

# Rapid Fear Detection Relies on High Spatial Frequencies

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## Abstract

Signals of threat—such as fearful faces—are processed with priority and have privileged access to awareness. This fear advantage is commonly believed to engage a specialized subcortical pathway to the amygdala that bypasses visual cortex and processes predominantly low-spatial-frequency information but is largely insensitive to high spatial frequencies. We tested visual detection of low- and high-pass-filtered fearful and neutral faces under continuous flash suppression and sandwich masking, and we found consistently that the fear advantage was specific to high spatial frequencies. This demonstrates that rapid fear detection relies not on low- but on high-spatial-frequency information—indicative of an involvement of cortical visual areas. These findings challenge the traditional notion that a subcortical pathway to the amygdala is essential for the initial processing of fear signals and support the emerging view that the cerebral cortex is crucial for the processing of ecologically relevant signals.

## Keywords

fear detection, fearful faces, spatial frequency, continuous flash suppression, sandwich masking, facial expressions, visual perception, consciousness, fear

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Throughout human evolution, the rapid analysis of emotionally significant sensory events—and of threat signals in particular—has been highly beneficial for survival and may have propelled the development of dedicated neural circuits (Öhman & Mineka, 2001; Tamietto & de Gelder, 2010). Studies on the neural processing of emotional stimuli have implicated the amygdala as an essential node in mediating adaptive responses to threat (Phelps & LeDoux, 2005; Vuilleumier, 2005). In rodents, the amygdala receives subcortical afferents that bypass cortical areas and convey coarse auditory information about aversive stimuli in a rapid fashion (LeDoux, 2000). Following these findings, the current dominant view of emotion processing in the human visual system holds that the initial analysis of threatening visual stimuli bypasses visual cortex and engages a specialized extrageniculate subcortical pathway projecting from the retina to the amygdala via the superior colliculus and the pulvinar (Öhman, 2005; Skuse, 2006; Tamietto & de Gelder, 2010). This subcortical “low road”

(LeDoux, 1996) to the amygdala is assumed to enable rapid processing of threatening stimuli such as fearful facial expressions and to operate largely automatically and outside of conscious awareness.

Although the idea of a subcortical pathway to the amygdala is commonly applied to the human visual system, there is no clear anatomical evidence for a feed-forward connection conveying visual information from the superior colliculus or the pulvinar to the amygdala in the primate brain (Pessoa & Adolphs, 2010). The existence of a retino-collicular-pulvinar-amygdala pathway in the human visual system is therefore usually inferred indirectly from findings that are consistent with the functional properties

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ascribed to the low road. For example, the faster and more accurate detection of fearful faces than of neutral faces (Milders, Sahraie, Logan, & Donnellon, 2006; Yang, Zald, & Blake, 2007) and amygdala activity to fearful faces found in the absence of awareness (Morris, de Gelder, Weiskrantz, & Dolan, 2001; Whalen et al., 1998) are taken as support for the low-road account.

Another approach has exploited the tuning properties of cells in subcortical structures belonging to the putative low road (Vuilleumier, Armony, Driver, & Dolan, 2003). Visually responsive neurons in the input layers of the superior colliculus, the gateway to the purported subcortical route, receive afferents mainly from magnocellular retinal ganglion cells that have large receptive fields and respond to gradual luminance changes over large regions of the input image, that is, to low-spatial-frequency (LSF) information (Leventhal, Rodieck, & Dreher, 1985; Schiller, Malpeli, & Schein, 1979). By contrast, parvocellular ganglion cells that have small receptive fields and respond to luminance changes that occur over smaller image regions, that is, to high-spatial-frequency (HSF) information, project mainly to cortical visual areas (Livingstone & Hubel, 1988; Merigan & Maunsell, 1993). Thus, if the subcortical pathway does convey visual information about fear signals, the processing of such stimuli should predominantly rely on coarse LSF information. In support of this notion, stronger amygdala activity to fearful than to neutral faces has been found for low-pass-filtered but not for high-pass-filtered face stimuli (Vuilleumier et al., 2003).

Contrary to these neuroimaging findings, however, psychophysical studies have shown that observers primarily use HSF rather than LSF information to discriminate fearful faces from other expressions (Adolphs et al., 2005; Smith, Cottrell, Gosselin, & Schyns, 2005; Smith & Schyns, 2009). Although these results demonstrate the central importance of HSF information in fear recognition, they do not rule out a functional role of the low road in other, more basic tasks, such as fear detection. It is conceivable that complex perceptual judgments on fearful faces involve cortical circuits that analyze fine-grained HSF information but do not tap into the rapid initial processing of fear signals attributed to the subcortical pathway. Rather, one important function ascribed to the putative low road is to support rapid access to awareness for emotional stimuli (Öhman, 2005; Tamietto & de Gelder, 2010; Yang et al., 2007).

To test the functional role of the putative low road in the conscious detection of fear signals, we examined whether the advantage of fearful over neutral faces in gaining access to awareness relies on LSF or HSF information. If the “fear advantage” in conscious detection is mediated by coarse visual signals transmitted through the subcortical pathway to the amygdala, it should depend more strongly on LSF than HSF information. Alternatively, if the fear advantage depends on similar visual cues as

the more sophisticated task of fear recognition, it should rely primarily on HSF information analyzed by visual cortical areas.

