

Research Article

Emotion Improves and Impairs Early Vision

Bruno R. Bocanegra and René Zeelenberg

Erasmus University Rotterdam

ABSTRACT—Recent studies indicate that emotion enhances early vision, but the generality of this finding remains unknown. Do the benefits of emotion extend to all basic aspects of vision, or are they limited in scope? Our results show that the brief presentation of a fearful face, compared with a neutral face, enhances sensitivity for the orientation of subsequently presented low-spatial-frequency stimuli, but diminishes orientation sensitivity for high-spatial-frequency stimuli. This is the first demonstration that emotion not only improves but also impairs low-level vision. The selective low-spatial-frequency benefits are consistent with the idea that emotion enhances magnocellular processing. Additionally, we suggest that the high-spatial-frequency deficits are due to inhibitory interactions between magnocellular and parvocellular pathways. Our results suggest an emotion-induced trade-off in visual processing, rather than a general improvement. This trade-off may benefit perceptual dimensions that are relevant for survival at the expense of those that are less relevant.

Results from a variety of paradigms indicate that emotion affects perceptual processing. For example, evidence for enhanced identification of emotionally significant stimuli has been obtained for briefly presented and masked arousing words (Anderson & Phelps, 2001; Zeelenberg, Wagenmakers, & Rotteveel, 2006) and for emotional faces, snakes, and spiders in visual search tasks (Fox et al., 2000; Öhman, Flykt, & Esteves, 2001). Also, brain-damaged patients who exhibit spatial neglect show less visual extinction for faces with happy or angry expressions than for faces with neutral expressions (Vuilleumier & Schwartz, 2001).

The effects of emotion on perception could arise at different stages of visual processing (Vuilleumier, 2005). That is, emotion-induced effects may be mediated by specialized neural

systems dedicated to the recognition of certain classes of stimuli, such as faces, words, and objects. Recent studies, however, indicate that even earlier stages of visual processing are affected by emotion. Evidence that emotion enhances early perceptual processing comes primarily from research in cognitive neuroscience (for a review, see Vuilleumier, 2005). Neuroimaging studies using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have shown that emotional images, compared with neutral images, enhance activations in early occipital cortex (Lang et al., 1998; Morris et al., 1998). Additionally, event-related potential (ERP) studies (Schupp, Junghöfer, Weike, & Hamm, 2003) suggest that early visual components are affected by the emotional significance of stimuli. Some studies have indicated that modulations of ERPs may be observed as early as 60 to 90 ms after stimulus onset (Stolarova, Keil, & Moratti, 2006).

Although the modulation of early visual processing by emotion has now been demonstrated in a number of studies, the behavioral consequences of this modulation remain largely unknown. The first and only behavioral study showing that emotion enhances low-level vision was published only recently. In this study, Phelps, Ling, and Carrasco (2006) presented fearful or neutral face cues prior to a target Gabor patch presented at low luminance contrast. Results showed that the fearful face cues enhanced threshold contrast sensitivity. The mechanisms underlying emotion-induced enhancement of low-level vision, however, are still largely unspecified. As a consequence, it is not clear whether all early dimensions of vision are enhanced by emotion, or whether the effects are restricted to certain basic visual attributes.

It has been proposed that the amygdala, a medial temporal lobe structure involved in emotional processing, may boost sensory processing via connections to the visual cortex (Anderson & Phelps, 2001; Morris et al., 1998). That is, emotional stimuli activate the amygdala (Vuilleumier, 2005), which in turn may modulate ongoing processing in the visual cortex. Neuroanatomical studies with primates indicate that the amygdala projects to the earliest levels of the ventral visual stream (Amaral, Behniea, & Kelly, 2003). A common distinction within the

Address correspondence to Bruno R. Bocanegra or René Zeelenberg, Erasmus University Rotterdam, Department of Psychology, Woudestein, P.O. Box 1738, 3000 DR Rotterdam, The Netherlands, e-mail: bocanegra@fsw.eur.nl or zeelenberg@fsw.eur.nl.

visual system is that between magnocellular and parvocellular visual channels. These channels differ in the nature of the visual information they carry. Whereas magnocellular channels process predominantly coarse, low-spatial-frequency (LSF) information, parvocellular channels process predominantly fine-grained, high-spatial-frequency (HSF) information. It has been shown that projections from the amygdala to occipital cortex are mostly of the magnocellular type, and therefore carry predominantly LSF information (Amaral et al., 2003). This raises the following question: Are the facilitatory effects of emotion restricted to the processing of LSF information, or is HSF information also affected? The fact that projections from the amygdala to early visual cortices are magnocellular (Amaral et al., 2003) suggests that only LSF information may benefit from the presentation of a fearful face.

