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Conscious awareness is necessary to assess trust and mimic facial expressions, while pupils impact trust unconsciously

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People make rapid inferences about others' thoughts and intentions. For example, they observe facial movements and pupil size of others and unwittingly make use of this information when deciding whether to trust someone or not. However, whether spontaneous mimicry depends on visual awareness of the stimulus and whether these processes underlie trust decisions is still unknown. To investigate whether visual awareness modulates the relationship between emotional expressions, mimicry and trust, participants played a series of trust games and saw either their partners' faces with a neutral, happy or fearful expression, or their partners' eyes in which the pupil size was large, medium or small. Subjects' trust investments, facial movements and pupil responses were measured. In half of the trials, the stimuli were rendered invisible by continuous flash suppression. Results showed that facial expressions were mimicked and influenced trust decisions during the conscious condition, but not during the unconscious (suppressed) condition. The opposite was found for pupil size, which influenced trust decisions during states of unawareness. These results suggest that the neurobiological pathway linking the observation of facial expressions to mimicry and trust is predominantly conscious, whereas partner pupil size influences trust primarily when presented unconsciously.

This article is part of the theme issue 'Cracking the laugh code: laughter through the lens of biology, psychology, and neuroscience'.

1. Introduction

Humans can decide whether to trust a complete stranger in a split second (38 ms) [1]. They do this seamlessly without making any effort, and often without being explicitly aware of how they reached such a decision. Apart from explicit facial expressions of emotion (a wide smile signalling happiness; a dropped jaw signalling fear), in real life, human and non-human primates exchange emotional signals in more subtle ways [2,3]. For example, people can detect irony in laughter by detecting slight changes in other's expressions. These expressions are not merely verbal, but involve several different bodily actions that can influence the interpretation of social interaction. An example of this is pupil mimicry [4–6]. It has been shown that people mimic each other's pupil size and if the interacting partners' pupils synchronously dilate, pupil mimicry enhances trust [7–9]. This implicitly formed intuition resembles a 'gut feeling', which plays an essential role in novel situations. The somatic marker hypothesis states that prior to a decision, a parallel somatic/visceral response generates information that helps people guide the decision in one direction or another [10]. During this process, rapid mimicry may reflect the transmission of affect between individuals (emotional contagion), potentially serving as a precursor to more complex social skills such as trust [4–6,11–13].

Given the speed with which emotional expressions affect our daily social interactions, it has been suggested that emotional information may be processed via the retino-collicular-pulvinar-amygdala pathway. This subcortical 'low road' is thought to enable rapid processing of emotional information bypassing the visual cortex, thereby facilitating physiological responses such as pupil dilation and facial expression without consciously perceiving the visual input [14–20]. The most direct evidence for the unconscious processing of emotional expressions comes from studies with blindsight patients. Although blindsight patients have a lesion in their primary visual cortex, they can still distinguish facial and bodily expressions of emotion without conscious awareness of perceiving them [21–23]. Crucially, these patients also show facial mimicry and pupillary reactions (indicative of autonomic arousal) to unconsciously perceived expressions of fear and happiness [22]. Notably, blindsight patients' physiological reaction was stronger when the affective stimuli were presented to their blind side. This suggests that unconscious visceral reactions (rapid mimicry) may be particularly informative when awareness of visual information is absent. In other words, human mimicry might be particularly useful during a subliminal presentation, when the visual input is noisy or difficult to encode. However, the extent to which unconscious emotional processing is shared by healthy participants remains unclear.

To explore unconscious emotional processing in healthy subjects, previous studies have used blinding methods such as continuous flash suppression (CFS). CFS is one of the most effective blinding techniques, in which one eye is presented with a stimulus while the other eye is shown rapidly changing 'Mondrian' masks [24]. This method allows suppression of presented stimuli from awareness up to several minutes. Many studies using binocular rivalry and CFS paradigms confirmed that the presentation of emotional expressions or eye stimuli evoke neurophysiological and behavioural responses even when they were not consciously perceived [25–27]. This evidence promoted the notion that the unconscious processing of emotional expressions might help people detect emotions rapidly. Yet such conclusions may be premature as other studies found no evidence of non-conscious affective processing in healthy participants [28–32]. A potential explanation is related to the measurement's issues of visual awareness in CFS studies. Specifically, previous findings indicate that (un)awareness is not an all-or-nothing mechanism, and levels of visual awareness vary during CFS [33]. Thereby, it has been argued that it is important to control not only for objective measures but also for subjective measures of awareness (see [28,34]). Moreover, it is possible that some emotional modalities are processed consciously, while others are processed unconsciously (for a review, see [12]). While facial muscle movements are largely a conscious process, autonomic movements which control pupil size are fully unconscious [35,36]. Accordingly, it is plausible that different emotional effectors may influence human behaviour (mimicry and trust) via diverse neurological pathways.

