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Unconscious processing of coarse visual information during anticipatory threat

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ABSTRACT

Rapid detection of threats has been proposed to rely on automatic processing of their coarse visual features. However, it remains unclear whether such a mechanism is restricted to detection of threat cues, or whether it reflects a broader sensitivity to even neutral coarse visual information features during states of threat. We used a backward masking task in which participants discriminated the orientation of subliminally presented low (3 cpd) and high (6 cpd) spatial frequency gratings, under threat (of shock) and safe conditions. Visual awareness of the gratings was assessed objectively using an additional localization task. When participants were unaware of the gratings, above chance and improved discrimination of low-spatial frequency gratings was observed under threat compared to safe trials. These findings demonstrate unconscious processing of neutral coarse visual information during threat state, supporting the view that automatic threat detection may rely on a general facilitation of coarse features irrespective of threat content.

1. Introduction

Detection of threat-relevant cues is crucial for survival. It has been proposed that this process is aided by a rapid and automatic processing of coarse visual features of cues that convey threat (Öhman, 2005). However, it remains unclear if this facilitation of coarse visual processing reflects a broader mechanism extending to the processing of neutral, non-threatening stimuli when already in a state of threat anticipation. Establishing whether such a process exists may be critical for advancing our understanding of visual processing under threat.

Threat stimuli can be processed automatically, i.e., in the absence of visual awareness or attention (Öhman, Carlsson, Lundqvist, & Ingvar, 2007). For example, cortically blind patients are able to discriminate emotional faces above chance level despite an inability to consciously perceive them (de Gelder, Vroomen, Pourtois, & Weiskrantz, 1999; Pegna, Khateb, Lazeyras, & Seghier, 2005). In addition, fearful and conditioned stimuli can evoke defensive responses in these patients, as well as in healthy participants when presented outside of visual awareness (Esteves, Dimberg, & Öhman, 1994; Tamietto et al., 2009; Vieira, Wen, Oliver, & Mitchell, 2017). The neural mechanism underlying this process has been proposed to involve the amygdala and anatomically connected extrastriate and subcortical visual areas, i.e., pulvinar and superior colliculus, which are activated by subliminally presented fearful faces (Morris, Öhman, & Dolan, 1999).

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A key characteristic of pathways connecting the amygdala with cortical and subcortical visual areas is that the majority of them is magnocellular in nature, and thus biased toward fast processing of coarse visual information (or low-spatial frequency, LSF; Amaral, Behniea, & Kelly, 2003; Schiller & Malpeli, 1977). Crucially, the subcortical regions that were previously found to be activated by subliminally presented fearful facial expressions also respond specifically to LSF, as opposed to high-spatial frequency (HSF), fearful faces (Burra, Hervais-Adelman, Celeghin, de Gelder, & Pegna, 2017; Mendez-Bertolo et al., 2016; Pegna et al., 2005). Indeed, recent work showed that masked (through continuous flash suppression) LSF, but not HSF threat stimuli (snakes) were perceived faster, implying prioritized unconscious processing of threats based on their LSF features (Gomes, Soares, Silva, & Silva, 2017). These observations lend support to the view that automatic processing of threats relies on coarse visual features which may serve as evolutionary adaptation facilitating their rapid detection and responses in often time-constrained threatening situations (Öhman, 2005; Soares, Maior, Isbell, Tomaz, & Nishijo, 2017). However, it remains unclear whether unconscious processing of LSF information is bound to threat cues, or whether it reflects broader sensitivity that would also facilitate processing of neutral LSF information under threat. Indeed, anticipatory threat was shown to facilitate perception of unmasked LSF information (Lojowska, Gladwin, Hermans, & Roelofs, 2015). Testing whether such a mechanism remains intact despite the absence of visual awareness is relevant as it would support an automatic mechanism relying on general sensitivity to LSF information irrespective of its threatening content.

