

Emotion-Induced Trade-Offs in Spatiotemporal Vision

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It is generally assumed that emotion facilitates human vision in order to promote adaptive responses to a potential threat in the environment. Surprisingly, we recently found that emotion in some cases impairs the perception of elementary visual features (Bocanegra & Zeelenberg, 2009b). Here, we demonstrate that emotion improves fast temporal vision at the expense of fine-grained spatial vision. We tested participants' threshold resolution with Landolt circles containing a small spatial or brief temporal discontinuity. The prior presentation of a fearful face cue, compared with a neutral face cue, impaired spatial resolution but improved temporal resolution. In addition, we show that these benefits and deficits were triggered selectively by the global configural properties of the faces, which were transmitted only through low spatial frequencies. Critically, the common locus of these opposite effects suggests a trade-off between magno- and parvocellular-type visual channels, which contradicts the common assumption that emotion invariably improves vision. We show that, rather than being a general "boost" for all visual features, affective neural circuits sacrifice the slower processing of small details for a coarser but faster visual signal.

Keywords: emotion, vision, fearful faces, spatial resolution, temporal resolution

In complex environments, observers rely on various types of visual cues to guide their actions. Facial expressions, for instance, are biologically meaningful signals that play an important role in guiding interpersonal interactions, motivational behavior, and cognition. From an evolutionary perspective, one might expect that emotionally significant visual signals should be subject to preferential perceptual analysis in order to promote adaptive behavior in situations that are relevant for survival or reproduction (Dolan, 2002; Phelps & LeDoux, 2005). Indeed, recent findings from various experimental paradigms indicate that emotion affects visual perception. For example, emotional words are identified more accurately than are neutral stimuli in masked visual identification tasks (Gaillard et al., 2006; Zeelenberg, Wagenmakers, & Rotteveel, 2006). Emotional words and faces are also identified more accurately during the "attentional blink" in rapid serial visual presentation tasks (Anderson, 2005; Anderson & Phelps, 2001; Fox, Russo, & Georgiou, 2005). In addition, emotional faces and pictures are detected faster and for prolonged durations during binocular rivalry (Alpers & Pauli, 2006; Yang, Zald, & Blake, 2007). Finally, various types of threat-related stimuli—such as emotional faces, snakes, and spiders—are identified more rapidly than are neutral stimuli in visual search tasks (Fox et al., 2000; Öhman, Flykt, & Esteves, 2001).

Emotional influences in perception could arise at different stages of visual processing (Bocanegra & Zeelenberg, 2009a; Mathewson, Arnell, & Mansfield, 2008). For example, emotion might facilitate the early processing of elementary visual features such as color, brightness, surfaces, and edges (Bocanegra & Zeelenberg, 2009b; Phelps, Ling, & Carrasco, 2006); the binding of these visual features into coherent object representations (MacKay, Hadley, & Schwartz, 2005; Mather, 2007); or the attentional selection of object representations when stimuli are in spatial or temporal competition with each other (Anderson, 2005; Fox, Russo, Bowles, & Dutton, 2001; Holmes, Green, & Vuilleumier, 2005).

In recent years, neurophysiological research on emotion has suggested that the affective significance of stimuli influences early stages of visual processing. Studies using positron emission tomography and functional magnetic resonance imaging (fMRI) have indicated that emotion boosts activations in visual cortex (Lang et al., 1998; Morris et al., 1998; Vuilleumier, Armony, Driver, & Dolan, 2001). Also, event-related potential (ERP) studies have suggested that the initial visual components are affected by emotion (Pourtois, Grandjean, Sander, & Vuilleumier, 2004; Schupp et al., 2004; Stolarova, Keil, & Moratti, 2006). Accumulating evidence points to the amygdala, a medial temporal lobe structure involved in emotion processing, as a critical mediator of these emotional modulations. That is, emotional stimuli may quickly and automatically activate the amygdala (Öhman, 2002; Whalen et al., 1998), which in turn modulates ongoing processing in the visual cortex (Hung et al., 2010; Vuilleumier, 2005). Anatomical studies have shown that the amygdala projects to all levels of the ventral visual stream (Amaral, Behnia, & Kelly, 2003). In addition, studies have consistently shown that fearful facial expressions, compared with neutral facial expressions, modulate activations in the amygdala and extrastriate visual areas (Morris et al., 1998; Vuilleumier et al., 2001). Importantly, a recent study

This article was published Online First March 28, 2011.

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We thank Mario de Jonge, Diane Pecher, and Lisa Vandenberg for helpful comments on an earlier version of this article.

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with patients with temporal lobe lesions has directly implicated the amygdala in modulating the visual cortex, presumably via feedback-type projections (Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004).

Although many neurophysiological findings have suggested that emotion facilitates early stages of visual processing, few studies have investigated whether emotion affects the actual perception of elementary visual features. The first psychophysical study to investigate this question presented a fearful face cue prior to low spatial frequency (LSF) Gabors at threshold contrast (faint sinusoidal luminance gratings with a spatial frequency of 2 cpd; Phelps et al., 2006). It was found that observers' perception of the Gabor targets improved when they were cued by a fearful compared with a neutral face cue. Although the fearful face cue was task-irrelevant, its mere presence had a beneficial effect, suggesting that it triggered a visual facilitation that carried over onto the processing of the subsequently presented Gabors. Although previous neurophysiological findings pointed toward an emotion-induced facilitation in early vision, the findings by Phelps et al. (2006) provided the first behavioral evidence for this effect.

Surprisingly, we recently found that emotion can also impair early vision. In a paradigm similar to that in Phelps et al. (2006), we investigated whether this emotion-induced facilitation generalizes across different spatial frequencies (Bocanegra & Zeelenberg, 2009b). We tested the effect of a fearful face cue on the perception of coarse LSF Gabors and fine-grained high spatial frequency (HSF) Gabors at suprathreshold contrast. Consistent with the previous finding of Phelps et al. (2006), our finding was that a fearful face cue improved the detection of a slight orientation tilt for an LSF Gabor. Unexpectedly, we found that a fearful face cue impaired tilt detection for an HSF Gabor (Bocanegra & Zeelenberg, 2009b). This finding suggests that the benefits of emotion do not extend to all basic properties of vision. Instead of emotion overall inducing facilitation in vision, it improves the processing of coarse features but impairs the processing of fine-grained details.