EXPERIMENT 1: DOES EMOTION DIFFERENTIALLY AFFECT LSF AND HSF VISION?

We investigated the effect of intact fearful face cues (i.e., unfiltered fearful faces of broadband spatial-frequency composition) on observers' sensitivity to orientation across a range of spatial frequencies. Both orientation and spatial frequency are processed early in the cortical visual stream (Itti, Koch, & Braun, 2000). Fearful faces activate the amygdala (Vuilleumier, Armony, Driver, & Dolan, 2003) and were shown to affect low-level visual processing in a recent behavioral study (Phelps et al., 2006). The main question of interest was whether face cues would enhance performance for both LSF and HSF target stimuli, or whether the effect would be limited to LSF targets.

Method

Participants

Eighteen observers with normal or corrected-to-normal vision participated in the experiment.

Stimuli and Apparatus

Visual stimuli were generated using MATLAB and the Psychophysics Toolbox (Brainard, 1997). They were presented on a computer with a gamma-corrected Iiyama 21-in. Vision Master monitor (100-Hz refresh rate; resolution of $1,600 \times 1,200$ pixels). Figure 1 illustrates the stimulus sequence. A light-gray fixation point ($0.2^\circ \times 0.2^\circ$, 25 cd/m^2) was presented at the center of a uniform gray background (15 cd/m^2) throughout each trial. The cue display consisted of two face stimuli (each 5.2° in diameter), presented at 10° eccentricity to the left and right of fixation. To manipulate emotion, we selected from the Pictures of Facial Affect (Ekman & Friesen, 1976) a set of facial photographs of 11 unique persons portraying prototypical *fearful* and *neutral* expressions. Each cue display consisted of a pair of fearful or a pair of neutral facial cutouts of the same person. The target display contained a single Gabor patch (2° Gaussian-

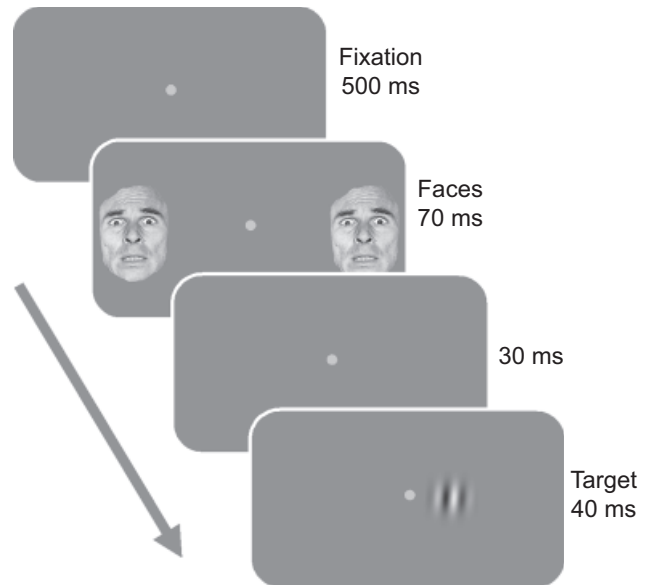


Fig. 1. Illustration of the display sequence for trials in the experiments. Subjects' task was to indicate whether the briefly presented Gabor patch was tilted or oriented vertically.

enveloped sinusoidal grating), randomly presented either to the left or to the right of fixation at 4° eccentricity. Gabor patches were presented at 30% Michelson luminance contrast and sampled from a set of spatial frequencies in five log increments from 1.5 to 6 cycles per degree (1.5, 2.1, 3.0, 4.2, and 6.0 cpd). Gabor eccentricity (4°) was chosen to ensure that performance over the entire range of spatial frequencies used in the experiment would be off floor and off ceiling (Pointer & Hess, 1989).

