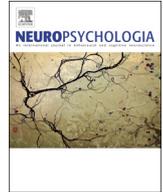




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Unconscious fearful body perception enhances discrimination of conscious anger expressions under continuous flash suppression

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ABSTRACT

The continuous flash suppression (CFS) paradigm is increasingly used to study unconscious visual perception. Our goal was to use CFS and to compare the results with previous findings from patients with brain lesions, and studies of healthy participants. We used an emotion discrimination task and bilaterally presented whole-body postures expressing fear or anger, rendering the stimuli invisible in either one of the visual fields. We found that the CFS presentation did not yield the classical redundant target effect of response facilitation when the unconsciously seen stimuli had congruent emotions; instead we found a facilitation effect in reaction times by body stimuli of incongruent emotions, especially by the unconscious fearful body facilitating discrimination of conscious angry body. Our results with healthy participants showed similarities to hemianopia patients without blindsight, but not to blindsight or neglect patients, indicating that unconscious visual processing is not a single phenomenon, but is likely to involve multiple mechanisms, processes and brain regions. Further studies are necessary to validate the facilitation effect of fearful bodies on other tasks, and to study the neural substrates of this effect.

1. Introduction

Unconscious visual perception is a topic that has long fascinated researchers. The dissociations between behavior and subjective awareness seen in studies of patients with brain lesions contribute to our understanding of unconscious processes in the intact brain. Patients lose conscious visual perception due to variable lesions in different locations of the brain, and the residual visual behavior may be different or not always have the same neural basis. Blindsight patients with V1 lesions could not report the presence of a visual target in the contralesional visual field, but could still react to the visual target above chance level (Danckert and Rossetti, 2005; Weiskrantz, 1986). Perception without awareness in blindsight patients was also reported for emotional stimuli (de Gelder et al., 1999). Patients with neglect usually due to parietal lesions would not consciously perceive a contralesional stimulus when another salient target was present in the ipsilesional visual field, unless explicitly asked to direct their attention to the contralesional side (Corbetta and Shulman, 2011; Driver and Vuilleumier, 2001). This makes the phenomenon of vision without awareness much more complex than assumed in the distinction between conscious and non-conscious perception. At present it is not clear whether a single distinction of conscious versus non-conscious

perception applies across a large range of stimulus conditions (low level, high level vision, affective or neutral images), and across different kinds of patients and lesion locations (neglect or blindsight), for different methods of making images invisible in neurologically intact participants (masking, binocular rivalry, continuous flash suppression) and for different experimental techniques and associated response measurements (direct or indirect effect).

Because patients with lesions are rare, several methodological paradigms have been applied to study unconscious processes in healthy participants, including masking and binocular rivalry. Masking has been applied to induce blindsight-like effects. When fearful and happy faces were bilaterally presented, with one visual field masked to emulate the blind visual field, the masked faces with congruent emotion to the visible faces showed a redundant target effect: a shortening of the reaction time (RT) (Tamietto and de Gelder, 2008). When the stimuli were bilaterally presented and consciously perceived by healthy participants, a facilitation effect for congruent emotional face stimuli was also observed (Tamietto et al., 2006).

However, the strength of masking has the risk of not fully rendering stimuli subliminal (Kouider and Dehaene, 2007; Lohse and Overgaard, 2017), and the duration of the stimulus dominance in binocular rivalry is not stable, and not freely controllable by the participant (Tong et al.,

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2006). Another recently developed method is continuous flash suppression (CFS). Utilizing interocular competitions similar to binocular rivalry, the subjective percept of a low-contrast target stimulus in one eye can be suppressed by a high-contrast and dynamic noise pattern in the other eye. Compared to backward masking and binocular rivalry, CFS has stronger suppression strength, and can reliably render a stimulus invisible for a few seconds (Tsuchiya and Koch, 2005; Tsuchiya et al., 2006). With the CFS paradigm, blindsight-like percepts, and dissociations between neural activity and percept have been found for emotional stimuli with healthy participants. For example, fearful faces have been found to break from CF-suppression (b-CFS) and enter into awareness faster than neutral and happy faces (Yang et al., 2007), and could induce amygdala activation when suppressed under CFS (Jiang and He, 2006).