To test the above theories, we examined the extent to which conscious awareness of facial expression or pupil size is required to influence participants': (i) trust decisions and (ii) rapid mimicry. We asked participants to play a series of trust games while presented with images of faces or eyes of different partners varying in facial expressions (happy, neutral, fearful) or pupil sizes (large, medium size, small). During these games, we used CFS to manipulate conscious perception in half of the trials [24] and participants' mimicry was tracked using facial electromyography (EMG) and pupil size was sampled with a novel method developed by Brascamp & Naber ([37], figure 1). This method was developed specifically for the purposes to measure pupil sizes under visual suppression, which is very well suited for the intent of this research. Still, considering that pupils are very sensitive to luminance changes and CFS creates flashing, we approach our pupil results with caution and recommend further replications, before drawing definitive conclusions. After the stimulus presentation, participants were asked how much money they wanted to invest in their partner; a task known to reflect trust in that partner. Previous findings indicate that levels of visual awareness vary during CFS [33]. We, therefore, applied a conservative approach in which awareness was measured continuously, and data were split into *Conscious*, *Semi-conscious* and *Unconscious conditions* (see Method for more details).

We hypothesize that if healthy subjects' trust decisions rely partly on unconscious affective processing (**H1**:) emotional information conveyed by faces and pupils will modulate trust-related investments under 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, we predict that, in line with earlier results with blindsight patients, (**H2**:) facial/pupil mimicry will occur during both conscious (control) and unconscious (suppressed) conditions. Finally, we examined the interaction between mimicry and trust. Specifically, we expected that (**H3**:) mimicry of partners' happy facial expressions/large pupils will be associated with higher trust levels, while the mimicry of frowning faces/small pupils will lower trust. This hypothesis was based on our previous studies, where we observed that when participants mimicked dilated pupils they trusted their partner more than when they perceived dilated pupils, but did not mimic [7,8].

2. Results

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

First, we conducted a series of multilevel models (Methods) to test our behavioural predictions. In the first model (electronic supplementary material, table S1), a significant main effect of emotion on trust ($F_{1,17808} = 79.913$, $p < 0.0001$) revealed that partners with happy facial expressions and large pupils were trusted more than partners with fearful faces and small pupils, in keeping with our hypothesis. Moreover, the main effect of awareness levels ($F_{1,17808} = 770.611$, $p < 0.0001$) showed that participants trusted their partner more during control (conscious) trials, compared to suppressed (CFS) semi-conscious trials and unconscious trials. This result suggests that people tend to withhold trust when they cannot consciously perceive their partners' eyes or face properly. Crucially, a significant three-way interaction between suppression, expression modality and emotion