Why does emotion impair fine-grained spatial vision? Current behavioral and neurophysiological accounts of emotion-induced modulations in perception do not predict this deficit (Anderson, 2005; Fox et al., 2001; Öhman et al., 2001; Phelps et al., 2006; Vuilleumier, 2005; Zeelenberg et al., 2006). One possibility is that emotion-induced decrements in spatial vision are related to emotion-induced gains in temporal vision. From an anatomical and functional point of view, the visual system consists of several parallel pathways that have adapted to complementary, though conflicting, aspects of visual information processing. For example, visual pathways responsible for transmitting fine-grained spatial information are inherently slower in their temporal response latencies. On the other hand, visual pathways responsible for transmitting coarse spatial information are relatively faster in their temporal responses (Callaway, 1998). In a complex visual world, an adaptive observer has to cope with the conflicting demands of spatial and temporal visual processing. By trading off the processing resources dedicated to spatial versus temporal visual features, emotional responses might allow observers to transiently optimize their visual performance in threatening situations. A temporal gain would speed up visual processing and intrinsically benefit the detection of threat-relevant features such as motion, depth, and direction. In this manner, individuals' affective neural circuits

might facilitate faster coarser pathways and temporarily inhibit slower fine-grained pathways. Within this perspective, emotion-induced deficits in spatial vision might not be incidental phenomena but instead could be functionally linked to benefits in temporal vision. Although it has been shown that fearful face cues cause decrements in fine-grained spatial vision (Bocanegra & Zeelenberg, 2009b), it is currently unknown whether these spatial impairments are related to improvements in the temporal domain.

What mechanisms could underlie an emotion-induced trade-off in spatiotemporal vision? Emotion-induced spatial deficits could be due to interactions between magno- and parvocellular-type channels in the visual system. Parvocellular channels have smaller receptive fields selective for fine-grained HSF stimuli at high luminance contrast, whereas magnocellular channels have larger receptive fields selective for coarse LSF stimuli at low contrast (Callaway, 1998). Apart from their differences in spatial receptive fields, magno- and parvocellular channels can also be differentiated in terms of their temporal response properties. Parvo cells exhibit slower and sustained responses compared with magno cells, which show fast and transient responses (Callaway, 1998; De Valois, Cottaris, Mahon, Elfar, & Wilson, 2000). Given that the amygdala receives magnocellular type visual input and projects to the visual cortices (Amaral et al., 2003), it seems reasonable to assume that the presentation of a fearful face cue would benefit low-contrast LSF information. Indeed, this is consistent with Phelps et al.'s (2006) finding that a fearful face cue improves the perception of threshold LSF Gabors. However, by itself this does not explain the deficit for suprathreshold HSF Gabors that we obtained in a recent study (Bocanegra & Zeelenberg, 2009b). Although benefits for low-contrast LSF stimuli (Phelps et al., 2006) suggest a facilitation of magnocellular processing, magno cells, compared with parvo cells, saturate quickly for visual presentations at higher contrasts (>0.10) and lack the spatial sensitivity that is required for processing HSFs (Derrington & Lennie, 1984). We therefore speculated that the spatial deficits might be due to a trade-off between systems receiving their visual input from predominantly magno- versus parvocellular visual channels. That is, emotion might enhance the sensitivity of magnocellular-type channels, which in turn inhibit parvocellular-type channels. Interchannel inhibitory mechanisms have been used previously to explain a wide variety of findings in various perceptual paradigms, such as metacontrast masking (Breitmeyer & Ogmen, 2000), saccadic suppression (Burr, Morrone, & Ross, 1994), and texture segmentation (Yeshurun & Carrasco, 2000). Such an interchannel mechanism would predict that the pattern of emotion-induced benefits and deficits that we obtained recently (Bocanegra & Zeelenberg, 2009b) generalizes to other visual dimensions. In particular, a facilitation in magnocellular processing would promote the *segregation* of visual signals over time (increasing temporal resolution), whereas an inhibition of parvocellular processing would promote the *integration* of visual signals in space (decreasing spatial resolution).

In the present study, we tested these predictions by assessing observers' spatial and temporal visual resolution threshold in gap detection tasks (Yeshurun & Carrasco, 1999; Yeshurun & Levy, 2003). In Experiment 1, we investigated the influence of a fearful face cue on spatial resolution and temporal resolution. If emotion induces a perceptual trade-off in vision, then different emotion-induced effects should be observed in these complementary as-

pects of visual perception. We expected that fearful face cues would elicit a deficit in spatial resolution and that this spatial deficit would be accompanied by a symmetrically opposite benefit in temporal resolution. In Experiment 2, we used face cues with different spatial-frequency compositions to test whether the effect of emotion on spatiotemporal resolution was driven by the LSFs or HSFs of the face cues. That is, in contrast manipulating the spatial frequency of the Gabor target, which we did in a recent study (Bocanegra & Zeelenberg, 2009b), we manipulated the spatial frequency content of the face cues. Because the amygdala is believed to receive subcortical visual input of the magnocellular type, we predicted that the emotion-induced effects would be obtained with LSF face cues but not with HSF face cues (Jones & Burton, 1976; Morris et al., 1998; Vuilleumier, Armony, Driver, & Dolan, 2003; Whalen et al., 1998). In Experiment 3, we used face cues that consisted of an LSF face and an HSF face, with one superimposed on the other (and one face presented upright and the other inverted), to test whether the effects of emotion on spatiotemporal resolution would be abolished when either LSFs or HSFs of the face cue were inverted. Because emotional facial expression is not readily processed when a face is inverted (Farah, Tanaka, & Drain, 1995), we predicted that emotion-induced effects would be obtained only when the LSFs of the faces were upright and the HSFs were inverted but not when the LSFs were inverted and the HSFs were upright.

Experiment 1

In Experiment 1 we investigated the influence of a fearful face cue on spatial resolution and temporal resolution. Similar to previous studies (Bocanegra & Zeelenberg, 2009b; Phelps et al., 2006), we presented a fearful or neutral face cue prior to a visual target. Participants performed a threshold spatial or temporal gap detection task with target Landolt circles containing either a small spatial or brief temporal discontinuity (see Figure 1). The presentation of an emotional cue was predicted to facilitate magnocellular processing at the expense of parvocellular processing. We predicted that, as a consequence, fearful cues, compared with neutral cues, would impair the detection of a small spatial gap in the target (requiring parvocellular visual processing) and improve the detection of a brief temporal gap in the target (requiring magnocellular visual processing).

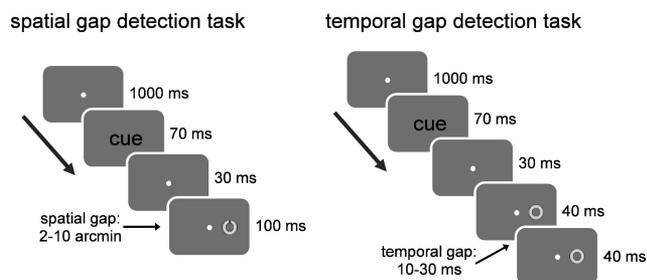


Figure 1. Illustration of the trial sequence for the spatial and temporal gap detection tasks in Experiments 1–3. The cue display consisted of either neutral or fearful faces. Examples of face cues are provided in Figure 2.