The redundant target effect is an indirect effect measurement that has shown useful to assess non-conscious perception. Initially demonstrated in healthy participants under conscious viewing conditions, the effect is observed when two targets are presented bilaterally and the reaction times (RTs) to one of the targets are shorter compared to the single target condition (Miller, 1982; Raab, 1962). Since loss of visual awareness for blindsight or neglect patients is visual field-specific, many patient studies have presented a redundant stimulus in the blind visual field, in addition to a stimulus in the intact visual field, as a means of testing residual vision in an indirect fashion. An effect of the redundant emotional target has been found in both blindsight patients and neglect patients. With blindsight patients, previous studies found that the RTs for detecting the emotional faces (fear and sad) in the intact visual field were shortened when faces with congruent expressions were shown in the blind field (de Gelder et al., 2005, 2001). With neglect patients, emotional faces were extinguished less than neutral faces (Vuilleumier and Schwartz, 2001). When extinguished, fearful faces activated the amygdala similar to when they were visible (Vuilleumier et al., 2002). When priming a visible target face (happy, sad) with extinguished emotional faces, primes with congruent emotion to the target elicited faster RT than incongruent emotions (Williams and Mattingley, 2004). However, with hemianopia patients that had unilateral lesions but did not show any classical blindsight effects, studies did not find a redundant target effect, instead found a facilitation effect of fearful faces in the blind visual field, for detecting happy faces in the intact visual field and enhancing its N170 component of ERP (Bertini et al., 2013; Cecere et al., 2014). They found that this facilitation effect was even present for non-emotional tasks, including gender discrimination and orientation discrimination of Gabor patches in the intact visual field (Bertini et al., 2013; Bertini et al., 2017). In two of the three studies, the facilitation was found only for patients with left hemispheric lesions (Bertini et al., 2017; Cecere et al., 2014).

Similar to faces, the human body is also a category conveying information of identity and emotion. Because of the behavioral relevance, body stimuli have also been used as an effective tool to probe unconscious visual processing. For blindsight patients, both neutral body and face stimuli induced BOLD activation in the superior temporal sulcus and the amygdala (Van den Stock et al., 2014). When presented to the blind field, happy and fearful bodies and faces both triggered fast facial muscle and pupillary reactions (Tamietto et al., 2009); angry dynamic body expressions could activate not only primary somatosensory, motor and premotor areas, but also bilateral superior colliculi, pulvinar, amygdala and the right fusiform gyrus (Van den Stock et al., 2011). In neglect patients, when two stimuli were presented simultaneously in the two visual fields, bodies expressing fear were less extinguished than bodies expressing happiness, when presented to the contralesional visual field, showing an attention-grabbing effect (Tamietto et al., 2007). Extinguished fearful bodies also induced activation in extrastriate body areas and the left amygdala (Tamietto et al., 2015). When investigating this in healthy participants, we also observed under the b-CFS paradigm that fearful bodies showed a longer suppression time than neutral bodies, while angry bodies were

suppressed shorter, indicating different unconscious/preconscious processing of these two bodily emotions (Zhan et al., 2015).

To further study the unconscious emotional body processing, and to compare to both previous patient studies and masking study of healthy participants, here we used the redundant target paradigm together with CFS. We bilaterally presented fearful and angry bodies under CFS in an emotion discrimination task, and suppressed one of the visual fields to emulate the effect of a blind visual field. We observed a facilitation effect of RT for unconscious emotional bodies incongruent to the emotion of the conscious targets, and this facilitation effect was present especially when the conscious targets were angry and the unconscious stimuli were fearful bodies.

2. Materials and method

2.1. Participants

Forty-one participants took part in the study. Forty participants had normal stereo and color vision, and normal or corrected-to-normal visual acuity. None of the participants had a history of neurological disorders. The participants provided written consents, and received either monetary or course credit rewards after participation. The experimental procedures were approved by the ethics committee of Maastricht University, and the experiments were carried out in accordance to the declaration of Helsinki. For each participant, we included the data for further analysis if they satisfied two criteria: 1. the participant performed the task properly (low number of incorrect trials); 2. the CFS suppressed the stimuli properly throughout the experiment, in which case the participant should not consciously perceive the suppressed stimulus in the noise at all. This was validated by a series of debriefing question after the experiment (Did you see anything in the noise? If yes, how many times? Did you see two boxes during the experiment? If yes, how many times?). In studies of perceiving non-conscious stimuli, a trial-by-trial report of visibility has been usually implemented, which could be a dichotomous report (seen/unseen), or a graded report (e.g. perception awareness scale, PAS, Ramsøy and Overgaard, 2004). For normal participants, hemianopia and blindsight patients, PAS has been a more sensitive measure of visual awareness than yes/no answers (Mazzi et al., 2016). It reflected the level of priming effects (Lohse and Overgaard, 2017), and correlated with the ERP amplitude of the visual awareness negativity (Mazzi et al., 2018). In the current study where participants' attention was directed to one of the visual fields, we did not implement a trial-by-trial measure of awareness. Apart from maintaining a design comparable to other redundant-target studies, we are aware of the possibility, that if participants report their subjective awareness on a trial-by-trial basis, they may expect to see stimuli in the noise, which may direct their attention to the noise side and in turn interfere with the emotion categorization task they perform. Consequently we chose a stringent criterion, and included participants who were completely unaware of the suppressed stimuli.