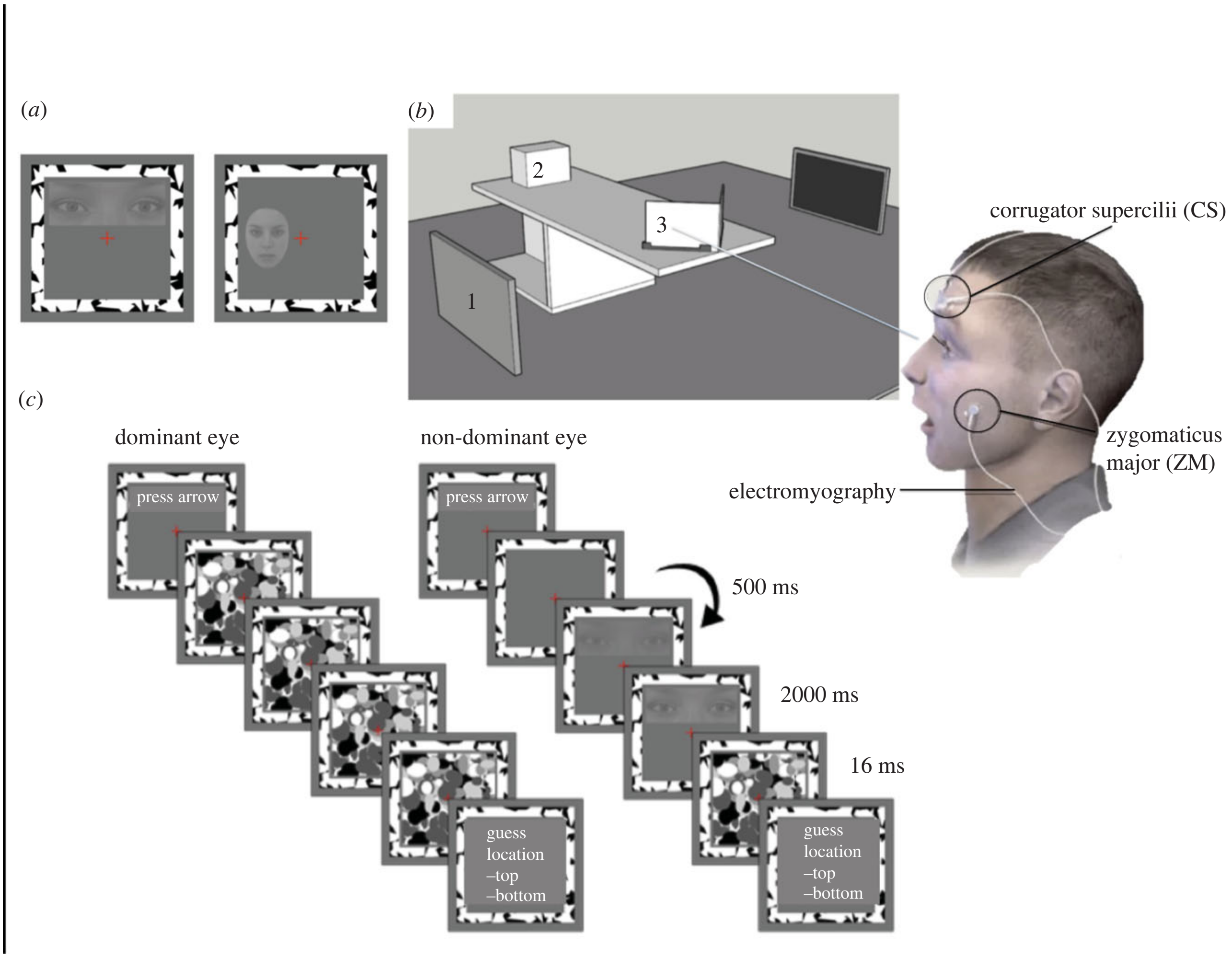

Figure 1. (*a*) Example of a neutral facial stimulus on the right, and medium-sized pupils on the left. All displays were surrounded by a black and white square border to facilitate stable convergence of the images in both eyes. The position was either above or below the fixation cross for the eyes' 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 sized 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 s, participants were asked to make a guess for the location. After this, they had to indicate confidence in their decision on a 4-point scale (guessing, not confident, quite confident and 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 s inter-trial interval, followed. Pictures adapted from Tamietto & De Gelder [20] (figure 3). (Online version in colour.)

($F_{2,17808} = 24.019$, $p < 0.0001$) clarified that facial expressions and pupillary signals modulated trust differently (figure 2).

Post hoc pairwise comparisons of the three-way interaction revealed that facial expression modulated trust investments during both conscious and semi-conscious conditions (happy > neutral > fearful: all $ps < 0.05$), but not when the stimuli were fully suppressed, and participants did not consciously perceive the stimuli at all—*unconscious condition* (all $ps > 0.05$, figure 2*a*). An opposite effect was observed with the pupillary expressions of arousal, as partners' pupil size influenced trust decisions during suppressed (CFS) trials but not during the control condition. Specifically, in the *semi-conscious* condition, partners with large pupils were trusted more than partners with medium ($p < 0.0001$) and small pupils ($p < 0.0001$). Also, during the *unconscious* (fully suppressed) condition, partners with large pupils were trusted more than partners with small pupils ($p < 0.05$). However, participants' investments did not differ between partners' pupil sizes in the control condition (all $ps > 0.05$, figure 2*b*).

Altogether, these data implicate that, in line with the first hypothesis, emotional expressions can influence participants' trust even under visual suppression. Nevertheless, after controlling for subjective awareness scores, our data clarify that some level of visual per cent is necessary for emotional facial expressions to influence trust evaluation. On the other hand, the partner's pupil size seems to impact trust mainly unconsciously.

(b) (H2:) Does facial/pupil mimicry occur during control and suppressed (CFS) conditions?

Figure 3 displays the mean *z*-scored zygomaticus major (ZM) responses minus mean corrugator supercilii (CS) responses split by condition and the level of awareness. We performed two general linear models on EMG amplitudes recorded on the CS and the ZM muscles to test how visual awareness influences facial muscle mimicry. Both models tested how partners' expression (happy, neutral, fearful) presented

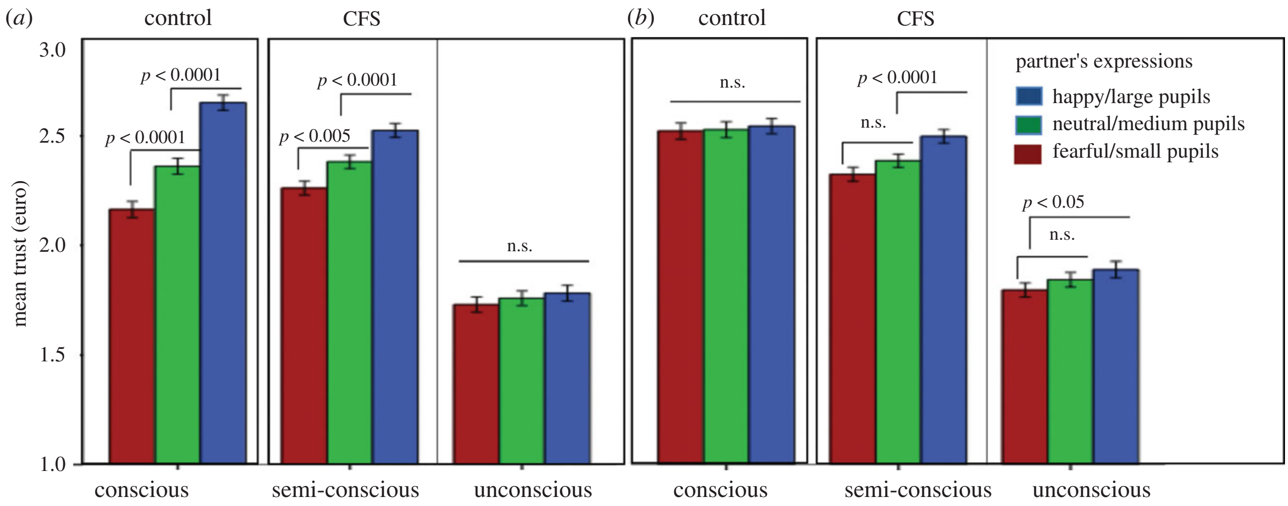

Figure 2. Bar plots display investment level (mean ± standard error) split by partners' expressions and subjects' level of awareness. (Online version in colour.)

under different awareness levels (conscious, semi-conscious, unconscious) affects responses in the muscles sampled.

