to account for linear, quadratic, and cubic trends in the growth curves. These models had a 3 level structure defined by time segments (level 1), nested in trials (level 2), nested in subjects (level 3), whereas time segments (100-ms time slots) were used as a repeated factor with a First-Order Autoregressive covariance structure (AR1) to control for autocorrelation while including a random intercept for individuals (no random effects were included in the final model, for full models see Supplementary Table 2-3).

6

Mimicry of frowns

Figure 3A displays the mean corrugator supercilii (CS) responses from pre-stimulus baseline. The main effect of partner's emotion [$F(2, 163802) = 9.935$, $p < 0.0001$] showed that on average participants frown more in response to fearful facial expressions compared to neutral ($p < 0.05$) and happy expressions ($p < 0.0001$). Intriguingly, in line with the second hypothesis, facial mimicry occurred during both control and suppressed (CFS) conditions. However, a significant interaction between emotion and awareness level [$F(4, 163802) = 2.540$, $p < 0.0001$] revealed that facial mimicry was influenced by the level of subjective awareness. Post-hoc pairwise comparisons (LSD tests) showed that in the control condition, participants displayed complete mimicry: they frowned more in response to fearful facial expressions compared to neutral and happy expressions (all ps < 0.05). In the semi-conscious condition, participants frowned more in response to fearful facial expressions compared to neutral and happy expressions (all ps < 0.005), but no difference was found between neutral and fearful expressions ($p > 0.05$). Finally, in the CFS fully unconscious condition, no difference was observed between happy and neutral faces or fearful and neutral faces (all *p*s > 0.05). This result implies that as the level of visual awareness declines, the influence of the partner's emotional expression on facial mimicry also decreases. Apart from the above effect with emotion, these results showed a main effect of awareness on CS muscle [F (1, 3094) = 6.355, $p < 0.05$], where participants' average CS activity increased with increasing awareness of the stimuli.