We combined a backward masking procedure with a visual task in which participants discriminated the orientation of subliminally presented LSF (3 cpd) and HSF (6 cpd) gratings under threat (of shock) and safe conditions. An additional localization task provided an objective validation of visual unawareness produced by backward masking. We predicted that if coarse visual input is processed unconsciously under state of threat, we should observe above-chance as well as improved discrimination of successfully masked LSF gratings under threat compared to safe conditions relative to performance for HSF gratings.

2. Methods

2.1. Participants

Twenty-four (17 female) participants (age 19–24, SD: 2.38) recruited form the Radboud University took part in the experiment. Sample size calculation using G*Power (Faul, Erdfelder, Lang, & Buchner, 2007) revealed that 24 participants is sufficient to achieve a medium effect size ($\eta_p^2 = 0.06$) with power of $\beta > 0.08$. Inclusion criteria were: no past or present neurological or psychiatric conditions, no use of psychotropic medications, normal or corrected-to-normal vision, no color-blindness. All participants provided signed informed consent and were reimbursed with 15 euros for their participation. All procedures were approved by the local ethical review board (CMO Region Arnhem-Nijmegen, The Netherlands).

2.2. Stimuli and apparatus

The experimental task was generated in MATLAB R2010a (The MathWorks, Inc.) with the Psychophysics Toolbox (Brainard, 1997) and presented on a BenQ XL2420T LCD monitor (refresh rate of 120 Hz, resolution of 1920 × 1080 pixels). During each trial, there was a fixation dot (size: 0.15°) presented on a uniform gray background (luminance: 71 cd/m^2) in the center of screen in one of the following three colors: gray (luminance: 98 cd/ m^2), orange (luminance: 56 cd/m^2) or blue (luminance: 56 cd/m^2). Four Gabor gratings (Gaussian-enveloped sinusoidal grating, 2° diameter) were displayed at 2° eccentricity from the center of the screen to the center of the gratings. Gabor gratings were presented at 30% Michelson contrast and in two spatial frequency ranges: 3 and 6 cycles per degree (cpd), referred to further as 'LSF' and 'HSF' gratings, respectively. Four masks were presented at the location of the gratings and consisted of a black and white checkerboard (size: 2°, spatial frequency: 4.5 cpd at 100%-Michelson contrast with no Gaussian filter applied, eccentricity: 2°). Prior pilot testing revealed that a full contrast of the mask with this spatial frequency was successful at masking both lower and higher spatial frequency gratings. Two white frames (size: 6° × 2° at 2° eccentricity) were displayed on the left and right side of the fixation. Participants performed the task at a distance of 51 cm with their head fixated in a chin rest.

Threat was induced by a chance of receiving an electric shock depending on the color of the fixation in each trial. Shocks were delivered transcutaneously through the participants' fourth and fifth distal phalanges of the right hand using a Digitimer Constant Current Stimulator DS7A (www.digitimer.com) and standard Ag/AgCl electrodes. The maximum intensity stimulus consisted of 10 pulses with 1-ms length and 19.75-ms ISI, administered during a 200-ms time interval at 50 Hz with a maximum intensity level of 6 mA.

2.3. Procedure and experimental task

The experimental procedure included the following steps: task instructions, practice session, shock calibration and the actual experiment. Participants first received task instructions and were informed that the color of the fixation (orange and blue) would indicate the chance of receiving an electric shock during its presentation. The association between the fixation color and potential receipt of a shock was counterbalanced across participants. Subsequently, they performed a practice task consisting of 32 trials of which half were masked. The practice session was the same as the actual discrimination task with the exception that no electric shocks were administered. Next, shock intensity was adjusted at the individual level to ensure that the shocks were unpleasant but not painful. Shock calibration was performed using a standardized staircase procedure comprising 5 shock presentations followed by