Method

Participants. Ten students at Erasmus University Rotterdam participated for course credit or a small monetary reward. All participants had normal or corrected-to-normal vision. Participants gave informed consent, and no one participated in more than one of the experiments reported here. All procedures were executed in compliance with institutional guidelines and were approved by the local ethics committee.

Stimulus materials and apparatus. A light gray fixation point ($0.2^\circ \times 0.2^\circ$, 45 cd/m^2) was presented at the center of a uniform gray background (25 cd/m^2) throughout each trial. To manipulate emotion, facial photographs of 11 unique persons portraying prototypical fearful and neutral expressions were selected from the Picture of Facial Affect series (Ekman & Friesen, 1976). The cue display consisted of two identical face stimuli (each 5.2° in diameter) that were either fearful or neutral and were presented at 10° eccentricity to the left and right of fixation. An example of a face cue is provided in Figure 2. The target display contained a single Landolt circle (0.8° , 75 cd/m^2), randomly presented either to the left or to the right of fixation at 4° eccentricity at 50% Michelson luminance contrast.

In our spatial and temporal resolution tasks, we exploited the contrasting spatiotemporal response properties of subcortical magno- and parvocellular channels and their afferent cortical circuits. In the spatial resolution task, the Landolt circle contained a small aperture at the top (2, 4, 6, 8, or 10 arcmin) on 50% of the trials and no aperture on the remaining trials. We used small apertures ($\sim 1/30$ – $1/6$ of its overall size), which are outside the sensitivity range of magnocellular-type pathways (Leonova, Pokorny, & Smith, 2003; McAnany & Alexander, 2008).

In the temporal task, two consecutive Landolt circles appeared on 50% of the trials. Both Landolt circles were presented for 40 ms each and separated by a variable interval (10, 15, 20, 25, or 30 ms). On the remaining trials, a single Landolt circle was presented for a duration ranging from 90 to 110 ms (i.e., 90, 95, 100, 105, or 110 ms). The smallest temporal interval between two spatially overlapping pulses that can still be discriminated from a single pulse indicates the limit of temporal resolution (Kelly, 1972). Both subcortical parvo cells and simple V1 cells that receive parvocellular input show sustained monophasic responses with latencies that exceed 70 ms (~ 80 – 100 ms). However, subcortical magno cells and simple V1 cells that receive magnocellular input show transient biphasic responses that have interpeak latencies below 70 ms (~ 40 – 65 ms; De Valois et al., 2000). Both the fast transient and biphasic nature of magno-type cells makes them especially sensitive to visual stimuli with fast onset asynchronies. In the temporal resolution task, the Landolt circle onset asynchronies ranged from 50 ms to 70 ms, which is outside the temporal sensitivity range of parvo-type cells.¹

Stimuli were presented on a gamma-corrected Iiyama 21-in. Vision Master Pro 514 monitor (spatial resolution task: 100-Hz refresh rate, $1,600 \times 1,200$ pixels; temporal resolution task: 200-Hz refresh rate, 800×600 pixels).

¹ Please note that we are not addressing a third visual pathway, the koniocellular pathway, which is involved in color vision but whose general contribution to spatiotemporal resolution is less explored.

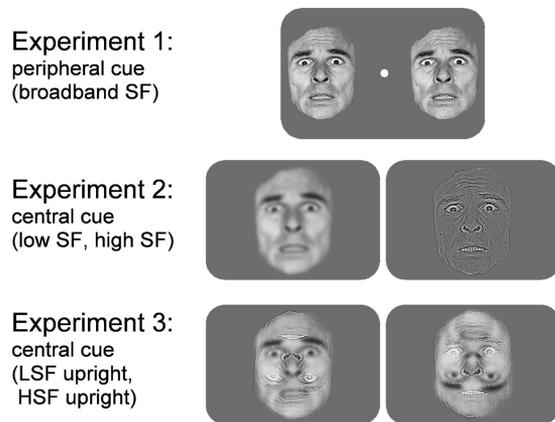


Figure 2. Illustration of the cue types in Experiments 1–3. Two peripheral face cues were presented on each trial in Experiment 1. A single central face cue was presented on each trial in Experiments 2 and 3. LSF = low spatial frequency; HSF = high spatial frequency. *Note.* Image from the Pictures of Facial Affect (POFA) database. Copyright 1993 by Paul Ekman, Ph.D./Paul Ekman Group, LLC. Reprinted and adapted with permission.

Procedure. Participants viewed the display binocularly at a distance of 57 cm with their heads stabilized by a chin rest. They were instructed to fixate on the central point throughout testing. The presentation procedure for Experiment 1 is illustrated schematically in Figure 1. Each trial started with the presentation of a fixation point for 1,000 ms. Next, the cue display (i.e., two neutral faces or two fearful faces) was presented for 70 ms, followed by a 30-ms blank screen. Finally, the target display was presented for 100 ms in the spatial task and 90–110 ms in the temporal task. The short duration between cue onset and target offset (~200 ms) precluded eye movements toward the stimuli (Mayfrank, Kimmig, & Fischer, 1987).

Participants performed both the spatial resolution task and the temporal resolution task. The order of the tasks was counterbalanced across participants, and the tasks were performed on different days; half of the participants completed the spatial resolution task on Day 1 and the temporal resolution task on Day 2, and the other half completed the tasks in reverse order. In the spatial task, participants indicated whether the Landolt circle contained a small spatial gap at the top or was intact. In the temporal task, participants indicated whether the circle was flickering (i.e., whether there was a brief temporal gap) or was temporally continuous. Participants pressed the *M* key when a spatial or temporal gap was present in the target stimulus and pressed the *Z* key when it was absent.

Prior to the main experiment, each participant performed 100 training trials in which targets contained the largest spatial or temporal gap size (respectively, 10 arcmin and 30 ms) to become familiar with the task at hand and to make sure the requirements of the experiment were clear. After completion of the training trials, participants performed the main experiment, which consisted of 880 trials (in either the spatial resolution task or the temporal resolution task, depending on the counterbalanced order for each participant). Each condition contained an equal number of trials, and all variables within each task varied randomly from trial to trial. Feedback on performance was given after each trial. We analyzed performance in terms of the signal detection theory

measure d' , which we calculated as $z(\text{hit}) - z(\text{false alarm})$ for each condition and participant (Macmillan & Creelman, 1991).

