

Spatial Frequency Modulates Neural Pathways for Fearful Facial Expression Processing

Authors: He Zeyu, Zhang Ziqi, Li Kexuan, He Weiqi, He Weiqi

Date: 2020-01-18T00:00:00+00:00

Abstract

Fearful emotions receive prioritized effective processing due to their threatening nature. Spatial frequency, as a fundamental component for processing facial information, influences the processing of fearful facial expressions via distinct neural pathways. The dual-pathway perspective posits that low spatial frequency information in fearful facial expressions exhibits preferential transmission along the subcortical pathway, whereas high spatial frequency information primarily undergoes fine-grained processing of fearful facial expressions through the cortical pathway; conversely, multiple pathways can more flexibly mediate the influence of spatial frequency on emotional processing. Future research should elucidate the functions of brain regions and their sub-regions across multiple pathways, thereby further validating how visual information impacts emotional processing.

Full Text

Neural Pathways Through Which Spatial Frequency Affects the Processing of Fearful Facial Expressions

HE Zeyu¹, ZHANG Ziqi¹, LI Kexuan¹, HE Weiqi¹

(1 Research Center of Brain and Cognitive Neuroscience, Liaoning Normal University, Dalian 116029, China)

Abstract

Fear is prioritized for effective processing due to its threatening nature. Spatial frequency, as a fundamental component of facial information processing, influences the processing of fearful facial expressions through distinct neural pathways. The dual-pathway view posits that low spatial frequency (LSF) components of fearful faces are preferentially transmitted via subcortical pathways, whereas high spatial frequency (HSF) information primarily engages cortical

pathways for refined processing of fearful expressions. More recently, multiple-pathway models have been proposed to more flexibly account for how spatial frequency influences emotional processing. Future research should clarify the roles of specific brain regions and their sub-regions across these multiple pathways to further elucidate how visual information modulates emotional processing.

Keywords: spatial frequency; fearful facial expression; subcortical pathway; cortical pathway; multiple pathways

Throughout human evolution, rapid analysis of emotionally significant events—particularly threat signals—has conferred substantial survival advantages. Previous research on emotional processing demonstrates that attentional resources are preferentially allocated to threatening stimuli over neutral ones (Vuilleumier, Armony, Driver, & Dolan, 2003). Fear represents a spontaneous defensive emotional response when individuals encounter threatening stimuli. In studying fear, facial expressions commonly serve as emotional carriers. Categorical theory of emotion posits that facial expressions are processed based on their structural features (Hassin, Aviezer, & Bentin, 2013), which can be decomposed through Fourier transformation of visual signals into fundamental components varying in spatial frequency, orientation, amplitude, and phase (Webster, De Valois, & Switkes, 1990).

Spatial frequency (SF) is defined as luminance variation per unit of spatial distance, typically expressed in cycles per degree of visual angle (c/d) (Jeanet, Caharel, Schwan, Lighezzolo-Alnot, & Laprevote, 2018). LSF information (<8 c/d) is associated with coarse, holistic face processing and rapid transmission via magnocellular channels to dorsal stream and subcortical regions (Cushing, Im, Adams Jr, Ward, & Kveraga, 2019), facilitating detection of threatening or urgent visual events (Carretié, Hinojosa, López-Martín, & Tapia, 2007). Conversely, HSF information (>24 c/d) subserves detailed face processing with slower transmission through parvocellular channels to ventral visual cortex (Cushing et al., 2019). Parvocellular ganglion cells possess smaller receptive fields that respond to luminance changes in localized image regions (Merigan & Maunsell, 1993). Consequently, LSF components convey holistic information and transmit coarse emotional signals, whereas HSF components convey fine-grained details such as wrinkles and eye whites associated with age features and facial expressions (Liu, Collin, Rainville, & Chaudhuri, 2000).

Unlike other emotional stimuli, threat-related information can be processed rapidly and efficiently through specialized mechanisms (Adolphs et al., 2005; LeDoux, 1998; Öhman & Mineka, 2001), driving the development of dedicated neural pathways (Öhman & Mineka, 2001; Tamietto & De Gelder, 2010). The dual-pathway model of emotional processing proposes two parallel routes: a subcortical “low road” providing rapid but coarse biological signals to the amygdala, and a longer, slower cortical “high road” delivering detailed information through cortical visual areas (LeDoux, 1998; Öhman, 2005; Tamietto & De Gelder, 2010). Bar (2003) demonstrated substantial correspondence between visual neural pathways processing spatial frequency and neural circuits handling

emotional stimuli, suggesting extensive connectivity between visual and emotional systems and between cortical and subcortical structures. This implies that spatial frequency information utilizes multiple neural pathways to process emotional stimuli (Vuilleumier et al., 2003).