## Experiment 1: Detection of Low- and High-Pass-Filtered Faces Under Continuous Flash Suppression (CFS)

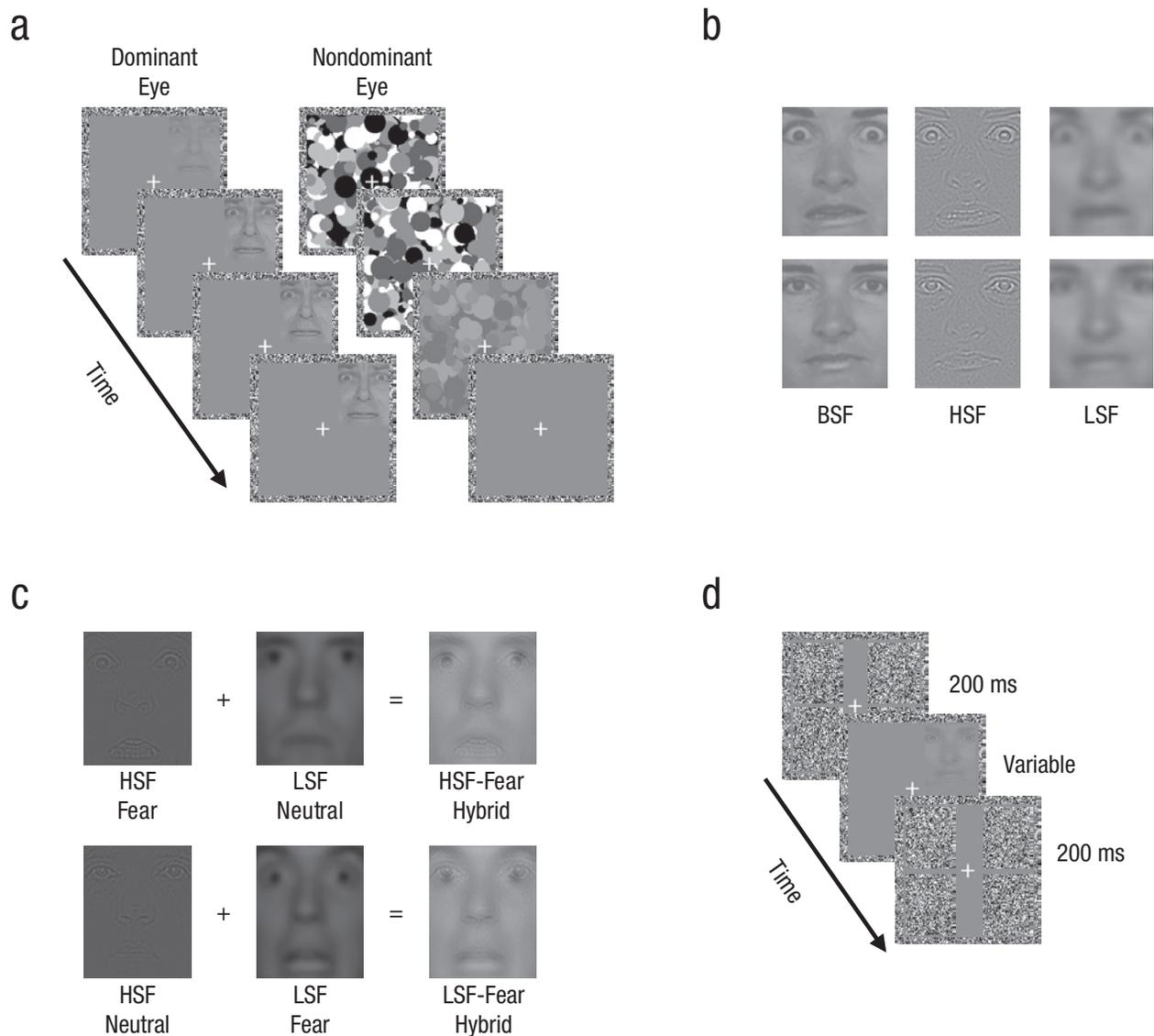
In Experiment 1, we used CFS (Tsuchiya & Koch, 2005), a potent interocular suppression technique, to test whether the advantage of fearful faces in accessing visual awareness relies on HSF or LSF information (Fig. 1a).

At the beginning of each trial, high- and low-pass-filtered fearful and neutral faces (Fig. 1b) presented to one eye were rendered invisible through CFS masks flashed at 10 Hz into the other eye. We measured the time needed for faces to overcome CFS and break into awareness (Jiang, Costello, & He, 2007; Yang et al., 2007). Because interocular suppression is known to reduce activity along the geniculostriate pathway and to strongly suppress neural processing in extrastriate visual cortex (for a review, see Lin & He, 2009), we considered this method particularly useful for uncovering a functional role of the low road. Indeed, neuroimaging studies have found fearful faces to activate the amygdala under interocular suppression, whereas no such differential neural activity has been detected in ventral cortical areas (Lin & He, 2009).

### Method

**Participants.** A total of 44 participants (33 female, 11 male; mean age = 26.3 years) gave informed consent to take part in Experiments 1a through 1c (for additional participant information, see the Supplemental Material available online). Twelve participants took part in Experiment 1a. Sixteen participants completed Experiments 1b and 1c, respectively.