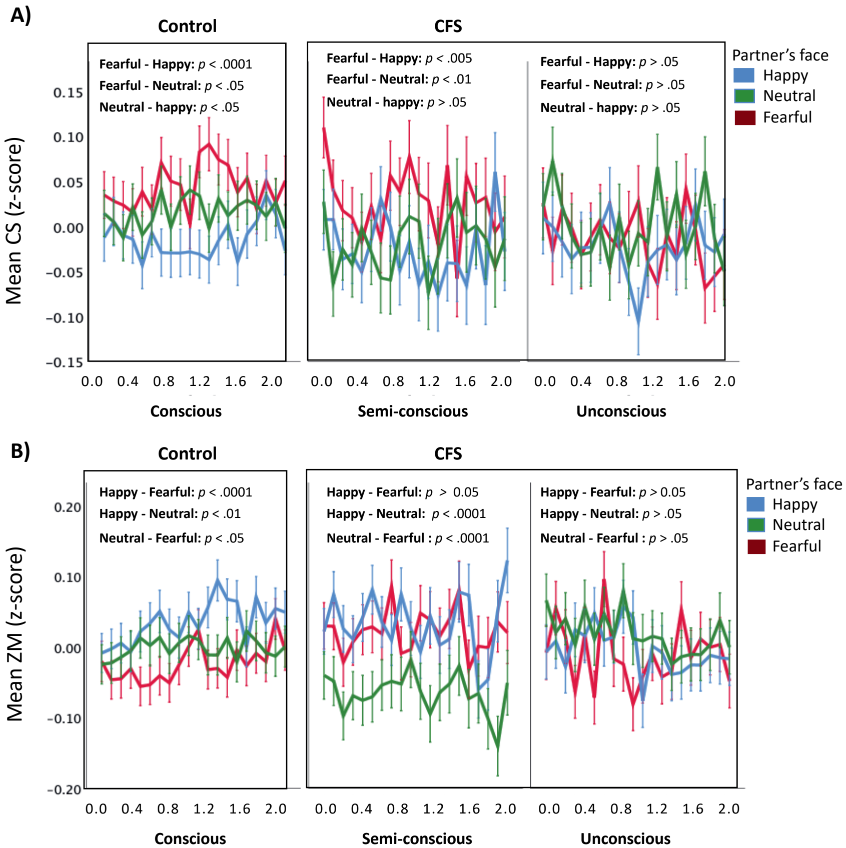
Mimicry of smiles

Figure 3B displays the mean z-scored zygomaticus major (ZM) responses from pre-stimulus baseline. We found a main effect of partner emotion [F (2, 163803) = 7.603, $p < 0.0001$] implying that participants smiled more in response to happy facial expressions compared to neutral expressions ($p < 0.0001$) and fearful expressions ($p < 0.01$). We found no difference between fearful and neutral expressions ($p > 0.05$). Importantly, a significant interaction between expression and awareness level [F (4, 163803) = 8.246, $p < 0.0001$] revealed that, while in the control (visible) condition, participants exhibited mimicry too all facial expressions, smiling more in response to happy facial expressions compared to neutral and fearful expressions (all $p < 0.01$). No difference in ZM activity was found between neutral and frowning ($p > 0.05$). In the semi-conscious condition, participants showed partial mimicry: they smiled more in response to happy facial expressions compared to neutral (all *p*s < 0.0001) but not fearful expression ($p > 0.05$). They also smiled more in response to fearful expressions than neutral expressions ($p > 0.0001$). Finally, in the CFS fully unconscious condition, there was no difference found between happy and neutral faces or fearful and neutral faces ($p > 0.05$).

Although the current results partially support the second hypothesis suggesting that facial mimicry emerges also during suppressed (CFS) conditions, after controlling for subjective awareness scores, our data imply that some level of visual perception is necessary for emotional facial expressions to influence muscle movements.

Pupil Mimicry

As in the previous facial mimicry analysis we used a Generalized linear model to predict participants' z-scored baseline-corrected pupil response (for full model see Supplementary Table 4). The main effect of awareness [F (1, 140,399) = 9.343, $p <$ 0.0001] demonstrated that pupil dilation was stronger during the CFS unconscious condition and the semiconscious than during the conscious control condition (both p < 0.001, Figure 3), no difference was found in the CFS conscious between semiconscious and unconscious conditions (p = 0.982). However, contrary to our expectations and previous research, we did not find evidence for pupil mimicry (Kret et al., 2015; Procházková et al., 2018; van Breen et al., 2018). Although Figure 3C shows that in the control condition, the mean pupil responses showed the expected pattern (participants' pupils were larger in response to partners' large pupils compared to medium sized and small pupils), this effect did not reach significance.



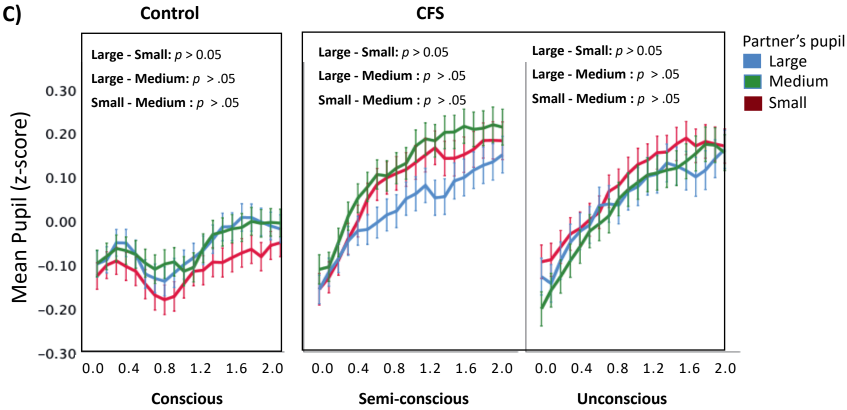


Figure 3. Line plots depict baseline corrected z-scored physiological signals per 2 seconds split by subjects' level of awareness. **(A)** The mean corrugator supercilii (CS) responses from pre-stimulus baseline shows that on average participants frown more in response to fearful facial expressions compared to neutral [β = 0.021, SE = 0.009, CI (0.003, 0.038), $p < 0.05$] and happy expressions [β = 0.040, SE = 0.009, CI (0.023, 0.058), $p < 0.0001$] during conscious and semi-conscious conditions but not during unconscious conditions. **(B)** The mean z-scored zygomaticus major (ZM) responses from pre-stimulus baseline shows that on average participants smile more in response to happy facial expressions compared to neutral expressions [β = 0.038, SE = 0.010, CI (0.018, 0.058), $p < 0.0001$] and fearful expressions [β = 0.028, SE = 0.010, CI (0.008, 0.048), $p < 0.01$] but not during semiconscious or unconscious conditions. **(C)** The mean z-scored pupil response from pre-stimulus baseline to partners' pupils split by subjects' level of awareness.