Procedure

Observers viewed the displays binocularly at a distance of 57 cm, with their heads stabilized by a chin rest. They were asked to fixate on the central fixation point throughout testing. The short duration between cue onset and target offset (140 ms) was chosen to preclude eye movements toward the cue stimuli (Mayfrank, Kimmig, & Fischer, 1987). The Gabor patches were either slightly tilted (clockwise or counterclockwise) or oriented vertically. Observers performed a tilt-detection task on the Gabor patches. If a target was tilted (clockwise or counterclockwise), they pressed the "m" key on the computer keyboard; if the target was not tilted (i.e., presented vertically), they pressed the "z" key. Each observer performed 100 training trials prior to the experiment. During this initial block, the tilt of the Gabor patches was adjusted for each observer (1.0° , 2.0° , 3.0° , or 4.0°) so that overall performance across the different spatial frequencies in the main experiment would approximate 80% correct ($d' \approx 1.68$). The main experiment consisted of 880 trials. All variables (cue emotion: fearful faces vs. neutral faces; target spatial frequency: 1.5–6.0 cpd; target tilt: present vs. absent) varied randomly from trial to trial. Feedback on performance was given after each trial.

Results and Discussion

Experiment 1 examined whether fearful faces influence orientation sensitivity as a function of spatial frequency. A 2 (cue emotion) \times 5 (target spatial frequency) repeated measures analysis of variance (ANOVA) was performed on d' accuracy, calculated as $z(\text{hits}) - z(\text{false alarms})$ (Macmillan & Creelman, 1991). Overall sensitivity varied as a function of spatial frequency, $F(4, 68) = 4.64, p < .01, \eta_p^2 = .21$, and showed a quadratic trend, $F(1, 17) = 29.57, p < .0001, \eta_p^2 = .64$. Additional analyses showed that the quadratic trend was significant for both the fearful-cue condition, $F(1, 17) = 12.813, p < .01, \eta_p^2 = .43$, and the neutral-cue condition, $F(1, 17) = 8.78, p < .01, \eta_p^2 = .34$. Of primary interest, the interaction between cue emotion and target spatial frequency was significant, $F(4, 68) = 10.04, p < .001, \eta_p^2 = .37$, indicating that fearful cues had a different effect depending on the spatial frequency of the Gabor target. Bonferroni-corrected comparisons indicated that fearful cues, compared with neutral cues, improved orientation sensitivity for low spatial frequencies (< 3 cpd; both $ps < .01$), but impaired sensitivity for high spatial frequencies (> 3 cpd; both $ps < .01$; see Fig. 2).

To further characterize the pattern of results, we fitted quadratic functions to predict performance as a function of spatial frequency, separately for each observer and condition (i.e., the fearful-cue and neutral-cue conditions). With the obtained parameters, we then calculated the estimated point of maximum orientation sensitivity.¹ A comparison showed that the estimated maximum orientation sensitivity was lower for fearful face cues ($M = 3.00$ cpd) than for neutral face cues ($M = 4.02$ cpd), $t(17) = 6.37, p < .001$,² suggesting that the observed LSF benefits and HSF deficits were due to a shift in the orientation-sensitivity function toward the lower spatial frequencies.

The observed emotion-induced improvement for LSF targets extends the findings of Phelps et al. (2006) to the processing of spatial orientation. Given that our Gabor patches were suprathreshold in contrast (30%), and that orientation thresholds are invariant for contrasts above 20% (Itti et al., 2000), it seems unlikely that the LSF benefits can be explained as a by-product of contrast detection. Complementary to the findings of Phelps et al., our results suggest that fearful faces modulate the sensitivity of visual channels tuned to specific orientations and spatial frequencies (Itti et al., 2000). More important, we obtained an emotion-induced impairment for HSF targets. Although we had anticipated that emotion-induced benefits might be limited to LSF targets, we had not anticipated an impairment for HSF targets.

¹The average R^2 was .92 for the fearful-cue condition and .94 for the neutral-cue condition.

²Although the distribution of peak differences was nearly normal, we also tested the presence of a shift using a nonparametric Wilcoxon signed-rank test. This test also indicated that maximum sensitivity was lower for the fearful-cue condition than for the neutral-cue condition, $Z = 3.63, p < .001$.

