Freezing Promotes Perception of Coarse Visual Features

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Freezing is an evolutionarily preserved defensive behavior, characterized by immobility and heart rate deceleration, which is thought to promote visual perception. Rapid perceptual assessment of threat is crucial in life-threatening situations; for example, when policemen need to make split-second decisions about the use of deadly force. Here, we hypothesized that freezing is specifically associated with better perception of rapidly processed coarse, low-spatial frequency (LSF) features. We used a visual discrimination task in which participants determined the orientation of LSF and high-spatial frequency (HSF) gratings under threat of shock and safe conditions. As predicted, threat anticipation improved perception of LSF at the expense of HSF gratings. Crucially, stronger decrease in heart rate, a parasympathetic physiological index of freezing, was linked to better perception of LSF. These results provide empirical evidence for the comobilization of physiological and perceptual processes, which may play an important role in decision making under acute stress.

Keywords: freezing, visual perception, spatial frequency, fear bradycardia

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Freezing is an evolutionarily preserved defensive behavior thought to promote rapid perceptual assessment of threat (Blanchard, Griebel, Pobbe, & Blanchard, 2011; Campbell, Wood, & McBride, 1997; Fanselow, 1994; Lang, Bradley, & Cuthbert, 1997; Öhman & Wiens, 2002). Optimal decision making under threat can save animals from predation (Blanchard et al., 2011; Eilam, 2005) and is also important in humans. For instance, police

officers must rely on limited visual information to make split-second decisions about using lethal force (Fleming, Bandy, & Kimble, 2010; Nieuwenhuys, Savelsbergh, & Oudejans, 2012). It remains unclear, however, whether and how visual perception is altered during freezing. Revealing the relationship between freezing and visual perception would not only advance our understanding of primary defensive reactions, but it may also inform training programs aiming to enhance performance under threat.

During threat exposure, the balance between activation of the sympathetic and parasympathetic branches of the autonomic nervous system shapes the expression of defensive behavior (Fanselow, 1994). Whereas sympathetic dominance facilitates active fight-or-flight reactions, parasympathetic activity underlies freezing (Fanselow, 1994). A defining characteristic of freezing in both humans and animals is a transient, parasympathetically driven, deceleration of heart rate (HR) or *fear bradycardia* (Azevedo et al., 2005; Campbell et al., 1997; Öhman & Wiens, 2002; Roelofs, Hagenaars, & Stins, 2010). Fear bradycardia is thought to support a state of reduced body motion and thereby decrease the chance of being detected by predators (Campbell et al., 1997). Freezing is also seen as a critical decision-making stage during which an organism has to choose the most adaptive defensive reaction in given circumstances; that is, to remain frozen or to switch to active fight-or-flight (Eilam, 2005). The probability of switching between passive and active defensive behaviors largely depends on external threat characteristics, such as its magnitude, distance, and ambiguity (Blanchard & Blanchard, 1989; Eilam, 2005; Fanselow, 1994). Freezing, and in particular HR deceleration (Graham & Clifton, 1966; Lacey & Lacey, 1970; Sokolov & Cacioppo, 1997) has therefore long been thought to put an organism into a state

conducive to sensory intake (Blanchard et al., 2011; Lang et al., 1997; Öhman & Wiens, 2002). However, how perceptual processes are altered during freezing has never been scrutinized empirically.

Recent studies have suggested that emotional cues have a selective effect on visual perception, enhancing perception of coarse visual features, that is, low-spatial frequencies (LSFs), at the expense of fine-grained details, that is, high-spatial frequencies (HSFs, Bocanegra & Zeelenberg, 2009; Nicol, Perrotta, Caliciuri, & Wachowiak, 2013). For example, presentation of phylogenetically threat-relevant stimuli, such as fearful faces, results in an immediate perceptual shift from HSF to LSF perception (Bocanegra & Zeelenberg, 2009; Nicol et al., 2013). A similar enhancement in LSF perception has also been observed following instructed fear (Lee, Baek, Lu, & Mather, 2014).

At the neural level, these findings have been explained in terms of a threat-induced interaction between visual pathways functionally engaged in processing of these two types of spatial information (Bocanegra, 2014; Breitmeyer & Williams, 1990). Specifically, LSF information is conveyed rapidly along the magnocellular pathway projecting to the dorsal visual stream involved in action modulation. In contrast, fine-grained HSF information is processed by the phylogenetically younger and slower parvocellular pathway, which projects to the ventral stream and provides fine-grained information for object recognition at the cost of speed (Goodale & Westwood, 2004; Maunsell, 1987). Along these lines of evidence, it has been suggested that threat-related improvement in LSF detection may be facilitated by enhanced activation of the magnocellular pathway which then inhibits the parvocellular pathway (Bocanegra, 2014; Bocanegra & Zeelenberg, 2009; Breitmeyer & Williams, 1990).