(H3) Does mimicry modulate trust-related investments?

In the final models, we examined whether facial mimicry modulates trust. Since we found no evidence for pupil mimicry, we focused on facial mimicry only (for detailed mimicry classification see Methods); (for a similar approach, see Procházková et al., 2018).

In this Generalized linear model, we used a two-level structure defined by trials (level 1) nested in subjects (level 2). Participants' trust (investment level) was predicted by partners' emotion (happy, fearful/ large, small), awareness levels (conscious, semi-conscious, unconscious), and occurrence of mimicry (mimicry, no-mimicry) as well as two and three-way interactions between these factors. Contrary to our third hypothesis, our results showed that there was no main effect of mimicry ($p > 0.05$), and no interaction effects predicting trust (all ps > 0.05, Supplementary Table 5). Results were descriptively consisted with our prediction; when participants mimicked their partners' happy facial expressions, they trusted their partner slightly more than when they did not mimic, this effect, however, was not significant (Figure S1).

Discussion

The present study investigated whether consciousness modulates the relationship between the processing of emotional expressions and the development of trust. Participants played a series of trust games with different virtual partners whose faces and eyes were rendered invisible with continuous flash suppression (CFS). We hypothesized that if trust relies on-unconscious processes, (H1) emotional information should modulate trust decisions during both conscious and non-conscious presentation. Moreover, we hypothesized that if mimicry is part of the unconscious emotional process which contributes to trust, (H2) facial/pupil mimicry will occur during both conscious (control) and unconscious (suppressed) conditions, and (H3) facial/pupil mimicry will modulate trust. The current study provided mixed findings. We found that facial expressions were mimicked and did influence trust decisions (regardless of mimicry) during the conscious condition, whereas partners' pupil size influenced trust non-consciously. This suggests that pupil mimicry and facial mimicry potentially influence trust via separate neurophysiological pathways.

These results are important from the perspective of emotion theories postulating that emotional expressions can influence social behavior without the observer's visual awareness (LeDoux, 2012; Tamietto and De Gelder, 2010). Prior research implies that blindsight patients potentially receive emotional information via interceptive feedback from their own body (Tamietto & De Gelder, 2010). Nevertheless, whether non-conscious processing is shared by healthy subjects is a debated topic (Hedger et al., 2016, 2015b, 2015a; Pessoa and Adolphs, 2010; Straube et al., 2010), and whether it extends to the more subtle expression of pupil size was still unknown. Several methodological variations may give rise to these inconsistencies in the literature. For instance, while in many studies researchers assume that participants did not perceive the stimuli under CFS, we show that even though in many trials participants did not break the suppression (b-CFS), they still reported to have some residual vision. This was confirmed by high stimuli detection accuracy (84%) during these trials. Thus, in order to prevent false positives and account for subjective awareness measures, we split the data into conscious, semiconscious and unconscious conditions.

With regards to trust, in line with the first hypothesis (H1), we found that during both visible (control) and CFS conditions, partners displaying happy facial expressions were trusted more than partners with neutral or fearful expressions. At first sight, this finding seems to support the view suggesting that emotional stimuli are recognized even when suppressed from visual awareness (e.g., Pasley et al., 2004; Williams et al., 2004). However, the comparison between semiconscious and unconscious conditions revealed that emotional expressions modulated trust only when participants had some level of awareness of the facial stimuli. When subjects had no awareness of their partners' facial expressions of emotion, they were not influenced by their expressions. Moreover, we found that participants trusted their partners more during control trials compared to CFS trials, where their vision was either partially or fully suppressed. This demonstrates that the ability to perceive partners' emotional expressions is vital for the establishment of trust.