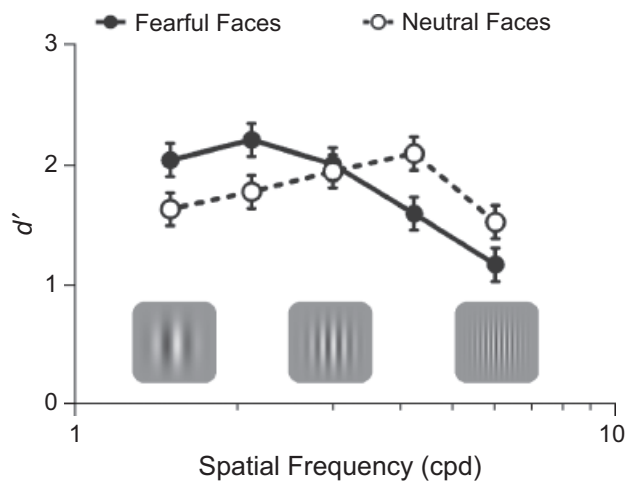


Fig. 2. Results from Experiment 1: accuracy of tilt-detection performance as a function of the spatial frequency of the target Gabor patch and the emotion of the facial cue. Error bars indicate within-subjects standard errors (Loftus & Masson, 1994).

EXPERIMENT 2: ARE THE OBSERVED LSF BENEFITS AND HSF DEFICITS BOTH DUE TO EMOTION?

Do the differential effects of fearful faces on HSF and LSF vision reflect a genuine shift in sensitivity due to global facial configuration, or are the effects due to local visual differences (e.g., in luminance, contrast, or complexity) between fearful and neutral faces? To answer this question, we conducted an experiment in which we inverted the face cues, so that local visual characteristics remained constant, but emotional content was not readily processed (Mayfrank et al., 1987; Phelps et al., 2006). If the LSF benefits and HSF deficits obtained in Experiment 1 were due to local differences between emotional and neutral faces, those benefits and deficits would be preserved when the faces were inverted. However, if they were caused by common underlying emotional mechanisms, face inversion would abolish both the benefits and the deficits.

Method

Participants

Sixteen additional observers with normal or corrected-to-normal vision participated in this experiment.

Stimuli, Apparatus, and Procedure

Experiment 2 was identical to Experiment 1 except for the inclusion of only two spatial-frequency conditions (2.1 and 4.2 cpd) and the addition of an inverted-cue condition in which cue displays consisted of inverted facial cutouts. The main experiment consisted of 704 trials.

Results and Discussion

A 2 (cue emotion: fearful faces vs. neutral faces) \times 2 (target spatial frequency: 2.1 vs. 4.2 cpd) \times 2 (face orientation: upright vs. inverted) repeated measures ANOVA showed a clearly in-

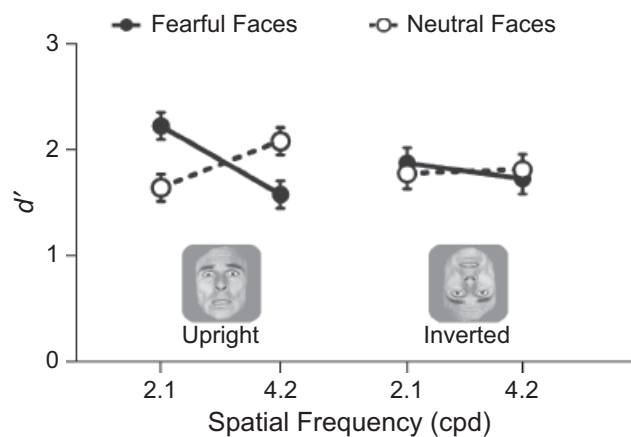


Fig. 3. Results from Experiment 2: accuracy of tilt-detection performance as a function of spatial frequency of the target Gabor patch, emotion of the facial cue, and orientation (upright or inverted) of the facial cue. Error bars indicate within-subjects standard errors (Loftus & Masson, 1994).

interpretable three-way interaction, $F(1, 15) = 17.99, p < .01, \eta_p^2 = .55$, indicating that the pattern of results differed for upright and inverted face cues (see Fig. 3). Separate two-way ANOVAs were performed for the upright- and inverted-face conditions. A significant crossover interaction between cue emotion and target spatial frequency was obtained with upright faces, $F(1, 15) = 28.67, p < .001, \eta_p^2 = .65$. The pattern observed in Experiment 1 was replicated: Both emotion-induced enhancement of LSF visual processing ($p < .01$, Bonferroni corrected) and emotion-induced impairment of HSF visual processing ($p < .01$, Bonferroni corrected) were observed. With inverted faces, however, no main effects or interaction were obtained (all F s < 1); both the improvement and the impairment were abolished.³ Thus, the emotional content conveyed through global facial configuration is responsible for both the benefits and the deficits observed across the orientation-sensitivity function.