Results and Discussion

Experiment 1 examined whether fearful face cues influence visual acuity in spatial and temporal resolution tasks. As is shown in Figure 3, the emotional status of the face cue had opposite effects on visual performance, depending on the task: Emotional faces impaired spatial resolution but improved temporal resolution.

These observations were confirmed by a repeated-measures analysis of variance (ANOVA; Cue Emotional Status \times Task \times Target Gap Size) performed on d' accuracy, using Greenhouse–Geisser corrections where appropriate. As expected, overall performance increased as a function of target gap size, $F(1, 9) = 177.03, p < .001, \eta_p^2 = .94$, indicating that larger gaps were easier to detect than smaller gaps.² The main effects of task and cue emotional status were not significant ($ps > .40$). Of primary interest, the interaction between emotional status of the cue and task was significant, $F(1, 9) = 70.03, p < .001, \eta_p^2 = .88$, indicating that fearful and neutral cues had different effects on d' accuracy depending on the visual dimension tested. Post hoc comparisons indicated that fearful cues, compared with neutral cues, improved performance in the temporal resolution task, $t(9) = 7.54, p < .001$, but impaired performance in the spatial resolution task, $t(9) = 5.33, p < .001$.

In addition to d' analyses, statistical analyses were performed on the hit and false-alarm rates for this and all subsequent experiments. The pattern of results for hit rates mimicked the pattern of results for d' : In all cases the effects that were found for d' were also obtained for hit rates. For false-alarm rates, no significant effects were present. Details of the analyses on hit and false-alarm rates for all experiments are reported in the Appendix.

In Experiment 1 we showed that fearful face cues, compared with neutral face cues, impair spatial resolution and improve temporal resolution. A related pattern of emotion-induced impairments and improvements was recently obtained by Bocanegra and Zeelenberg (2009b). They found that a fearful face cue impaired tilt detection of HSF Gabors but improved tilt detection of LSF Gabors. This selective improvement for LSF Gabors is consistent with physiological data suggesting that the amygdala receives subcortical visual input of the magnocellular type (Vuilleumier et al., 2003). The unexpected impairment for HSF Gabors might be explained by cross-inhibition between magno- and parvocellular processing (cf. Breitmeyer & Williams, 1990; Yeshurun & Levy, 2003). Experiment 1 tested a critical prediction of this hypothesis. If the counterintuitive pattern of impairments and improvements obtained by Bocanegra and Zeelenberg is indeed due to inhibition between magno- and parvocellular-type channels, similar effects should be obtained with entirely different stimuli provided that they are presented in tasks that rely primarily on either magno- or parvocellular processing. The finding of an emotion-induced impairment in spatial resolution coupled with an emotion-induced improvement in temporal resolution confirms these predictions.

² The gap size factor did not interact with any of the other factors in this and subsequent experiments. Because we were not primarily interested in the effect of gap size, these effects are not further discussed.

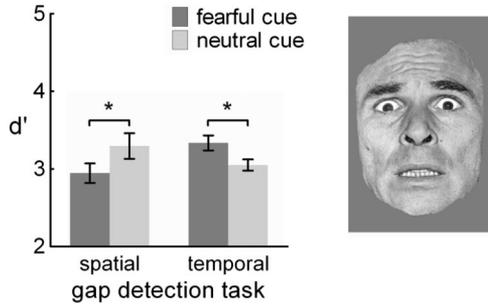


Figure 3. Spatial and temporal discriminability (d') as a function of expression of the face cue in Experiment 1. Error bars indicate standard error of the mean. Significant differences ($p < .05$) are indicated by an asterisk. Note. Image from the Pictures of Facial Affect (POFA) database. Copyright 1993 by Paul Ekman, Ph.D./Paul Ekman Group, LLC. Reprinted with permission.

Experiment 2

It is often assumed that the amygdala receives direct visual input via a subcortical route apart from the cortical visual input from the ventral visual stream (Jones & Burton, 1976; Morris et al., 1998; Vuilleumier et al., 2003; for arguments against the existence of a subcortical visual pathway to the amygdala see Cowey, 2004; Pessoa, 2005). The subcortical structures that are thought to provide direct visual input to the amygdala (pulvinar and superior colliculus) are of the magnocellular type. As a result, this direct subcortical route would provide mainly LSF information to the amygdala. The consequences of these structural characteristics were tested in a study by Vuilleumier et al. (2003). In an fMRI study they looked at emotional modulations of amygdala activation and activations of the visual cortex. Participants were presented with neutral or fearful faces that were frequency-filtered so that they contained either low, high, or broadband (i.e., unfiltered) spatial frequency components. Vuilleumier et al. found that, consistent with the idea that the amygdala receives its subcortical input via magnocellular channels, LSF components of fearful faces modulate activation of the amygdala and extrastriate areas, whereas HSF components do not. Also, it has been shown that LSF components of fearful faces influence reaction times in a dot-probe task but that HSF components do not (Holmes et al., 2005).

In Experiment 2 we used face cues with different spatial-frequency compositions to test whether the effects obtained in Experiment 1 were driven by LSFs or HSFs (or both) in the face cues. Considering the evidence suggesting that the amygdala receives subcortical visual input via a magnocellular pathway (Jones & Burton, 1976; Morris et al., 1998; Vuilleumier et al., 2003), we predicted that both the emotion-induced benefits in temporal resolution and deficits in spatial resolution would be obtained with LSF face cues but not with HSF face cues.

Method

Twenty students participated for course credit. The type of task was manipulated as a between-subjects factor: Ten participants performed a spatial resolution task, and the remaining 10 participants performed a temporal resolution task.

To generate HSF and LSF face cues, we applied low-pass and high-pass two-dimensional Gaussian filters to the set of faces used in Experiment 1 (Schyns & Oliva, 1999). We chose a low-pass filter cutoff that would target magnocellular-type channels (< 2 cpd) and a high-pass filter cutoff that would target parvocellular-type channels³ (> 4 cpd; De Valois, Albrecht, & Thorell, 1982; Vuilleumier et al., 2003; Winston, Vuilleumier, & Dolan, 2003). On each trial, a single face cue (5.2° in diameter), rather than two peripheral face cues, was presented at fixation. This was done to ensure that participants could easily discriminate the facial expressions in both the LSF and HSF conditions. Examples of an LSF face cue and an HSF face cue are provided in Figure 2. The main experiment consisted of 1,760 trials. All within-subject variables (emotional status of face cue, spatial frequency of the face cue, and target gap size) varied randomly from trial to trial. All other aspects of the methods were identical to those of Experiment 1.