Participant trust also increased when they could see their partner's eye-region as compared to seeing their partner's whole face. These results aligns with previous studies showing that when it comes to emotion processing, eyes are the most important part of the face (Adolphs et al., 2005; Farroni et al., 2002). This evidence suggests that in healthy subjects: (a) the ability to perceive partners' face and eyes is vital for the establishment of trust, and (b) the neurological path linking emotional expressions and trust requires visual awareness.

Apart from facial expressions, partner pupil size also modulated trust, yet not entirely according to our expectations. In contrast to prior research, participants did not trust partners with large pupils more than partners with smaller pupils – at least not during the visible (control) condition (Kret et al., 2015; Procházková et al., 2018;

Wehebrink, Koelkebeck, Piest, de Dreu, & Kret, 2018). Instead, partner pupil size influenced participants' trust decisions during the suppressed condition only. Why pupil influenced trust during suppression but not during fully visible control condition is open to interpretation. One possible explanation ties to prior research suggesting that observed pupil size influences emotion perception primarily unconsciously (Harrison et al., 2007, 2006). Another possibility is that autonomic cues (e.g. pupil dilation, blushing, sweating) are processed via distinct neurological pathway (e.g., retino-collicular-pulvinar-amygdala pathway) from facial mimicry, however future research is needed to establish to veracity of this interpretation. Finally, it is important to note methodological differences between our design and previous studies. The stimuli in the current study were presented for a shorter duration than in earlier studies, and it is possible that participants' pupils were not given enough time to mimic the stimulus pupils, an effect we know influences trust.

Facial mimicry was also affected by the level of subjective awareness. Our results showed that participants displayed facial mimicry during both conscious (control) and suppressed conditions. However, after we controlled for subjective measures of awareness, we did not find strong evidence for facial mimicry during the fully suppressed unconscious condition. Again, while the current results support our second hypothesis (H2) suggesting that facial mimicry emerges also during the suppressed (CFS) condition, our findings imply that facial mimicry deteriorates with a decline in visual awareness. Finally, we did not find significant evidence for mimicry-trust-linkage in the current study (H3). Together these finding suggest that while facial muscles might unconsciously move in response to partners' facial expressions (Fig. 2a), trust decisions are not significantly influenced by participants' own facial muscle responses.

Moreover, in contrast to prior literature (Kret et al., 2015; Procházková et al., 2018; Wehebrink et al., 2018), we did not observe pupil mimicry in our participants. There were several methodological distinctions that may provide a possible explanation for the lack of mimicry in current study. First of all, to keep the stimuli comparable to static facial expressions that were used in a prior blindsight study (Tamietto et al., 2009), in the current study we adapted static pupil sizes. Compared to dynamic expressions used in prior research (Kret et al., 2015; Procházková et al., 2018; Wehebrink et al., 2018), the drawback of static stimuli is that the accuracy of emotion expressions identification decreases – especially if the expression is subtle (Ambadar et al., 2005). Therefore, the lack of dynamic movement could be one of the reasons why pupil mimicry did not reach significance in the current experiment. Furthermore, to make the experimental procedure directly comparable with the blindsight study, this study also adapted a two-second window to measure pupillary signals (Tamietto et al., 2009). Yet, this time window may not be sufficient to capture the full pupil mimicry response (prior experiments measured pupil mimicry during longer windows; Kret et al., 2015; Procházková et al., 2018). Finally, we used a novel technology developed by Brascamp and Naber (2017) that has been designed to track pupil changes under CFS. To our knowledge, this method has only been used once in the literature. Thus, more research is required to validate this method. For instance, Figure 2 shows that the initial light dip that commonly occurs when a new stimulus is presented disappeared during CFS. The concern is that the continually flashing effect of CFS could potentially disrupt pupillary responses. We recommend that future studies adapt dynamic pupil stimuli, use a longer time window than two seconds and try an alternative 'blinding' method (e.g. Masking) to verify results.