The following participants' data were excluded from the analyses: one participant had a lazy eye; two participants saw the stimuli in the noise; another two participants did not see any suppressed stimuli but saw two boxes once and twice respectively during the experiment, indicating imperfect merging; another participant had only 5 trials of correct responses. In total 35 participants' data were included in subsequent analysis (mean age = 21.97, range 18–27 years, 4 males, 3 left-handed). These participants were not aware of the presence of suppressed stimuli.

2.2. Stimuli

The stimuli consisted of 6 fearful and 6 angry whole-body postures, performed by 6 actors (3 males), adapted from Stienen and de Gelder (2011). Facial information had been removed, and the images were aligned with each other at the feet level, and were all positioned at the

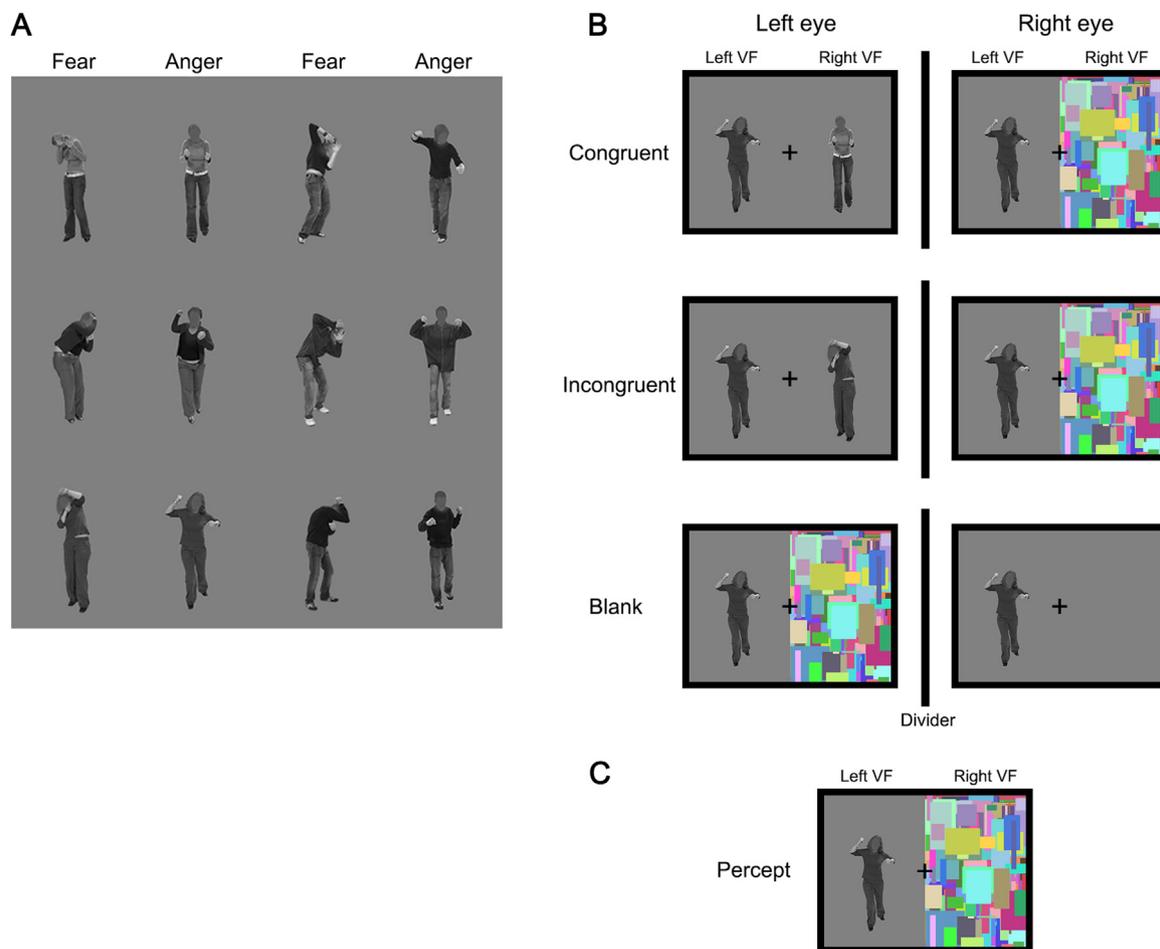


Fig. 1. A. All body stimuli used in this experiment, performed by 6 actors. B and C. Stimuli presentation, with examples showing an angry body in the left visual field as the target, while the noise pattern suppressing stimuli in the right visual field. B. Conditions of angry-congruent, angry-incongruent, and angry blank. VF: visual field. C. The 3 conditions in B all resulted in the same percept. The fearful conditions were constructed in the same way. In the experiment the visual field that the noise patterns were projected into for each trial was randomized. This figure shows right-visual-field projection of noise patterns.

center of a gray rectangle (160×240 pixels, RGB value = 128,128,128). The bodies occupied a region within 131×193 pixels.