**Display and stimuli.** Participants viewed stimuli on a 19-in. gamma-corrected CRT screen at a viewing distance of 50 cm, with their heads stabilized by a chin- and headrest. Stimuli were viewed dichoptically through a mirror stereoscope, such that each eye was presented with approximately half of the screen. Each eye was shown a frame surrounded by fusion contours consisting of random black and white pixels ( $8.5^\circ \times 8.5^\circ$ ; Fig. 1a). The gray background of the frames was assigned the mean luminance of the face stimuli. Faces were presented in one of the quadrants of one of the frames, centered at a vertical distance of  $2.0^\circ$  and a horizontal distance of  $2.3^\circ$  relative to a central white fixation cross. Participants were asked to maintain stable fixation.



**Fig. 1.** Procedure and stimuli for the three experiments. In Experiments 1 and 2, a face was gradually introduced to the participant's dominant eye (a), while masks were presented at 10 Hz to the nondominant eye using continuous flash suppression (CFS). Participants localized as quickly and accurately as possible the quadrant in which the face or any part of the face became visible. This illustration of an example trial depicts the standard, unfiltered CFS masks and an original, unfiltered broad-spatial-frequency (BSF) fearful face. Other face stimuli (examples of which are shown in (b)) consisted of high-spatial-frequency (HSF) and low-spatial-frequency (LSF) filtered fearful faces (top row) and neutral faces (bottom row). Faces were presented either upright (as shown here) or inverted. Examples of hybrid faces from Experiment 2 are shown in (c). HSF-fear hybrid faces were composed of a fearful, low-contrast HSF face and a neutral, high-contrast LSF face. Conversely, LSF-fear hybrids were composed of a neutral, low-contrast HSF face and a fearful, high-contrast LSF face. In Experiment 3 (d), a face displayed in one quadrant for a variable duration was preceded and followed by noise masks presented for 200 ms each. Participants localized as accurately as possible the quadrant in which the face was presented.

We selected eight face identities with fearful and neutral expressions, four from the Ekman and Friesen (1976) face set, and four from the NimStim set of facial expressions (Tottenham et al., 2009). These standard broad-spatial-frequency (BSF) faces were fit to a rectangle ( $3.2^\circ \times 3.8^\circ$ ) that excluded outer facial features (Yang et al., 2007) and were assigned identical luminance and root-mean-square (RMS) contrast values (Fig. 1b). To create HSF and LSF

faces, we manipulated spatial-frequency content by passing the BSF images through a second-order Butterworth filter, using a high-pass cutoff of more than 6 cycles per degree for the HSF faces and a low-pass cutoff of less than 2 cycles per degree for the LSF faces, following previous studies (Vlamings, Goffaux, & Kemner, 2009). Finally, the filtered faces were again normalized for luminance and RMS contrast. Subjective ratings demonstrated

that HSF and LSF fearful faces did not differ in perceived fearfulness (see the Supplemental Material). Following previous studies (Yang et al., 2007), we also generated inverted versions of all face stimuli (i.e., faces were rotated 180°).

The CFS masks ( $8.0^\circ \times 8.0^\circ$ ) used in Experiment 1a consisted of randomly arranged white, black, and gray circles (diameter =  $0.3^\circ$ – $1.4^\circ$ ). In Experiments 1b and 1c, we controlled for the possibility that these CFS masks were more effective in suppressing LSF than HSF information (Yang & Blake, 2012) and manipulated their spatial-frequency content using the same procedure and cutoffs as for the face stimuli. For Experiment 1b, we generated hybrid masks that were combinations of high- and low-pass-filtered CFS masks with identical contrast energy in both spatial-frequency bands, each having a lower mean luminance. In Experiment 1c, we used CFS masks containing HSF information only.

**Procedure.** Trials began with a 1-s presentation of the blank frames and the fixation cross only. Next, a face was introduced to the participant's dominant eye by linearly ramping up its contrast over a period of 1.1 s while CFS masks flashing at 10 Hz were presented within the frame shown to the nondominant eye. Beginning 1.1 s after trial onset, the contrast of the CFS masks was linearly ramped down to zero over 4.0 s (Experiments 1a and 1b) or 7.0 s (Experiment 1c). Trials ended when participants responded or after a maximum duration of 7.0 s (Experiments 1a and 1b) or 10.0 s (Experiment 1c). Participants pressed one of four keys on a QWERTY keyboard corresponding to the four quadrants ("F" or "V" with their left hand and "J" or "N" with their right hand) to indicate as quickly and accurately as possible in which quadrant a face or any part of a face became visible. Trials with incorrect responses or no response (< 2%) were excluded from the computation of mean suppression durations.

**Design.** Experiment 1a consisted of 576 trials in which all combinations of the eight faces' spatial frequency (BSF, HSF, or LSF), emotion (fearful or neutral), and face orientation (upright or inverted) were presented equally often. The quadrant for face presentation was selected at random for each trial, the order of all experimental conditions was randomized, and there were mandatory breaks every 96 trials. Experiments 1b and 1c were the same but contained 384 trials because we omitted the BSF condition.