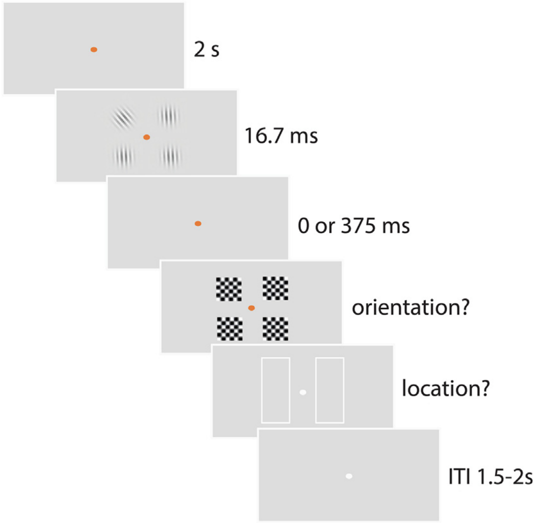

Fig. 1. *Example trial from the experiment.* The fixation color (orange or blue) signaled the threat condition and thus indicated whether or not there was a chance of receiving an electric shock during the trial. Participants were first required to indicate the orientation, i.e., left or right, of the tilted grating randomly presented in one of the four possible locations together with the three remaining vertical gratings. The presented gratings consisted of either all low or all high spatial frequencies. Next, participants had to indicate if the location of the tilted grating was left or right relative to the fixation, as indicated by the two frames (awareness check). The two questions were not time-constrained. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

participants' verbal reports of their unpleasantness on a scale from 1 to 5. The final shock intensity obtained with this procedure was used in the actual task.

The actual experiment consisted of the orientation discrimination and localization task. The orientation task was the task of interest. We based this operationalization on previous work in which the same localization task was used as an objective measure of unawareness in tasks where stimulus features (emotional expressions) were of main interest (Jolij & Lamme, 2005). The localization task is a more conservative measure of unawareness because even if participants would not perceive the orientation, they could have still seen the location (i.e., target onset) of the stimulus, which would be degraded to a lesser degree than orientation in case of less successful masking. Previous research found the effect of threat on orientation performance of consciously perceived gratings (Lojowska et al., 2015; Lojowska, Ling, Roelofs, & Hermans, 2018), and the use of the same task as an index of unconscious processing makes it also possible to test whether the same facilitation occurs in the absence of visual awareness.

The orientation discrimination task consisted of the following conditions: Threat Condition (threat, safe), Spatial Frequency (3 cpd, 6 cpd) and Mask Condition (Masked, Unmasked). Each trial started with the presentation of an orange or blue fixation (indicating threat or safe conditions) in the middle of the screen for 2 s, immediately followed by four gratings displayed around the fixation (see Fig. 1). Three of the gratings had a vertical orientation and one of the gratings could be oriented either 45° clockwise or counterclockwise relative to the vertical orientation (deviant grating). Gratings were presented for 16.67 ms (exactly two screen refresh cycles) and all four gratings had a spatial frequency of either 6 or 3 cpd. In the masked condition, the presentation of the gratings was immediately followed by masks (with no delay in between), whereas in the unmasked condition, the checkerboard masks were presented 375 ms after offset of the gratings. Participants could receive an electric shock from the moment a shock-related color of the fixation was displayed until the onset of the checkerboard masks. During mask presentation, participants were required to indicate as accurately as possible whether the orientation of a deviant grating was clockwise (UP arrow key) or counterclockwise (DOWN arrow key on the keyboard) relative to the vertical orientation. The masks remained on screen until the response was given. In order to motivate participants, feedback was displayed on screen in the form of "correct" or "incorrect" above the fixation after each response. After the orientation task and within the same trial, participants performed the localization task. Participants were instructed to indicate the location of the deviant grating, i.e., whether it was on the left (z key) or right (x key) side of the fixation. The frames remained on screen until the response was given, which was followed by 1.5–2 s inter-stimulus interval (ITI) before the next trial began.

Participants were instructed to fixate the central dot throughout the task. The task was divided into two blocks with a short break in between. Each block consisted of 192 trials representing the following conditions: Threat LSF, Threat HSF, Safe LSF, Safe HSF for Masked and Unmasked conditions (48 trials in total for each condition). Trials were fully randomized and the proportion of trials with shocks (i.e., reinforcement rate) was 9.5% (10 threat trials with shocks in each block, which were excluded from the analysis). The task lasted approximately 40 min.