2.3. Procedure

The experiment was presented with Psychtoolbox 3 (Brainard, 1997; Pelli, 1997) in MATLAB (version 2012b, the MathWorks, Natick, MA, USA). For stable refresh rates and precise timing of the stimuli presentation, the experiment was presented with a 3D-capable LCD screen (Acer VG248, resolution = 1920×1080 , refresh rate = 60 Hz). The dichoptic display of stimuli was achieved by presenting stimuli in two rectangular regions (320×240 pixels) side-by-side at the center of the screen, while the participants viewed the screen through a pair of prism glasses (diopter = 12), which bent the light from the screen and projected the ipsilateral image to the center of the view of each eye. The background of the screen was set to gray (RGB value = 128,128,128). To aid fusing of the stimuli for participants, two rectangular frames (thickness = 10 pixels) were placed around the stimuli presentation regions, and two fixation crosses were placed at the center of each region. To prevent crosstalk of the two images, a cardboard was placed between the screen and the participant, which separated the screen in two equal halves. Participants rested their head on a chin rest 59 cm from the screen. Under this setup, each eye of the participant saw the content within one rectangle, and the participant's left and right visual fields corresponded to the left and right side of the fixation cross for both eyes. Upon a stable fusion of the two rectangles, participants saw

one single rectangle, and one single fixation cross at the center of the screen.

To indicate the start of each trial, the fixation cross would change to white color one second before the trial, and remain white throughout the trial. Participants were instructed to keep their heads as still as possible, remain fixated on the fixation cross, and not to blink within a trial if possible.

In each trial, the same target stimulus was presented in one visual field of both rectangles. In the other visual field of one rectangle, either no stimulus (blank, baseline conditions), or a stimulus with congruent or incongruent emotion was presented. In the corresponding visual field of the other rectangle, a dynamic and colorful noise pattern (flash rate = 10 Hz) was presented. The noise pattern suppressed the perception of the other stimulus in the corresponding visual field, which rendered a percept of only one stimulus presented side by side with a noise pattern. The noise pattern consisted of overlapping small rectangles of different colors (height and width within 20×15 pixels). Six hundred unique noise images were created, and were randomly selected for each individual trial.

To decrease the possibility that the target stimulus escapes suppression, the target stimulus was faded in from 0% to 50% contrast in 0.5 and then faded out to 0% contrast in 0.5. Participants performed the 2AFC task, where they reported the emotion they saw in the non-noise side as quickly but as accurately as possible during stimulus presentation, by pressing one of the two buttons (numpad button 1 and 2). If the participant didn't make a response, the noise would continue to flash

for 2 more seconds after the target stimulus faded out. Thus the response window was 3 s upon stimulus onset. To eliminate the possibility of seeing afterimages in the suppressed visual field, the noise pattern would be presented in both eyes for 1 more second immediately following the participant's response, or after the response window closed. The inter-stimulus interval was jittered amongst 3.5, 4, 4.5, 5, 5.5 s.

There were 6 conditions of suppressed stimuli and a total of 192 trials: fear-congruent, fear-incongruent, fear-blank, anger-congruent, anger-incongruent, anger-blank. To balance the number of times that a certain stimulus was seen, the congruent and incongruent conditions had 24 trials each, and the blank conditions had 48 trials each. For the same reason, the noise pattern was presented in the right eye for congruent and incongruent trials, and was presented in the left eyes for blank trials. The visual field that the noise pattern was project into was balanced across trials, and later served as a factor in the analysis. See Fig. 1 for the stimuli and conditions.

For the conditions where two bodies were presented in the same rectangle, the identities of the bodies were always different from each other, although both were from the same gender.

Before the actual experiment, participants underwent a short practice of 12 trials, where fearful and angry bodies different from the actual experiment were presented unilaterally (the side suppressed by the noise pattern was blank).

In the actual experiment, the button assignments (button 1 and 2) corresponding to the fear and anger responses were balanced across participants.

2.4. Data analysis

For accuracy, the numbers of correct trials per condition were counted. Since the total number of trials for blank conditions and for the congruent/incongruent conditions were not the same, and the trial counts in most of the conditions were not normally distributed, two Friedman tests were performed respectively for the 4 blank conditions (fear/happy, L/R visual field that the target was projected into), and for the 8 congruent/incongruent conditions.