In sum, the unique combination of a trust game, physiological measures, and CFS allowed us to test how emotional expressions dynamically shape participants' trust and physiology. Our data imply that by diminishing people's ability to read other's facial expressions, trust breaks down – thus supporting the view that trust depends on visual input. We further found that facial expressions were mimicked and influenced trust decisions during the control condition but not during the unconscious (suppressed) condition. On the one hand, this result contradicts the proposed hypotheses suggesting that emotional cues influence trust and facilitate mimicry unconsciously via subcortical pathway. On the other hand, the current results are some of the first to show that pupil size influences trust primarily through unconscious processes. Our findings support the empirical view (Procházková and Kret, 2017) that autonomic cues and facial expressions influence social behavior via two separate neurophysiological pathways. In line with this theory, we conclude that in healthy subjects, the path from facial expressions to mimicry and trust is predominantly conscious, while pupil size influences trust unconsciously.

Method

The CFC experiment aimed to replicate and extend the results of a blind sight study by (Tamietto et al., 2009) while measuring facial mimicry and pupil mimicry during trust games (Kret et al., 2015; Procházková et al., 2018).

Participants

We planned to include *N* = 50 participants in our main analyses. This sample sizes was determined by sample sizes in previous studies using CFS (Vieira et al., 2017) and measuring physiology (Kret et al., 2015; Schlossmacher, Junghöfer, Straube, & Bruchmann, 2017). Data collection was terminated when this sample size was achieved, after exclusion of participants fulfilling the exclusion criteria related to above-chance prime discrimination (see below).

We recruited 65 Leiden University students to participate in our experiment (77% female, mean age 23.6 years, range 18-60 years old). They had normal vision or corrected-to-normal vision (contact lenses only), no history of neurological or psychopathological conditions, and no history of substance use or abuse. Four participants were excluded from all analyses because they did not return for their second session, and for eleven other participants the eye-tracking and physiological data had to be excluded because of physiological artefacts resulting in more than 50% of their data missing (for similar outlier-criteria, see Kret et al., 2015). This left us with 50 full datasets for behavioral and facial mimicry analyses. Five additional subjects were excluded from the pupil analysis as they were missing more than half of their pupil data. Thus, we had valid pupil data for 45 people. The ethics committee of Leiden University approved the experimental procedures (ethics number: CEP18-0403/201).

Design

This study consisted of 2 (face versus eyes) × 2 (suppressed versus conscious) × 3 (positive versus neutral versus negative) within-subject design (32 trials per condition). Participants completed two independent sessions on two different days, each session consisted of two blocks where they either saw faces (CFS/control) or eyes (CFS/control). Each block had 96 trials (96 x 4 = 384 trials per subject). In both tasks, participants had to make an investment in a virtual partner during each trial.

Participants were told that they would sometimes see an image of this partner right before the investment decision. For the first task, they were presented with images of an eye region with different pupil sizes (small, medium, large size). For the second task, they were presented with whole faces that showed different emotional expressions (fearful, neutral, happy). Each expression appeared 32 times per block. The order of the tasks (eye or face) was random for each participant. In both investment tasks, stimuli in half of the trials were suppressed with CFS (implicit test condition), while stimuli in the other half of the trials were not suppressed and therefore consciously perceivable (explicit control condition). In each session, participants first completed the implicit CFS test block followed by the explicit control block. This was done to prevent a recognition effect from interfering with the suppression time: If participants were repeatedly exposed to the stimuli in the conscious condition before they completed the suppressed condition, this might cause the stimuli to break through suppression more easily because of familiarization. The session order of eyes and face conditions was randomly varied between participants. As outcome variables, we measured investment decisions as a reflection of perceived trust and response accuracy. In addition, we assessed the participant's pupil size, facial muscle activity (frowning and smiling), and skin conductance as physiological measures over 2 seconds of stimulus presentation. Skin conductance measures were collected for control purposes to assess whether the observed mimicry effects (e.g., increased EMG activity) were a mere by-product of arousal responses. If true, such a response would not necessary reflect mimicry but rather a general arousal response reflected in increased phasic skin conductance. The control analysis confirmed that phasic skin conductance did not significantly differ between any of the tested conditions (see Supplementary Figure 2).