LSF fearful faces elicit greater activation in the amygdala, superior colliculus (SC), and pulvinar (Pulv) than HSF fearful faces, indicating preferential rapid transmission of coarse fear information through subcortical pathways (Vuilleumier et al., 2003). However, recent research suggests observers primarily use HSF rather than LSF information to discriminate fearful from other facial expressions (Stein, Seymour, Hebart, & Sterzer, 2014). Alternative hypotheses propose flexible processing of spatial frequency information based on task demands or strategies (Goffaux, Jemel, Jacques, Rossion, & Schyns, 2003; Peyrin et al., 2005). LSF information signals face presence while HSF information specifies face identity—both essential for threat detection. Rapidly transmitted LSF information may generate an initial, coarse impression of a face to guide subsequent processing of detailed HSF information (Bar, 2003; Bullier, Hupé, James, & Girard, 2001). Overall, visual stimulus perception depends on both LSF and HSF information, and integrating both will provide a more complete understanding of threat processing.

This review synthesizes evidence and controversies regarding neural pathways through which spatial frequency influences fearful face processing, summarizing current perspectives and future directions.

2.1 Subcortical Neural Pathways for LSF Processing of Fearful Faces

Early visual processing of emotional information reveals a specific pathway: a subset of retinal fibers reaches the superior colliculus and pulvinar via subcortical routes before projecting to the amygdala, the central hub of emotional processing. The superior colliculus, a key component of this subcortical pathway, represents the first retino-recipient subcortical structure responding to coarse (LSF) emotional stimuli, primarily featuring magnocellular neurons tuned to lower spatial frequencies (Márkus et al., 2009). The pulvinar serves as a critical intermediate relay, transmitting visual information from the superior colliculus to the amygdala (陈珊珊, 蔡厚德, 2015). The amygdala constitutes a crucial node for transmitting threat-related information and generating adaptive responses (Phelps & LeDoux, 2005; Vuilleumier, 2005).

Morris et al. (1999) proposed that this subcortical pathway is essential for automatic, rapid processing of visual emotional information, operating largely unconsciously to quickly handle threatening stimuli such as fearful facial expressions. Garvert et al. (2014) further confirmed that subcortical amygdala pathways facilitate rapid sensory processing of faces, particularly during early stimulus processing. Subcortical pathways exhibit faster synaptic integration times (80–90 ms) than cortical visual streams (145–170 ms), supporting the concept of rapid subcortical amygdala input (Silverstein & Ingvar, 2015). Intracranial electroen-

cephalogram (iEEG) data reveal amygdala responses to fearful faces as early as 74 ms, significantly faster than latencies observed in fusiform cortical regions (Méndez-Bértolo et al., 2016). Recent diffusion tensor imaging (DTI) studies have provided additional anatomical evidence for subcortical pathways (McFadyen, Mattingley, & Garrido, 2019; Tamietto, Pullens, de Gelder, Weiskrantz, & Goebel, 2012), further demonstrating that subcortical routes deliver rapid but coarse threat-related signals to the amygdala.

2.2 Evidence for LSF Effects on Fearful Face Processing

Behavioral data reveal differential sensitivity to LSF and HSF information affecting emotional valence. LSF processing of fearful stimuli yields faster responses (Holmes, Green, & Vuilleumier, 2005; Mermillod, Droit-Volet, Devaux, Schaefer, & Vermeulen, 2010), with LSF-filtered faces detected more rapidly than HSF-filtered faces (Holmes et al., 2005; Vlamings, Goffaux, & Kemner, 2009). When judging face gender under different spatial frequency conditions, recognition accuracy for LSF fearful faces significantly exceeds that for HSF fearful faces (Bocanegra & Zeelenberg, 2009; Holmes et al., 2005). Given that coarse facial information judgments require less precision, LSF information demonstrates advantages in both processing speed and accuracy.