EXPERIMENT 3: DOES EMOTIONAL MODULATION OF EARLY VISION EXTEND BEYOND THE LOCATION OF THE CUE?

Are the influences of a fearful face cue on early vision restricted to the location of the cue, or do they extend to other spatial lo-

³Although cue emotion and target spatial frequency did not have an interactive effect on performance in the inverted-face condition, a reviewer pointed out that the inverted faces (whether fearful or neutral) and upright neutral faces appeared to have different effects on sensitivity. This raises the question of whether upright neutral faces modulate sensitivity (relative to inverted neutral faces) in a way that is opposite to the effect of upright fearful faces (relative to inverted fearful faces). Two additional ANOVAs indicated that face orientation (upright vs. inverted) interacted with spatial frequency for fearful faces, $F(1, 15) = 9.74, p < .01, \eta_p^2 = .39$, but not for neutral faces, $F(1, 15) = 1.49, p = .24, \eta_p^2 = .09$. Thus, when performance is compared with an inverted-face baseline, the crossover pattern of LSF benefits and HSF deficits is mostly due to the effect of fearful faces, and less due to an opposing effect of neutral faces. Although neutral faces did show numerical effects in the opposite direction, these failed to reach significance.

cations?⁴ To answer this question, we conducted an additional experiment that included cue displays with one fearful face and one neutral face and varied whether the Gabor patch was presented on the side of the fearful face or on the opposite side (note that in Experiments 1 and 2, either both face cues were fearful or both were neutral). If the emotional modulation in early vision reflects a local change in perceptual processing, the pattern of LSF benefits and HSF deficits would be expected to vary as a function of location. In particular, the fearful face cue might affect performance only if it is presented on the same side as the Gabor patch. However, if the influence of a fearful face cue extends significantly beyond its location, the pattern of LSF benefits and HSF deficits might be obtained even when the fearful face cue is presented on the side opposite the Gabor patch.

Method

Participants

Sixteen additional observers with normal or corrected-to-normal vision participated in the experiment.

Stimuli, Apparatus, and Procedure

The most important change in the design of this experiment was the addition of two new types of cue displays. In the same-side condition, a fearful face cue was presented on the same side as the Gabor patch, and a neutral face cue was presented on the opposite side. In the opposite-side condition, a neutral face cue was presented on the same side as the Gabor patch, and a fearful face cue was presented on the opposite side. In total, there were four cue types: (a) two fearful faces, (b) two neutral faces, (c) same side, and (d) opposite side. All faces were presented upright, and two spatial-frequency conditions (2.1 and 4.2 cpd) were included. The main experiment consisted of 704 trials.

Results and Discussion

A two-way interaction indicated that the effect of the different cue types on orientation sensitivity differed for HSF and LSF targets, $F(3, 45) = 9.53, p < .01, \eta_p^2 = .39$ (see Fig. 4). To further characterize the interaction, we conducted separate ANOVAs for the HSF and LSF conditions. The ANOVA on the LSF targets showed an effect of cue type on performance, $F(3, 45) = 4.55, p < .01, \eta_p^2 = .23$. As in Experiments 1 and 2, Bonferroni-corrected comparisons showed that performance was better when both faces were fearful than when both faces were neutral ($p < .05$). More important, performance benefits (relative to the condition with two neutral face cues) were present both when the fearful face was presented on the same side as the Gabor patch ($p < .05$) and when the fearful face was presented on the opposite side ($p < .01$). There was no significant difference in performance between the same-side and opposite-side conditions ($p > .10$).

⁴We thank an anonymous reviewer for suggesting this experiment.

