Rapid fear detection relies on high spatial frequencies

Timo Stein\textsuperscript{1,2,3}, Kiley Seymour\textsuperscript{1}, Martin N. Hebart\textsuperscript{2,4}, & Philipp Sterzer\textsuperscript{1,2,4}

\textsuperscript{1} Department of Psychiatry, Charité Universitätsmedizin Berlin, Charitéplatz 1, 10117 Berlin, Germany
\textsuperscript{2} Berlin School of Mind and Brain, Humboldt-Universität zu Berlin, Luisenstraße 56, 10099 Berlin, Germany
\textsuperscript{3} Center for Mind/Brain Sciences, CIMeC, University of Trento, Corso Bettini 31, 38068 Rovereto, Italy
\textsuperscript{4} Bernstein Center for Computational Neuroscience, Humboldt-Universität zu Berlin, Philippstraße 13, 10115 Berlin, Germany

Author for correspondence:
Timo Stein
Center for Mind/Brain Sciences (CIMEC)
Palazzo Fedrigotti
Corso Bettini 31
38068 Rovereto (TN)
Italy
timo@timostein.de
phone +39 0464808722
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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 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
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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 feedforward 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 ascribed to the low road. For example, the faster and more accurate detection of fearful faces compared to 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, i.e. to low spatial frequency (LSF) information (Leventhal, Rodieck, & Dreher, 1985; Schiller, Malpeni, & Schein, 1979). By contrast, parvocellular ganglion cells that have small receptive fields and respond to luminance changes that occur over smaller image regions, i.e. 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 compared to neutral faces has been found for low-pass but not for high-pass filtered face stimuli (Vuilleumier et al., 2003).

Contrary to these neuroimaging findings, however, 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 to 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 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**

In Experiment 1, we used continuous flash suppression (CFS; Tsuchiya and 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 (Figure 1a). At the beginning of each trial, high- and low-pass filtered fearful and neutral faces (Figure 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). Since 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, while no such differential neural activity has been detected in ventral cortical areas (Lin & He, 2009).
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Method

Participants. A total of 72 participants (54 female, age range 18–39 years, mean age 26.7 years) gave informed consent to take part in the present experiments (for additional participant information and experimental details, see Supplemental Material available online). Twelve observers participated in Experiment 1a. Sixteen participants completed Experiments 1b and 1c, respectively.

Display and stimuli. Participants viewed a 19-inch gamma-corrected CRT screen at a viewing distance of 50 cm dichoptically through a mirror stereoscope, with their head stabilized by a chin-and-head rest, 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° × 8.5°; Figure 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 the frames, centered at a vertical distance of 2.0° and a horizontal distance of 2.3° relative to a central white fixation cross. Participants were asked to maintain stable fixation.

We selected eight face identities with fearful and neutral expressions, four from the Ekman and Friesen (1976) face set, and four from the Nimstim face set (Tottenham et al., 2009). These standard broad spatial frequency (BSF) faces were fit to a rectangle (3.2° × 3.8°) that excluded outer facial features (Yang et al., 2007) and were assigned identical luminance and RMS contrast values (Figure 1b). To create HSF and LSF faces, spatial frequency content in these BSF images was manipulated by passing them through a second order Butterworth filter, using a high-pass cutoff of > 6 cycles/degree for the HSF faces and a low-pass cutoff of < 2 cycles/degree for the LSF faces, based on previous studies (Vlamings, Goffaux, & Kemner, 2009). Finally, the filtered faces were again normalized for luminance and RMS contrast. Importantly, subjective ratings demonstrated that HSF and LSF fearful
Fear detection relies on high spatial frequencies (see Supplemental Material available online). Following previous studies (Yang et al., 2007), for Experiment 1 we also generated inverted versions of all face stimuli (i.e. faces were rotated by 180 degrees).

The CFS masks \((8.0^\circ \times 8.0^\circ)\) used in Experiment 1a consisted of randomly arranged white, black, and gray circles (diameters \(0.3^\circ–1.4^\circ\)). 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 high spatial frequency 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 non-dominant 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 trial 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% in all CFS experiments) were excluded from the computation of mean suppression durations.