Functional magnetic resonance imaging (fMRI) supports the dominant hypothesis that coarse visual information—LSF components—receives early processing in the superior colliculus-pulvinar-amygdala rapid pathway (Vuilleumier et al., 2003; Zhang, Zhou, Wen, & He, 2015). Studies show that fearful faces activate the superior colliculus and pulvinar, particularly LSF fearful faces, suggesting this subcortical pathway may transmit coarse fear-related information to the amygdala (Vuilleumier et al., 2003). Burra et al. (2017) found that in patient TN with bilateral visual field “blindsight,” only LSF fearful faces activated the amygdala, further indicating that LSF fear information transmission may depend on the subcortical superior colliculus-pulvinar-amygdala pathway. The prevailing view in human visual emotion processing holds that initial analysis of threatening visual stimuli bypasses visual cortex, projecting from retina to amygdala via a specialized subcortical pathway involving the superior colliculus and pulvinar.

However, hemodynamic signals provide no information about response latencies of visual cortex to LSF emotional stimuli. Event-related potential (ERP) studies with high temporal resolution can further validate LSF advantages in subcortical pathways. Research demonstrates that during early emotional processing stages, LSF information rapidly extracts threat-related stimuli (faces and scenes), as reflected by P1 and N170 components showing larger amplitudes for LSF emotional versus neutral faces, with LSF-evoked P1 and N170 amplitudes exceeding those evoked by HSF (Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005; Tian et al., 2018; Vlamings et al., 2009). Intracranial EEG provides direct electrophysiological evidence for amygdala responses during spatial frequency-modulated fear processing, revealing that rapid amygdala responses

are restricted to LSF fearful faces (Méndez-Bértolo et al., 2016). Thus, the relevance of LSF to emotional neural processing receives clear support. Overall, emotional processing is selectively tuned to different spatial frequency information across distinct temporal stages, with LSF primarily conferring processing advantages during early emotional processing phases.

2.3 Challenges to LSF Effects on Fearful Face Processing

Some fMRI studies find that the pulvinar responds not to the emotional significance of visual stimuli but to whether stimuli are consciously perceived. These results contradict claims of pulvinar involvement in unconscious processing and are inconsistent with its proposed major role in subcortical pathways (Padmala, Lim, & Pessoa, 2010). Furthermore, measuring and comparing response latencies across brain regions reveals that subcortical visual processing does not identify information faster than cortical processing (Pessoa & Adolphs, 2010). This has led researchers to question the widely documented subcortical pathway and consider whether fear responses are genuinely accelerated by prioritized LSF processing.

McFadyen et al. (2017) used magnetoencephalography (MEG) to measure neural activity while participants judged the gender of neutral and fearful faces filtered by LSF and HSF, applying dynamic causal modeling to explore all possible information-transmitting neural networks. Data-driven neural simulations of both pathways revealed a temporal advantage for subcortical connections during amygdala activity, supporting a broad role for subcortical pathways in rapidly transmitting raw, unfiltered information to the amygdala. However, pulvinar-to-amygdala connections were not modulated by spatial frequency or facial expression, suggesting that amygdala subcortical pathways are non-selective for face spatial frequency or emotion—contrasting with previous views of prioritized LSF fear processing in subcortical routes (McFadyen, Mermillod, Mattingley, Halász, & Garrido, 2017). ERP studies have yielded conflicting results: some find N170 components unaffected by facial emotion or spatial frequency (Holmes et al., 2005), while others show N170 is more sensitive to HSF than LSF information regardless of emotional content (Alorda, Serrano-Pedraza, Campos-Bueno, Sierra-Vázquez, & Montoya, 2007).

Addressing these controversies, McFadyen et al. suggest that superior colliculus may have been omitted from dynamic causal models, despite evidence that its inputs primarily convey LSF visual face information. This implies that rapid pulvinar-amygdala information transfer likely represents multiple sources, capable of processing both LSF and HSF stimuli from retinal and cortical inputs (Tamietto & Morrone, 2016). Recent research matching luminance and contrast across spatial frequency conditions reveals that contrast equalization is particularly crucial during early (100 ms) visual processing (Vlamings et al., 2009). Intracranial EEG studies using luminance- and contrast-equalized stimuli support this, showing no significant differences between HSF and LSF faces until 240 ms (Willenbockel, Lepore, Nguyen, Bouthillier, & Gosselin, 2012). Thus,

spatial frequency effects on emotion can be further investigated by controlling stimulus luminance differences. Future studies should employ higher spatial resolution methods to identify additional information transmission pathways in humans and non-human primates.

In summary, visual information can reach the amygdala via primary visual cortex, providing evidence for threat-related information transmission—particularly fear—through the subcortical superior colliculus–pulvinar–amygdala pathway, with LSF conferring transmission priority in this subcortical route, enabling rapid and efficient processing of LSF fearful faces.

