Social threat perception and the evolution of paranoia

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Abstract

Rapid and efficient judgments about the significance of social threat are important for species survival and may recruit specialized neurocognitive systems, consistent with biological models of threat processing [1]. We review cognitive, psychophysiological, neuropsychological, and neuroimaging evidence in support of specialized neural networks subserving the processing of facial displays of threat. Cognitive research suggests that faces depicting anger are detected quickly when presented amongst other facial expressions, on the basis of distinguishing facial features. Psychophysiological investigations using visual scanpath techniques provide evidence for increased foveal attention to facial features of threat-related expressions (anger, fear), which may facilitate rapid detection and subsequent appraisal of the significance of threat (such as the direction of impending threat). Neuropsychological and neuroimaging studies implicate a primary role for the amygdala and pre-frontal cortices in interpreting signs of danger from facial expressions and other social stimuli. Subtle disturbances in these neurocognitive systems underlying efficient threat detection (manifesting in attentional biases and aberrant neural activity) may result in abnormally heightened perception of social threat, as seen in clinical levels of social anxiety and/or persecutory delusions in schizophrenia. Clinical states of paranoia may therefore reflect normal variation (i.e. biases) in the adaptive mechanisms which have evolved, in the Darwinian sense, to facilitate efficient threat detection in humans. As such, clinical levels of paranoia may represent the inevitable cost of efficient threat perception—or ‘justified’ suspicion—that is necessary for survival of the human species.

Keywords: Threat perception; Faces; Emotions; Persecutory delusions; Paranoia; Schizophrenia; Anxiety; Attention; Neurobiology

1. Introduction

Accurate interpretation of emotions conveyed through facial expressions is central to effective social communication, and may encompass distinct perceptual and neurocognitive processes according to the emotion [2]. Considerable physiological [3] and cross-cultural [4] research has established the existence of basic facial expressions of emotion (see Ref. [5] for a review), and recent neuroimaging evidence has provided support for the existence of discrete neural systems subserving the perception of negative emotions such as fear, anger, and disgust [6,7]. The influence of anxiety and mood upon the ability to
detect and respond appropriately to emotion conveyed through facial expression has been well-documented, with increased attention to negative facial expressions (and decreased attention to positive expressions) reported in depression [8,9], and increased pre-attentive orienting to threat-related facial expressions associated with social anxiety [10–15] and delusional ideation [16].

Rapid detection of threat in the social environment is critical for species survival. The neurocognitive mechanisms responsible for fast and efficient threat detection may thus have survived as an adaptive advantage in accord with Darwinian evolution theory [17], and consistent with recent models of threat perception [1]. Studies in healthy subjects indeed suggest that the detection of angry facial expressions is fast and efficient [18–21]. In line with these behavioural data, neurobiological evidence supports a primary role for the amygdala in initiating a rapid response to threat, while slower cortical processing serves to inhibit the limbic response following conscious appraisal of the significance of threat [1].

Here, we review studies which have examined the neurocognitive basis of threat perception, including cognitive research, psychophysiological studies employing visual oculography as an overt index of attention to threat, and studies which have revealed a distinct pattern of neural activity when viewing threat-related social information (e.g. faces depicting emotional expressions of fear and anger). We have focused upon studies examining the neurocognitive basis of threat perception not only in healthy populations, but also within psychiatric patients who experience inappropriately increased anxiety and threat perception in everyday social contexts: in particular, schizophrenia patients with abnormal beliefs (delusions) and hallucinations of a persecutory nature.

### 1.1. Cognitive research

Cognitive studies in healthy individuals suggest that faces depicting emotional expressions of anger are detected more rapidly than faces depicting other (non-threatening) expressions. For example, angry faces are detected faster in homogeneous crowds of discrepant faces in visual search tasks employing schematic face stimuli [18–20]. Furthermore, when displays contain the same faces (congruent affect), detection of the absence of an incongruent face is slower if all the faces display angry (or sad/angry) rather than happy expressions [18], suggesting that angry faces engage attention. However, discrepant findings in visual search tasks have been noted, which suggest that the faster detection of angry schematic faces may be due to low level features of the stimulus (e.g. contrast artifact), rather than threat detection per se [22].\(^1\)

\(^1\) Of course, it may be that pre-attentive attention to low level features of faces (e.g. eyebrows, eyes) may facilitate rapid detection of expressions of threat, as suggested by previous studies [23,24].