**Design.** Experiment 1a consisted of 576 trials in which all combinations of the faces’ spatial frequency (BSF, HSF, or LSF), emotion (fearful or neutral), face orientation (upright
Fear detection relies on high spatial frequencies or inverted), and eight face exemplars 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 ANOVA on the mean suppression durations 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, $F(1, 11) = 16.18, p = .002$, as reported previously (Jiang et al., 2007; Yang et al., 2007). There were no significant interactions with face orientation, all $F < 1$. 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. Importantly, 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 LSF faces, $F(1, 11) = 3.36, p = .094$ (Figure 2a). Reducing the analysis to HSF and LSF faces only, a significant spatial frequency-by-emotion interaction, $F(1, 11) = 22.00, p < .001$, 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
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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, $F(1, 15) = 17.40$, $p = .001$, meaning that the fear advantage was larger for HSF than for LSF faces (Figure 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 Supplemental Material available online) 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 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-orientation 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, $F(1, 15) = 16.47$, $p = .001$, but not for LSF faces, $F(1, 15) = 2.42$, $p = .140$ (Figure 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.
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**Experiment 2:**

**Detection of hybrid faces under continuous flash suppression**

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 a HSF fearful face and an LSF neutral face to LSF-fear hybrids containing an LSF fearful face and a HSF neutral face (Figure 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 observers took part in Experiment 2.

**Stimuli, procedure, and design.** The general experimental settings were identical to 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 four from the Ekman and Friesen set), each having a lower mean luminance than in Experiment 1 (Figure 1c). 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 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 Supplemental Material available online).

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.
Results and discussion

Suppression durations were significantly shorter for HSF-fear hybrids than for LSF-fear hybrids, *t*(11) = 4.15, *p* = .002 (Figure 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.

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 (Figure 1d). As these masks contained a broad range of spatial frequencies, this method minimized potential interactions with the faces’ spatial frequency.

Method

Participants. Sixteen observers participated in Experiment 3.

Display and stimuli. Participants viewed a 17-inch gamma corrected TFT screen binocularly. A single black frame was displayed in the center of the screen. The CFS masks were replaced by noise masks (consisting of random black and white pixels) that were presented in the same locations as the face stimuli (Figure 1d). 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 piloting revealed no evidence for generally better detection of HSF faces under sandwich masking (for a control experiment demonstrating that overall detection accuracies
Fear detection relies on high spatial frequencies were actually higher for LSF than for HSF faces, see Supplemental Material available online).

**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, combining 16 identities of HSF- and LSF-fear hybrids, six different presentation durations, and four face locations in random order.

**Results and discussion**

As can be seen from Figure 4, detection accuracies were 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
Fear detection relies on high spatial frequencies 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).

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 shows that amygdala activity does not differentiate between fearful and neutral HSF faces (Vuilleumier et al., 2003). One possibility for this apparent inconsistency with our 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), providing strong evidence against an essential role of the amygdala in rapid fear detection. Also, since 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, Lazeyra, & 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,
Fear detection relies on high spatial frequencies. 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 only studied 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 high spatial frequency information.

Another important limitation of the present study is that we only contrasted 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 non-expressive 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, since 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, calling for a reconsideration of the current views on the neural processing of emotionally significant stimuli.
Authorship