3.1 Cortical Neural Pathways for HSF Processing of Fearful Faces

Many visual stimuli can be processed rapidly through initial cortical responses, suggesting sufficient time for extensive feedback processing even within cortex (Pessoa & Adolphs, 2010). Given that processing involves both amygdala and visual cortex, distinct neural pathways emerge for conscious emotional stimulus processing: cortical pathways.

Fear information activates visual cortex extensively through the lateral geniculate nucleus (LGN)–primary visual cortex V1–amygdala pathway (Das et al., 2005; Hariri, Mattay, Tessitore, Fera, & Weinberger, 2003; Morris et al., 1999; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004). The LGN receives direct projections from retina and superior colliculus and feeds back to retinotopically organized regions in occipital cortex (Shi & Davis, 2001). De Valois et al. measured spatial frequency tuning properties of V1 cells in macaques, finding that both frequency ranges activate neuronal populations in V1, meaning any differential responses to HSF and LSF stimuli are reflected in activity patterns of distinct V1 visual neuron groups (De Valois, Albrecht, & Thorell, 1982). Consequently, V1 activation levels are commonly used as a baseline for investigating spatial frequency properties in other visual areas (Skottun, 2015).

3.2 Evidence for HSF Effects on Fearful Face Processing

Cortical pathways operating at conscious levels primarily transmit HSF information representing fine-grained processing (Furl, Henson, Friston, & Calder, 2013). Stein et al. (2014) provided behavioral evidence for HSF effects on fearful face processing in cortical pathways. In Experiment 1, using continuous flash suppression, participants judged the emotional valence (fearful or neutral) of faces under HSF and LSF conditions, revealing faster recognition of HSF fearful faces during conscious processing, indicating a processing advantage. Experiments 2 and 3 used hybrid faces: high-fear hybrids (HSF fearful face + LSF neutral face) and low-fear hybrids (LSF fearful face + HSF neutral face). Experiment 2 showed faster recognition of high-fear hybrids in continuous flash suppression, with significantly shorter suppression durations. Experiment 3 used sandwich masking to minimize potential interactions between HSF and LSF, finding higher detection accuracy for high-fear hybrids. These findings

demonstrate that rapid fear processing does not exclusively depend on LSF information but is also influenced by HSF information, reflecting involvement of cortical visual areas (Stein et al., 2014).

Because different neural pathways in the visual system exhibit varying sensitivity to spatial frequency ranges, researchers have analyzed processing characteristics of different SF face stimuli to investigate differential inputs to amygdala and ventral visual cortex in healthy brains. Results show that although HSF information is processed more slowly at conscious levels, it yields higher recognition accuracy (Vuilleumier et al., 2003). Studies of atypical brains provide converging evidence: intracranial EEG data from epilepsy patients show delayed onset of emotional expression effects for HSF compared to LSF information (Tessari, 2012). A study of patients with bilateral amygdala lesions revealed that impaired fear recognition stemmed from compromised processing of the eye region, specifically an inability to actively process HSF-filtered eye regions (Adolphs et al., 2005).

MEG evidence further demonstrates that HSF fearful faces elicit more pronounced brain activation than LSF fearful faces. Dynamic causal modeling analyzed effects of spatial frequency and/or fear on neural pathway connection strength, comparing cortical, medial, and subcortical connectivity patterns. Results showed larger effect sizes for HSF faces in cortical pathways, with significant HSF modulation of information transmission from V1 to amygdala and stronger cortical pathway connections—indicating that cortical pathways rely on HSF information processing (McFadyen et al., 2017). These findings underscore the importance of HSF information in fear recognition and confirm the amygdala’s necessity for such visual and emotional processing.

3.3 Challenges to HSF Effects on Fearful Face Processing

Although rapid fear detection dependent on HSF supports emerging views of cortex’s role in detecting ecologically relevant signals, neuroimaging data also show that the amygdala cannot discriminate fearful from neutral HSF faces (Vuilleumier et al., 2003). Some researchers argue the amygdala may not participate in initial fear face processing but instead modulates later attentional and cognitive processes based on stimulus valence and behavioral significance (Adolphs, 2008; Pessoa, 2010). Additionally, because visual cortical regions project substantial signals to the amygdala with minimal delay, and fMRI studies demonstrate that amygdala responses do not require intact primary visual cortex (Burra et al., 2013), the information transmission characteristics of cortical pathways require further investigation.