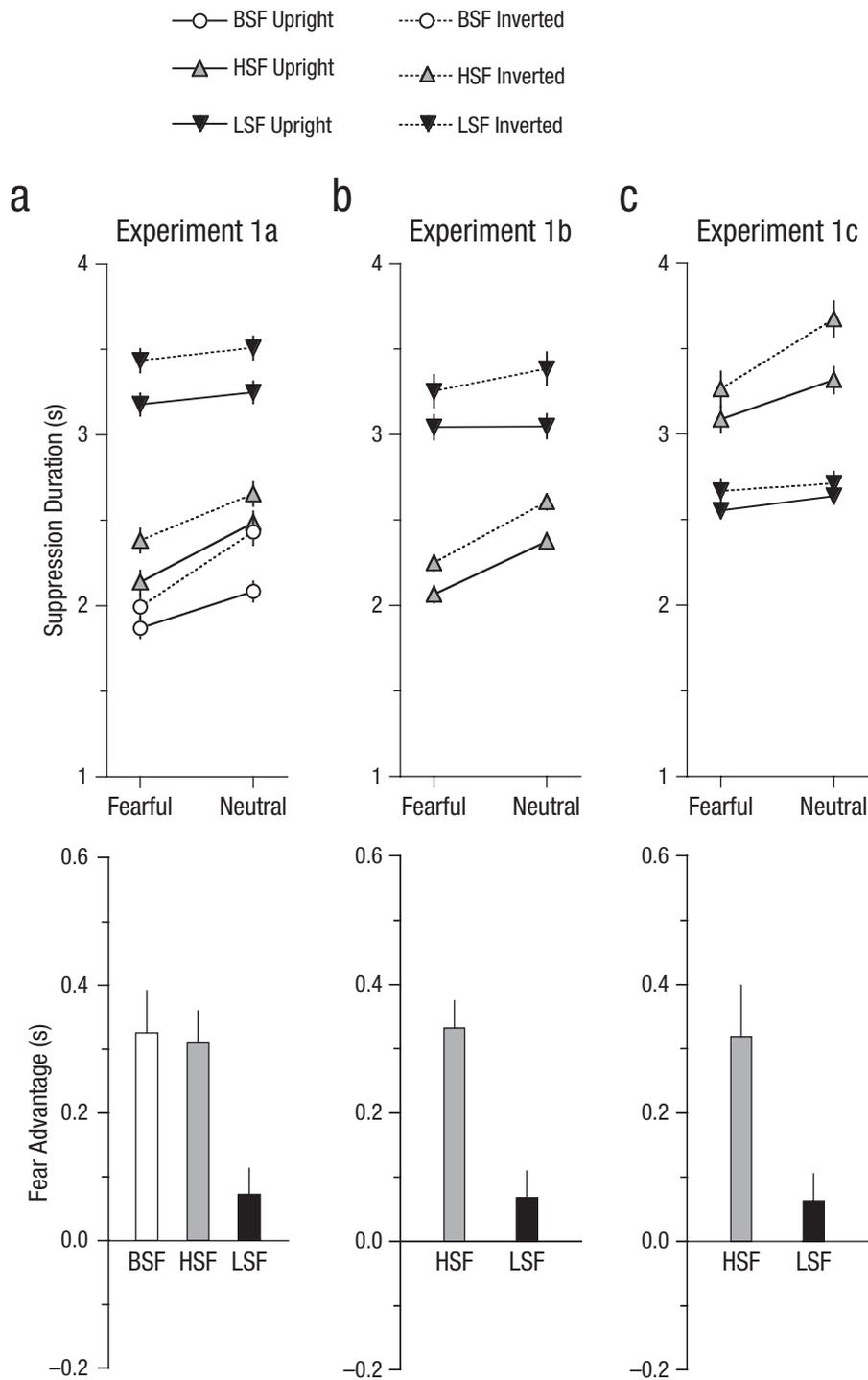
## Results and discussion

A repeated measures analysis of variance on the mean suppression duration from Experiment 1a revealed a general advantage of fearful over neutral faces in overcoming suppression,  $F(1, 11) = 33.81$ ,  $p < .001$ , overall

shorter suppression durations for BSF and HSF than for LSF faces,  $F(2, 22) = 19.00$ ,  $p < .001$ , and shorter suppression durations for upright than for inverted faces,  $F(1, 11) = 16.18$ ,  $p = .002$ ; these findings are consistent with previous research (Jiang et al., 2007; Yang et al., 2007). There were no significant interactions with face orientation, all  $F$ s < 1. This is consistent with previous findings (Yang et al., 2007) indicating that the advantage of fearful faces in gaining access to awareness does not rely on configural face processing but on salient image features that are preserved in inverted faces. Our central question was whether this increased saliency of fearful faces would rely on LSF or on HSF information. Crucially, there was an interaction between spatial frequency and emotion,  $F(2, 22) = 12.04$ ,  $p < .001$ , with significant advantages of fearful over neutral faces in accessing awareness for BSF faces,  $F(1, 11) = 25.03$ ,  $p < .001$ , and HSF faces,  $F(1, 11) = 39.20$ ,  $p < .001$ , but not for LSF faces,  $F(1, 11) = 3.36$ ,  $p = .094$  (Fig. 2a).

Reducing the analysis to HSF and LSF faces only, we found a significant spatial-frequency-by-emotion interaction,  $F(1, 11) = 22.00$ ,  $p < .001$ , which demonstrated that the advantage of fearful faces was larger for HSF than for LSF faces. A potential reason for the observed HSF specificity of the fear advantage is that the CFS masks were more effective in suppressing LSF than HSF fear information (Yang & Blake, 2012). To exclude this possibility, in Experiment 1b, we filtered the spatial-frequency content of the CFS masks and created hybrid CFS masks that consisted of identical contrast energy in both the low- and high-spatial-frequency bands. The results were similar to those of Experiment 1a. There were significant main effects of spatial frequency,  $F(1, 15) = 11.06$ ,  $p = .005$ , emotion,  $F(1, 15) = 60.94$ ,  $p < .001$ , orientation,  $F(1, 15) = 36.87$ ,  $p < .001$ , and, critically, a significant interaction between spatial frequency and emotion,  $F(1, 15) = 17.40$ ,  $p = .001$ , which means that the fear advantage was larger for HSF than for LSF faces (Fig. 2b). The fear advantage was significant for HSF faces,  $F(1, 15) = 65.89$ ,  $p < .001$ , but not for LSF faces,  $F(1, 15) = 2.87$ ,  $p = .111$ . Additional control experiments (see the Supplemental Material) showed that these results were not due to local contrast differences in the eye or mouth regions and that the HSF specificity of the fear advantage extended to faces presented further in the periphery.

