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A Critical Evaluation of the Claim that the Amygdala's Primary Function in Social Perception is in Underpinning the Perception and Experience of Fear

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Humans are inherently social and make complex inferences regarding others' emotional states. Research examining the neurological basis of social perception has implicated the amygdala in the perception and experience of fear. In some psychological difficulties, fear is assumed to become 'pathological,' such that it prevents the individual from functioning at an optimal level (Myles, 2021a, 2021b; Myles & Merlo, 2021; Myles et al., 2020, 2021). This article will argue that the amygdala is involved in the perception and experience of fear but that its primary function in social perception is to promote rapid responses to threatening stimuli, before directing attention towards socially salient events. Firstly, evidence for the role of the amygdala in experiencing and perceiving fear will be discussed, before outlining research implicating the amygdala in processing a variety of facial expressions. The differing functions of the amygdala with respect to response latency will then be reviewed, before evaluating its role in the perception of other emotional and non-emotional stimuli.

The literature is saturated with evidence for the role of the amygdala in experiencing fear. For example, patient SM had bilateral amygdala damage (BAD) and failed to exhibit fear in response to trauma, dangerous animals or emotionally evocative movies (Feinstein et al., 2011). SM

displayed no other emotional deficits, emphasising the selectivity of her impairment (Tranel et al., 2006). However, SM identified that others experience fear in similar situations, demonstrating that her deficit was not derived from failure to understand fear. Contrarily, another BAD patient did not exhibit such impairments, suggesting that the amygdala is not causally involved in experiencing fear (Anderson & Phelps, 2002); however, differential damage may underly incongruous findings. Therefore, research with neurological patients provides equivocal evidence that the amygdala entails a role in experiencing fear.

Further support for the role of the amygdala in experiencing fear comes from neurologically intact individuals. Intracranial amygdala stimulation manifests feelings of fear (Halgren et al., 1978) and both abnormal structural and functional connectivity within the amygdala has been implicated in anxiety (Etkin et al., 2009). Whilst distinct, anxiety and fear share emotional similarities and the authors postulated that the amygdala underlies such emotions. However, the amygdala is not necessary for the conscious experience of fear. Evidence for this comes from reports that panic attacks can be induced in BAD patients by carbon dioxide inhalation (Feinstein et al., 2013) or injection of adrenergic agonists (Khalsa et al., 2016). These results indicate that the amygdala is involved in the experience of fear arising from exteroceptive stimuli but suggest that the amygdala is not crucial for the conscious experience of fear.

The amygdala's role extends beyond the experience of fear to the perception of threatening emotions. For example, BAD manifests disproportionate impairment in recognising fearful facial expressions in both static (Adolphs & Spezio, 2006) and dynamic stimuli (Graham et al., 2007). Further, BAD also impairs identification of the intensity of fearful expressions (Adolphs et al., 1994), implicating the amygdala in fear perception. Indeed, neuroimaging studies have demonstrated a linear relationship between left amygdala activity and the intensity of fearful expressions (Morris et al., 1996), advocating the role of the left amygdala in fearful expression perception. Whilst meta-analytic evidence supports the left-hemispheric lateralisation of responses to fearful faces (Baas et al., 2004), such findings may reflect poor temporal resolution associated with functional imaging, as the response of the right amygdala may be more rapid than the left. Future research is required to fully elucidate the lateralisation of emotion perception.

Indeed, the amygdala has been suggested to selectively respond to threatening social stimuli. For example, faces modulate amygdala activity in patients with social phobia but not healthy controls (Birbaumer et al., 1998), suggesting that the amygdala is involved in the subjective evaluation of social threat. Further, BAD patients display deficits in identifying other negative

emotions, including sadness, anger and disgust (Adolphs et al., 1999, 2003). Interestingly, BAD patients can recognise happiness; the stereotypical smile has been suggested to propagate such ease of recognition (Adolphs et al., 1996). Such evidence suggests that the amygdala is involved in the perception of threatening social stimuli, with a disproportionately large involvement in fear, perhaps due to its adversity.

Moreover, contemporary literature implicates the amygdala in the perception of facial expression intensity, irrespective of valence. For example, intracranial studies have identified neurons that are selectively responsive to the intensity of happy expressions (Rutishauser et al., 2015). Stimulation of the amygdala can also induce positive affect (Bijanki et al., 2014), implicating the amygdala in the experience of positive emotionality. Additionally, after habituation to facial expressions within an expression-specific category, the amygdala releases from adaptation as a face morph crosses a subjective boundary between expressions (Harris et al., 2012). These results suggest that the amygdala is involved in the categorical perception of expressions. This indicates that the amygdala encodes both the intensity and categorical valence of facial expressions, with an additional role in the experience of positive emotionality.

Theorists have also postulated that the amygdala processes positive facial expressions, which subsequently promote avoidance behaviour. For example, BAD patients demonstrate a positive bias when interpreting the trustworthiness of a face (Adolphs et al., 1998) and, unlike neurotypicals, fail to exhibit avoidance behaviour when internal facial features are occluded (Harrison et al., 2015). Neuroimaging evidence suggests that, whilst right amygdala activity entails an inverse relationship with perceived trustworthiness (Engell, 2007), the left amygdala exhibits a quadratic relationship (Todorov et al., 2008). These findings highlight the amygdala's involvement in the perception of both positive and negative expressions, with hemispheric segmentation in processing emotional valence.