2.4. Data analysis

Validation of threat of shock procedure. Prior to the experiment, shock intensity level was calibrated using a work-up procedure during which participants indicated on a scale from 1 to 5 how unpleasant the shock was. The average shock value was 4.5 (SD = 0.59) with none of the participants scoring below 4. This implies that individually adjusted shock intensity levels used in the experiment were generally unpleasant for all participants. Furthermore, to confirm the experimental procedure, after the experiment participants were asked to report the contingencies between the color of the fixation dot and threat condition. All participants reported the correct contingencies.

Awareness check. Performance in the localization task was used to objectively assess visual unawareness of the gratings. A successful masking procedure should be evidenced by at-chance performance (50% correct) for masked conditions (i.e., performance not significantly larger than test value of 0.5), and significant above-chance performance for unmasked conditions (i.e., performance significantly larger than test value of 0.5). To test these predictions, average performance for all participants and each condition was tested against chance level performance using one-tailed one-sample *t*-tests.

Orientation task. Provided that visual unawareness was not achieved for all masked conditions (see Results Localization Task), in order to assure that performance in the discrimination task represents unseen gratings, subsequent analysis of discrimination performance for masked trials was restricted exclusively to those trials in which participants responded incorrectly in the localization task (for similar procedure, see e.g.; Jolij & Lamme, 2005). Likewise, analysis of discrimination performance for unmasked trials was restricted exclusively to those trials in which participants responded correctly in the localization task. Due to this difference in trial selection, masked and unmasked trials were analyzed in separate models.

An analysis of discrimination performance was performed using a general linear mixed-effects with the *glmer* function (lmer4 package; version: 3.3.1; Bates, Maechler, & Bolker, 2015). This was done to accommodate the binary and nonparametrically distributed data, and to account for individual differences in performance. Each model included a fixed intercept, a fixed effect for the factors threat condition (threat, safe) and spatial frequency (LSF, HSF), and a fixed effect for the interaction between threat condition and spatial frequency. Within-subject repeated measures were modelled by including a per-participant random adjustment to the fixed intercept (‘random intercept’), as well as per-participant random adjustments to the slopes of predictors, i.e., threat condition, spatial frequency, and interaction between them. All correlations among random effects were also included in the model. This resulted in a model “maximal with respect to the random effects” to avoid inflated Type-1 errors (Barr, Levy, Scheepers, & Tily, 2013). Point estimates (B) were used as a measure of the magnitude of the effects. *p*-values were determined using Type 3 Likelihood Ratio Tests implemented in the *mixed* function of the package *afex* (Singmann, Bolker, Westfall, & Aust, 2018).

To test if the orientation performance differed from chance level (i.e., is significantly larger than 50% correct performance), the mean orientation performance for all participants and each masked and unmasked condition was tested using one-sample one-tailed *t*-tests. All statistical analyses were performed in RStudio (version 1.0.143; R Core Team, 2015).

3. Results

3.1. Awareness check

To examine visual awareness of the gratings, the average performance accuracy for all participants for all eight conditions (threat LSF, HSF; safe LSF, HSF for masked and unmasked trials) in the localization task was tested against chance level performance (50% correct). As expected, localization accuracy of all unmasked conditions was significantly above chance level [threat LSF: M = 0.84, $t(1,23) = 9.57$, $p < .001$, $\eta_p^2 = 0.80$; safe LSF: M = 0.82, $t(1,23) = 8.97$, $p < .001$, $\eta_p^2 = 0.77$; threat HSF: M = 0.69, $t(1,23) = 5.58$, $p < .001$, $\eta_p^2 = 0.57$; safe HSF: M = 0.71, $t(1,23) = 6.50$, $p = .001$, $\eta_p^2 = 0.65$], implying that the gratings were visible in unmasked trials. All these effects remained significant after Bonferroni correction (adjusted *p* threshold = 0.0065, initial *p* value of 0.05 divided by 8 *t*-tests).