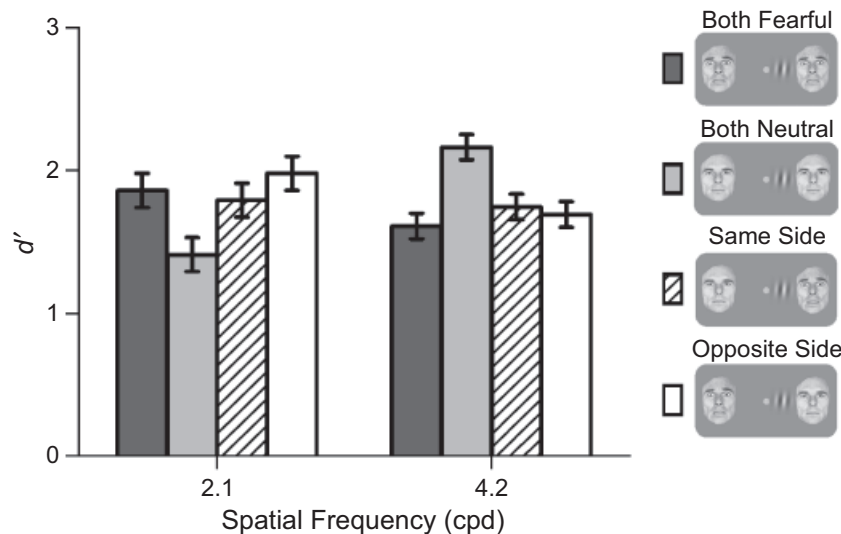


Fig. 4. Results from Experiment 3: accuracy of tilt-detection performance as a function of spatial frequency of the target Gabor patch and cue type. Error bars indicate within-subjects standard errors (Loftus & Masson, 1994).

The ANOVA on HSF targets also showed an effect of cue type, $F(3, 45) = 7.07$, $p < .01$, $\eta_p^2 = .32$. Bonferroni-corrected comparisons showed that performance was worse when both faces were fearful than when both faces were neutral ($p < .01$), again replicating the results of Experiments 1 and 2. Performance deficits (relative to the condition with two neutral face cues) were present both when the fearful face was presented on the same side as the Gabor patch ($p < .01$) and when the fearful face was presented on the opposite side ($p < .01$). Again, performance did not differ significantly as a function of the location of the fearful face cue ($p > .10$). The results of Experiment 3 indicate that the effect of a fearful cue on LSF and HSF vision extends beyond the location of the cue.

GENERAL DISCUSSION

A large number of studies of emotional enhancements in early vision have been reported in the neuroimaging literature (Lang et al., 1998; Morris et al., 1998; Vuilleumier, 2005; Vuilleumier et al., 2003), but there has been only one behavioral study, published only recently (Phelps et al., 2006). In the present study, we found evidence for an emotion-induced enhancement in orientation sensitivity for LSF targets, extending the results of Phelps et al. to a new visual dimension. More important though, we found an emotion-induced impairment for HSF targets, demonstrating for the first time that emotion impairs early vision. An important topic for future studies is whether our results generalize to other emotional facial expressions. Most studies investigating the influence of emotion on early vision (e.g., Phelps et al., 2006; Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005; Vuilleumier et al., 2003), including the present study, have used fearful faces. However, different expressions may differ in the degree to which they induce arousal and ac-

tivate the amygdala (Kesler/West et al., 2001) and in the way they carry diagnostic information across the spatial-frequency spectrum (Smith, Cottrell, Gosselin, & Schyns, 2005). Thus, the effect of emotional modulations on early vision might vary depending on facial expression (e.g., angry, happy).

Our results extend previous behavioral studies by showing that emotion affects visual perception in the absence of simultaneous distractors or trailing masks (Anderson & Phelps, 2001; Phelps et al., 2006; Zeelenberg et al., 2006), suggesting that emotion modulates signal strength, rather than the impact of external noise (Itti et al., 2000). Specifically, the finding that the presentation of a task-irrelevant fearful face selectively improves orientation sensitivity in LSF ranges points toward an enhancement of magnocellular channels transmitting coarse visual signals. The selective LSF benefit agrees with physiological and anatomical data indicating that the amygdala relays its visual input to striate and extrastriate areas via predominantly magnocellular-type projections (Amaral et al., 2003).

Vuilleumier et al. (2003) also investigated the relation between emotion and early vision as a function of spatial frequency. In their fMRI study, participants were presented with neutral or fearful faces, and activation of the amygdala and visual cortices was examined. The faces were frequency-filtered so that they contained LSF, HSF, or broadband components. The results indicated that LSF components of fearful faces modulate activation of the amygdala and extrastriate areas, whereas HSF components do not. Vuilleumier et al. explained their findings as due to a tecto-pulvinar pathway from the retina to the amygdala.⁵

⁵Some researchers (e.g., Cowey, 2004; Pessoa, 2005) have questioned the existence of a subcortical visual pathway to the amygdala. Note, however, that the interpretation of our results does not depend on the existence of such a pathway.