Stimuli

Stimuli consisted of 8 pictures of faces and 8 pictures of eyes (each appeared 12 times per block). The stimuli were similar to those used in a previous study by Kret, Fischer, and De Dreu (2015). Pictures of the eye region of four men and four women with Caucasian nationality were used. Everything between the eyelashes was removed from the images and replaced with artificial eye white, an artificial iris, and an artificial pupil to allow for precise control over pupil size. Three sizes of pupil were used: small, medium, and large. The medium size pupil was considered to be the reference pupil size and was set at 100%; the large pupil had a size of 160% relative to the reference; the small pupil had a size of 60% relative to the reference. The same sizes were used across all eyes so no other differences were present. All pictures were converted to grayscale to remove any impact potential impact of eye or skin color. The contrast of the pictures was brought down to 30% to allow for better masking (Carmel, Arcaro, Kastner, & Hasson, 2010) and prevent luminance differences within the eye region for the different pupil sizes. The pictures of the whole faces were taken from the Amsterdam Dynamic Facial Expression Set (ADFES; van der Schalk, Hawk, Fischer, & Doosje, 2011). Four men and four women with fearful, neutral and happy expressions were selected. The images were standardized, converted to grayscale and cropped to only reveal the facial area without hair or ears (see Figure 1). All facial images were scaled to have the same dimensions in order to prevent differences in detectability. After cropping, the contrast was decreased to 30% to allow for better masking. In order to make sure that both the eye and face images had the same luminance level, the average luminance of all images was checked with a MATLAB script and then adjusted in Adobe Photoshop to a brightness of 113 out of 255.

Apparatus

In order to combine CFS with eye-tracking, a custom-built stereoscope designed by Brascamp and Naber (2016) was used (see Figure 1b). Pupil and gaze data were collected with an Eyelink 1000 Plus (SR Research Ltd., Mississauga, Ontario, Canada) at a rate of 2000 Hz. It was placed in between two monitors of 23.8 inches, displaying at a 60 Hz refresh rate with a 1920x1080 resolution. The brightness of the screen was set to 70%. Two cold mirrors were placed in such a way that they directed the participant's sight towards the monitors while allowing the infrared light of the eye tracker to pass through. The distance between participants' eyes and the monitors was 63 cm, the visual angle of the displayed images was 16.6° horizontal and vertical. Testing was done in a dark room without artificial illumination. The experiment was programmed in MATLAB® 2012b and Psychtoolbox-3. The timing of behavioral and physiological responses was synchronized by means of pulses sent through a parallel port.

Procedure

Task outline

Each trial started with a message telling the participant that they could start the new trial by pressing the corresponding key. A gray background and a red fixation cross were present during the whole trial (see Figure 1c for an overview of a trial). After the participant's keypress, random Mondrians were presented to the dominant eye with a frequency of 10 Hz. At the same time, the image of the eyes or faces was presented to the non-dominant eye over a period of 2.5 seconds on a gray background. The opacity of the stimulus was increased from 0 to 100% in the first 0.5 seconds. After this, the fully opaque image remained on the screen for another 2 seconds. The position was either above or below the fixation cross for the eyes stimuli and left or right of the fixation cross for the faces stimuli. The fixation cross remained visible throughout the whole trial. Participants had to respond as soon as they could determine the location of the upcoming stimulus. If the participant did not press during the 2.5-second period, a screen appeared that asked participants to make their best guess regarding the location of the stimulus. After this, they had to indicate confidence in their decision on a 4-point scale (guessing, not confident, quite confident, very confident). Finally, they were asked to make an investment decision of €0 - €6 in their virtual partner for each trial. There was no time limit for answering the confidence question and the investment decision. If participants responded within the first 2500 ms of a trial, the screen that asked participants to make their best guess was skipped. After the questions, a 5-second break was implemented to allow physiological response to come down and establish the next trial's physiological baseline. A full trial lasted for around 10 seconds depending on the participant's response times.