The analysis of masked trials revealed that localization performance for threat and safe HSF conditions did not differ significantly from chance level [threat HSF: M = 0.50, $t(1,23) = 0$, $p = 0.5$; safe HSF: M = 0.48, $t(1,23) = -1.35$, $p = .91$, $\eta_p^2 = 0.073$], confirming that the gratings were unseen in these trials. However, despite backward masking, localization performance for threat and safe LSF gratings in masked trials was above chance level [threat LSF: M = 0.55, $t(1,23) = 3.11$, $p = .002$; safe LSF: M = 0.54, $t(1,23) = 1.82$, $p = .041$, $\eta_p^2 = 0.12$], implying that despite backward masking, participants were still able to localize the gratings in these conditions. Performance in threat LSF condition furthermore remained significantly above chance level after Bonferroni correction (adjusted *p* threshold = 0.0065). In order to assure that discrimination performance in masked trials represents unseen gratings, subsequent analyses of the discrimination task were exclusively restricted to those masked trials in which participants responded incorrectly in the localization task (for similar procedure, see e.g.; Jolij & Lamme, 2005). In a similar vein, the analysis of discrimination performance for unmasked trials was restricted to those trials in which participants responded correctly in the localization task. Masked and unmasked trials were analyzed in separate models.

3.2. Discrimination task

In the discrimination task, we tested the prediction that if coarse visual input is processed unconsciously in a state of threat, we should observe above-chance and improved discrimination of successfully masked LSF stimuli under threat compared to safe trials relative to performance for HSF gratings.

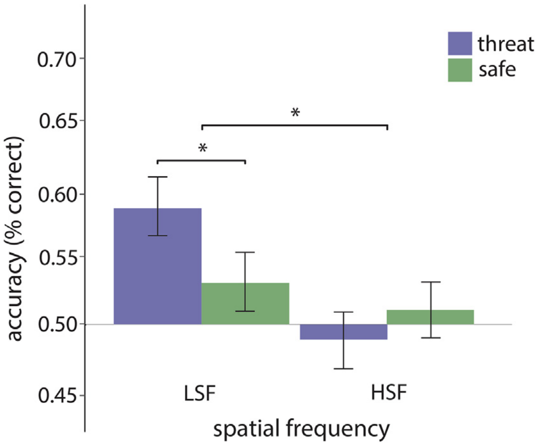

Fig. 2. Performance on the discrimination task for unseen masked trials in threat and safe conditions. LSF, low-spatial frequency; HSF, high-spatial frequency; *, $p < .05$. The horizontal line indicates chance performance (50% accuracy).

Masked trials. To test our hypothesis that unconscious processing of coarse visual information is present under state of threat, we first tested whether discrimination performance within incorrectly localized masked trials is better than chance level (50% correct). As can be seen in Fig. 2, discrimination performance for masked threat LSF trials was significantly above chance level, [M = 0.59, $t(1, 23) = 5.07, p < .001, \eta_p^2 = 0.53$). In contrast, performance in the remaining three masked conditions was not above chance level [safe LSF: M = 0.53, $t(1, 23) = 1.62$, $p = .060$, $\eta_p^2 = 0.10$; threat HSF: M = 0.48, $t(1, 23) = -0.74$, $p = .77$, $\eta_p^2 = 0.023$; safe HSF: M = 0.51, $t(1, 23) = 0.71$, $p = .24$, $\eta_p^2 = 0.021$]. Performance for masked LSF trials under threat remained significantly above chance after Bonferroni correction (adjusted p threshold = 0.0065).

Subsequently, we tested whether LSF discrimination under threat is significantly better relative to safe trials. We first found that an interaction between threat condition (threat, safe) and SF (LSF, HSF) was significant ($B = 0.35$, $SE = 0.14$, $\chi^2(1) = 5.56$, $p = .018$, see Fig. 2). Follow-up analyses revealed that the interaction between threat condition and SF was driven by a significant difference between threat and safe trials for LSF ($B = 0.44$, $SE = 0.21$, $\chi^2(1) = 4.39$, $p = .036$), but not for HSF trials ($B = 0.25$, $SE = 0.20$, $\chi^2(1) = 1.51$, $p = .21$). The remaining main effects of threat condition ($B = -0.095$, $SE = 0.15$, $\chi^2(1) = 0.42$, $p = .52$) and SF ($B = -0.26$, $SE = 0.15$, $\chi^2(1) = 3.19$, $p = .074$) were nonsignificant. These results indicate that when participants were objectively unaware of the stimuli, they were able to discriminate the orientation of LSF gratings, but only in a state of threat.