Such a trade-off between LSF and HSF perception may be particularly relevant during freezing. A bias toward LSF perception may, on the one hand, facilitate rapid decision making through enhanced perception of coarse threat-relevant features such as location. Impairment in HSF perception, on the other hand, would compromise detailed analysis of the threat which would be too time consuming to benefit immediate survival. However, no studies to date have investigated this putative perceptual shift in relation to freezing and its psychophysiological concomitants.

The aim of Experiment 1 was, therefore, to examine whether the parasympathetically dominated state of freezing is associated with a shift in spatial vision toward LSF. To test this hypothesis, we used a visual discrimination task in which participants determined the orientation of LSF and HSF gratings under conditions of threat (anticipation of mild electrical shock) versus safety (no shock). HR and skin conductance were measured throughout the task to assess the activation of the parasympathetic and sympathetic nervous system, respectively. If freezing is indeed associated with a shift toward LSF perception, the following results should be expected: (1) Perception of LSF gratings should be improved on threat of shock versus safe condition, possibly at the expense of HSF detection; (2) Most critically, fear bradycardia as a *parasympathetically* controlled physiological index of freezing should be associated with the improvement of LSF perception. This relationship should remain significant after controlling for *sympathetically* dominated changes in skin conductance (Hermans, Henckens, Roelofs, & Fernández, 2013); and (3) No relationship between skin conductance and perceptual performance should be observed im-

plying that sympathetically controlled arousal, even though present during freezing, does not drive the perceptual changes. In Experiment 2, we aimed to estimate the orientation sensitivity function across a broader range of spatial frequencies in a nonthreatening condition. This allowed us to determine whether threat effects observed in Experiment 1 could be interpreted in terms of a threat-induced shift in the peak of this function. Such interpretation would be supported if this performance peak would fall in between the low and high spatial frequencies tested in Experiment 1.

Experiment 1

Method

Participants and design. Using G*Power 3 software (Faul, Erdfelder, Lang, & Buchner, 2007), we calculated that to achieve results at adequate power $(1 - \beta > 0.8)$ and medium effect size $(\eta_p^2 = .06)$, a minimum sample size of 23 participants was required to test. The maximum sample size was set to 34. Data collection was stopped when this number was reached provided exclusion criteria. A total number of 51 subjects with normal or corrected to normal vision were tested in a within-subjects design. Inclusion criteria were: no past or present neurological, psychiatric, or cardiovascular disease, and no use of psychotropic medications. All participants provided signed informed consent and were reimbursed with 20 euro for their participation. Data of 11 participants were excluded from the analysis because of technical problems $(N = 4)$, premature task termination $(N = 2)$, noncompliance with task instructions $(N = 3)$, and failure to reach the criterion of 75% performance accuracy $(N = 2)$. Participants with depressive psychopathology were excluded on the basis of the Beck Depression Inventory-II (BDI, Beck, Rush, Shaw, & Emery, 1979) score higher than 10 (Beck, Steer, & Brown, 1996, $N = 6$) as symptoms of depression have been linked to general cognitive impairments (Lee, Hermens, Porter, & Redoblado-Hodge, 2012) and dysfunctional emotional responses in particular during threat of shock (Grillon, Franco-Chaves, Mateus, Ionescu, & Zarate, 2013; Robinson, Overstreet, Letkiewicz, & Grillon, 2012). Data of a total 34 subjects aged between 18 and 30 years (mean age = 22.8 years; males = 11) were included in the analysis. All procedures were approved by the local institutional ethical board. We used a factorial design with two within-subject factors: threat condition (threat, safe) and spatial frequency (LSF, HSF).

Stimuli and apparatus. Visual stimuli were generated using MATLAB (MATLAB R2010a, The MathWorks, Inc.) in conjunction with the Psychophysics Toolbox (Brainard, 1997) and presented on a gamma-corrected liyama 19-in. Vision Master monitor (refresh rate of 100 Hz, resolution of 1024 × 768 pixels). Throughout the task, a fixation dot (size of 0.2° × 0.2°, luminance: 89 cd/m²) was displayed on a uniform gray background in the center of the screen (luminance: 79 cd/m²). The color of the fixation dot could change from gray to green, red, or yellow (see *Procedure and Experimental Task*). On each trial, a single Gabor grating (Gaussian-enveloped sinusoidal grating, 2.0° diameter size) was presented at 4° eccentricity from the fixation dot. Gabor gratings were presented at 30% Michelson contrast and in two frequency ranges: 3 cycles per degree (cpd) and 6 cpd, referred further as to LSF and HSF gratings, respectively. Given that the ability to detect targets outside of overt attention may be particu-

larly adaptive in threatening situations, peripheral presentation of gratings was chosen to increase the ecological validity of the task. In addition, by presenting stimuli at 4° eccentricity corresponding to approximately similar concentration of LSF-sensitive rods and HSF-sensitive cones in the retina (Purves et al., 2001), we aimed at reducing the bias toward any of the two frequencies. Participants performed the task at a distance of 66 cm with their head fixated in a chin rest.