T.S. and P.S. developed the study concept. All authors contributed to the study design. Testing, data collection, and data analyses were performed by T.S. The paper was drafted by T.S., and all co-authors provided critical revisions. All authors approved the final version of the paper for submission.
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Figure 1. Procedure and stimuli. (a) Face detection under continuous flash suppression (CFS). In Experiments 1 and 2, a face was gradually introduced to the observer’s dominant eye, while CFS masks were flashed at 10 Hz to the non-dominant eye. Participants localized as quickly and accurately as possible the quadrant in which the face or any part of the face became visible. This schematic of an example trial depicts the standard, unfiltered CFS masks and an example of an original, unfiltered broad spatial frequency (BSF) fearful face. (b) Examples of high spatial frequency (HSF) and low spatial frequency (LSF) filtered fearful (top row) and neutral (bottom row) faces. (c) Examples of hybrid faces from Experiment 2. HSF-fear hybrid faces were composed of a fearful low-contrast HSF and a neutral high-contrast LSF face. Conversely, LSF-fear hybrids were composed of a neutral low-contrast HSF and a fearful high-contrast LSF face. (d) Face detection under sandwich masking. In Experiment 3, a face displayed for variable durations 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.
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**Figure 2.** Detection of low and high-pass filtered faces under CFS. The top panels show mean suppression durations for upright and inverted BSF, HSF, and LSF faces, separately for fearful and neutral faces. Error bars represent the SE of the difference between fearful and neutral faces. The bottom panels show the ‘fear advantage’, i.e. the difference in suppression durations between neutral and fearful faces, averaged across upright and inverted faces, separately for BSF, HSF, and LSF faces. Error bars represent SEMs. (a) Results from Experiment 1a, in which we used standard, unfiltered CFS masks. (b) Results from Experiment 1b, in which high- and low-pass filtered faces competed against hybrid CFS masks. (c) Results from Experiment 1b, in which we used high-pass filtered CFS masks.
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Figure 3. Detection of hybrid faces under CFS. Bars denote mean suppression durations for HSF-fear and LSF-fear hybrids in Experiment 2. Error bars represent the SE of the difference between HSF-fear and LSF-fear hybrids.
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**Figure 4.** Detection of hybrid faces under sandwich masking in Experiment 3. The panel shows the mean proportion of correct responses as a function of stimulus onset asynchrony (SOA) between the forward and the backward masks, separately for HSF-fear and LSF-fear hybrids. Error bars represent the SE of the difference between HSF-fear and LSF-fear hybrids or fearful and neutral faces, separately for each SOA.
Supplemental experimental procedures and results

Additional experimental details

Participants. Volunteers were recruited from the Humboldt University subject pool and received either course credit or a monetary compensation for their participation. All observers had normal or corrected-to-normal vision. For the participants in Experiments 1 and 2 we established ocular dominance by the Miles (1930) test. As culture modulates facial expression recognition (e.g. Jack, Blais, Scheepers, Schyns, & Caldara, 2009), it should be noted that all participants were Western Caucasian observers.

Congruence between race of observers and stimuli. Some of the face stimuli did not match the race of our observers (in Experiment 1, one of the eight faces, in Experiments 2 and 3 four of the 16 faces). Given that incongruence between the race of observers and facial stimuli may be associated with perceptual differences (such as in the other-race effect, Meissner & Brigham, 2001), it is worth mentioning that the removal of these faces from the analyses did not lead to qualitatively different patterns of results in any of our experiments.

Choice of filter cutoffs. The low- and high-pass filter cutoffs for the face stimuli were selected based on previous studies as carefully reviewed by Vlamings, Goffaux, and Kemner (2009) to optimally stimulate magno- and parvocellular pathways, respectively. These cutoffs (> 6 cycles/degree of visual angle (c/deg) for the HSF faces and < 2 c/deg for the LSF faces), although identical to those used by Vlamings et al., deviated from the filter cutoffs employed in a previous fMRI study that provided strong support for a central role of an LSF-selective subcortical pathway in the processing of fearful faces (Vuilleumier, Armony, Driver, & Dolan, 2003). Expressed in c/deg, Vuilleumier et al. (2003) used lower cutoff values for both LSF and HSF faces. However, the faces used in their study were considerably larger than the stimuli used in our present experiments, as the interocular suppression technique employed in
Fear detection relies on high spatial frequencies (e.g., Blake, O’Shea, & Mueller, 1992). With the filter settings of Vuilleumier et al., our LSF face stimuli would have been blurred to an extent where fearful and neutral LSF faces would have been barely discriminable. Furthermore, the filter settings recommended by Vlamings et al. had the advantage that the LSF and HSF cutoffs were both falling roughly into the peak visibility range on the contrast sensitivity function (Campbell & Robson, 1968).