Because the visual input to the amygdala from this pathway is magnocellular (from pulvinar and superior colliculus), only LSF information is relayed to the amygdala by this pathway. Hence, Vuilleumier et al. argued, LSF components of faces modulate activation of the amygdala, whereas HSF components do not.

Both our results and those of Vuilleumier et al. (2003) indicate that spatial frequency is a critical factor in the effect of emotion on early perceptual processing. There are, however, a number of important differences between these studies. Vuilleumier et al. manipulated the spatial-frequency information present in their facial stimuli, whereas the faces in our study were always intact (broadband spatial frequency). Thus, the results of Vuilleumier et al. could be entirely due to the visual-input properties of the amygdala: Emotional faces with different spatial-frequency content activate the amygdala to different degrees. However, the results of our study are likely due to the visual-output properties of the amygdala (Amaral et al., 2003). Because projections from the amygdala to the visual cortices are mainly of the magnocellular type, only the processing of LSF Gabor patches was facilitated. Another important difference between the two studies is that we demonstrated effects on visual performance, whereas Vuilleumier et al. showed differences in brain activity. Our study indicates that the interaction between emotion and spatial frequency in early visual processing has important behavioral consequences.

Surprisingly, our findings show that fearful faces impair performance in response to HSF targets. This counterintuitive HSF deficit is possibly indicative of cross-inhibition between magno- and parvocellular pathways. From this perspective, these deficits may be due to an increased sensitivity of magnocellular neurons, which in turn inhibit parvocellular neurons (Breitmeyer & Williams, 1990; Yeshurun & Carrasco, 2000). This type of interchannel inhibition is consistent with the shift in peak sensitivity toward lower spatial frequencies observed in Experiment 1 (Carrasco, Loula, & Ho, 2006). In a similar vein, previous studies investigating various phenomena in metacontrast masking (Breitmeyer & Williams, 1990), texture segmentation (Yeshurun & Carrasco, 2000), and saccadic eye movements (Burr, Concetta Morrone, & Ross, 2002) have posited interchannel inhibition to account for interactions across spatiotemporal visual frequencies.

Although not predicted by previous data and models (Morris et al., 1998; Vuilleumier, 2005; Vuilleumier et al., 2003), the observed pattern of benefits and deficits shows that the neural mechanisms underlying emotional vision sacrifice the detection of fine visual details for the processing of coarse information. Rather than causing an overall improvement in visual processing, emotion results in a trade-off that may be due to magnocellular-parvocellular inhibition. The magnocellular pathway plays an important role in the perception of features that are potentially important for detecting threat in the environment—motion, depth, direction, and global configuration—and allows for faster processing than the parvocellular pathway. Thus, the present findings show an emotion-induced bias in the

visual system that may serve to facilitate survival-enhancing responses to danger.

Acknowledgments—We thank Sandra Langeslag, Bjorn de Koning, and Diane Pecher for helpful comments on earlier versions of this article.