Visual search studies, a recent investigation of the time taken to identify basic emotional expressions revealed a processing advantage for facial expressions of anger in healthy individuals; that is, angry faces were identified more quickly than other non-threat facial expressions (happy, sad, neutral faces) [21].

Whilst this evidence suggests that healthy individuals detect and identify facial expressions of anger with rapid efficiency, several studies of facial affect recognition in schizophrenia have revealed greater differential impairment for the recognition of negative emotions of fear [25,26], anger [27] and sadness [25,28]. Of course, this finding has been revealed in the context of a long history of evidence for a broader impairment in facial affect recognition in schizophrenia [26,29–33], and support for a differential deficit that is specific to negative emotion recognition remains equivocal [30,34] (indeed, some studies report no evidence for any deficit in facial affect recognition in schizophrenia [35,36]). Specific impairments in the identification of negative facial affect may therefore not be robust, or expressed in all schizophrenia patients. Indeed, one study examining schizophrenia patients on a case-by-case basis demonstrated that the recognition of threat-related emotions thought to rely upon intact amygdala function was impaired overall, yet no universal emotional identification deficits were demonstrated, and not all patients demonstrated specific deficits in the recognition of threat-related expressions [37].

The specificity of emotion recognition deficits in schizophrenia therefore requires further investigation in studies which examine the processing of particular emotional states in association with symptom variations in schizophrenia. For example, it may be that only sub-groups of schizophrenia patients with negative symptoms (i.e. anhedonia, social withdrawal) demonstrate impaired recognition of negative facial affect such as sadness, while other symptom profiles may be associated with aberrant processing of other emotions in various ways. For example, in contrast to the evidence for impaired recognition of negative facial affect in heterogeneous schizophrenia groups, there is robust evidence for superior emotion perception in paranoid schizophrenia patients (i.e. those experiencing predominantly persecutory delusions and/or hallucinations, compared with non-paranoid patients) [38]. This finding has been reported specifically with regard to negative emotions [38–42], and suggests that heightened perception of certain negative emotions may be relevant to the genesis of persecutory delusions.

### 1.2. Cognitive bias for social threat and persecutory delusions

Investigations of cognitive biases in schizophrenia have accumulated to implicate biased processing of threat-related information in relation to persecutory delusions. Some of the first investigations of this type employed a variation of
the original Stroop [43] procedure, to investigate pre-attentive processing of words referring to delusional themes (rather than colour words). Using this paradigm, schizophrenia patients with persecutory delusions are slower in naming the ink-colour of ‘paranoid’ or threat-related words, versus meaningless strings of O’s, neutral words, or words signifying negative affect, compared with depressed and normal controls [44]. These findings have been interpreted as evidence for heightened pre-attentive processing of threatening information in schizophrenia patients with persecutory delusions.

In attempting to demonstrate a similar bias in selective attention, two studies examined memory for threatening information in patients with persecutory delusions [45,46]. In one study [46], subjects listen to stories that differed in terms of threatening content; when asked to recall as many propositions from the stories as possible, persecutory deluded subjects recalled more of the threatening propositions from the stories than the healthy control group. Similarly, Bentall et al. [45] asked schizophrenia patients with persecutory delusions, depressed patients, and healthy participants to recall items from a list of threat-related, depression-related and neutral words. The deluded participants displayed better memory for threat- and depression-related words than the normal controls, and demonstrated a significant tendency to repeat threat-related words during recall. In a related study [47], groups of patients suffering from persecutory delusions, depression, and healthy controls were asked to rate the frequency with which selected positive, negative, and neutral events had actually happened to them, as well as the predicted likelihood of these events happening to them in the future. All patient groups rated negative events as occurring relatively more frequently in comparison to the control subjects, and levels of magical ideation (e.g. paranormal beliefs) were associated with estimates of the frequency of negative events for both self and others. Collectively, the studies by Bentall and colleagues suggest that persecutory delusions are associated with biased attention and memory for material associated with personal threat; memory biases may be a consequence of deeper encoding of threatening material due to increased pre-attentive processing of threat, thus facilitating greater recall and expectation of threatening information and personal experiences.