The average reaction times (RT) for each condition of suppressed stimuli were calculated for each visual field of each participant (LVF, RVF). For this analysis, independent of the correctness of the responses, the trials that had an RT outside 1.96 standard deviations of the average RT within each participant were first excluded (4.91% of all trials). Trials not responded (.36% of all trials) and trials with a wrong response (5.22%) were also excluded from subsequent analysis. A total of 10.49% trials were excluded for the RT analysis. The 12 conditions were then entered into a repeated-measures ANOVA with factors of conscious emotion (fear/anger), congruency (blank/congruent/incongruent), and visual field (L/R). We also performed an ANOVA by using the same inputs but coding the conditions differently, with factors of conscious emotion, unconscious emotion (blank/fear/anger), and visual field. To examine the whole distribution of the RTs for individual participants, which provides more information comparing to using only the mean RT per participant, we further computed the cumulative distribution functions (CDF) for each condition (Ratcliff, 1979). Because no visual field laterality effect was found in the two ANOVAs (see results), we first rank-ordered the RT in individual participants for the 6 conditions (conscious emotion: fear/anger, congruency: blank/congruent/incongruent) across both visual fields, divided the RTs in 10% quantiles, then calculated the mean for each quantile. This procedure was performed with the excel plugin CDF-XL (Houghton and Grange, 2011). These RTs were then entered into a repeated-measures ANOVA of conscious emotion \times congruency \times quantiles.

For all the ANOVAs performed, when the sphericity is violated, Greenhouse-Geisser corrections were applied. Multiple comparisons were adjusted with the Sidak method in post-hoc simple effect analysis.

In addition, we also checked whether a Simon effect was present in the data, between the situations that the side of the button assignment

was congruent with the stimulus presentation side, versus those incongruent ones (e.g. if the participant was assigned the buttons of 1 = fear and 2 = anger, a trial where fear was presented at the left visual field would be a congruent trial). The Simon effect on accuracy showed a trend to significance in the two-sided Wilcoxon signed ranks test, $Z = -1.928$, $p = .054$, where the accuracy for the congruent side was slightly higher. In the ANOVA conscious emotion (fear/anger) \times congruency (blank /congruent/incongruent) \times button congruency (congruent/incongruent), the congruent button condition showed faster RTs with a trend to significance (mean difference = .010 s, $F(1,34) = 4.083$, $p = .051$, $\eta_p^2 = .107$), but did not have interactions to the other two main effects ($F(1,34) = .617$, $F(1,34) = .022$ respectively), thus the Simon effect was not included as a factor in the main analysis.

3. Results

The numbers of correct trials did not differ among the 4 blank conditions (Fblank_Lfield, Fblank_Rfield, Ablank_Lfield, Ablank_Rfield), $\chi^2(3) = 3.137$, $p = .371$. The numbers of correct trials among 8 congruent and incongruent conditions were also not different, $\chi^2(7) = 2.294$, $p = .942$.

The repeated measures ANOVA (conscious emotion \times congruency \times visual fields) for the RTs showed a main effect of congruency, $F(2,68) = 9.535$, $p = .00022$, $\eta_p^2 = .219$, where the incongruent conditions had a shorter RT than both the blank and the congruent ones (RT mean difference = .014 s, $p = .020$, and RT mean difference = .020 s, $p = .00081$, respectively). Examining fear and anger separately with post-hoc simple effect analysis, the RT of conscious angry body together with an incongruent fearful body was significantly shorter than with a congruent angry body (mean difference = .031 s, $p = .00074$), and also shorter than presenting the conscious angry body alone (mean difference = .021 s, $p = .011$). See Fig. 2A.

There was also a trend to significance for the interaction of conscious emotion \times visual fields, $F(1,34) = 3.956$, $p = .055$, $\eta_p^2 = .104$. Post-hoc simple effects analysis showed that, in the right visual field, the conscious angry bodies across 3 congruency conditions in general had a longer RT than the conscious fearful bodies (RT mean difference = .019 s, $p = .023$).

None of the other main effects or interactions was significant.

In the ANOVA of conscious emotion \times unconscious emotion \times visual fields, where the conditions were coded differently, we found a significant interaction of conscious and unconscious emotions, $F(2,68) = 8.982$, $p = .00035$, $\eta_p^2 = .209$. There was a trend to significance for conscious emotion \times visual field, $F(1,34) = 3.956$, $p = .055$, $\eta_p^2 = .104$, the same to the ANOVA above. There was also a trend to significance for unconscious emotion, $F(2,68) = 2.863$, $p = .064$, $\eta_p^2 = .078$, where the unconscious fearful bodies had a slightly shorter RT, although pairwise comparisons were not significant.