In summary, fearful face transmission through cortical pathways is primarily mediated by fine-grained HSF information. The priority of HSF for conscious fear processing aligns with its central role in fear recognition, demonstrating that rapid fear face processing does not necessarily imply a direct subcortical route to the amygdala—cerebral cortex is also critical for processing ecologically

relevant signals (Stein et al., 2014).

4 Multiple Pathways for Spatial Frequency Effects on Fearful Face Processing

Pessoa et al. (2010) discussed and revised the “traditional” subcortical pathway, which was thought to process emotional visual stimuli unconsciously and rapidly via the superior colliculus and pulvinar to the amygdala. However, during fear responses, fast but coarse visual processing represents only one necessity in dangerous environments. Research shows that other visual pathways also serve this function: visual stimulus processing can involve multiple brain regions—including amygdala, orbitofrontal cortex (OFC), anterior insular cortex (AIC), and anterior cingulate cortex (ACC)—through “multiple activation waves” in visual cortex and beyond, enabling direct processing of behaviorally relevant responses. Thus, rapid emotional processing is possible without a specialized subcortical pathway. This suggests multiple parallel visual information processing routes exist, and the subcortical pathway may not be purely “subcortical” but connects directly with cortex, such as between amygdala and OFC or ACC (Pessoa & Adolphs, 2010; Tamietto & De Gelder, 2010). Observations of orbitofrontal regions reveal that different sub-regions specialize in processing specific emotions and respond faster to facial expressions than the amygdala, suggesting OFC may modulate amygdala activity (Tessari, 2012). Moreover, when subcortical pathways or key regions (e.g., amygdala) are damaged, emotional information continues to be transmitted effectively and rapidly (Pessoa & Adolphs, 2010), leading some to propose emotional stimulus processing along a medial pathway from pulvinar through primary visual cortex to amygdala (Furl et al., 2013).

Consequently, some studies have moved beyond isolated examination of HSF and LSF effects in different neural pathways, challenging traditional single-pathway views. ERP research provides new evidence: You and Li (2015) investigated threatening scenes processed by HSF and LSF, finding an interaction between spatial frequency and emotion on early visual component P1. Fear and disgust elicited opposite response patterns under LSF (confined to dorsal visual stream) and HSF (localized to ventral visual stream) conditions, indicating that both HSF and LSF information can influence threat processing during early visual stages, albeit with different response patterns and visual streams. Additional findings show that cells in ventral stream area V4 respond not only to higher but also to lower spatial frequencies, precluding selective activation of dorsal/ventral streams by a single spatial frequency (Skottun, 2015). This mechanism is adaptive, as an organism’s survival is maximized when it can simultaneously utilize both HSF and LSF visual information for rapid threat detection (Fradcourt, Peyrin, Baciú, & Campagne, 2013; Stein et al., 2014).

However, research on how spatial frequency influences fearful face processing across multiple pathways remains limited and controversial. Regarding the proposed medial pathway from pulvinar through V1 to amygdala, DCM analysis of MEG data yields inconsistent results. While the presence of pulvinar-V1

connections in optimal models confirms previous anatomical evidence from humans and primates (Bridge, Leopold, & Bourne, 2016), the model also reveals that neither spatial frequency nor emotion influences V1 activity via pulvinar or LGN (McFadyen et al., 2017).

Overall, current research has focused primarily on unilateral investigation of emotional or visual information processing in key brain regions and pathways. The impact of incorporating spatial frequency information on emotional processing across multiple pathways requires further study. Existing results have examined transmission of fearful stimuli within neural pathways involving thalamus, amygdala, and sensory cortex (inferior occipital, fusiform regions), as well as dorsal-ventral opposing modulation by anterior cingulate cortex (ACC) (Das et al., 2005). Other research shows that processing threat information such as fearful faces correlates with bilateral amygdala activation, while cognitive evaluation of these stimuli associates with increased right ventral orbitofrontal responses. Additional prefrontal regions, such as ventral and dorsal prefrontal cortex, may transmit information to amygdala via reciprocal influences on OFC and through thalamus and striatum. Thus, the ability to modulate emotional experience and responses likely depends on interactions between amygdala and these more lateral prefrontal cortices (Hariri et al., 2003). Future research should shift from cortical- versus subcortical-centered frameworks to focus on longitudinal and lateral integration of emotional information (Pessoa & Adolphs, 2011).