Unmasked trials. As expected, discrimination performance in all correctly localized unmasked trials was robustly above chance level [threat LSF: M = 0.86, $t(1, 23) = 11.65$, $p < .001$, $\eta_p^2 = 0.85$; safe LSF: M = 0.86, $t(1, 23) = 12.17$, $p < .001$, $\eta_p^2 = 86$; threat HSF: M = 0.80, $t(1, 23) = 10.01$, $p < .001$, $\eta_p^2 = 0.81$; safe HSF: M = 0.79, $t(1, 23) = 9.08$, $p < .001$, $\eta_p^2 = 0.78$]. The main effects of threat condition and SF, and the interaction between them, were nonsignificant (all $p_s > .05$). The fact that we did not replicate the effect of threat on behavioral performance in unmasked trials may be due to close-to-ceiling performance resulting from a relatively low task difficulty (i.e., only two orientations), which was necessary for the challenging masked condition.

4. Discussion

The current study shows that in the absence of visual awareness, anticipation of threat can induce above-chance and improved discrimination of low-spatial frequency information.

Our results demonstrate that although participants may have felt like they were guessing in masked trials, their behavioral responses were influenced by the anticipatory threat state, leading to above-chance discrimination performance for LSF gratings. Our results therefore offer behavioral support to the view that automatic visual processing in threatening situations relies on coarse visual information. The current findings are in line with previous neural evidence showing that subcortical visual regions (i.e., amygdala, pulvinar, SC), which are typically activated by unseen threat stimuli, respond specifically to LSF but not HSF fearful faces (Burra et al., 2017; Liddell et al., 2005; Mendez-Bertolo et al., 2016; Morris et al., 1999; Vuilleumier, Armony, Driver, & Dolan, 2003). They are also in line with behavioral evidence showing faster access of LSF relative to HSF threat stimuli (such as snakes) to consciousness, implying enhanced unconscious processing of LSF information (Gomes et al., 2017; but see Gayet, Stein, & Peelen, 2018; Stein, Seymour, Hebart, & Sterzer, 2014 for different results and interpretation using continuous flash suppression task).

By separating threat induction from the visual task, the current study extends these findings, and shows that the mechanism of automatic processing of LSF is not only restricted to threat cues, but reflects a broader sensitivity to LSF information observed also for neutral LSF information in a threat state. This suggests that initial threat detection mechanisms may rely on a general facilitation of LSF information irrespective of its threatening content, which may be evaluated later in the course of visual processing. We propose that such a general mechanism may underlie enhanced LSF processing of both neutral and threatening visual information during a threat state. The fact that we found it for neutral LSF information is particularly relevant for the etiology of anxiety disorders where rough configural information is equally used in processing of both neutral and threat cues (e.g., faces Langner, Becker, & Rinck, 2009;

Langner, Becker, Rinck, & van Knippenberg, 2015).

At the neural level, this observation raises the possibility that state-induced activation of the amygdala, through its efferent projections to visual areas, may exert control over ongoing visual processing by increasing its sensitivity to incoming coarse visual input, regardless of its threat relevance (Diano, Celeghin, Bagnis, & Tamietto, 2016; Pessoa & Adolphs, 2010; Tamietto & de Gelder, 2010). Given that activation of a subcortical visual pathway in response to unseen threat stimuli was observed using backward masking procedures, and that backward masking is thought to interfere with cortical processing (Fahrenfort, Scholte, & Lamme, 2007; Lamme & Roelfsema, 2000), it is possible that such a priming effect could operate at the subcortical level. Future neuroimaging or electrophysiological studies are needed to reveal whether such a mechanism underlies the current finding.