To conclusively rule out that the masks used in the previous experiments were more effective in suppressing LSF than HSF fear information, in Experiment 1c, we used CFS masks that contained HSF information only. Again, we found significant main effects of emotion,  $F(1, 15) = 22.52$ ,  $p < .001$ , and orientation,  $F(1, 15) = 9.20$ ,  $p = .008$ , and a significant spatial-frequency-by-emotion interaction,  $F(1, 15) = 7.07$ ,  $p = .018$ . Thus, even when the face stimuli competed against high-pass-filtered masks, the fear advantage was significant for HSF faces,



**Fig. 2.** Results for Experiments 1a, 1b, and 1c (a–c, respectively). The top row shows mean suppression duration as a function of face type (fearful and neutral) and face orientation (upright and inverted), separately for broad-spatial-frequency (BSF), high-spatial-frequency (HSF), and low-spatial-frequency (LSF) faces. Error bars represent standard errors of the difference between fearful and neutral faces. The bottom row shows the “fear advantage” (i.e., the difference in suppression duration between neutral and fearful faces, averaged across upright and inverted faces) as a function of faces’ spatial frequency. Error bars represent standard errors of the mean.

$F(1, 15) = 16.47, p = .001$ , but not for LSF faces,  $F(1, 15) = 2.42, p = .140$  (Fig. 2c). Because overall suppression durations in Experiment 1c were considerably longer for HSF

than for LSF faces,  $F(1, 15) = 10.86, p = .005$ , these results also show that the HSF specificity of the fear advantage cannot be ascribed to ceiling effects for LSF faces.

## Experiment 2: Detection of Hybrid Faces Under CFS

Another way to examine which spatial-frequency band is read out by the visual system is to present hybrid faces that combine HSF and LSF information of two different facial expressions in one stimulus (Schyns & Oliva, 1999; Winston, Vuilleumier, & Dolan, 2003). In Experiment 2, we compared the duration of perceptual suppression for HSF-fear hybrids constructed from an HSF fearful face and an LSF neutral face with LSF-fear hybrids consisting of an LSF fearful face and an HSF neutral face (Fig. 1c). If the fear advantage is driven by LSF information conveyed by the low road, LSF-fear hybrids should overcome CFS more quickly than HSF-fear hybrids.

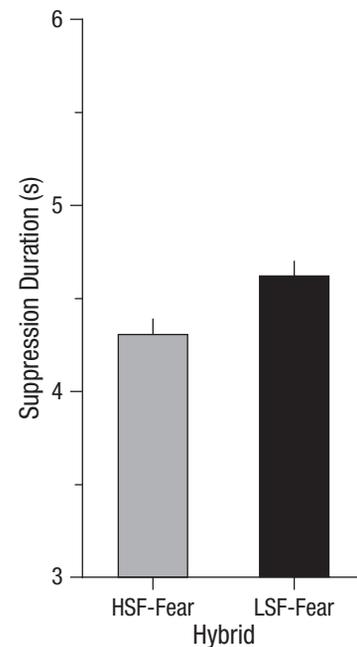
### Method

**Participants.** Twelve participants (10 female, 2 male; mean age = 28.3 years) took part in Experiment 2.

**Stimuli, procedure, and design.** The stimuli, procedure, and design were identical to those in Experiment 1c, except that we now presented (only upright) HSF-fear and LSF-fear hybrid faces and hybrid CFS masks. We constructed hybrid faces from another set of 16 high- and low-pass-filtered face exemplars (12 from the NimStim set and 4 from the Ekman and Friesen set), each having a lower mean luminance than in Experiment 1. Each HSF-fear hybrid face was composed of a fearful, low-contrast HSF face and a neutral, high-contrast LSF face. Conversely, each LSF-fear hybrid was composed of a neutral, low-contrast HSF face and a fearful, high-contrast LSF face. The HSF images were assigned only one third of the RMS contrast of the LSF images to rule out that faster detection of HSF-fear hybrids than of LSF-fear hybrids could have been due to overall shorter suppression for HSF stimuli (for a validation of this manipulation and for a control experiment using HSF and LSF images with identical contrast, see the Supplemental Material). Participants completed 128 trials in which the 16 face exemplars were presented four times as HSF-fear hybrids and four times as LSF-fear hybrids, in randomized order. As in Experiment 1, trials with incorrect responses or no response (< 2%) were excluded from the computation of mean suppression durations.

### Results and discussion

Suppression durations were significantly shorter for HSF-fear hybrids than for LSF-fear hybrids,  $t(11) = 4.15$ ,  $p = .002$  (Fig. 3). Thus, although the contrast of the HSF content in these hybrid faces was reduced relative to the LSF content, the fear advantage was mediated by this contrast-reduced HSF fear content.