(i) Mimicry of frowns (CS)

According to expectations, the first generalized linear model (GLM) with CS as dependent variable showed a main effect of the partner's emotion ($F_{2,163802} = 9.935$, $p < 0.0001$)—demonstrating that participants frown more in response to fearful facial expressions compared to neutral ($p < 0.05$) and happy expressions ($p < 0.0001$). Importantly, a significant interaction between emotion × awareness level ($F_{4,163802} = 2.540$, $p < 0.0001$) revealed that facial mimicry was impacted by the level of subjective awareness (electronic supplementary material, figure S1A and table S2). The *post hoc* pairwise comparison (LSD tests) disclosed that participants displayed complete mimicry in the control condition: 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 n difference was found between neutral and fearful expressions ($p > 0.05$). Finally, there was no difference between happy and neutral faces or fearful and neutral faces in the fully unconscious condition (all $ps > 0.05$). This result implies that when visual awareness declines, the influence of partners' emotional expression on facial mimicry also decreases.

(ii) Mimicry of smiles (ZM)

The second GLM on the ZM also showed a main effect of the partner's emotion ($F_{2,163803} = 7.603$, $p < 0.0001$) and demonstrated that participants smiled more in response to happy facial expressions compared to neutral expressions ($p < 0.0001$) and fearful expressions ($p < 0.01$, electronic supplementary material, figure S1B and table S3). No difference was found between fearful and neutral expressions ($p > 0.05$). Notably, a significant interaction between expression × awareness level ($F_{4,163803} = 8.246$, $p < 0.0001$) revealed that in the control condition, participants were mimicking others' expressions; they smiled 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 expressions ($p > 0.05$). Similarly, in the semi-conscious condition, participants showed mimicry; they smiled more in response to happy facial expressions compared to neutral (all $ps < 0.0001$), but not fearful expressions ($p > 0.05$). They also smiled more in response to fearful expressions than neutral expressions ($p > 0.0001$). However, similarly to the previous analysis, there was no difference between happy and neutral faces in the fully unconscious condition or fearful and neutral faces ($p > 0.05$).

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

(iii) Pupil mimicry

In the following analysis (figure 4), we used GLM to predict participants' *z*-scored baseline-corrected pupil response (for full model, see electronic supplementary material, table S4). Because pupil size is a slow signal, in contrast to previous EMG analysis, we analysed the pupil size after the 1500 ms baseline, which is common in the pupil mimicry studies [5,7,8] and in the pupillometry literature (e.g. [35]). The GLM showed a main effect of awareness ($F_{1,38713} = 165.104$, $p < 0.000$), indicating that pupil dilation was more substantial during *unconscious* and *semi-conscious* conditions than during conscious conditions (both $p < 0.001$). No difference was found in the CFS conscious between semi-conscious and unconscious conditions ($p > 0.05$).

Notably, a significant interaction between awareness level × emotion ($F_{1,38713} = 6.182$, $p < 0.001$) was found, suggesting that emotional expressions modulated pupil responses differently across awareness conditions. Figure 4 shows that in the *control* condition, participants' pupils were larger in response to partners' large pupils compared to small pupils ($p < 0.001$), a pattern that we have seen in most of our previous studies [4–6]. The opposite pattern was found during CFS conditions, as in the *unconscious* condition, participants displayed larger pupils in response to partners' small pupils versus large pupils ($p < 0.05$). During the semi-conscious condition, participants' pupils were larger in the medium partners' pupil condition than in the partners' large pupil condition ($p < 0.01$).