In general, automatic prioritization of coarse visual input regardless of threat content may aid threat detection according to a '*better safe than sorry'* principle (LeDoux, 1998). Namely, detection of potentially threatening cues could be initiated by rapidly processed coarse visual information, even at the cost of false positives (Gao, LoBue, Irving, & Harvey, 2017). From an evolutionary perspective, and in line with this view, localization of threats is of critical importance, and being able to discriminate the identity of a predator may be less helpful survival-wise if one does not know where it is. Discrimination of LSF gratings in our task is more likely to represent perception of crude visual characteristics of a cue which may not be sufficient to discriminate stimulus identity. With regard to the localization, we also observed improved localization of masked LSF stimuli under threat, which is in line with threat-related enhancement in unconscious detection of stimulus location in previous work (e.g., Gomes et al., 2017). The fact that we observed improved orientation discrimination despite the absence of localization ability suggests that the neural pathways responsible for these processes may not fully overlap, or that despite a successful masking procedure, the coarse features of the stimulus could still be processed unconsciously. This is in line with previous studies that showed that orientation discrimination can take place notwithstanding the absence of visual awareness of discriminated stimuli (Boyer, Harrison, & Ro, 2005; Koenig & Ro, 2018; Ro, Shelton, Lee, & Chang, 2004).

Some interpretational issues should be considered when evaluating the current findings. Because the current study is the first one to test the effects of anticipatory threat on unconscious perception of spatial frequency information, it was important to use the same spatial frequencies, i.e., 3 and 6 cpd, for which threat effects were previously shown for conscious perception (Lojowska et al., 2015, 2018). Anticipatory threat effects on a wider range of spatial frequencies should be tested in follow-up studies to test the generalizability of the current findings. In particular, the claim that unconscious threat effects are mediated through the magnocellular pathway could be validated by future studies showing threat effects for other spatial frequencies falling within the sensitivity range of this pathway ($SF < 4$ cpd, Leonova, Pokorny, & Smith, 2003). Future studies should also test to what extent the current and future threat-related effects on individual spatial frequencies can mediate previously observed threat effects on perception of real-life stimuli (Jusyte & Schonenberg, 2014; Roelofs, Hagenaars, & Stins, 2010; Vuilleumier et al., 2003), naturally consisting of a wider spectrum of spatial frequencies.

One could ask whether the masking procedure, despite making the stimulus subliminal, could have also influenced how strong or impoverished the sub-threshold representations of LSF and HSF stimuli were. Although we cannot exclude this possibility, previously found unconscious prioritization of LSF, but not HSF stimuli, using continuous flash suppression, suggests that our results may not be exclusive for the backward masking procedure (Gomes et al., 2017, but see Gayet et al., 2018). Future research using methods other than backward masking (e.g., continuous flash suppression or TMS over V1, Jolij & Lamme, 2005; Koenig & Ro, 2018) is necessary to shed more light on a potential contribution of sub-threshold representations to the observed findings.

Another potential methodological issue is that performance of the localization task might have been influenced by cognitive load during performance of the primary orientation task. We consider this unlikely as the difficulty of the experiment was relatively low by having only two orientations (45°, left and right) and two locations (left and right). Nevertheless, we cannot exclude the possibility that some of the incorrect localization trials represent seen, but not-remembered locations, resulting in a less conservative awareness check. Future studies could address this issue through balancing the order of localization and orientation tasks across participants.

Together, our findings show that unconscious processing of neutral coarse visual information can be induced by threat state, implying that a general facilitation of coarse visual information, irrespective of its threat content, may be part of an initial threat detection mechanism.

Authors' contribution

ML, MM, EJH, KR designed research. ML performed research. ML, MM analyzed data. ML, MM, EJH, KR wrote the paper. All authors approved the final version of the manuscript for submission.

Data availability statement

The data that support the findings of this study are available from the corresponding author (Maria Lojowska) upon request.

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