To further examine the whole distribution of the RTs in individual participants, we calculated the means of rank-ordered RTs in 10% quantiles, and performed an ANOVA of conscious emotion \times congruency \times quantiles. There was a significant main effect of congruency ($F(2,68) = 13.277$, $p = .0000135$, $\eta_p^2 = .281$), that the incongruent conditions had the shortest RT ($p = .002$ versus congruent conditions, $p = .00026$ versus blank conditions), consistent with the ANOVA results calculated with condition means. There was a trend to significance for the main effect of conscious emotion, that the RT for conscious fear was marginally shorter than that of conscious anger ($F(1,34) = 3.574$, $p = .067$, $\eta_p^2 = .095$). The main effect of quantiles was significant, due to the rank-ordering process. Interestingly, there is an interaction of congruency \times quantiles ($F(2.819,95.845) = 5.696$, $p = .002$, $\eta_p^2 = .143$), that the difference of RT for incongruent conditions was bigger for the longer RTs, comparing to the blank and congruent conditions.

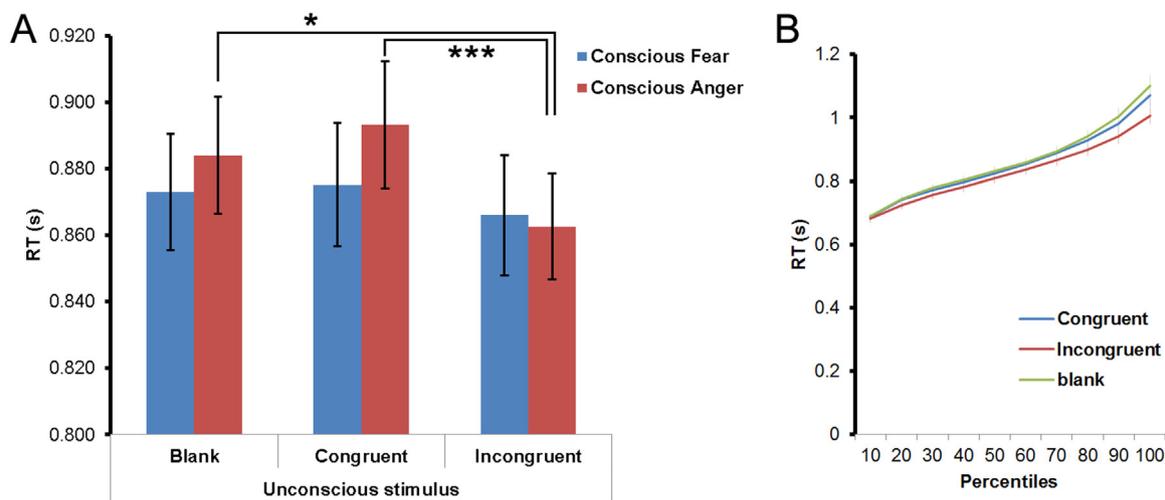


Fig. 2. A. Reaction times (RTs) of conscious fear and anger, presented together with an unconscious stimulus, which was a blank stimulus, a congruent stimulus, or an incongruent stimulus ($n = 35$). Error bars denote SEM. *: $p < .05$, ***: $p < .001$. B. Cumulative distribution functions of rank-ordered RTs, averaged for congruent, incongruent and blank conditions ($n = 35$). Error bars denote SEM.

4. Discussion

Our goal was to find evidence for perception of emotional body expressions outside visual awareness in healthy participants by using the CFS paradigm in combination with the redundant target effect, and to compare our findings with results from patient studies. We found an interaction between the body expressions of the consciously and the unconsciously seen stimuli. We expected that here the RT would typically be shorter when comparing the congruent condition to the single-stimulus condition, in line with the classical redundant target effect observed with stimuli under both fully visible conditions and backward-masked conditions. However, we did not find a facilitation effect by the congruent conditions, but instead found a faster RT for the incongruent conditions. This indicates that the unconscious process during CFS measured here may be sustained by different mechanisms than at stake in backward masking, and under conditions of full visibility. Under CFS, the unconscious bodies were processed to some extent, but the processing was not at a level that would allow a redundant target effect to appear, unlike the findings for healthy participants with conscious perception or under masking conditions, and for blindsight patients. However we found that the incongruent condition showed a bigger RT difference than congruent and blank conditions. This may reflect that the information of the suppressed incongruent stimuli accumulates over time, that some information was indeed processed, despite the strong suppression effect of CFS.