**Fig. 3.** Results from Experiment 2: mean suppression duration as a function of stimulus type. Each stimulus was composed of either a fearful, low-contrast high-spatial-frequency (HSF) face and a neutral, high-contrast low-spatial-frequency (LSF) face (HSF-fear hybrids) or a neutral, low-contrast HSF face and a fearful, high-contrast LSF face (LSF-fear hybrids). Error bars represent standard errors of the difference between HSF-fear and LSF-fear hybrids.

## Experiment 3: Detection of Hybrid Faces Under Sandwich Masking

Finally, in Experiment 3, we tested whether the HSF specificity of the fear advantage would generalize to another detection paradigm not involving interocular suppression. We devised a sandwich-masking protocol in which hybrid faces that were displayed for variable durations were forward and backward masked by random noise pixels (Fig. 1d). Because these masks contained a broad range of spatial frequencies, this method minimized potential interactions with the faces' spatial frequency.

### Method

**Participants.** Sixteen participants (11 female, 5 male; mean age = 26.3 years) took part in Experiment 3.

**Display and stimuli.** Participants binocularly viewed a 17-in. gamma-corrected thin-film-transistor screen. A single black frame was displayed in the center of the screen. The CFS masks used in the previous experiments were replaced by noise masks (consisting of random black and white pixels) that were presented in the same locations as the face stimuli. The size and the position of the stimuli were the same as in the previous CFS experiments.

We used the same set of 16 face exemplars as in Experiment 2 to create HSF-fear and LSF-fear hybrids, but HSF and LSF faces now had identical RMS contrast values, as informal pilot studies revealed no evidence for generally better detection of HSF than of LSF faces under sandwich masking (for a control experiment demonstrating that overall detection accuracies were actually higher for LSF than for HSF faces, see the Supplemental Material).

**Procedure.** Trials began with a 1-s presentation of the blank frame without a fixation cross, followed by a 2-s presentation of the fixation cross only. Next, four noise masks, randomly generated for each trial, were displayed within four quadrants of the frame for 200 ms, followed by the presentation of a face in one quadrant for a variable duration (17, 50, 83, 117, 167, or 217 ms). Another four random noise masks presented for 200 ms immediately followed face presentation. We asked participants to indicate as accurately as possible, without speed pressure, the quadrant in which the face was presented. Participants received feedback.

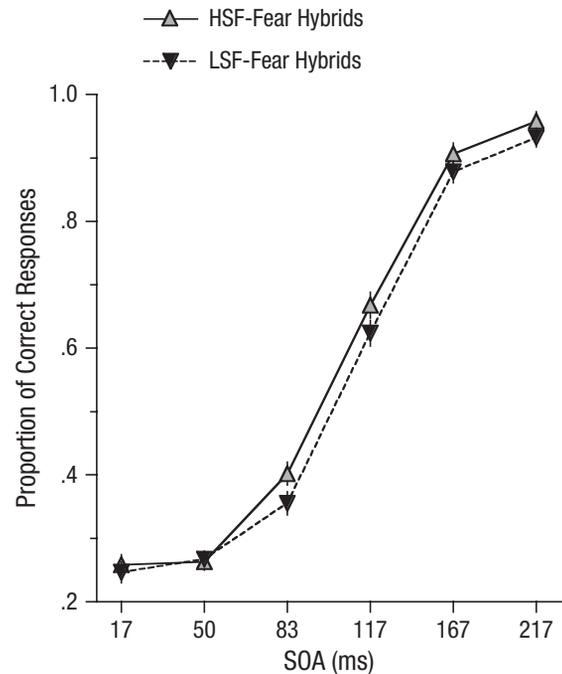
**Design.** There were 768 trials, which combined 16 identities for both HSF- and LSF-fear hybrids, six different presentation durations, and four face locations in random order.

## Results and discussion

As can be seen in Figure 4, detection accuracy was higher for HSF-fear hybrids than for LSF-fear hybrids,  $F(1, 15) = 7.61, p = .015$ , thus replicating the HSF specificity of the fear advantage revealed by the previous CFS experiments.

## General Discussion

To examine whether the rapid conscious detection of fear signals involves a distinct extrageniculate subcortical pathway to the amygdala, we tested whether the advantage of fearful over neutral faces in accessing visual awareness (Yang et al., 2007) relies on low or high spatial frequencies. Contrary to the purported role of a subcortical “low road” to the amygdala that transmits mainly coarse LSF information, our data show that rapid detection of fearful faces is mediated predominantly by fine-grained HSF information. As HSF image content is conveyed by parvocellular ganglion cells that project primarily to visual cortical areas via the geniculostriate pathway (Livingstone & Hubel, 1988; Merigan & Maunsell, 1993), these results challenge the prevailing theory that a retino-collicular-pulvinar-amygdala pathway is essential to rapid fear detection (Öhman, 2005; Tamietto & de Gelder, 2010).



**Fig. 4.** Results from Experiment 3: mean proportion of correct responses as a function of stimulus onset asynchrony (SOA) between the forward and the backward masks, and stimulus type. Each stimulus was composed of either a fearful, low-contrast high-spatial-frequency (HSF) face and a neutral, high-contrast low-spatial-frequency (LSF) face (HSF-fear hybrids) or a neutral, low-contrast HSF face and a fearful, high-contrast LSF face (LSF-fear hybrids). Error bars represent standard errors of the difference between HSF-fear and LSF-fear hybrids or fearful and neutral faces.