Results and Discussion

Experiment 2 examined whether the emotion-induced deficits in spatial resolution and benefits in temporal resolution were due to the LSF or HSF in the face cues. A mixed ANOVA with cue emotional status, cue spatial frequency, and target gap size as within-subject factors and task as a between-subjects factor was performed on d' accuracy, using Greenhouse–Geisser corrections where appropriate.

As in Experiment 1, overall performance increased as a function of target gap size, $F(4, 72) = 243.71, p < .001, \eta_p^2 = .93$. Also, performance was higher for the participants in the temporal resolution task than for the participants in the spatial resolution task, $F(4, 72) = 14.20, p < .01, \eta_p^2 = .44$. The main effect of cue emotional status was not significant ($p > .30$). Most important, we obtained a clearly interpretable three-way interaction, $F(1, 18) = 62.56, p < .001, \eta_p^2 = .77$, indicating that the pattern of results differed for LSF and HSF face cues (see Figures 4 and 5). Separate two-way ANOVAs were performed for the LSF and HSF conditions. A significant crossover interaction between cue emotional status and task was obtained with LSF cues, $F(1, 18) = 56.83, p < .001, \eta_p^2 = .75$. Post hoc comparisons showed an emotion-induced enhancement of temporal resolution, $t(9) = 5.27, p < .001$, and an emotion-induced impairment of spatial resolution, $t(9) = 5.72, p < .001$. With HSF cues, in contrast, no interaction or main effects of emotion ($ps > .12$) were found, indicating that both the improvement and impairment were abolished.

We found that, consistent with our predictions, fearful LSF faces, compared with neutral LSF faces, improved temporal resolution (see Figure 4). In addition, we found no differences in temporal performance between fearful HSF faces and neutral HSF faces (see Figure 5). As shown in Figure 4, compared with neutral LSF cues, fearful LSF cues impaired spatial gap detection, but as in the temporal task, we observed no differences for the HSF cues (see Figure 5). This finding is consistent with the idea that an emotion-induced facilitation in magnocellular processing (triggered by the LSFs in the face cues) results in an inhibition of parvocellular processing (as assessed by the spatial resolution task).

³ These cutoff frequencies are consistent with psychophysical data on contrast sensitivity of the magno and parvo pathways for spatial frequencies in the range 0.25–12 cpd (Leonova et al., 2003).

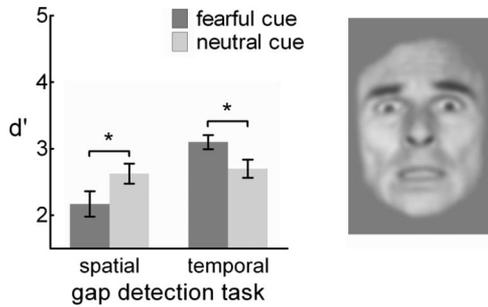


Figure 4. Spatial and temporal discriminability (d') as a function of expression of the face cue for low spatial frequency cues in Experiment 2. Error bars indicate the standard error of the mean. Significant differences ($p < .05$) are indicated by an asterisk. *Note.* Image from the Pictures of Facial Affect (POFA) database. Copyright 1993 by Paul Ekman, Ph.D./Paul Ekman Group, LLC. Adapted with permission.

Another relevant aspect of the present experiment is that we obtained emotion-induced modulations in low-level vision with face cues that were presented in the center of the screen. In Experiment 1 of the present study as well as our previous study (Bocanegra & Zeelenberg, 2009b), we used peripheral cues rather than central cues. The present experiment shows that emotion-induced benefits and deficits in low-level vision can also be obtained with central cues. This is consistent with the findings of Phelps et al. (2006), who demonstrated emotion-induced benefits in contrast sensitivity for both central and peripheral face cues. Clearly, emotion-induced modulations in low-level vision are robust and can be found under different cuing conditions.

Experiment 3

In Experiment 2 we demonstrated that both the spatial deficits and temporal benefits were selectively triggered by the LSFs in the face cues. In Experiment 3, we tested whether these effects were genuine emotional effects elicited by the configural properties of the facial expressions. It could be that the performance differences observed between fearful LSF cues and neutral LSF cues were due to differences in basic visual attributes in the faces (e.g., differences in overall luminance, spatial frequency composition, con-

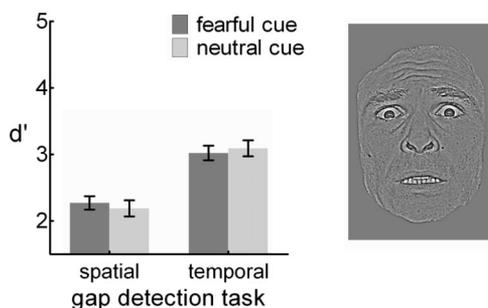


Figure 5. Spatial and temporal discriminability (d') as a function of expression of the face cue for high spatial frequency cues in Experiment 2. Error bars indicate the standard error of the mean. *Note.* Image from the Pictures of Facial Affect (POFA) database. Copyright 1993 by Paul Ekman, Ph.D./Paul Ekman Group, LLC. Adapted with permission.

trast energy, or featural complexity). To address this possibility, we superimposed HSF and LSF faces on each other, inverting either one or the other. When a face is inverted, all basic visual attributes remain constant, but emotional expression is not readily extracted (Farah et al., 1995). Thus, we expected an emotion-induced modulation of spatial and temporal resolution only when the LSF face was upright and the HSF face was inverted and not when the HSF face was upright and the LSF face was inverted.

Method

Twenty students participated for course credit. As in Experiment 2, 10 participants performed a spatial resolution task and 10 participants performed a temporal resolution task. All aspects of the methods were identical to those of Experiment 2, except that we superimposed HSF and LSF faces on each other, inverting either one or the other. This spatial frequency orientation factor was crossed with the emotionality (neutral vs. fearful) of the face. This resulted in four types of face cues; LSF-upright/HSF-inverted neutral cues, LSF-inverted/HSF-upright neutral cues, LSF-upright/HSF-inverted fearful cues, and LSF-inverted/HSF-upright fearful cues (see Figure 2). The main experiment consisted of 1,760 trials. All variables within each task varied randomly from trial to trial.

Results and Discussion

Experiment 3 examined whether the emotion-induced deficits in spatial resolution and benefits in temporal resolution were due to the configural properties of the emotional facial expressions. A mixed ANOVA with cue emotional status, cue spatial frequency orientation, and target gap size as within-subject factors and task as a between-subjects factor was performed on d' accuracy, using Greenhouse–Geisser corrections where appropriate.