**Control experiments**

In addition to the experiments reported in the main manuscript, we ran six control experiments. In the first two control experiments, we used CFS to rule out that the HSF-specificity of the fear advantage was due to local contrast differences in the eye or mouth regions of the faces (Control Experiment 1) and to ensure that the HSF-specificity of the fear advantage would extend to faces presented further in the periphery (Control Experiment 2). In Control Experiment 3, in order to validate that the higher-contrast LSF faces were indeed overcoming CFS more quickly than the lower-contrast HSF faces, we measured suppression durations for the HSF and LSF faces that formed the basis of the HSF-fear and LSF-fear hybrids used in Experiment 2. In Control Experiment 4, we ensured that the advantage of HSF-fear over LSF-fear hybrids was equally present when both the HSF and the LSF components were displayed with identical contrast. In Control Experiment 5, in order to validate that there was no overall detection advantage for HSF faces under sandwich masking, we examined detection accuracies for the HSF and LSF faces that formed the basis of the hybrid faces used in Experiment 3. Finally, in Control Experiment 6 we collected...
subjective ratings of perceived fearfulness for HSF and LSF faces to ensure that fearful and neutral faces could be equally well distinguished in both spatial frequency bands.

**Participants**

Twelve observers participated in Control Experiment 1a (11 female, mean age 24.6 years), 14 in Control Experiment 1b (all female, mean age 24.7 years), 12 in Control Experiment 2 (11 female, mean age 26.8 years), 18 in Control Experiment 4 (13 female, mean age 24.9 years), and 18 in Control Experiment 5 (17 female, mean age 26.8 years). In Control Experiment 3, we tested the same 12 observers (10 female, mean age 28.3 years) as in Experiment 2 (in counterbalanced order). Finally, 14 observers who had participated in Experiment 1 took part in Control Experiment 6.

**Control Experiment 1: Local contrast differences**

In this control experiment, we included faces that were not only normalized for global RMS contrast, but also for local contrast in the eye and mouth regions. For each face identity, we created a “region of interest” (ROI) that covered the eyes and another ROI that covered the mouth. Stimuli were generated as for Experiment 1, but after adjusting global contrast and luminance (“Global” condition), we additionally equalized the RMS contrast of fearful and neutral faces in the eye ROI (“Eyes” condition), in the mouth ROI (“Mouth” condition), or in both ROIs (“Eyes & mouth” condition). In Control Experiment 1a we first tested whether these adjustments affected suppression durations for upright BSF faces competing against the standard CFS masks. The procedure of this experiment was identical to Experiment 1a. In 384 trials, we presented upright fearful and neutral BSF faces, equally often in the four contrast conditions (Global, Eyes, Mouth, Eyes & mouth). As can be seen from Figure S1, fearful faces were detected more quickly than neutral faces, $F(1, 11) = 11.68, p = .006,$ and
there was neither a significant main effect of contrast, nor a significant interaction between emotion and contrast, both $F < 1$.

In Control Experiment 1b, we presented upright fearful and neutral HSF and LSF faces that competed against hybrid masks (as in Experiment 1b). There were 768 trials and the procedure was identical to Experiment 1b. For the HSF faces, the main effect of emotion was significant, $F(1, 13) = 91.27, p < .001$, with shorter suppression durations for fearful faces, while the main effect of contrast and the interaction were not significant, both $F < 1$ (see Figure S1). Thus, the fearful face advantage for HSF stimuli was independent of the local contrast adjustment (as confirmed by separate $t$-test for the individual contrast conditions, all $t(13) > 5.04$, all $p < .001$). By contrast, the analysis for LSF faces revealed no significant main effects of emotion, $F < 1$, or contrast, $F(1, 13) = 1.09, p = .365$, but a significant emotion-by-contrast interaction, $F(1, 13) = 6.62, p = .001$. In the Global, Eyes, and Eyes & mouth conditions, there were no significant differences between suppression durations of fearful and neutral faces, largest $t(13) = 1.83$, whereas in the Mouth condition neutral faces were detected somewhat more quickly than fearful faces, $t(13) = 2.60, p = .022$.