Two recent studies have also investigated the time taken to recognize facial emotions in delusion-prone individuals and schizophrenia patients with persecutory delusions. Both delusion-prone and clinically deluded individuals were significantly slower to identify angry faces, reflecting a lack of the processing advantage shown by healthy control subjects [21,48]. The delayed processing of angry faces in relation to delusional ideation may reflect a prolonged, conscious evaluation of threat that is not undertaken during the normal efficient and automatic processing of directly threatening social material. Persecutory delusions may therefore be associated with an extended early processing of threat, or problems disengaging threat from conscious attention. Notably, recent studies have shown delayed disengagement of threat-related faces in association with high trait-anxiety [49] and delusion-proneness in healthy participants [16]. Again, it is plausible to suggest that this extended processing of threat may result in deeper encoding of threat-related information in long-term memory stores, coinciding with heightened recall of threatening material and higher expectation of negative events in paranoid schizophrenia as reported in previous studies (reviewed above).

1.3. Evidence from eye-movements

Visual scanpaths comprise voluntary eye movements (saccades) and foveal fixations, and represent a psychophysical measure of visual attention [50]. During examination of a visual stimulus, rapid eye movements direct the fovea to areas of interest, where ‘fixations’ occur. Fixations involve the fovea remaining relatively stationary on a particular region of the stimulus, usually for a few hundred milliseconds, depending upon task requirements [51]. Foveal input during fixations provides the visual system with detailed information about the stimulus, while cognitive processes operate in parallel, using parafoveal and peripheral retinal information to determine the location of the subsequent fixation, a process termed visual scanning [52].

Studies using brief (less than 200 ms) tachistoscopic presentations of objects have shown that coarse discrimination of visual stimuli occurs very quickly, but that the perception of finer details about the stimuli are governed by later, controlled processes of selective attention [53]. The distinction between controlled and automatic processing [54] has been prominent in the study of cognitive processes in both normal and schizophrenic cognition [55]. Controlled processes involve a slow sequence of temporary mental operations that are under voluntary control of the individual, placing demands upon limited attentional resources. Automatic processes, on the other hand, involve a fixed sequence of mental operations occurring relatively quickly in response to a particular stimulus, which occur outside of conscious awareness and involve access to long-term memory [55]. The study of visual scanpaths thus enables the investigation of information processing during both controlled stages of selective attention, and automatic processing of sensory information [56]. In terms of face processing, visual scanning paradigms can therefore be used to assess automatic sequences involved in early perceptual processing (e.g. recognition of an object as a face), as well as providing a real time measure of controlled attention to stimulus features (i.e. particular facial regions) during later stages of face processing that may be necessary for the discrimination of particular facial expressions (such as those depicting direct threat).

The first study of visual scanpaths to facial expressions depicting threatening emotions was conducted with
primates [57]. In this study, macaque monkeys spent more time attending to the eye regions of conspecific and human faces exhibiting obvious displays of social threat (i.e. furrowed brow, bared teeth). These authors concluded that increased attention to specific facial features (e.g. eyes) may be useful to detect the significance (i.e. directed at self versus others) of impending social threat.

Following from this study, a recent investigation has revealed the existence of distinct visual scanpath strategies in human subjects for threat-related (i.e. anger, fear) facial expressions [58]. Visual scanning of threat-related faces was characterized by increased fixations to feature areas (i.e. eyes, nose, and mouth) and extended lengths between fixations, when compared with non-threat facial expressions that included both emotion-laden (happy, sad) and non-emotional (neutral) faces. The increased attention to feature areas of threat-related faces may thus facilitate the detection of threat from facial expressions, consistent with previous behavioural research that attests to the role of feature-based detection of threat from facial expressions of anger and fear [23,24].