As in Experiments 1 and 2, overall performance increased as a function of target gap size, $F(4, 72) = 220.51, p < .001, \eta_p^2 = .96$. The main effects of task and cue emotional status were not significant ($ps > .15$). Most important, we obtained a clear three-way interaction, $F(1, 18) = 20.01, p < .001, \eta_p^2 = .53$, indicating that the pattern of results differed for upright LSF and upright HSF cues (see Figures 6 and 7). Separate two-way ANOVAs were performed for these conditions. A significant crossover interaction

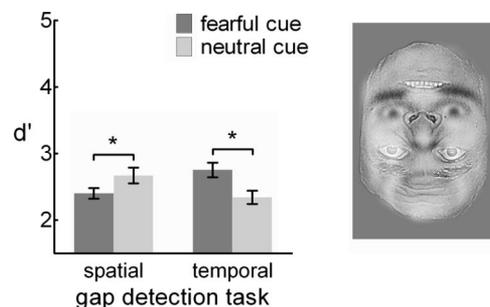


Figure 6. Spatial and temporal discriminability (d') as a function of expression of the face cue for low spatial frequency upright cues in Experiment 3. Error bars indicate the standard error of the mean. Significant differences ($p < .05$) are indicated by an asterisk. *Note.* Image from the Pictures of Facial Affect (POFA) database. Copyright 1993 by Paul Ekman, Ph.D./Paul Ekman Group, LLC. Adapted with permission.

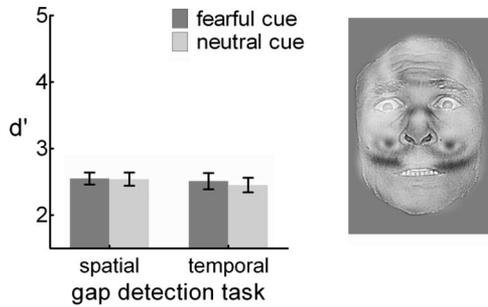


Figure 7. Spatial and temporal discriminability (d') as a function of expression of the face cue for high spatial frequency upright cues in Experiment 3. Error bars indicate the standard error of the mean. *Note.* Image from the Pictures of Facial Affect (POFA) database. Copyright 1993 by Paul Ekman, Ph.D./Paul Ekman Group, LLC. Adapted with permission.

between cue emotional status and task was obtained with upright LSF cues, $F(1, 18) = 45.21, p < .001, \eta_p^2 = .71$. Post hoc comparisons showed an emotion-induced enhancement of temporal resolution, $t(9) = 5.14, p < .01$, and an emotion-induced impairment of spatial resolution, $t(9) = 4.51, p < .01$. With upright HSF cues, in contrast, no interaction or main effects ($ps > .56$) were found, indicating that both the improvement and impairment were abolished.

Thus, fearful cues improved temporal resolution only when the LSFs were upright. Similarly, fearful cues impaired spatial resolution only for upright LSFs (see Figure 6). Thus, we observed both temporal benefits and spatial deficits in acuity with superimposed upright LSFs and inverted HSFs. However, with inverted LSFs and upright HSFs both effects were abolished (see Figure 7). This finding concurs with previous studies in which face inversion abolished the emotion-induced benefits in contrast sensitivity (Phelps et al., 2006) and deficits in orientation tilt detection (Bocanegra & Zeelenberg, 2009b) and shows that performance differences we observed in Experiment 2 are unlikely due to differences in basic visual attributes between the fearful and neutral faces (e.g., differences in luminance, spatial frequency composition, contrast energy, or featural complexity). Moreover, the current experiment extends previous findings by combining face inversion and spatial frequency filtering (see Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005). This combined manipulation demonstrated that the emotion-induced benefits and deficits in vision are due to a common affective system that detects coarse LSF facial features at a global configural level.

General Discussion

In the present study we tested whether emotion elicits a visual trade-off between systems that receive their input from predominantly magno- versus parvocellular channels. Specifically, we hypothesized that emotion boosts magnocellular processing but inhibits parvocellular processing. Because magno- and parvocellular visual channels differ in their spatial and temporal response properties, this trade-off hypothesis predicts that emotion promotes the segregation of visual signals over time and the integration of visual signals over space. Experiment 1 showed that, consistent

with these predictions, fearful face cues, compared with neutral face cues, caused a deficit in spatial gap detection and a benefit in temporal gap detection. Experiment 2 showed that these emotion-induced effects were due to the LSFs in the faces; emotion-induced deficits and benefits were present when LSF faces were presented prior to the target but absent when HSF faces were presented. Finally, in Experiment 3 we showed that emotion-induced effects on visual processing were obtained when the LSF content of the face cue was presented upright and the HSF content was inverted but not when the LSF content of the face cue was inverted and the HSF content was upright.

Although the peripheral and central cues in our experiments were task-irrelevant and uninformative as to the target location, one might ask whether the salient fearful face cues might in some way have influenced observers' willingness to respond "yes" or might have inadvertently alerted or distracted observers during an emotional trial. However, due to the opposite directionality of the emotional modulations we observed (spatial deficits vs. temporal benefits), it seems unlikely that our findings can be attributed to nonspecific affective facilitation or interference effects that are not intrinsic to the visual system (e.g., selective response strategies or momentary changes in observers' alertness). Importantly, these nonspecific mechanisms would predict similar effects of fearful face cues in both the temporal and spatial resolution tasks, which we did not observe.

In Experiments 2 and 3 we manipulated the spatial frequency content of the face cues. One might ask whether the facial features were as salient in the HSF face cues compared with the LSF face cues. Note, however, that we presented the cues foveally to ensure that the facial expressions would be easily discriminable for both types of cues. It has previously been shown that gender judgments for low-pass and high-pass filtered faces are equally accurate in the spatial frequency ranges we used (Vuilleumier et al., 2003). Because both fearful and neutral HSF faces are clearly detectable to observers and readily activate the fusiform cortex (Vuilleumier et al., 2003), HSF faces do not simply lack the contrast energy required to activate the visual system. Thus, it seems unlikely that a difference in featural salience per se can explain the null effects we observed for HSF cues.

We argue that the spatial deficits are due to an interchannel trade-off (cf. Yeshurun & Levy, 2003), in which a facilitation of magnocellular processing is accompanied by an inhibition of parvocellular processing. Our Experiments 2 and 3 showed that the spatial deficits were driven selectively by the LSFs of the facial expressions. By low-pass-filtering the faces, we drastically reduced the parvo-activating HSFs and retained the magno-activating LSFs in the face cues. Note that a trade-off mechanism predicts that the magnocellular facilitation induced by a fearful LSF face cue should be sufficient to elicit a symmetrical parvocellular inhibition, despite the fact that LSFs by themselves do not readily stimulate parvocellular channels. In other words, the presence of magno-activating features in the fearful cue (LSFs) should impair performance in a task that taps into parvocellular processing (spatial resolution). Indeed, LSF face cues caused the same decrement in spatial resolution that we initially obtained with unfiltered faces. This decrement was completely absent for the HSF face cues, even though HSFs by themselves target parvocellular processing. This selective dissociation strongly suggests that the emotion-induced deficits in spatial resolution depend on the

same cue-driven facilitation in magnocellular processing that elicited the emotion-induced benefits in temporal resolution.