REFERENCES

- Amaral, D.G., Behniea, H., & Kelly, J.L. (2003). Topographical organization of projections from the amygdala to the visual cortex in the macaque monkey. *Neuroscience*, *118*, 1099–1120.
- Anderson, A.K., & Phelps, E.A. (2001). Lesions of the amygdala impair enhanced perception of emotionally salient events. *Nature*, *411*, 305–309.
- Brainard, D.H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436.
- Breitmeyer, B.G., & Williams, M.C. (1990). Effects of isoluminant-background color on metacontrast and stroboscopic motion: Interactions between sustained (P) and transient (M) channels. *Vision Research*, *30*, 1069–1075.
- Burr, D.C., Concetta Morrone, M., & Ross, J. (2002). Selective suppression of the magnocellular visual pathway during saccadic eye movements. *Nature*, *371*, 511–513.
- Carrasco, M., Loula, F., & Ho, Y.X. (2006). How attention enhances spatial resolution: Evidence from selective adaptation to spatial frequency. *Perception & Psychophysics*, *68*, 1004–1012.
- Cowey, A. (2004). The 30th Sir Frederick Bartlett lecture: Fact, artefact, and myth about blindsight. *Quarterly Journal of Experimental Psychology: Section A. Human Experimental Psychology*, *57*, 577–609.
- Ekman, P., & Friesen, W. (1976). *Pictures of facial affect*. Palo Alto, CA: Consulting Psychologists Press.
- Fox, E., Lester, V., Russo, R., Bowles, R.J., Pichler, A., & Dutton, K. (2000). Facial expressions of emotion: Are angry faces detected more efficiently? *Cognition & Emotion*, *14*, 61–92.
- Itti, L., Koch, C., & Braun, J. (2000). Revisiting spatial vision: Towards a unifying model. *Journal of the Optical Society of America A*, *17*, 1899–1917.
- Kesler/West, M.L., Andersen, A.H., Smith, C.D., Avison, M.J., Ervin Davis, C., Kryscio, R.J., & Blonder, L.X. (2001). Neural substrates of facial emotion processing using fMRI. *Cognitive Brain Research*, *11*, 213–226.
- Lang, P.J., Bradley, M.M., Fitzsimmons, J.R., Cuthbert, B.N., Scott, J.D., Moulder, B., & Nangia, V. (1998). Emotional arousal and activation of the visual cortex: An fMRI analysis. *Psychophysiology*, *35*, 199–210.
- Loftus, G.R., & Masson, M.E.J. (1994). Using confidence intervals in within-subject designs. *Psychonomic Bulletin & Review*, *1*, 476–490.
- Macmillan, N.A., & Creelman, C.D. (1991). *Detection theory: A user's guide*. New York: Cambridge University Press.
- Mayfrank, L., Kimmig, H., & Fischer, B. (1987). The role of attention in the preparation of visually guided saccadic eye movements in man. In J.K. O'Regan & A. Levy-Schoen (Eds.), *Eye movements: From physiology to cognition* (pp. 162–163). Amsterdam: Elsevier.
- Morris, J.S., Friston, K.J., Buchel, C., Frith, C.D., Young, A.W., Calder, A.J., & Dolan, R.J. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain*, *121*, 47–57.

- Öhman, A., Flykt, A., & Esteves, F. (2001). Emotion drives attention: Detecting the snake in the grass. *Journal of Experimental Psychology: General, 130*, 466–478.
- Pessoa, L. (2005). To what extent are emotional visual stimuli processed without attention and awareness? *Current Opinion in Neurobiology, 15*, 188–196.
- Phelps, E.A., Ling, S., & Carrasco, M. (2006). Emotion facilitates perception and potentiates the perceptual benefits of attention. *Psychological Science, 17*, 292–299.
- Pointer, J.S., & Hess, R.F. (1989). The human contrast sensitivity gradient across the human visual field: With emphasis on the low spatial frequency range. *Vision Research, 29*, 1133–1151.
- Pourtois, G., Dan, E.S., Grandjean, D., Sander, D., & Vuilleumier, P. (2005). Enhanced extrastriate visual response to bandpass spatial frequency filtered fearful faces: Time course and topographic evoked-potentials mapping. *Human Brain Mapping, 26*, 65–79.
- Schupp, H.T., Junghöfer, M., Weike, A.I., & Hamm, A.O. (2003). Emotional facilitation of sensory processing in visual cortex. *Psychological Science, 14*, 7–13.
- Smith, M.L., Cottrell, G.W., Gosselin, F., & Schyns, P.G. (2005). Transmitting and decoding facial expressions. *Psychological Science, 16*, 184–189.
- Stolarova, M., Keil, A., & Moratti, S. (2006). Modulation of the C1 visual event-related component by conditioned stimuli: Evidence for sensory plasticity in early affective perception. *Cerebral Cortex, 16*, 876–887.
- Vuilleumier, P. (2005). How brains beware: Neural mechanisms of emotional attention. *Trends in Cognitive Sciences, 9*, 585–594.
- Vuilleumier, P., Armony, J.L., Driver, J., & Dolan, R.J. (2003). Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nature Neuroscience, 6*, 624–631.
- Vuilleumier, P., & Schwartz, S. (2001). Emotional facial expressions capture attention. *Neurology, 56*, 153–158.
- Yeshurun, Y., & Carrasco, M. (2000). The locus of attentional effects in texture segmentation. *Nature Neuroscience, 3*, 622–627.
- Zeelenberg, R., Wagenmakers, E.-J., & Rotteveel, M. (2006). The impact of emotion on perception: Bias or enhanced processing? *Psychological Science, 17*, 287–291.

(RECEIVED 8/4/08; REVISION ACCEPTED 10/30/08)