Although reliance on high spatial frequencies for rapid fear detection supports the emerging view that the cortex plays an important role in the detection of ecologically relevant signals (Pessoa & Adolphs, 2010), neuroimaging data show that amygdala activity does not differentiate between fearful and neutral HSF faces (Vuilleumier et al., 2003). One possibility for this apparent inconsistency with the understanding of the amygdala’s role in mediating responses to fear signals is that the amygdala is not crucially involved in the initial processing of fearful faces but modulates later attentional and cognitive processes according to stimulus valence and behavioral significance (Adolphs, 2008; Pessoa, 2010). Indeed, a recent study on a patient with bilateral amygdala damage revealed a fear advantage at full strength under CFS and during visual search (Tsuchiya, Moradi, Felsen, Yamazaki, & Adolphs, 2009), which provides strong evidence against an essential role of the amygdala in rapid fear detection. Also, because visual cortical areas not only send massive efferents to the amygdala (Amaral, Price, Pitkanen, & Carmichael, 1992) but can also exhibit short latency

responses (Lamme & Roelfsema, 2000), rapid detection of fearful faces is not necessarily indicative of a direct subcortical route to the amygdala. Rather, our data are consistent with information about fearful faces being conveyed to the amygdala via the cerebral cortex, possibly including direct subcortical projections to extrastriate visual cortex (Morris et al., 2001; Pegna, Khateb, Lazeyras, & Seghier, 2005).

The HSF selectivity of the fear advantage in conscious detection dovetails with the central role of HSF information in the recognition of fearful faces (Adolphs et al., 2005; Smith et al., 2005; Smith & Schyns, 2009). For example, fearful faces are poorly recognized at longer viewing distances, as there is little HSF information available (Smith & Schyns, 2009). It is thus conceivable that both detection and recognition of fearful faces depend on similar facial features represented in the HSF band, such as sharp edges in the eye and mouth regions. An important question for future studies is to determine whether this HSF selectivity of fear processing extends to other stimuli, such as snakes (Isbell, 2006; Öhman, 2005) or emotional body postures (Tamietto & de Gelder, 2010), and to other effects that have been linked to the subcortical low road, such as attentional orienting to threatening stimuli (Ward, Danziger, & Bamford, 2005). Also, as we studied only access to awareness here, it remains to be seen whether the processing of invisible emotional stimuli (e.g., Lin & He, 2009) or the preserved ability to discriminate unseen facial expressions in patients with damage to primary visual cortex (de Gelder, Vroomen, Pourtois, & Weiskrantz, 1999) are similarly dependent on HSF information.

Another important limitation of the present study is that we contrasted only fearful with neutral faces. Our findings are therefore not necessarily specific to fearful facial expressions but may reflect a more general difference between expressive and nonexpressive faces. For example, a similar pattern might be obtained with other facial expressions, such as surprise, which is physically and conceptually similar to fear. On a related note, the advantage of fearful over neutral faces in gaining access to awareness could reflect the prioritized processing of either a fear signal or a more primitive threat or danger signal. It is still possible that the processing of simple threat signals, such as large eye whites, which are components of both fear and surprise signals (Jack, Blais, Scheepers, Schyns, & Caldara, 2009), relies on LSF information. Here, we specifically focused on the comparison between fearful and neutral faces to determine the spatial-frequency band mediating the fear advantage, because this particular contrast has in the past provided notable support for a functional role of the low road (Vuilleumier et al., 2003; Yang et al., 2007).

Taken together, the findings of our experiments argue against a functional role of a retino-collicular-pulvinar-amygdala pathway and cast doubt on the existence of such a subcortical fear module in the human brain. These findings thus call for a reconsideration of the current views on the neural processing of emotionally significant stimuli.

### Author Contributions

T. Stein and P. Sterzer developed the study concept. T. Stein, K. Seymour, M. N. Hebart, and P. Sterzer contributed to the study design. Testing, data collection, and data analyses were performed by T. Stein. The manuscript was drafted by T. Stein, and all coauthors provided critical revisions. All authors approved the final version of the manuscript for submission.

### Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

### Supplemental Material

Additional supporting information may be found at <http://pss.sagepub.com/content/by/supplemental-data>

### References

- Adolphs, R. (2008). Fear, faces, and the human amygdala. *Current Opinion in Neurobiology*, *18*, 166–172.
- Adolphs, R., Gosselin, F., Buchanan, T. W., Tranel, D., Schyns, P., & Damasio, A. R. (2005). A mechanism for impaired fear recognition after amygdala damage. *Nature*, *433*, 68–72.
- Amaral, D. G., Price, J. L., Pitkanen, A., & Carmichael, S. T. (1992). Anatomical organization of the primate amygdaloid complex. In J. P. Aggleton (Ed.), *The amygdala: Neurobiological aspects of emotion, memory, and mental dysfunction* (pp. 1–66). New York, NY: Wiley-Liss.
- de Gelder, B., Vroomen, J., Pourtois, G., & Weiskrantz, L. (1999). Non-conscious recognition of affect in the absence of striate cortex. *NeuroReport*, *10*, 3759–3763.
- Ekman, P., & Friesen, W. (1976). *Pictures of facial affect*. Palo Alto, CA: Consulting Psychologists Press.
- Isbell, L. A. (2006). Snakes as agents of evolutionary change in primate brains. *Journal of Human Evolution*, *51*, 1–35.
- Jack, R. E., Blais, C., Scheepers, C., Schyns, P. G., & Caldara, R. (2009). Cultural confusions show that facial expressions are not universal. *Current Biology*, *19*, 1543–1548.
- Jiang, Y., Costello, P., & He, S. (2007). Processing of invisible stimuli: Advantage of upright faces and recognizable words in overcoming interocular suppression. *Psychological Science*, *18*, 349–355.
- Lamme, V. A., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences*, *23*, 571–579.
- LeDoux, J. E. (1996). *The emotional brain: The mysterious underpinnings of emotional life*. New York, NY: Simon & Schuster.