**Control Experiment 2: Eccentricity**

In the second control experiment, faces were presented further in the periphery compared to their placement in the other experiments where faces were centered at a vertical distance of 2.0° and a horizontal distance of 2.3° relative to the fixation cross (i.e. eccentricity of the stimuli’s center 3.0°; eccentricity of the stimuli’s pixel closest to fixation 0.7°). In Control Experiment 2, the face stimuli were centered at a vertical distance of 4.2° and at a horizontal distance of 4.0° relative to the fixation cross (i.e. eccentricity of the stimuli’s center 5.8°; eccentricity of the stimuli’s pixel closest to fixation 3.3°). As shown in Figure S2a, we therefore changed the visual displays compared to the other CFS experiments.
Fear detection relies on high spatial frequencies

Instead of presenting one large frame to each eye, we displayed four small frames (each surrounded by fusion contours) of the same size to each eye, at all four possible face positions. In each of these four frames we presented a sequence of hybrid CFS masks to the non-dominant eye. Beginning 1.1 s after trial onset, these masks were ramped down to 0% contrast over 7.0 s. The maximum trial duration was 10.0 s. Upright face stimuli were presented within one of the four frames to the participants’ dominant eye. Control Experiment 2 contained 256 trials in which all combination of the faces’ spatial frequency (HSF, LSF), emotion, and 16 facial identities (from Experiments 2 and 3) were presented equally often, in random order. Results revealed a significant interaction between spatial frequency and emotion, $F(1, 11) = 19.75, p = .001$, but no significant main effect of spatial frequency, $F < 1$. The main effect of emotion approached significance, $F(1, 11) = 3.89, p = .074$. As can be seen from Figure S2b, suppression durations for HSF fearful faces were significantly shorter than for HSF neutral faces, $t(11) = 3.39, p = .006$. For LSF faces, there was no significant difference between fearful and neutral faces, only a trend towards faster detection of neutral faces, $t(11) = 1.97, p = .074$.

Control Experiment 3: HSF and LSF faces that formed the basis for the hybrids used in the CFS Experiment 2

We used the same experimental setup employed in Experiment 2, but measured suppression durations for the low- and high-pass filtered fearful and neutral faces that formed the basis of the HSF-fear and LSF-fear hybrid faces used in Experiment 2. Half of the participants were first tested in Experiment 2, and the other half began with Control Experiment 3. This control experiment consisted of 256 trials containing all combinations of spatial frequency (HSF, LSF), emotion, and 16 face identities. Trial order was randomized. As expected, the higher-contrast LSF faces overcame CFS much more quickly than the
Fear detection relies on high spatial frequencies, $F(1, 11) = 55.32, p < .001$ (Figure S3). There was also a significant main effect of emotion, $F(1, 11) = 19.81, p = .001$, and a significant interaction between spatial frequency and emotion, $F(1, 11) = 7.13, p = .022$. Consistent with our previous findings, the fear advantage was significant for HSF faces, $t(11) = 4.71, p = .001$, but not for LSF faces, $t < 1$.

**Control Experiment 4: Hybrid stimuli with identical contrast in the HSF and LSF bands**

In Control Experiment 4, we compared suppression durations for (upright) HSF-fear and LSF-fear hybrids that were constructed from high- and low-pass filtered faces (the same eight exemplars as in Experiment 1) with identical RMS contrast, each having a lower mean luminance than in Experiment 1. The experimental setup was identical to Experiment 2, except that on each trial the hybrid faces were presented to one randomly selected eye. There were 96 trials (eight exemplars of upright HSF- and LSF-fear hybrids and two eyes for face presentation occurred equally often). As in Experiment 2, we found that suppression durations for HSF-fear hybrids ($M = 4.05$ s) were significantly shorter than for LSF-fear hybrids ($M = 4.42$ s), $t(17) = 4.21, p = .001$ ($SE$ of the difference 0.09).