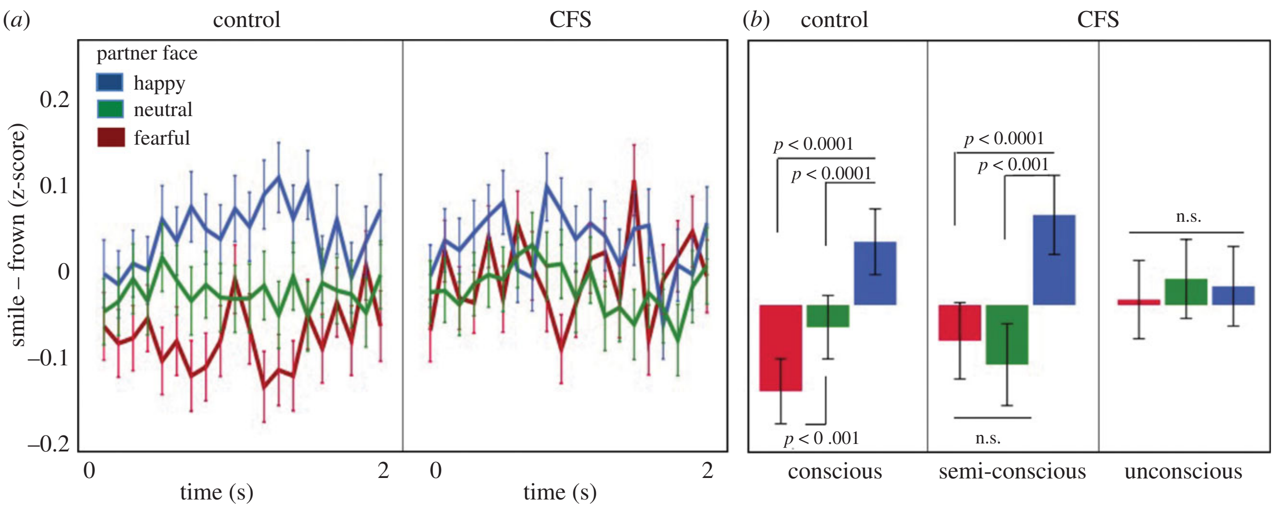

Figure 3. (*a*) Displays the mean *z*-scored zygomaticus major (ZM) responses minus mean corrugator supercilii (CS) responses (mean ± standard error) over 2 s, split by condition. (*b*) Displays the mean *z*-scored ZM responses minus CS responses split by subjects' level of awareness. For each muscle displayed separately, see electronic supplementary material, figure S1A,B.

(c) (H3:) Does mimicry modulate trust-related investments?

In the final two models, we examined if the mimicry of partners' happy facial expressions/large pupils were associated with higher trust levels, whilst the mimicry of frowning faces/small pupils would lower trust. In the first model, we selected trials where faces were shown. In the second model, we selected trials where pupils were shown. In both GLMs, 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 the two- and three-way interactions between these factors (for a similar approach, see [8]).

When participants mimicked partners' happy facial expressions, they trusted their partner slightly more than when they did not mimic; a trend in line with our predictions. However, this pattern did not reach the conventional threshold of statistical significance. The results showed that there was no main effect of mimicry ($p > 0.05$), and no interaction effects predicting trust (all $ps > 0.05$, electronic supplementary material, tables S5 and S6).

3. Discussion

Apart from recognizing emotional expressions such as smiling or laughing, most people can evaluate whether someone's laugh is being genuine or not. This is because communicative acts are not merely verbal, but involve a number of different bodily signals which can enact irony or sincerity. These types of expressions are particularly important when evaluating whether someone is genuine/trustworthy. These subtle expressions can be detected with remarkable speed, potentially via the subcortical 'low road' bypassing the visual cortex. This pathway is thought to enable rapid processing of emotional information and facilitates physiological responses such as pupil dilation and facial mimicry, outside of perceivers' conscious awareness of the visual input [15–17,19,22,38]. Supporting evidence comes from prior research with blindsight patients [20]. Nevertheless, whether healthy subjects share nonconscious processing is a debated topic. Likewise, it is still unknown whether the nonconscious processing of affective signals extends to pupil size [30,39–42]. In the present study, participants played a series of trust games with different virtual partners, whose faces and eyes were invisible with CFS. We hypothesized that if trust relies on unconscious processes, (H1:) emotional information should modulate trust decisions during conscious and nonconscious presentations. 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.

First, we found that participants trusted their partners more during control trials than CFS trials, where their vision was either partially or fully suppressed. This demonstrates that the ability to perceive partners' emotional expressions is pivotal for the establishment of trust. Participants' trust also increased when they could see their partner's eye region as compared to seeing their partner's whole face. This finding corresponds to research showing that the size of the eyes plays a significant role in communicating trustworthiness [43–45]. In the pupil, condition eyes were exaggerated. Although cropping to reveal just the eye region threatens ecological validity, this manipulation also enables improved measurement, which shows that the eyes play an important social role during trust detection.

Regarding the first trust-related 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 notion that emotional stimuli are recognized even when suppressed from visual awareness (e.g. [18,27]). However, the comparison between semi-conscious and unconscious conditions revealed that facial expressions modulated trust only when participants had some awareness of the facial stimuli. Therefore, contrary to previous findings [46–48], this evidence suggests that the ability to consciously perceive partners' expressions is critical to prime behaviour in healthy subjects. Apart from facial expressions, partners'