- LeDoux, J. E. (2000). Emotion circuits in the brain. *Annual Review of Neuroscience*, *23*, 155–184.
- Leventhal, A. G., Rodieck, R. W., & Dreher, B. (1985). Central projections of cat retinal ganglion cells. *Journal of Comparative Neurology*, *237*, 216–226.
- Lin, Z., & He, S. (2009). Seeing the invisible: The scope and limits of unconscious processing in binocular rivalry. *Progress in Neurobiology*, *87*, 195–211.
- Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science*, *240*, 740–749.
- Merigan, W. H., & Maunsell, J. H. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, *16*, 369–402.
- Milders, M., Sahraie, A., Logan, S., & Donnellon, N. (2006). Awareness of faces is modulated by their emotional meaning. *Emotion*, *6*, 10–17.
- Morris, J. S., de Gelder, B., Weiskrantz, L., & Dolan, R. J. (2001). Differential extrageniculostriate and amygdala responses to presentation of emotional faces in a cortically blind field. *Brain*, *124*, 1241–1252.
- Öhman, A. (2005). The role of the amygdala in human fear: Automatic detection of threat. *Psychoneuroendocrinology*, *30*, 953–958.
- Öhman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review*, *108*, 483–522.
- Pegna, A. J., Khateb, A., Lazeyras, F., & Seghier, M. L. (2005). Discriminating emotional faces without primary visual cortices involves the right amygdala. *Nature Neuroscience*, *8*, 24–25.
- Pessoa, L. (2010). Emotion and cognition and the amygdala: From “what is it?” to “what’s to be done?” *Neuropsychologia*, *48*, 3416–3429.
- Pessoa, L., & Adolphs, R. (2010). Emotion processing and the amygdala: From a “low road” to “many roads” of evaluating biological significance. *Nature Reviews Neuroscience*, *11*, 773–782.
- Phelps, E. A., & LeDoux, J. E. (2005). Contributions of the amygdala to emotion processing: From animal models to human behavior. *Neuron*, *48*, 175–187.
- Schiller, P. H., Malpeli, J. G., & Schein, S. J. (1979). Composition of geniculostriate input to superior colliculus of the rhesus monkey. *Journal of Neurophysiology*, *42*, 1124–1133.
- Schyns, P. G., & Oliva, A. (1999). Dr. Angry and Mr. Smile: When categorization flexibly modifies the perception of faces in rapid visual presentations. *Cognition*, *69*, 243–265.
- Skuse, D. (2006). Genetic influences on the neural basis of social cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *361*, 2129–2141.
- Smith, M. L., Cottrell, G. W., Gosselin, F., & Schyns, P. G. (2005). Transmitting and decoding facial expressions. *Psychological Science*, *16*, 184–189.
- Smith, M. L., & Schyns, P. G. (2009). Smile through your fear and sadness: Transmitting and identifying facial expressions over a range of viewing distances. *Psychological Science*, *20*, 1202–1208.
- Tamietto, M., & de Gelder, B. (2010). Neural bases of the non-conscious perception of emotional signals. *Nature Reviews Neuroscience*, *11*, 697–709.
- Tottenham, N., Tanaka, J. W., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., . . . Nelson, C. (2009). The NimStim set of facial expressions: Judgments from untrained research participants. *Psychiatry Research*, *168*, 242–249.
- Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience*, *8*, 1096–1101.
- Tsuchiya, N., Moradi, F., Felsen, C., Yamazaki, M., & Adolphs, R. (2009). Intact rapid detection of fearful faces in the absence of the amygdala. *Nature Neuroscience*, *12*, 1224–1225.
- Vlamings, P. H. J. M., Goffaux, V., & Kemner, C. (2009). Is the early modulation of brain activity by fearful facial expressions primarily mediated by coarse low spatial frequency information? *Journal of Vision*, *9*(5), Article 12. Retrieved from <http://www.journalofvision.org/content/9/5/12>
- 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.
- Ward, R., Danziger, S., & Bamford, S. (2005). Response to threat following damage to the amygdala. *Current Biology*, *15*, 571–573.
- Whalen, P. J., Rauch, S. L., Etcoff, N. L., McInerney, S. C., Lee, M. B., & Jenike, M. A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *Journal of Neuroscience*, *18*, 411–418.
- Winston, J. S., Vuilleumier, P., & Dolan, R. J. (2003). Effects of low-spatial frequency components of fearful faces on fusiform cortex activity. *Current Biology*, *13*, 1824–1829.
- Yang, E., & Blake, R. (2012). Deconstructing continuous flash suppression. *Journal of Vision*, *12*(3), Article 8. Retrieved from <http://www.journalofvision.org/content/12/3/8.full>
- Yang, E., Zald, D. H., & Blake, R. (2007). Fearful expressions gain preferential access to awareness during continuous flash suppression. *Emotion*, *7*, 882–886.