Freezing was induced through a possibility of receiving mild electric shocks. 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.

Psychophysiological measurements, that is, HR and skin conductance, were recorded throughout the task using a Biopac MP 150 system (Biopac Systems, Goleta, CA) connected to a computer running AcqKnowledge software (Biopac Systems). The sample rate was set to 200 Hz. HR was measured with an earclip HR sensor attached to the participant's right ear lobe. Skin conductance was acquired through 8-mm diameter Ag/AgCl electrodes positioned on the third and fourth distal phalanges of the left hand.

Procedure and experimental task. The experiment started with filling out the BDI and other questionnaires (see supplemental material, available online) administered for sample characterization, which was followed by task instructions. Participants were informed about the association between the color of the fixation dot and the possibility of receiving an electric shock. A red fixation dot signaled a 50% chance of receiving an electrical shock at any time during its presentation. A green fixation dot, on the other hand, signaled a safe condition where no shocks were given. In addition, all participants were explicitly instructed to fixate the dot throughout the whole task, avoid excessive eye blinking during the red and green dot presentations, and not to shift their gaze toward the randomly presented grating in the left or right visual field. Next, they performed a practice session consisting of 12 trials with visual feedback about their performance (i.e., "Correct!", "Incorrect!", "Too late") and without shock administration. This was followed by the calibration of electrical shock intensity to ensure that its level was unpleasant but not painful for each individual participant.

Subsequently, participants performed a modified visual orientation discrimination task (Bocanegra & Zeelenberg, 2009; Nicol et al., 2013). The task required discrimination of the orientation of single LSF and HSF gratings under safe and threat conditions. In total, there were four conditions: threat LSF, threat HSF, safe LSF, and safe HSF trials, each consisting of 56 trials. Each trial started with a presentation of the red or green fixation dot, which remained on the screen for a period of 6 seconds (Figure 1). During this 6-s period, a LSF or HSF stimulus was presented at a random interstimulus interval (ISI), and for 40 ms at 4° eccentricity either to the left or to the right of the fixation dot. Given that the saccadic eye movement to peripheral stimuli takes about 160 ms (Walker, Deubel, Schneider, & Findlay, 1997), brief presentation of a stimulus for 40 ms was used to prevent from making saccadic eye movements toward the gratings. After 6 s, the color of the fixation
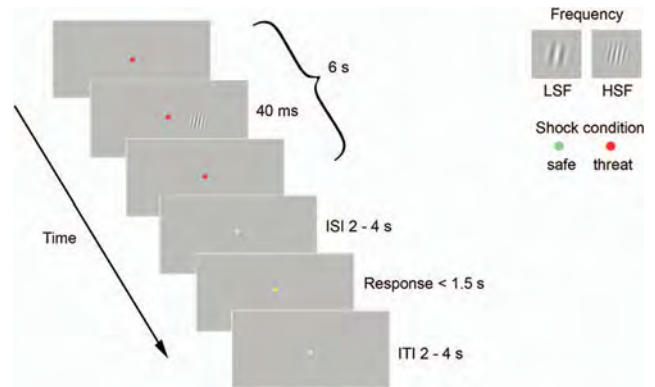

Figure 1. Visual orientation discrimination task. Green and red fixation dot (depicted as light and dark grey colors in a non-color version of the article, respectively) signaled none and 50% chance of receiving an electric shock, respectively. Participants were instructed to indicate, via button press, whether a LSF or HSF grating presented to the left or right of the fixation dot was tilted clockwise or counterclockwise. Responses were given after a 2–4 s ISI following trial offset. ISI, interstimulus interval; inter-trial interval (ITI), intertrial interval; HSF, high-spatial frequency; LSF, low-spatial frequency. See the online article for the color version of this figure.

dot changed from green or red to gray and remained onscreen for 2–4 s (ISI). The fixation dot then turned into yellow, prompting a response. Participants were required to indicate, through button press, whether the orientation of the grating was counterclockwise (arrow down on the keyboard) or clockwise (arrow up on the keyboard) with respect to a vertical orientation. If the reaction time (RT) exceeded a response window (1.5 s), visual feedback was presented ("Too late"). The response was followed by an intertrial interval of 2–4 s indicated by a gray fixation dot. An additional 12% of all trials (24 trials) with electric shocks were equally distributed across threat trials and excluded from the final analysis. In total, the task consisted of 192 trials (including shock trials) divided equally into 3 blocks with short breaks in between.

In order to maintain task difficulty at a constant 75% accuracy level on each condition, we used QUEST (Watson & Pelli, 1983). QUEST is a toolbox that uses Bayesian statistics to calculate the most probable perceptual threshold (here: orientation offset, deviation from a vertical orientation) based on trial-by-trial dynamics of behavioral responses (correct and incorrect responses) to reach a preset performance criterion (here: 75% correct responses). Therefore, correct responses resulted in adjusting the orientation threshold to a smaller angle on subsequent trials, and vice versa for incorrect responses. This procedure was applied separately for each of the four conditions and the resulting changes in the orientation offsets were used as the measure of behavioral performance. The initial orientation offsets for each condition were determined in a training block (14 trials per condition) preceding the task.