The congruency effect we found appears to have emotion specificity, as it was stronger when the consciously perceived bodies were angry ones. Unconscious fearful bodies facilitated the conscious perception of angry bodies, but unconscious angry bodies did not. Previously we found that angry bodies were suppressed for a shorter time span than the fearful bodies (Zhan et al., 2015), which may in part explain the differential effects between the unconscious emotions observed here. The unconscious angry bodies may be more salient, thus slowing down the RT comparing to unconscious fearful bodies.

The facilitation effect of unconscious fearful bodies was previously found in neglect patients, where the fearful bodies in the contra-lesional side were less extinguished (Tamietto et al., 2007). However, this attention-grabbing effect of fearful bodies would correspond to a slower RT for the consciously perceived emotion in our study, which we did not observe here. Also, neglect is thought to be induced by a disruption of balance in the spatial and non-spatial attentional controlling systems (Corbetta and Shulman, 2011). However, the CFS paradigm itself did not require participants to switch attention to another location, or

interfere with this process. In our experimental design the switch of attention was explicitly driven by task instructions in each block. Thus, it seems that the CFS disrupts the conscious percept based on a different mechanism than neglect. On the other hand, our results showed similarities to results obtained with the hemianopia patients without blindsight. These studies found a facilitation effect for unconscious fearful faces, in both emotional and non-emotion-related tasks (Bertini et al., 2013, 2017). In one of the studies, the fearful faces presented to the blind visual field did not show a facilitation effect when the intact field also perceived a conscious fearful face (Bertini et al., 2013), which was similar to what we found for congruent fearful bodies. The authors postulated that the conscious presentation of fearful faces may have inhibited the unconscious processing of fear through subcortical routes (Bertini et al., 2013). Future fMRI studies are necessary to validate this assumption. Interestingly, a follow-up study applied inhibitory transcranial direct current stimulation (tDCS) on either the vertex or the left occipital cortex (corresponding to O1 of the EEG 10/20 system) of healthy participants, both controlled with sham stimulations. Participants performed a go/no-go task to bilaterally presented emotional faces (fear, happy), masked by a neutral face. The study found that both under the sham condition and when inhibiting the vertex, the RTs for happy and fearful target faces were facilitated when the masked face had congruent emotions, a redundant target effect similar to those found in other masking and blindsight studies. However, inhibiting the occipital cortex showed a facilitation effect of masked fearful faces on target happy faces, similar to hemianopia patients without blindsight (Cecere et al., 2013). Given that the interocular competition utilized by the CFS paradigm is thought to occur in V1 or LGN (Tong et al., 2006), this tDCS study presented particularly intriguing similarities to CFS.

Although the previous hemianopia studies and our study showed a facilitation effect for unconscious fear, no matter whether it was expressed by faces or bodies, it is still not fully clear whether both stimulus categories convey emotional information through similar neural substrates, or whether these neural substrates differ for different types of participants. Faces convey fear with raised eyebrows and increased eye-white regions (Whalen et al., 2004), and in both sighted participants and blindsight patients this may rely on a fast subcortical pathway, processing both broadband and low spatial frequency information, through the superior colliculus, inferior pulvinar, to amygdala (Burra et al., 2017; Mendez-Bertolo et al., 2016). The importance of intact superior colliculi for blindsight is supported by an RTE effect for gestalt-like dots in blindsight patients with hemispherectomy, for whose blind visual fields, no other intact structure in the visual

pathway existed apart from the superior colliculus (Georgy et al., 2016). However the involvement of the amygdala for faces may be linked to the eye region of the faces, in both masking and CFS experiments (Gray et al., 2013; Whalen et al., 2004; Yang et al., 2007). Compared to faces, perception of bodily emotions involves more action-related processing (Dael et al., 2012; de Gelder et al., 2010). Although extinguished fearful bodies in a neglect patient could activate the amygdala (Tamietto et al., 2015), the preferred spatial frequency conveying emotional information for bodies is yet to be determined. The processing of fearful faces and bodies is also likely to be different under CFS, as we previously found a shorter suppression time for fearful faces than angry ones, but a longer suppression time for fearful bodies than angry ones (Zhan et al., 2015). Given the facilitation effect of fear (bodies/faces) in our findings and in hemianopia patients without blindsight, the difference between our findings and blindsight may be more related to the individual processing mechanisms (e.g. stages in different pathways) disrupted by these conditions, rather than stemming from the stimuli.