Experiment procedure

Upon arrival at the laboratory, participants read the information letter, signed an informed consent form, and filled in a short questionnaire assessing demographic information. They were then seated in front of the set-up and rested their heads in a chinrest. Participants performed a short test to determine if their left or right eye was dominant. This test is an adjusted version of the test described in Yang, Blake & McDonald (2010) and consisted of 32 trials total. Instead of using a square Mondrian image to suppress the arrow, we decided to use the same circle, Mondrian, we use during the experiment to ensure no differences were present. This dominance test indicated right eye dominance for 56% of the participants. After this, participants were familiarized with the different parts of a trial and the keys they had used to respond. They were also introduced to the rules of the trust game and were familiarized with some example scenarios. The trust game was always referred to as an “investment game” to prevent priming participants that trust was a key element in the study. Participants were asked to make an investment of €0, €2, €4, or €6 in their virtual partner for each trial. Their investments were tripled and the partner would then decide how much money they wished to return. Participants were informed that we had recordings of their partners and that these would be shown prior to making an investment decision. They were told that no feedback would be given between trials but that their investments and partner choices would determine the bonus received at the end of the experiment. Four practice questions were given to ensure participants understood the investment game and were aware of the consequences of their answers. Partner payments were based on decisions made by 15 students in the role of trustee, who was given a form with four investment decisions of others and asked how much they would give back if they received a certain amount of money. After the experiment, participants chose a random number and were matched with the corresponding partner. That partner’s investment decision was used to determine the amount of bonus money received. When everything was clear, the physiological equipment was applied to the participants' face and hand, after which the real experiment began.

Participants were asked to ensure that they could put their head on the chin rest comfortably. Stable binocular fusion was achieved by letting participants adjust the coordinates of the screen where stimuli were presented so that they merged into one clear picture. After a nine-point calibration of the eye tracker, participants performed two practice trials after which they could ask their final questions. The test block followed the practice trials. Participants were provided with the option to take a break after they had completed half of the trials. If they chose to take the break, the screen and eye tracker were calibrated again. After the test block, all participants took a break and they were allowed to rest as long as they wanted. Next, the control block began, in which they again were provided with the option to take a break. At the end of the second session, participants were debriefed and compensated with either money or participant credits. Each participant also received a monetary bonus ranging between € 0 and € 3 based on their performance in the investment game.

Data acquisition and preparation

Pupil size

Pupil diameter was sampled with a rate of 1000 Hz per eye and was later down-sampled to 100-ms slots. Gaps smaller than 250 ms were interpolated, and a 10th-order low-pass Butterworth filter was used to smooth the data in PhysioData Toolbox v0.3.5. If the pupil sizes across two-time samples exceeded two standard deviations, the data were identified as outliers and excluded from the analysis. For each trial, we averaged 500 ms prior to stim onset, which served as a baseline measure. Pupil responses were then expressed as differences from baseline by subtracting the mean baseline pupillary diameter from all subsequent samples. Participants that missed more than 50% of their pupil data had been excluded (for similar outlier-criteria, see Kret et al., 2015). Control analysis confirmed that participants blinked or missed pupil data equally across all conditions. Moreover, the distribution of pupil was comparable across CFS and control conditions (see Supplementary Materials for details).

Electromyography

The parameters for facial EMG acquisition and analysis were selected according to the guidelines by van Boxtel (2010). Flat-type active electrodes were used and activity was measured bipolarly over the zygomaticus major (smiling muscles) and the corrugator supercilii (frowning muscles) on the left side of the face at a sample rate of 1,024 Hz. The grounding electrode was positioned behind the left ear. Before attachment, the skin was cleaned with alcohol and the electrodes were filled with electrode paste. Raw data were first filtered offline in the PhysioData Toolbox v0.3.5 with a 28 Hz high-pass and 500 Hz low-pass FIR filter. Data were smoothed with a

Boxcar filter of 100ms and visually inspected for artefacts. Parts of the data considered problematic were discarded. Subsequently, data were segmented into 2,500 ms epochs, including 500 ms of prestimulus baseline and 2,000 ms of stimulus exposure for each muscular region separately, full-wave rectified and smooth signal. Per trial, a baseline of EMG signals was calculated by averaging the activity recorded during the 500 ms preceding stimulus onset (the last 500 ms of the 5000 ms inter-trial interval period). Phasic EMG responses were averaged over 100 ms intervals starting from stimulus onset (overall corresponding to 20 time-bins) and expressed as μV of difference from baseline activity by subtracting the mean baseline EMG signal from all subsequent samples.