5 Summary and Future Directions

In summary, substantial evidence supports the dual-pathway model of spatial frequency effects on fearful face processing: LSF fearful faces undergo rapid, effective processing in subcortical pathways, while HSF information influences fearful face processing in cortical pathways engaged during conscious processing. However, controversies persist regarding how fearful faces are processed in neural pathways to the amygdala. Multiple-pathway models propose that visual information influences emotional stimulus processing through early parallel transmission across multiple routes, activating numerous key brain regions and sub-regions. This shift from single, specialized pathways to multiple pathways encourages researchers to focus on connections between brain regions, sub-regions, and cortical-subcortical interactions.

Future research should address several key considerations:

First, whether to control task relevance to emotional content remains controversial. Unlike other domains where experimental paradigms are tightly controlled, studies on spatial frequency effects on emotional processing have focused on whether results relate to emotional content. Because stimulus and task parameters can significantly influence information transmission across neural pathways, and to enable productive cross-study comparisons, many studies have employed tasks unrelated to emotional expression, such as gender discrimination (Garvert et al., 2014; McFadyen et al., 2017; Méndez-Bértolo et al., 2016; Vuilleumier

et al., 2003). However, some researchers propose that future studies should examine whether cortical pathways for HSF face processing can drive amygdala activation during tasks requiring explicit emotional expression judgments, rather than relying solely on gender discrimination tasks (Vuilleumier et al., 2003).

Second, methodological limitations leave the assessment and comparison of processing speeds in cortical and subcortical structures unresolved. Although the concept of rapid amygdala processing via subcortical pathways is commonly applied to human research, no clear anatomical evidence demonstrates that visual information reaches the amygdala via superior colliculus or pulvinar in primate brains (Pessoa & Adolphs, 2010). Some researchers question whether such a subcortical fear processing pathway exists in humans, noting that the retina-superior colliculus-pulvinar-amygdala pathway lacks direct supporting evidence and is typically inferred indirectly from results, then assumed to align with human neural pathways for LSF face processing. Therefore, the critical question is not which brain region activates first, but which neural pathway more efficiently facilitates integration of stimuli and visual factors. Reconceptualizing subcortical pathways as playing a generalized rather than specialized role in face processing may explain contradictory results across spatial frequencies (De Cesare & Codispoti, 2013). Some researchers recommend redefining subcortical pathway “coarseness” as “unfiltered” (McFadyen et al., 2017). Recent tractography studies have reconstructed subcortical pathways to demonstrate that connections between amygdala and subcortical sensory nerves facilitate fear recognition (McFadyen et al., 2019). Future research should advance technical applications and methodological innovations, such as fMRI and intracranial recording, to clarify the temporal and spatial frequency characteristics of inputs to each brain region in these pathways, validating previous speculative findings while minimizing interference from confounding factors (Méndez-Bértolo et al., 2016).

Third, as a dimension independent of valence and arousal, how emotional motivation operates in spatial frequency effects on fearful face processing remains unexplored. Visual processing of emotional stimuli depends on motivational systems that prompt individuals to act and respond, implementing appropriate behaviors to avoid threatening stimuli (Vuilleumier, 2005). Research supports that HSF information correlates with rapid recognition of self-relevant emotional experience, while rapid identification of emotional motivation (avoidance, approach, or inaction) requires LSF information, confirming that motivational features of emotion influence visual processing (Fradcourt, Peyrin, Baciú, & Campagne, 2013). Future studies should further investigate how emotional motivation affects neural pathways for facial expression processing.

Finally, whether similar conclusions extend to other threatening emotional stimuli or comparable emotions beyond fearful faces requires investigation. Since detection and recognition of fearful faces both depend on similar facial features represented in HSF bands, such as sharp edges in eye and mouth regions, a key

question for future research is whether HSF selectivity in fear processing generalizes to other stimuli (Isbell, 2006; Öhman, 2005) or body postures (Tamietto & De Gelder, 2010). Another important limitation is that most studies compare fearful faces to neutral faces, meaning results may not be specific to fearful expressions but could reflect more general distinctions between expressive and non-expressive faces. For example, other facial expressions (e.g., surprise) may show similar processing patterns, as they share morphological features with fear (e.g., widened eyes) and overlapping facial action units (Du, Tao, & Martinez, 2014). The advantage for threatening stimuli in conscious processing may reflect prioritization of primitive danger signals, suggesting that spatial frequency processing of other simple threat signals remains possible (Jack, Blais, Scheepers, Schyns, & Caldara, 2009).

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