Although we suggest that our observed spatiotemporal effects are due to inhibitory interactions *between* visual channels, one might argue that both effects may be explained by an overall increase in average receptive field size *within* visual channels. This mechanism would impair spatial resolution and additionally increase spatial summation between overlapping receptive fields. Enhanced summation, in turn, would improve signal-to-noise ratios that could benefit temporal resolution. However, this mechanism appears unlikely, considering that our Landolts were small (0.8°) and spatial summation becomes negligible for field sizes below 1° – 2° (Mäkelä, Rovamo, & Whitaker, 1994; Yeshurun & Levy, 2003). Our results are therefore more readily explained by interchannel inhibition.

Previous studies have postulated that, independent of emotion, interchannel interactions (i.e., inhibition between magno- and parvocellular-type channels) explain a wide variety of perceptual phenomena. Interchannel inhibition may account for results in various paradigms, such as pattern-masking effects in contrast sensitivity (Itti, Koch, & Braun, 2000), metacontrast masking effects in contour and brightness perception (Breitmeyer & Ogmen, 2000), saccadic suppression effects in contrast sensitivity (Burr et al., 1994), and attentional cuing effects in texture segmentation and spatiotemporal resolution⁴ (Yeshurun & Carrasco, 2000; Yeshurun & Levy, 2003). For example, metacontrast masking occurs when the perception of a target stimulus is impaired by the subsequent presentation of a spatially nonoverlapping mask stimulus. Although observers can readily detect the occurrence of a masked target, the metacontrast mask strongly impairs the perception of a target's fine-grained contour. To account for this effect, it has been proposed that the magnocellular activity of the transient mask inhibits the parvocellular activity of the target's contour (Breitmeyer et al., 2006; Breitmeyer & Ogmen, 2000). Thus, our explanation of emotion-induced trade-offs in visual processing concurs with findings reported in the nonaffective visual perception literature.

Our finding that the temporal benefits and spatial deficits were absent for HSF facial features fits neatly with studies showing that HSF fearful faces, compared with HSF neutral faces, do not differentially activate the amygdala or the visual cortex (Pourtois et al., 2005; Vuilleumier et al., 2003). Anatomical evidence suggests that the amygdala does not receive subcortical parvocellular input (Jones & Burton, 1976). It has been suggested that LSF magnocellular input from the pulvinar is critical for amygdala processing of brief emotional stimuli (<300 ms; Vuilleumier et al., 2003; Ward, Danziger, & Bamford, 2005). Although our findings concur with previous fMRI data indicating that the enhanced amygdala and visual cortical responses to fearful faces are driven exclusively by LSFs (Vuilleumier et al., 2003; Winston et al., 2003), we cannot make strong claims about the neural substrates underlying our spatiotemporal effects. Our experimental predictions were based on global aspects of amygdala connectivity. However, detailed structural knowledge is lacking about the amygdala's subcortical magnocellular input, its interlaminar connectivity, and how its output projections feed back onto the magno- and parvocellular dominant circuits of V1. An important question for future research is how and at what level in the visual system emotion-induced interchannel inhibition is instantiated.

An interesting question is whether the perceptual modulations observed in our study are restricted to specific types of emotional stimuli or whether they reflect a general affective mechanism governing emotion-perception interactions. Do our results generalize to other stimulus types (e.g., other facial expressions, affective pictures), and does the pattern of results depend on the specific affective state of the participants? Are the results specific to threat processing, or are they possibly more broadly applicable to other negative emotions? As with most studies investigating the influence of emotion on early visual processing (Phelps et al., 2006; Pourtois et al., 2005; Vuilleumier et al., 2003), we used fearful faces because they have consistently been shown to activate the amygdala (Vuilleumier, 2005). However, different underlying emotional dimensions could be critical for the trade-off effects observed in our study (e.g., arousal, valence, threat relevance). For instance, different types of stimuli may differ in the degree to which they induce emotional arousal and activate the amygdala (Hariri, Tessitore, Mattay, Fera, & Weinberger, 2002). Furthermore, findings have suggested that different emotional facial expressions may have evolved as informationally orthogonal signals (Smith, Cottrell, Gosselin, & Schyns, 2005) in order to maximize the decoding and transmission efficiency for different types of affective messages. Conceivably, different affective messages (e.g., anger vs. happiness) may induce different prioritizations of basic visual features in the environment. Thus, emotion-induced trade-offs in perception might vary depending on the type of emotional cue used. An additional question is whether faces need to be consciously perceived in order to influence early visual processing. Studies have shown that masked fearful faces activate the amygdala (Öhman, 2002; Whalen et al., 1998), suggesting that faces that are not consciously perceived may still have an impact on performance in the tasks used in the present study.

In a recent study, Becker (2009) observed that fearful face cues, presented prior to a search display consisting of nonemotional stimuli, enhanced the rate of visual search. That is, search slopes were lower when fearful face cues were presented compared with when neutral or happy face cues were presented. These findings are somewhat similar to the findings of the present study and those of Phelps et al. (2006) and Bocanegra and Zeelenberg (2009b) in that they show a carryover effect of fearful faces on the perception of neutral stimuli. The extent to which similar processes underlie effects in these different paradigms remains to be determined. For example, can fearful face cues also cause a decrease in the rate of visual search? Such a finding would be analogous to those reported

⁴ Interestingly, these findings indicate that attentional cuing, independently of emotion, can induce spatial *benefits* and temporal *deficits* at a cued spatial location (i.e., the inverse of the effects we obtained in the present study). However, it appears that the trade-off effects induced by emotion are distinct from the spatially localized trade-off effects induced by attentional cuing. Evidence from a previous study directly has suggested that emotion-induced trade-offs are not constrained to the spatial location of the emotional cue (Bocanegra & Zeelenberg, 2009b, Experiment 3). Using the same emotional cuing paradigm, emotion-induced benefits and deficits were obtained for Gabors that differed in spatial frequency. Importantly, these emotion-induced effects did not vary as a function of the spatial location of the fearful face: Identical effects were obtained when the fearful face was presented ipsilaterally and contralaterally to the target Gabor location.

here. Moreover, it remains to be seen whether fearful face cues influence performance in visual search paradigms and paradigms such as those of the present study under the same sorts of circumstances. The findings of Becker were obtained in a design in which faces within a block of trials were all of the same type, whereas studies showing effects of face cues on low-level perception have all used designs in which the type of cue (fearful vs. neutral) varied randomly from trial to trial.