The amygdala's involvement in the evaluation of emotional valence led to its implication in avoidance behaviour (Adolphs et al., 2010). Recent evidence suggests that the amygdala processes threatening stimuli, through the pulvinar and superior colliculus, without necessitating cognitive appraisal (LeDoux, 2000). Support for this comes from reports that amygdala neurons are responsive to fearful faces 74 milliseconds after stimulus onset (Méndez-Bértolo et al., 2016); this early activity precedes conscious awareness. Indeed, these neurons are not modulated by high spatial frequency (HSF) fearful faces, suggesting that they are selective for low spatial frequency (LSF) information (Vuilleumier et al., 2003). Activity was observed at congruent latencies in the pulvinar and superior colliculus, supporting their role in this network. Further,

neurotypical individuals rapidly respond to threatening faces whereas BAD patients cannot (Bach et al., 2015), elucidating a causal role of the amygdala in social threat detection. This system also functions independently of attentional resources, as visual neglect patients show increased right amygdala activity in response to fearful faces in their blind hemifield (Liddell et al., 2005). Therefore, the amygdala constitutes part of a rapid network that constructs a coarse representation of potentially threatening stimuli at early latencies.

After the amygdala's initial rapid response to threatening stimuli, it directs attention towards socially salient events to elucidate their nature. A recent meta-analysis of intracranial studies reported that amygdala neurons respond to LSF fearful faces at early latencies of 50-290 milliseconds but respond to HSF faces at greater latencies (Méndez-Bértolo et al., 2016). For example, amygdala neurons selective for both happy and fearful faces respond up to 1.5 seconds after stimulus onset (Wang et al., 2014). Thus, the amygdala may entail a latent role in directing attention towards social stimuli (Adolphs, 2008). The eyes have also been suggested to represent a socially salient region in expression perception. Indeed, BAD patients fail to utilise the eye region to decipher emotions (Spezio et al., 2007) but can recover fear recognition abilities when instructed to attend to the eye region (Adolphs et al., 2005). Further, basolateral amygdala neurons are responsive to eyes (Meletti et al., 2012), irrespective of expression, implicating the amygdala in directing attention towards the eyes. Such findings account for the disproportionate impairment in fear recognition with BAD, as the eye region is highly diagnostic in the perception of fear (Barrett, 2018). These results suggest that the amygdala is fundamental in directing attention towards socially salient stimuli.

Indeed, the amygdala's role in directing attention facilitates the disambiguation of stimuli (Adolphs et al., 2010). Evidence for this comes from Adams et al (2003), who reported greater amygdala activity in response to fearful faces with direct gaze and angry faces with averted gaze, as compared to the respective expressions with contrary gaze patterns. As the former expressions are more ambiguous, this suggests that the amygdala is recruited to disambiguate the expressions with respect to the contextual information. Further, when viewing face morphs between happy and fearful expressions, distinct neural populations respond to ambiguity in different expressions (Wang et al., 2017). This suggests that different areas of the amygdala encode the ambiguity of different facial expressions. Thus, the amygdala appears to entail a latent function of directing attention towards socially salient events to disambiguate the nature of facial expressions.

Emotion selectivity in the amygdala also extends beyond the visual domain. For example, amygdala activity is modulated by auditory crying or laughter (Sander & Scheich, 2001). Further, BAD patients have been reported to fail to recognise fear and anger from vocal prosody (Scott et al., 1997), elucidating a causal role in auditory emotion perception. The amygdala is also responsive to fearful body postures (Grezes et al., 2007), with evidence that BAD impairs recognition of fearful postures (Sprengelmeyer et al., 1999). However, BAD patients demonstrate normal emotion recognition from body postures when the face is occluded (Atkinson et al., 2007). As the amygdala directs attention towards the eyes, this suggests that the inability to utilise the eye region in posture identification manifests impaired fearful posture recognition.

Moreover, the amygdala processes postural information in a network of brain regions and has been suggested to allocate cognitive resources to areas processing body information. Recent evidence reported that the modulation of amygdala activity in response to bodily expressions was correlated with the enhancement of activity in other body-selective areas (Van de Vliet et al., 2018). However, BAD patients failed to exhibit such modulations, despite possessing no impairment in emotion categorisation tasks. This suggests that the amygdala is involved in allocating cognitive resources to body-processing regions. Subsequent research is required to evaluate whether it aids other domains of expression recognition by allocating cognitive resources to relevant neural areas.

In conclusion, the amygdala is critically involved in the experience and perception of fear. However, its primary role extends to the experience and perception of both positive and negative emotions, modulating subsequent approach and avoidance behaviour. Indeed, the amygdala responds rapidly to potentially threatening stimuli, before directing attention towards socially salient events to disambiguate their nature. Moreover, the role of the amygdala in emotion perception extends beyond the visual domain to vocal prosody, with evidence of its subsidiary functions in processing emotional body postures, social categorisation and facial identity. Nevertheless, despite its subsidiary roles in other perceptual and experiential domains, the amygdala's primary function in social perception involves proliferating rapid responses to potentially threatening stimuli, before directing attention to explicate the nature of socially salient events. Understanding the role of the amygdala in these psychological processes brings us closer to elucidating its role in 'clinical' fear (Myles, 2021a, 2021b).

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Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any potential conflict of interest.

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