Another mechanism that possibly supports blindsight is the inter-hemispheric integration and cooperation. Two experiments in blindsight patients showed that, when responding to stimuli in either visual field with one of the hands, for the intact visual field the RT was shorter when the hand was controlled by the motor cortex ipsilateral to the hemisphere processing the visual information; for the blind visual field the opposite pattern of RT emerged, indicating that the visual information needed additional processing time in the intact hemisphere, which involved the parietal and premotor areas through the corpus callosum (Celeghin et al., 2015, 2017). In our current experiment, participants used different fingers of the same hand to respond, thus we were not able to make direct comparisons. Instead we could examine whether a Simon effect was present, which may also be related to inter-hemispheric cooperation. With a Simon effect, ipsilateral RT to the target side is facilitated. In our data we did not find a significant Simon effect of the responding side and visual field, nor any interaction to other factors though. For the CFS mechanism which mainly involves interocular competition within the same hemispheres, it is not yet clear whether inter-hemispheric cooperation would also be involved. Further CFS studies combining both the RTE and two-hand responses would be suitable to investigate this hypothesis.

Two recent studies with the CFS paradigm used a similar bilateral presentation design. One presented one arrow and 4 flanker arrows dichoptically, with the flanker arrows either masked with CFS or not masked. They found that the non-masked flanker arrows with direction incongruent to the target arrow slowed down the RT for the target, but this effect was abolished when the flanker arrows were suppressed, where no difference was found comparing to the conditions without flankers (Wu et al., 2015). Another study used faded-in fearful and happy faces under CF-suppression 600 ms before presenting the target (thus was a much longer prime), while participants categorized the emotion of a visible target face presented for 200 ms. The study found a facilitation effect on RT for the unconscious faces with congruent emotions (Ye et al., 2014). The difference between the results of these two studies may therefore be related to the different levels of their suppression under CFS, with and without priming effects.

In our case, since the classical redundant target gain effect shown with backward-masking was not seen here, residual vision under CFS suppression is likely to be abolished more thoroughly than with backward-masking. However, as the unconscious fearful bodies facilitate the processing of conscious angry bodies, does the amount of information transmitted under CFS allow integration between the two emotions?

When brain activity of healthy participants was observed under fMRI, consciously seeing two incongruent body expressions (fear and happy) induced weaker activity across the brain than seeing two congruent body expressions, indicating interference between the incongruent emotions (de Borst and de Gelder, 2016). When participants consciously observed two actors interacting in a violent social scene,

participants' attention on the aggressor induced activation of body-processing areas (extrastriate body area) and emotion-related areas (Van den Stock et al., 2015). In our study, although two body stimuli were bilaterally presented, with one of them unseen, the cognitive process induced by our design may be different from these two conscious viewing situations. First, we did not observe a facilitation effect by the congruent emotions, or interference by the incongruent emotions. Second, there was no intrinsic social interaction between our bilaterally presented stimuli: both were facing the observer (participant), but not facing each other. Although in our case the participant's percept could be treated as "attending to an aggressor (angry) or a victim (fearful)", both cases were "interacting" with the observer, this percept was the same when there was only one unilateral stimulus presented, for which we did not find a main effect of the consciously perceived emotion. Thus our results suggest that unconscious perception of bodies under CFS is very different from perception that is fully conscious, and its brain substrates still await future examinations.

A range of different methods have been used in the consciousness literature to render a stimulus unconscious, and several studies had made efforts to compare them. Almeida et al. observed an influence of happy faces on the likability rating for neutral stimuli (Chinese characters) under backward masking, but did not observe this effect under CFS (Almeida et al., 2013). Faivre et al. compared CFS with conscious viewing and several other non-conscious paradigms, including gaze-contingent crowding and masking. They found that the preference bias for angry, neutral, happy emotional faces was different across these methods, but the stimuli rendered unconscious by masking and CFS did not influence subsequent preference judgments (Faivre et al., 2012). Another recent fMRI study further compared the brain responses between CFS and chromatic flicker fusion, and found the categorical information of stimuli could be decoded from temporal and frontal areas under chromatic flicker fusion, but not with CFS (Fogelson et al., 2014). We observed in our current study that the facilitation of incongruent emotions was also different from the classical redundant target effect under backward masking. The evidence thus points to a difference in the mechanisms rendering stimulus unconscious in healthy participants. It indicates that the phenomenon of being visually unconscious of a stimulus is likely to involve multiple stages and processes in healthy participants and patient groups, and the links of them to CFS and other methods rendering stimuli unconscious are yet to be fully established. Similar to hemianopia patients not displaying above-chance performance for a range of visual stimuli, it is also possible for the methods applied to healthy participants, where the stimulus information was processed in some way in the brain, but did not induce dissociation or was not captured in either behavioral measures or brain signal measures. Apart from finding a more sensitive behavioral measure with participants, future fMRI and EEG/MEG research with more sensitive measures or neural signatures for unconscious processing would be necessary to better understand unconscious processes.

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Conflict of interest

The authors declare no competing financial interests.

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