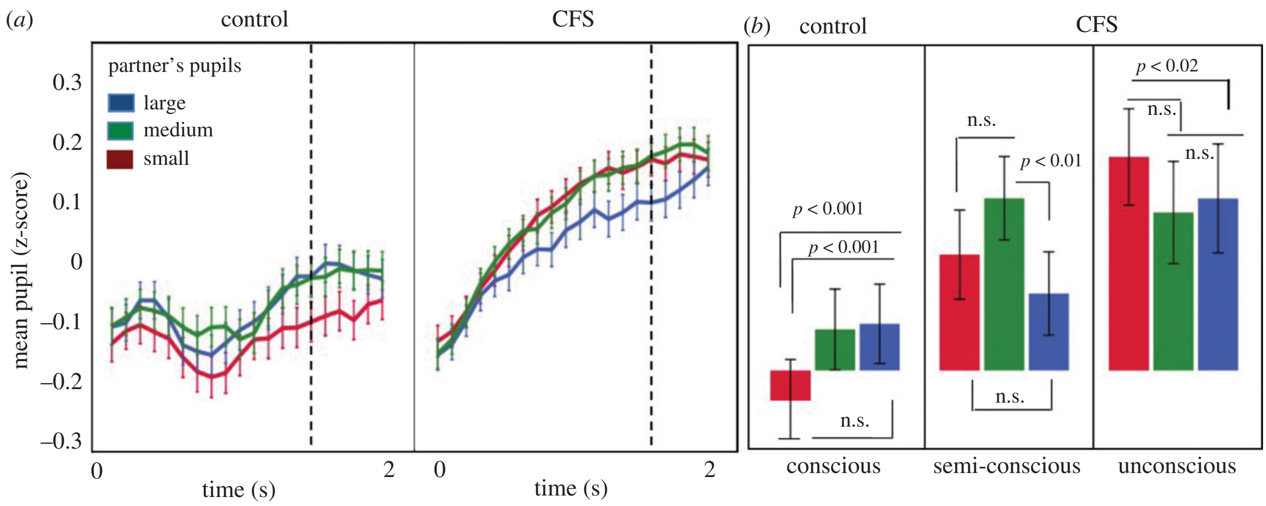

Figure 4. (*a*) The mean *z*-scored pupil response from pre-stimulus baseline to partners' pupils over 2 s time, split by subjects' level of awareness. The dashed line shows the timepoints after the 1500 ms included in the analysis. (*b*) Mean *z*-scored pupil response after the 1500 ms baseline split by subjects' level of awareness. For each muscle displayed separately, see electronic supplementary material, figure S2. (Online version in colour.)

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. Although the pattern was in the expected direction, it did not reach significance [7,8,49]. Instead, partners' pupil size influenced participants' trust decisions during the suppressed condition. Specifically, we observed that when subjects had no awareness of partners' eyes, they were influenced by their pupils. The reason pupils influenced trust during unconscious conditions, but not during fully visible control conditions, is open to interpretation. However, a possible explanation ties to prior evidence suggesting that observed pupil size influences emotion perception primary unconsciously [5,50]. Accordingly, this result fits with the theory submitting that autonomic cues and facial expressions influence social behaviour via distinct neurophysiological pathways. Specifically, autonomic cues may be processed via the retino-collicular-pulvinar-amygdala pathway, while facial expressions require the visual cortex [12].

We further hypothesized that emotional mimicry might occur unconsciously (H2). At first sight, similarly to the above trust-related findings, the results showed that participants displayed facial mimicry during both the conscious (control) condition and CFS conditions (figure 3*a*). Yet, we did not find strong evidence for facial mimicry during the fully suppressed unconscious condition after controlling for subjective awareness measures. Thus, our findings implicate that rapid facial mimicry also deteriorates as visual awareness declines. While some research suggests that emotive processes continue without visual awareness [25–27], the level of processing afforded by CFS is a controversial topic. For example, research has shown that low-level features within the face can be processed without visual awareness. In contrast, high-level features of the face require visual awareness [51]. Here, we demonstrate that CFS prevented information reaching high-level brain structures responsible for trust, but also prevented facial mimicry. This result aligns with the theory that (in contrast to unconscious autonomic mimicry) facial mimicry is more cognitive, controlled by high-level brain structures [8,12].

Furthermore, in line with prior findings [7,8,49], we observed a pupil mimicry response in the control condition—participants' pupils were larger in response to partners' large pupils compared to small pupils. Interestingly, the opposite pattern was found in the unconscious condition, where participants displayed larger pupils in response to partners' small pupils versus large pupils. During the semi-conscious condition, participants' pupils were larger when partners' pupil sizes were medium in size rather than large. The fact that pupillary response increases as awareness level decreases (figure 4*b*) also points toward the theory that pupil signals are processed mainly unconsciously [12]. However, before we can support such an interpretation, we need to consider a potential confounding effect that CFS could have on pupils. We have used a novel technology developed by Brascamp & Naber [37] that has been specifically designed to track pupil changes under CFS. However, figure 4 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 potentially disrupts pupillary responses, in which case the pupil data during CFS conditions may not be valid. To our knowledge, this method has only been used once in the literature and therefore it lacks extensive validation. Thus, more research is needed before we can draw definite conclusions about the pupil mimicry effects found during the semi-conscious and unconscious conditions.

Finally, contrary to the third hypothesis (H3) and previous research [7,8,49], we did not find significant evidence for the mimicry–trust-linkage in the current study. This suggests that even though facial muscles and pupils unconsciously move in response to partners' facial expressions and pupil sizes (figure 2*a*), participants' mimicry was not associated with a significant increase/decrease in participants' investments (trust). Although we fail to reject the null hypothesis, it does not transmit any meaningful information about the viability of the null hypothesis, as there is a probability of making a Type II error. Several methodological limitations may provide a possible explanation for the lack of mimicry–trust-related effect. First, although we used similar stimuli as was used in previous pupil mimicry research [7,8,49], in contrast to these studies, which used dynamic videos of changing pupils, we used pictures of static pupil sizes to keep the stimuli comparable to static facial expressions used in a prior study with blindsight patients [22]. The drawback of static stimuli is that the accuracy of emotion expressions identification decreases—especially if the expression is subtle [2]. Therefore, the lack of movement could be one of the reasons why mimicry did not modulate trust in the current experiment. To make the experimental procedure directly comparable with the blindsight study, this study also adopted a 2 s window to measure all the signals [22]. This time window may not have been sufficient to capture the full mimicry response (prior experiments measured pupil mimicry during 10+ second windows; [7,8]). It is, therefore, possible that participants' pupils were not given enough time to mimic the partners' pupils, an effect we know influences trust [7,8,49].