Data reduction and statistical analyses. Performance for each of the four conditions was defined as the mean orientation offset required to perform at 75% accuracy. Mean orientation offsets were calculated for each of the four conditions and across all three experimental blocks. Behavioral data were analyzed statistically using a repeated-measures analysis of variance

(ANOVA) with threat condition, spatial frequency, and block number as within-subjects factors.

Off-line analyses of event-related changes in HR and skin conductance level (SCL) were performed in MATLAB (MATLAB R2010a, The MathWorks, Inc.). HR responses were analyzed using in-house software for interactive visual artefact correction and peak detection, according to procedures detailed elsewhere (Hermans et al., 2013). For each trial, event-related HR responses were calculated as the difference between the averaged HR 2–6 s after stimulus onset and the averaged −25 s to −1 prestimulus baseline. This relatively long baseline window was chosen to account for fluctuations of HR with the respiratory cycle, that is, respiratory sinus arrhythmia (Hermans et al., 2013). The difference in averaged HR change between threat and safe conditions was calculated for each participant and used as an index of fear bradycardia (Azevedo et al., 2005; Hermans et al., 2013). Because of non-normal distribution of HR data (as indicated by Shapiro-Wilk test), the difference in HR between threat and safe conditions was assessed with a permutation t test with 50,000 random permutations.

To quantify changes in SCL during trials, we took the average SCL of 2–6 s after stimulus onset and subtracted the average SCL during a 1-s baseline period preceding trial onset. We chose this measure of averaged changes in SCL during trials because peak skin conductance response amplitudes are not representative of sympathetic arousal for longer trial durations (Phelps et al., 2001). The difference in averaged SCL changes between threat and safe conditions was calculated for each participant and used as an index of sympathetic arousal. SCL changes were analyzed at the group level using t-statistics.

To assess the relationship between fear bradycardia and perceptual performance, we correlated the fear bradycardia index (difference in averaged and baseline-corrected HR between threat and safe conditions) with the threat-induced difference in orientation offset (orientation offset threat minus orientation offset safe) separately for LSF and HSF trials. Furthermore, we examined the relationship between arousal and perceptual performance by correlating the index of sympathetic arousal (difference in averaged and baseline - corrected SCL between threat and safe conditions) with the threat-induced difference in orientation offset (orientation offset threat minus orientation offset safe), also separately for LSF and HSF trials. Because the physiological measures deviated from a normal distribution we used a Spearman's rank order correlation. Finally, to examine whether the relationship between the fear bradycardia index and perceptual performance can be explained by shared variance with the sympathetic arousal index, we partialed out the sympathetic arousal index in the correlation between the fear bradycardia index and the threat-induced difference in orientation offset.

Results

Behavioral results.   To test our first hypothesis that LSF detection is enhanced under conditions of threat, we conducted a 2 (threat condition: shock, no-shock) × 2 (spatial frequency: LSF, HSF) × 3 (block number, 1–3) repeated measures ANOVA. In line with our predictions, there was a significant threat condition by spatial frequency interaction, $F(1, 33) = 6.74$, $p = .014$, $\eta_p^2 = .17$; Figure 2), indicating that threat of shock resulted in *lower*
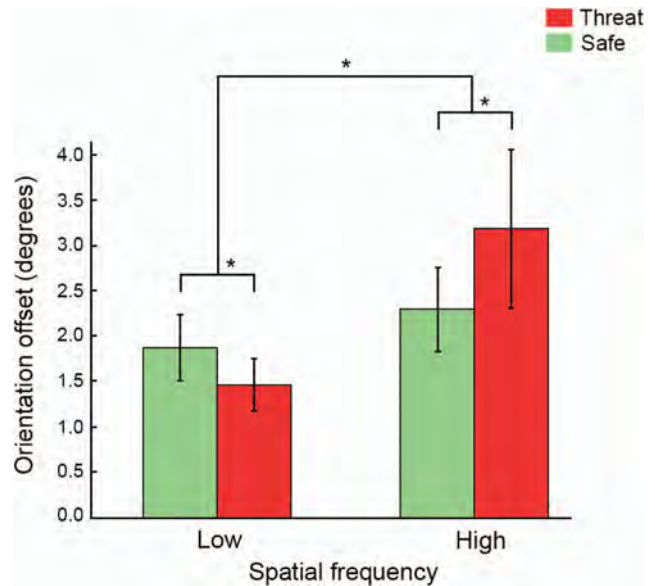

Figure 2.   Change in the orientation offset as a function of threat and spatial frequency condition. Threat of shock improves and impairs perception of low-spatial frequency (LSF) and high-spatial frequency (HSF) gratings, respectively. Error bars represent 95% confidence intervals. Asterisks indicate significant differences (* $p < .05$). See the online article for the color version of this figure.