Skin conductance

Disposable electrodes filled with isotonic gel were used. They were placed on the inside distal phalanx of the ring finger and middle finger of the left hand. Raw data were first filtered offline with a 2 Hz low-pass filter and a 0.05 Hz phasic high-pass filter in PhysioData Toolbox v0.3.5. Data were visually inspected for artefacts and parts considered problematic were discarded. The average skin conductance response (SCR) was expressed by the skin conductance level difference from the baseline (the last 500 ms of the inter-stimuli interval, preceding stimulus onset). Upon baseline correction, all physiological measurements (EMG, Pupil, SCR) were normalized using the two-step transformation by Templeton (2011).

Statistical analysis

Multilevel models

Because the data had a hierarchical structure, results were analyzed by using multilevel modelling. This method allowed us to not only account for between-person variation but also for within-person variation. Analyses were performed in IBM SPSS Statistics (v25) by means of generalized linear mixed models. We took a backward selection approach, starting with a full model. One by one, insignificant interaction effects were removed from the model, followed by insignificant main effects. If the model fit improved, the factor was deleted from the model. If the model fit became worse, we used the log-likelihood test (LRT) to check if the change in fit statistic was significant. In favor of parsimony, the non-significant effect was left out when the model fit did not decline significantly.

Defining Facial Mimicry

Facial mimicry was conceptualized as increased smiling Zygomaticus major (ZM) muscle activity in response to happy expressions, and an increase in frowning Corrugator Supercilii (CS) muscle in response to fearful expressions. First, we z-scored the ZM and CS signals for each participant across four conditions (Face/eyes), (CFS/Control). We then subtracted the z-scored ZM signal from the CS signal combining the data into a continuous EMG (smile-frown) signal. As a result, the positive values represented increase smiling and negative values represented an increase in frowning. We then excluded all neutral trials (neutral faces/middle pupil size) and averaged the continuous z-scored EMG (smile-frown) signal over each trial. This mean value represented a mean increase/decrease in smiling/pupil size per trial. If participants saw happy expression (coded as 1) and they displayed baseline increase in smiling (mean EMG > 0), this trial would result in positive values, which would be classified as mimicry (coded as 1). On the other hand, if smiling activation decreased during the smiling trial resulting in negative values (mean EMG < 0), we classified this as no-mimicry (coded as -1). If participants saw fearful expression (coded as -1) and they displayed higher EMG activation (mean EMG > 0) this would be a non-mimicry trial. On the other hand, if they displayed lower EMG activation (mean EMG < 0) this would be mimicry trial.

Defining Pupil Mimicry

Pupil mimicry is described as synchrony in pupil sizes between a participant and a (virtual) partner (Kret et al., 2015). To define pupil mimicry, first, we z-scored participants' pupil size over trials and conditions. This resulted in a mean-centered continuous pupil variable (20 bins of 100 ms in each trial) with positive values corresponding to participant's pupil dilation and negative values to constriction. We classified each trial as mimicry/non-mimicry trial: if participants displayed a mean increase in pupil size during large trial and decrease during small trial, we would classify this as pupil mimicry trial. On the other hand, if participants' pupil decreased during partners' large trials and increased during the partner's small trials, this would be classified as a non-mimicry trial. We would like to note that our stimulus presentation duration was on the short side compared to previous literature (Kret et al., 2015; Procházková et al., 2018). In these previous studies, the eye regions were presented for 4 seconds. The pupils were static for the first 1.5 second and then dilated, remained static, or constricted. In those studies, the pupil mimicry response was analyzed over 2.5 seconds (from 1.5 – 4 seconds), whereas in the current, it was analyzed over 2 seconds. In addition, in order to be in line with research conducted by Tamietto & Castelli (2009), we decided to analyze pupil size directly after 500 ms of prestimulus baseline, while this is not common in the pupil mimicry (Harrison et al., 2006; Kret et al., 2015; Procházková et al., 2018) or pupillometry literature in general (e.g. Bradley et al., 2008).