To summarize, we demonstrate that by testing visual acuity either in space or time, it is possible to dissociate the detrimental and beneficial consequences of emotion. Furthermore, these opposite effects were modulated by the same perceptual properties of the fearful face cues. The most important conclusion that can be drawn from these commonalities is that emotion-induced visual deficits are not incidental phenomena. Previously, it was unclear why emotion should impair the perception of small spatial details. Here we show that these impairments are the result of an adaptive visual bias that enhances the detection of fast temporal features at the expense of slower spatial features. Within this framework, one might say that the beneficial and detrimental consequences of “emotional” vision are two sides of the same coin. Importantly, this functional link demonstrates that emotion does not merely “turn up the volume” for all types of visual features. Instead, our results indicate a trade-off between visual channels tuned to different visual features, which challenges the generally accepted notion that emotion invariably facilitates visual performance. By trading off the processing of spatial versus temporal visual features, observers might transiently optimize their visual performance in threatening situations. A gain in temporal resolution could benefit the perception of features that are potentially important for the detection of threat in the environment, features such as motion, depth, and direction. Thus, we propose that emotion facilitates fast temporal features that are more relevant for survival at the expense of fine-grained spatial features that are less relevant.

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(Appendix follows)

Appendix

Analyses for Hits and False Alarms

The observed hit and false-alarm rates for Experiments 1–3 are presented in Table A1; details of the statistical analyses are presented next.

Experiment 1

We examined whether fearful face cues influence visual acuity in spatial and temporal resolution tasks. Separate repeated-measures analyses of variance (ANOVAs; Cue Emotional Status \times Task) were performed on the hit and false-alarm rates, using Greenhouse–Geisser corrections where appropriate.

Hit rate. The main effects of task and cue emotional status were not significant ($ps > .05$). Of primary interest, the interaction between emotional status of the cue and task was significant, $F(1, 9) = 12.39, p < .01, \eta_p^2 = .88$, indicating that fearful and neutral cues had different effects on hit rates depending on the visual dimension tested. Post hoc comparisons indicated that fearful cues, compared with neutral cues, increased hit rates in the temporal resolution task, $t(9) = 3.99, p < .01$, but decreased hit rates in the spatial resolution task, $t(9) = 2.89, p < .02$.

False-alarm rate. Neither the main effects of task and cue emotional status nor their interaction was significant ($ps > .13$).

Experiment 2

We examined whether the emotion-induced deficits in spatial resolution and benefits in temporal resolution were due to the low spatial frequency (LSF) or high spatial frequency (HSF) in the face

cues. Separate mixed ANOVAs with cue emotional status and cue spatial frequency as within-subject factors and task as a between-subjects factor were performed on the hit and false-alarm rates, using Greenhouse–Geisser corrections where appropriate.

Hit rate. Hit rates were higher for the participants in the temporal resolution task compared with the participants in the spatial resolution task, $F(1, 18) = 8.65, p < .01, \eta_p^2 = .32$. The main effect of cue emotional status was not significant ($p > .16$). Most important, we obtained a clearly interpretable three-way interaction, $F(1, 18) = 7.93, p < .01, \eta_p^2 = .31$, indicating that the pattern of results differed for LSF and HSF face cues. Separate two-way ANOVAs were performed for the LSF and HSF conditions. A significant crossover interaction between cue emotional status and task was obtained with LSF cues, $F(1, 18) = 18.21, p < .001, \eta_p^2 = .50$. Post hoc comparisons showed an increase in hit rates due to emotion in the temporal resolution task, $t(9) = 3.22, p < .01$, and a decrease in hit rates due to emotion in the spatial resolution task, $t(9) = 2.87, p < .02$. With HSF cues, in contrast, no interaction or main effect of emotion ($ps > .10$) were found, indicating that both the increase and decrease in the hit rates due to emotion were abolished.

False-alarm rate. Neither the main effects of task, cue emotional status, and cue spatial frequency nor their interactions were significant ($ps > .35$).

Experiment 3

We examined whether the emotion-induced deficits in spatial resolution and benefits in temporal resolution were due to the configural properties of the emotional facial expressions. Separate mixed ANOVAs with cue emotional status and cue spatial frequency orientation as within-subject factors and task as a between-subjects factor were performed on the hit and false-alarm rates, using Greenhouse–Geisser corrections where appropriate.

Hit rate. The main effects of task, cue emotional status, and cue spatial frequency orientation were not significant ($ps > .28$). Most important, we obtained a clear three-way interaction, $F(1, 18) = 7.75, p < .01, \eta_p^2 = .30$, indicating that the pattern of results differed for upright LSF and upright HSF cues. Separate two-way ANOVAs were performed for these conditions. A significant crossover interaction between cue emotional status and task was obtained with upright LSF cues, $F(1, 18) = 15.39, p < .001, \eta_p^2 = .46$. Post hoc comparisons showed an increase in hit rates due to emotion in the temporal resolution task, $t(9) = 3.10, p < .02$, and a decrease in hit rates due to emotion in the spatial resolution task, $t(9) = 2.93, p < .02$. With upright HSF cues, in contrast, no interaction or main effects ($ps > .59$) were found, indicating that both the increase and decrease in the hit rates due to emotion were abolished.

False-alarm rate. Neither the main effects of task, cue emotional status, and cue spatial frequency orientation nor their interactions were significant ($ps > .17$).

Table A1

Hit and False-Alarm Rates in Experiments 1–3 as a Function of Cue Condition and Task

Experiment, cue, and task	Hit rate		False-alarm rate	
	Fearful cue	Neutral cue	Fearful cue	Neutral cue
Experiment 1				
Temporal task	.921	.884	.078	.069
Spatial task	.790	.876	.045	.037
Experiment 2				
LSF cue				
Temporal task	.887	.737	.052	.045
Spatial task	.586	.756	.039	.044
HSF cue				
Temporal task	.849	.800	.040	.033
Spatial task	.674	.610	.043	.035
Experiment 3				
LSF upright cue				
Temporal task	.846	.650	.073	.045
Spatial task	.736	.805	.045	.051
HSF upright cue				
Temporal task	.750	.765	.062	.031
Spatial task	.775	.731	.064	.046

Note. LSF = low spatial frequency; HSF = high spatial frequency.

Received March 29, 2010

Revision received January 17, 2011

Accepted January 24, 2011 ■