Masking, attentional blink and CFS paradigms are all blinding methods that can suppress visual input. The difference in these methods is that the manipulation or visual perception happens at a different level of processing. For instance, a recent study showed that unconscious processing was present with masking but absent with CFS [52]. The authors concluded that CFS allows very little perceptual processing, if at all, and that previous reports of high-level and complex unconscious processing during CFS may result from partial awareness. It is, therefore, worth mentioning that CFS is a particularly 'aggressive' method and other 'softer' blinding methods could bring different results. Another important fact to consider is that people with lesions create new types of axonal connections with other parts of the brain [53,54]. This neuroplasticity effect may explain the dichotomy in unconscious processing found between healthy subjects compared to subjects with blindsight. If we consider the speed with which mimicry happened combined with the fact that participants were not instructed to react to the stimuli in any way, it could be argued that the occurrence of spontaneous mimicry (the tendency to smile in response to seeing smiling faces) suggests that healthy subjects also engage in 'unconscious' processing of emotional stimuli. While the decision to trust is more cognitive and potentially conscious, the tendency to smile is more implicit. This study demonstrates that both reactions co-occur at the same time, but the causality between them cannot be directly established in this experiment.

The limitation of this experiment is that we cannot directly determine what is happening during the semi-conscious condition. This is because we asked participants about the location of the stimuli, but not the content of the stimuli. For example, it is possible that participants detected the location of the stimuli, but did not recognize the emotional content of the stimuli (e.g. only detected ambiguous shape in the upper visual field). To probe the 'grey zone' further, we recommend future studies use an alternative approach in which visual experience can be graded on a scale, including multiple responses ranging from 'no visual experience at all' to 'a clear and complete visual experience' on the other [55]. These subjective reports would allow us to further understand whether 'semi-conscious' condition functions at a similar unconscious processing level to other blinding methods. Given the above limitations, we recommend that future studies adopt dynamic pupil stimuli, use a time window longer than 2 s, and try an alternative 'blinding' method (e.g. masking) to verify our results. We further argue that a reliable method to manipulate mimicry has not been definitively established. Until then, the causal link between autonomic mimicry and pro-social behaviour will remain largely speculative. Thus, researchers should be cautious when comparing naturally occurring effects with findings from (invasive) manipulation studies.

In conclusion, the unique combination of a trust game, physiological measures and CFS allowed us to test how emotional expressions dynamically shape participants' trust and mimicry. In contrast to previous research, a distinction was made between 'motor mimicry' (e.g. facial expression mimicry) controlled by the motor muscles and 'autonomic mimicry' (pupil mimic) controlled by the autonomic nervous system. Accordingly, the results revealed that facial expressions were mimicked and influenced trust decisions during the conscious condition, while partners' pupil size influenced trust decisions primarily non-consciously. These results are significant for emotion theories postulating that unseen emotional stimuli can influence human behaviour and social decisions [19,20,56]. Instead, here we demonstrate the ability to assess trust, as well as how the more basic tendency to mimic facial expressions breaks down by diminishing people's ability to read others' facial expressions. On the other hand, the current study is one of the first to show that pupil size influences trust mainly unconsciously. We conclude that the path from facial expressions to mimicry and trust in healthy subjects is predominantly conscious. Meanwhile, we provide evidence that pupil size influences trust mainly unconsciously.

4. Method

The CFC experiment aimed to replicate and extend the results of a blindsight study by Tamietti *et al.* [22] while measuring facial mimicry and pupil mimicry during trust games [7,8].

(a) Participants

We planned to include $N = 50$ participants in our main analyses. These sample sizes were determined by sample sizes in previous studies using CFS [57] and measuring physiology [7,8,58]. Data collection was terminated when this sample size was achieved, after the 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). The main focus of the study was on expressions and the expressions were equally distributed across pictures, we do not see a problem in the inequality of the sample. 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 11 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 [7]). This left us with 50 full datasets for behavioural 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 no. CEP18-0403/201).

(b) 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 × 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 s of stimulus presentation. Skin conductance measures were collected for control purposes to assess whether the observed mimicry effects (e.g. increased EMG activity) were no mere by-product of arousal responses. If true, such a response would not necessarily 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 electronic supplementary material, figure S3).

(c) Stimuli

Stimuli consisted of eight pictures of faces and eight pictures of eyes (each appeared 12 times per block). The pupil stimuli set was acquired from Kret *et al*. [7]. To convert videos of dynamically changing pupils into a static stimulus, we took the last frame of the videos. In the case of constricting pupils, we used the final frame of the video when the pupils were the smallest (60%). For the dilating pupils, we used the last frame of the video where the pupils were the largest (140%; example in electronic supplementary material, figure S4). The pictures of the whole faces were taken from the Amsterdam Dynamic Facial Expression Set (ADFES; [59]). For details see electronic supplementary material.