orientation offsets for LSF gratings, $M_{safe} = 1.47$ vs. $M_{threat} = 1.88$, $t(33) = -2.31$, $p = .027$, $d = .40$, and *higher* orientation offsets for HSF gratings, $M_{safe} = 2.30$ vs. $M_{threat} = 3.19$, $t(33) = 2.04$, $p = .049$, $d = .35$. We did not find a main effect of threat condition, $F(1, 33) = 1.19$, $p = .28$, $\eta_p^2 = .03$, indicating that threat of shock did not lead to a nonspecific improvement of perception. Thus, our findings show that threat specifically improves detection of LSF information at the expense of HSF information.

There were additional main effects of spatial frequency, $F(1, 33) = 23.58$, $p < .001$, $\eta_p^2 = .42$, and block number, $F(1, 39.9) = 17.64$, $p < .001$, $\eta_p^2 = .35$, indicating that participants' perceptual performance was in general better for LSF information, and that performance improved over time. Block number did not interact with threat condition, $F(1.1, 37.7) = 0.001$, $p = .99$, $\eta_p^2 = .00$; spatial frequency, $F(1.2, 40.5) = 3.40$, $p = .064$, $\eta_p^2 = .093$, nor with threat condition by spatial frequency interaction, $F(1.1, 37.6) = 1.64$, $p = .21$, $\eta_p^2 = .05$.

Physiological results.   To examine whether threat of shock was associated with freezing, we tested whether the threat condition was associated with stronger averaged HR decelerations (fear bradycardia) than the safe condition using a permutation paired-samples t test. As expected, we found stronger HR deceleration in the threat condition compared with the safe condition, $t(33) = -4.02$, $p < .001$, $d = .88$ (Figure 3A). We also found stronger SCL increases in threat versus safe conditions, $t(33) = 2.45$, $p = .014$, $d = .65$. These findings show that threat of shock induces both parasympathetically (HR deceleration) and sympathetically (SCL increases) driven autonomic responses. Notably, no correlation between threat-induced changes in HR and SCL was observed, $\rho(32) = .048$, $p = .79$.
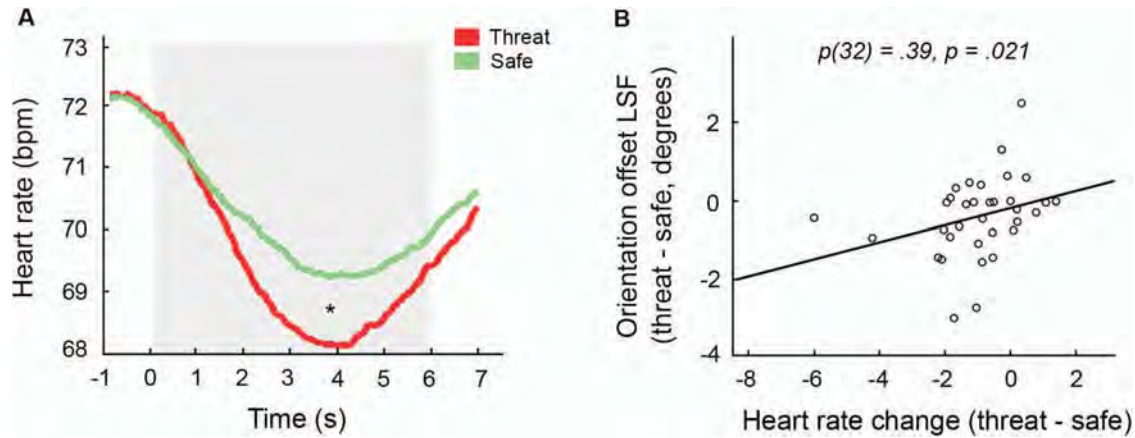
Figure 3. (A) Significant difference in HR on threat as compared with safe conditions. Although both threat and safe conditions were characterized by HR deceleration, threat condition: $t(33) = -9.11$, $p < .001$, $d = 1.56$; safe condition: $t(33) = -5.54$, $p < 001$, $d = .95$, relative to baseline, a stronger decrease in HR was observed in the threat condition. (B) Positive correlation between threat-induced changes in low-spatial frequency (LSF) orientation offset and fear bradycardia. Bpm, beats per minute; shaded area represents a period of stimulus and possible shock presentation; * $p < .05$. See the online article for the color version of this figure.

Behavior—HR relationship. To test our second hypothesis that freezing is associated with increased visual perception of LSF information, we calculated a correlation between threat-induced differences in LSF orientation offset and individual scores of fear bradycardia, and found them to be positively correlated, $\rho(32) = .39$, $p = .021$ (Figure 3B). Notably, this relationship remained significant after partialing out the effects of sympathetically driven changes in SCL, $\rho(31) = 0.35$, $p = .046$, implying that threat-related improvement in LSF perception is specifically associated with parasympathetic activation.