**Control Experiment 5: HSF and LSF faces that formed the basis for the hybrids used in the sandwich masking Experiment 3**

The procedure for Control Experiment 5 was identical to Experiment 3, except that we used only three presentation durations (83, 117, or 167 ms). In Control Experiment 5a, we presented the same HSF-fear and LSF-fear hybrids as in Experiment 3; in Control Experiment 5b, we presented the separate low- and high-pass filtered fearful and neutral faces that constituted these hybrid faces. In Control Experiment 5a, there were 384 trials combining...
Fear detection relies on high spatial frequencies

16 identities of HSF- and LSF-fear hybrids, three presentation durations, and four face locations. Control Experiment 5b contained 384 trials with all combinations of spatial frequency (HSF, LSF), emotion, three presentation durations, and 16 face identities. Trial order was randomized. Half of the participants began with Control Experiment 5a, and half began with Control Experiment 5b. The results from Control Experiment 5a replicated those of Experiment 3: Participants were more accurate in localizing HSF-fear hybrids than LSF-fear hybrids, $F(1, 17) = 26.76, p < .001$ (Figure S4a). Control Experiment 5b ruled out that this effect resulted from a generally better performance for HSF stimuli: Detection accuracies were significantly higher for LSF faces than for HSF faces, $F(1, 17) = 68.52, p < .001$ (Figure S4b). The main effect of emotion was also significant, $F(1, 17) = 8.79, p = .009$, with fearful faces being detected more accurately than neutral faces. The interaction between spatial frequency and emotion approached significance, $F(1, 17) = 4.23, p = .055$, indicating that the fear advantage was largely specific to HSF faces, $F(1, 17) = 8.98, p = .008$, and not present for LSF faces, $F < 1$.

**Control Experiment 6: Face stimuli rated for fearfulness**

Finally, we collected subjective ratings of perceived fearfulness for our experimental stimuli. After completing the experimental session, observers rated the face stimuli used in Experiment 1 for “fearfulness” on a scale from 1 (“not fearful”) to 5 (“very fearful”). Faces were presented for 500 ms in the center of the frame shown to the participants’ dominant eye (no masks were presented to the non-dominant eye) and observers were asked to indicate their subjective impression of fearfulness, with no speed pressure. Of particular interest here was the comparison between the ratings for HSF and LSF faces (see Table S1). Repeated measures ANOVAs with the factors spatial frequency (HSF, LSF) and emotion (fearful, neutral) revealed no significant interaction between spatial frequency and emotion, neither for
upright faces, \( F(1, 13) = 2.33, p = .151 \), nor for inverted faces, \( F(1, 13) = 3.64, p = .079 \), meaning that the difference in rated fearfulness between fearful and neutral faces used in our experiments did not differ significantly between high- and low-pass filtered faces.
Supplemental References


Fear detection relies on high spatial frequencies

Table S1

*Face stimuli rated for fearfulness*

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Figure S1. Control for local contrast differences. Mean suppression durations from Control Experiment 1a (BSF faces) and Control Experiment 1b (HSF and LSF faces), shown separately for faces with globally normalized contrast and luminance (“Global” condition), and for faces in which we additionally normalized the RMS contrast locally in the eye regions (“Eyes”), in the mouth region (“Mouth”), or in both the eye regions and in the mouth region (“Eyes & Mouth”). Error bars represent the SE of the difference between fearful and neutral faces.
Figure S2. Control for eccentricity. (a) In Control Experiment 2, faces were presented in separate small frames further in the periphery. (b) Mean suppression durations for high- and low-pass filtered fearful and neutral faces. Error bars represent the SE of the difference between fearful and neutral faces.
Figure S3. Results from Control Experiment 3, in which we measured suppression durations for low-contrast HSF and high-contrast LSF fearful and neutral faces that formed the basis of the hybrid faces used in Experiment 2. Error bars represent the SE of the difference between fearful and neutral faces.
Figure S4. Detection of hybrid faces under sandwich masking. (a) Results of Control Experiment 5a, in which participants detected HSF-fear or LSF-fear hybrids. (b) Results of Control Experiment 5b. In this experiment, participants detected fearful and neutral high- and low-pass filtered faces that formed the basis of the hybrid stimuli used in Control Experiment 5a. Error bars represent the SE of the difference between HSF-fear and LSF-fear hybrids or fearful and neutral faces, separately for each SOA.