(d) Procedure

Each trial started with a message telling the participant that they could start the new trial by pressing the corresponding key. A grey background and a red fixation cross were present during the whole trial (figure 1*c* 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 s on a grey background. The opacity of the stimulus was increased from 0% to 100% in the first 0.5 s. After this, the fully opaque image remained on the screen for another 2 s. The position was either above or below the fixation cross for the eyes stimuli and left or right of the fixation cross for the face's 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 s 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 and very confident). Finally, they were asked to make an investment decision of €0–€4 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 s break was implemented to allow physiological responses to return to normal and establish the next trial's physiological baseline. A full trial lasted for around 10 s depending on the participant's response times. For details of the experimental procedure see electronic supplementary material.

(e) Suppression

In our dataset, on average, the suppression broke in 24.3% of the CFS trials (25.9% face trials and in 22.7% eye condition trials), (which is in line with earlier work e.g. [60]). While many studies use the time until suppression (b-CFS) as the dependent variable (e.g. [31,61]; for b-CFS results see electronic supplementary material, tables S7–S9), the main goal of the current study was to test how conscious awareness of a partner's expression (facial and pupil size) shape (i) trust decisions, (ii) and mimicry (iii) the effect of mimicry on trust decisions. This required using awareness as an 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 [34]). 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); [47,62]. As expected, the CFS objective measure (the location detection performance) significantly correlated with participants' 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 the chance level: (binomial test: $p < 0.001$). In the rest of the CFS trials (57% of the total number of CFS trials), participants' 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 4 = very confident (22.1% trials), after excluding trials where the suppression broke (b-CFS), participants' detection performance reached 84% (above 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.

Importantly, during CFS the level of awareness varied (electronic supplementary material, table S9), in half of the CFS trials, participants were not consciously aware of the stimuli at all but 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: (i) *Conscious condition* represents the control trials where participants perceived the stimuli without suppression and were confident in seeing it (confidence level = 4). (ii) *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, (iii) *Unconscious condition* represents the trials where stimuli were shown under suppression and subjects reported that they were guessing the stimulus location (confidence level = 1). For physiological details regarding data acquisition and preparation see electronic supplementary material.

(f) Statistical analysis

(i) Multilevel models

Because the data had a hierarchical structure, results were analysed 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 (v. 25) 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. Because parsimonious explanations are preferred, the non-significant effect was left out when the model fit did not decline significantly.

(ii) Analysis 1: (H1:) does emotional information influence trust during control and suppressed (CFS) conditions?

To test the first hypothesis evaluating the effect of experimental conditions on trust, we used a GLM 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 $2 \times 3 \times 3$ 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 (apart from a random intercept for subject, no other random factors were included).

(iii) Analysis 2: (H2:) will facial mimicry occur during control and suppressed (CFS) conditions?

To test for facial muscle mimicry, we selected trials where participants observed partners' faces. We then used two separate GLMs to predict the changes in the two EMG amplitudes of the CS and the ZM muscles. As predictors, we used partners' expressions in the three 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 three-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 (apart from a random intercept for subject, no other random factors were included).

(iv) Analysis 3: (H2:) will pupil mimicry occur during control and suppressed (CFS) conditions?

As in the previous facial mimicry analysis, we used GLM to predict participants' z-scored baseline-corrected pupil response. As predictors, we used partners' expressions in the three 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 three-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). We would like to note that our stimulus presentation duration was on the short side compared to previous literature [7,8]. In these previous studies, the eye regions were presented for 4 s. The pupils were static for the first 1.5 s and then dilated, remained static or constricted. In those studies, the pupil mimicry response was analysed over 2.5 s (from 1.5 to 4 s) whereas in the current study it was 2 s (that is, the full stimulus presentation time). While knowing that this brief stimulus presentation time might be suboptimal for measuring pupil mimicry, we did not increase it because we matched the methods with the study conducted by Tamietto & Castelli [63]. Also, if we had extended the window to 4 s, most people would break the suppression and perceive the stimuli. With a 2 s window, we achieved that in 43.0% of cases participants reported not being able to see the stimuli at all, which was crucial for our hypotheses. Thus, we decided to analyse pupil size in the last 500 ms of the stimuli presentation (after the 1500 ms baseline), which is common in pupil mimicry studies [5,7,8] or pupillometry literature in general (e.g. [35]).

(v) Analysis 4: (H3:) does facial/pupil mimicry modulate trust-related investments?

We run two separate GLMs (one for eyes, one for faces). In these models, 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 the two- and three-way interactions between these factors.

For classification of mimicry see electronic supplementary material.

Ethics. The ethics committee of Leiden University approved the experimental procedures (ethics no. CEP18-0403/201).

Data accessibility. The article's supporting data and code can be accessed here: https://osf.io/wzs73/?view_only=d14b2f215d574a4199840a1a64c5d37e. Data and materials will also be uploaded to DataverseNL, accessible to anyone.

Supplementary material is available online [64].

Authors' contributions. E.P.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, supervision, visualization, writing—original draft, writing—review and editing; D.V.: data curation, formal analysis, investigation, methodology, project administration; R.d.Z.: conceptualization, data curation, formal analysis, investigation, methodology; M.T.: conceptualization, formal analysis, methodology, writing—review and editing; M.E.K.: conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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