No significant correlation between individual scores of fear bradycardia and threat-induced differences in HSF orientation threshold was observed, $\rho(32) = .19$, $p = .27$. Furthermore, in accordance with our third hypothesis, no significant correlations between changes in SCL and orientation offset for LSF, $\rho(32) = .23$, $p = .19$, and HSF, $\rho(32) = .19$, $p = .28$ were observed.

Following publication guidelines (Simmons, Nelson, & Simonsohn, 2011), below we report the main statistical results including participants excluded based on a BDI score above 10. Including these six participants resulted in no significant interaction effect between threat condition and spatial frequency, $F(1, 39) = 1.57$, $p = .22$. Using the BDI score as a covariate to control for depressive symptoms resulted in a significant interaction, $F(1, 38) = 5.63$, $p = .023$, $\eta_p^2 = .13$. Furthermore, including these subjects in a correlation analysis resulted in a significant correlation between individual scores of fear bradycardia and threat-induced differences in LSF orientation offset, $\rho(38) = .44$, $p = .005$, but not between fear bradycardia scores and threat-induced HSF orientation offset, $\rho(38) = .16$, $p = .34$. The results therefore remained significant in the total group when taking the severity of depression into account.

Experiment 2

Previous studies have shown that emotional cues shift the perceptual sensitivity function toward lower spatial frequencies (Bo-canegra & Zeelenberg, 2009; Lee et al., 2014). To be able to evaluate our results from Experiment 1 in light of those findings, we conducted a second experiment in which we estimated the orientation sensitivity function across a wider range of spatial frequencies in the nonthreatening condition. Particularly, we aimed to estimate the peak of this function, because an interpretation of our findings in terms of a shift toward lower spatial frequencies would require the performance peak to lie between the two spatial frequencies tested in Experiment 1 (i.e., between 3 cpd and 6 cpd).

Method

An additional sample of 22 participants was tested in a nearly identical design with the following range of spatial frequencies: 0.5, 1.5, 3.0, 4.5, 6.0, 7.5, and 8.0 cpd. The ISI and ISI were shortened to 1–2 s, and we included only a safe condition. The task was divided into 4 blocks of 98 trials each (14 trials for each spatial frequency in each block) and took about 1 hr. The first block was used for the stabilization of the QUEST adaptive staircase (titrating performance to 75%) and was discarded from the final analysis. All remaining procedures were the same as in Experiment 1. Mean orientation offsets were calculated for each of the seven spatial frequencies and analyzed statistically with a repeated measures ANOVA.

Results

First, we assessed the difference in orientation offsets between 3 and 6 cpd; that is, the two spatial frequencies that were used in Experiment 1 using *t*-statistics. As expected, and replicating the results from Experiment 1, LSF gratings were perceived significantly better than HSF gratings, $t(21) = -3.08$, $p = .006$, $d = .66$. Furthermore, in line with previous findings, orientation sensitivity across all frequencies varied as a function of spatial frequency, $F(6, 96) = 7.51$, $p < .001$, $\eta_p^2 = .32$, and showed a quadratic trend, $F(1, 16) = 19.65$, $p < .001$, $\eta_p^2 = .55$.

Next, we fitted the quadric function and used its parameters to estimate the frequency of maximum orientation sensitivity (Figure 4). This peak was reached at a spatial frequency of 3.56 cpd (i.e., between the 3cpd and 6 cpd used in Experiment 1; Figure 4). These findings support thus an interpretation of the Experiment 1 results in terms of a threat—induced shift of the baseline performance-peak toward lower spatial frequencies.

Discussion

The aim of this study was to examine how visual perception is altered during freezing. Four major findings emerge from the present investigation. First, anticipatory fear induced a spatial frequency shift in visual perception characterized by improved perception of LSF information, at the cost of detection of HSF information. Second and most critically, participants with stronger parasympathetically driven decrease in HR, a physiological index of freezing, exhibited a better discrimination of LSF targets. This relationship remained significant after controlling for sympathetically driven changes in skin conductance level. Third, no relation between perceptual performance and changes in skin conductance level were found, implying that observed improvement in LSF perception is linked specifically to parasympathetic activity during freezing. Finally, the estimation of the orientation sensitivity function revealed that the observed LSF benefit at the expense of HSF may be accounted for by a shift of the sensitivity function toward lower spatial frequencies.

Our results extend previous studies showing emotional modulation of low-level visual perception (Bocanegra & Zeelenberg, 2009; Nicol et al., 2013; Phelps, Ling, & Carrasco, 2006). Improvement of LSF at the expense of HSF perception was previously found shortly (30 ms, 34 ms ISI) following presentation of fearful faces (Bocanegra & Zeelenberg, 2009; Nicol et al., 2013). Our finding shows that this is not a short-lived and stimulus-

Figure 4. The average orientation offset across seven spatial frequencies at 30% Michelson contrast (lower tilt indicates better performance). Error bars represent 95% confidence intervals. Dotted line signifies the vertex of the fitted quadratic function [min tilt: 1.88 degrees at spatial frequency of 3.56 cpd]. The asterisk indicates a significant difference between 3 cpd and 6 cpd-frequencies used in Experiment 1 (* $p < .05$); cpd, cycles per degree. See the online article for the color version of this figure.

dependent effect, but it persists at least up to seconds during a state of anticipatory fear. A recent study furthermore demonstrated increased contrast sensitivity for LSF following threat of shock cues (Lee et al., 2014). Based on the observation that threat of shock triggered skin conductance responses, the latter study suggested that the observed peak in contrast sensitivity toward LSF can be accounted for by arousal (Lee et al., 2014). However, no direct relationship between skin conductance responses and perceptual performance was reported, raising the question as to whether this behavioral effect may have been alternatively attributed to parasympathetically controlled physiological changes accompanying threat of shock. Here, we demonstrate that threat of shock results in both sympathetically driven skin conductance responses and parasympathetically driven HR deceleration. Critically, improvement in LSF perception was exclusively associated with HR deceleration and this relationship remained significant after controlling for skin conductance responses. These findings, therefore, link the perceptual shift toward LSF directly to an autonomic parasympathetic physiological response profile associated with freezing.

So far, perceptual improvement during freezing has been mainly described as part of conceptual models of animal defensive behaviors based on their threat-oriented bodily responses, such as visual scanning of the environment and slow head movements, among others (for a review, see Hagenaars, Oitzl, & Roelofs, 2014). Here, we provide empirical evidence supporting this concept in humans. Our findings show however that, in contrast to animal models, freezing does not prompt a *general* improvement in visual perception, but rather a *specific* shift in the direction of LSF. The evolutionary significance of improved LSF perception may be twofold. First, it may promote detection of threat-relevant features such as its presence or location (Bocanegra & Zeelenberg, 2011) which is important for initial threat assessment and action selection when detailed analysis of the source of threat is less relevant. Second, LSF information is processed relatively fast in the brain (Maunsell, 1987) and the prioritization of LSF information during freezing may be crucial for rapid behavioral choices in often time-constrained threatening situations (Eilam, 2005; Nieuwenhuys et al., 2012). This prioritization of faster information processing at lower spatial resolutions at the expense of slower high spatial resolution information during freezing would thus serve rapid threat assessment according to a "better safe than sorry" principle. On the contrary, such specific LSF versus HSF gain may be less relevant in a fight-or-flight state where the fine-tuning and monitoring of generated actions may be more crucial for successful overcoming of threat. These notions are in line with psychophysiological theories emphasizing the role of HR in the control of visual sensitivity (Graham & Clifton, 1966; Lacey & Lacey, 1970; Sokolov & Cacioppo, 1997). These theories suggest that while situations requiring less openness for external cues, such as motor regulation (Konttinen, Lyytinen, & Viitasalo, 1998), are signified by HR *increases*, perceptual effort and lower perceptual thresholds are reflected in HR *decreases* (Lacey & Lacey, 1970).

The relation between fear bradycardia and improved LSF perception may imply that these two processes are regulated by overlapping neural mechanisms. Fear bradycardia and visual processes are likely to be regulated by efferent projections from the amygdala to the brainstem periaqueductal gray (PAG; Fanselow, 1994; Hermans et al., 2013) and to different levels of the visual
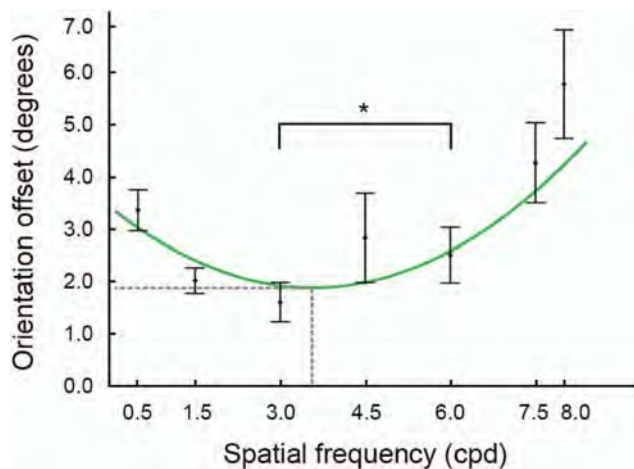
system (Amaral, Behniea, & Kelly, 2003; Pessoa & Adolphs, 2010; Tamietto, Pullens, de Gelder, Weiskrantz, & Goebel, 2012; Vuilleumier, Armony, Driver, & Dolan, 2003), respectively. The PAG and its afferent connections from the amygdala have been linked to the generation of freezing in animals and humans (Fanselow, 1994; Gozzi et al., 2010; Hermans et al., 2013; Kim, Rison, & Fanselow, 1993). On the other hand, the amygdala may enhance the activation of the LSF–sensitive magnocellular pathway, although the neural mechanism underlying this interaction is still unclear and may involve both subcortical and cortical visual circuits (Bocanegra, 2014; Pessoa & Adolphs, 2010; Tamietto & de Gelder, 2010). Future studies are needed to reveal the neural substrates of this interaction, and the extent to which neural mechanisms regulating perceptual and psychophysiological responses to threat do indeed show an overlap. Such findings would not only explain the current findings but would also support current motivational accounts of defensive behavior implying that in threatening situations, a common neural mechanism is involved in the mobilization of physiological responses to optimally counter threat, and perceptual processing to prompt information gathering (Blanchard et al., 2011; Bradley, 2009; Lang & Bradley, 2010; Lang et al., 1997).

In addition to theoretical significance, the present study has also practical implications. Our results may be relevant for better understanding of decision making in stressful situations, where perceptual assessment of threat is crucial for optimal fight-or-flight decisions. For example, police officers often have to make shooting decisions based on split-second threat assessment (Fleming et al., 2010; Nieuwenhuys et al., 2012). In contrast to HSF features associated with fine object recognition, enhanced perception of LSF under threat may facilitate the generation of coarse object representations (Bar, 2003), which in turn may contribute to faulty defensive reactions in situations where safe objects (e.g., phone) are mistakenly perceived as threat (e.g., gun). In addition, these results may be also relevant for training programs intended for improving object perception by means of HR regulation in combat situations. It should be noted, however, that the dynamics of freezing and its relevance for decision making in real-life situations and in response to more complex percepts (e.g., objects and scenes), still need to be addressed by means of more ecologically valid paradigms.

Some interpretational issues should be considered when evaluating the present findings. First, although our results support the notion that threat-triggered modulation of spatial vision relies on the shift of the baseline response peak toward lower spatial frequencies (i.e., toward the left of the response curve, Bocanegra & Zeelenberg, 2009; Lee et al., 2014), in previous work the perceptual shift was found for even lower frequencies (i.e., around 2 cpd compared with 3 cpd found here). This suggests that the range of LSFs facilitated by threat depends on the baseline response pattern (in nonthreatening situation) and specific experimental configurations.

Second, fear bradycardia was not associated with HSF performance. The lack of such a relationship in our study may be explained by the fact that impairment of HSF perception may be a secondary outcome resulting from the inhibitory effect of magnocellular pathway on HSF—sensitive parvocellular pathway (Bocanegra, 2014; Breitmeyer & Williams, 1990).

Third, one may argue that increased pupil dilation during threat anticipation may result in optical aberrations on the retina impairing mainly fine-grained vision (DeValois & DeValois, 1988). Although the present study did not include pupillometry, skin conductance and pupil dilation are known to be highly correlated measures controlled by common sympathetic neural pathways (Bradley, Miccoli, Escrig, & Lang, 2008). We did not find any correlation between skin conductance and perceptual performance, and the correlation between HR deceleration and performance for LSF targets remained significant when controlling for skin conductance. Therefore, our findings are unlikely to be explained by changes in pupil dilation. In addition, even though pupil dilation may theoretically result in worsened HSF perception, it cannot explain the improved LSF perception, which is thought to be unaffected or even slightly impaired in conditions of pupil dilation (DeValois & DeValois, 1988). Nonetheless, future studies including pupillometry are needed to investigate the exact relationship between pupil dilation and spatial frequency perception during freezing.

On a similar note, some studies have suggested that microsaccades facilitate perception of fine-grained visual information (Rucci, Iovin, Poletti, & Santini, 2007). Reduction of microsaccades during freezing could therefore account for the weaker perception of HSF targets observed in the current study. However, previous studies have shown a lack of difference in fixation-driven microsaccades on threat versus safe conditions (Laretzaki et al., 2011), suggesting that changes in microsaccades should not be observed during freezing either. Nevertheless, future studies with eye-tracking are needed to clarify this issue. Likewise, further research should also investigate the role of attention in altered perception during freezing. Although direct empirical evidence is lacking, it also it cannot be ruled out that processing of coarse visual features could be facilitated by increased attention to this type of features under threat of shock.

Finally, threat of shock was independent of perceptual choices, that is, participants could not avoid electrical shock by giving correct responses. This was done to achieve comparable levels of motivation on both threat and safe conditions, as the possibility to avoid threat has been suggested to engage motivational brain circuits and facilitate defensive behavior (Delgado, Jou, Ledoux, & Phelps, 2009; Lang & Bradley, 2010; Miskovic & Keil, 2014). Future studies should examine the contribution of motivational processes to affect-driven perceptual effects observed here.

In conclusion, our findings reveal that freezing is associated with improved perception of coarse LSF features. This change in perceptual sensitivity may play an important role in initial threat assessment and the choice of optimal defensive behavior during freezing.

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