Increased attention to the features of threat-related faces may also provide information about the spatial location of impending threat [57], consistent with cognitive research showing the normal tendency to attend in the direction of another person’s gaze [59]. This pattern of visual appraisal is consistent with the way that monkeys view expressions of facial threat, suggesting that increased attention to the feature areas of threat-related expressions may be have evolved to facilitate cognitive appraisal of the significance (i.e. identification of threat as direct?) of impending social threat. Furthermore, the extended scanpaths (longer distance between fixations) exhibited by human subjects might reflect normal ‘vigilance’, or excessive monitoring of salient cues for social threat.

1.4. Visual attention to threat and delusional ideation

Further investigations of visual attention to social threat in delusion-prone and clinically deluded individuals have revealed an overt avoidance of fixating upon facial threat in healthy individuals with a vulnerability to delusional thinking [58], and schizophrenia patients with persecutory delusions [60]. That is, delusion-prone individuals exhibited fewer fixations and extended scanpaths for faces depicting anger and fear, compared to age matched controls with low scores on a measure of delusional ideation [58]. Similarly, schizophrenia patients with predominant persecutory delusions spent less time viewing (i.e. showed fewer fixations of shorter duration) the feature areas of negative facial expressions (anger, sad), compared to healthy controls [60], and showed significantly fewer fixations to expressions of fear when compared to a non-deluded schizophrenia group. The pattern of viewing directly threatening facial expressions (i.e. anger) in delusion-prone and deluded schizophrenia subjects thus reflects a controlled attentional bias away from threat.

Reduced visual scanning of the feature areas of threat-related faces in deluded schizophrenia patients suggests that regions such as the eyes may be particularly threatening for paranoid individuals, consistent with an earlier study in which schizophrenia patients with persecutory delusions spent less time viewing the feature areas of neutral faces during an identity recognition task [61]. Of course, it is important to consider these findings in the context of previous studies of visual scanpath aberrations in schizophrenia, in which a robust pattern of ‘restricted’ scanning (comprising fewer fixations of longer duration and shorter distances between fixations) emerged consistently when viewing neutral faces [61–65] and emotional faces [66,67]. This pattern of restricted visual scanning in schizophrenia has also been demonstrated when viewing complex geometric and scene stimuli, most commonly in association with negative symptoms [68–72]. By contrast, an opposing style of ‘extensive’ scanning (characterized by fewer fixations of shorter duration and longer distances between fixations) was associated with positive symptoms (e.g. delusions) of schizophrenia [73,74] in early investigations of relatively long periods (e.g. 1 min) of viewing complex scene stimuli.

There have been two other visual scanpath studies of threat perception in deluded schizophrenia, which employed complex stimuli comprising photographs of social scenes depicting various degrees of threat [75,76]. Freeman et al. [75] found that patients with persecutory delusions displayed reduced visual appraisal for ‘happy’ and ‘potentially threatening’ scenes, compared to scenes depicting ‘direct’ and ‘hidden’ threat (which were viewed in a similar fashion to control groups). In the study by Phillips et al. [76], participants viewed social situations rated as neutral, ambiguous, or overtly threatening in content. During an initial free-viewing task, all subjects viewed an overtly threatening scene to a greater extent than an ambiguous (potentially threatening) scene, but schizophrenia patients with persecutory delusions demonstrated reduced appraisal of threatening areas of the ambiguous scene, and a corresponding increase in the number and duration of fixations to non-threatening areas. Additionally, deluded participants repeatedly viewed (checked) threatening foreground areas of all scenes less than normal and psychiatric controls.

These findings using social scene stimuli suggest that persecutory delusions may be associated with the perception of threat in inappropriate places within ambiguous contexts, while the reduced re-appraisal of foreground areas might reflect hasty decision-making about the content of the scenes. Moreover, the results do not support a direct association between persecutory delusions and increased attention to threat, as suggested by earlier studies of pre-attentive cognitive bias toward threat-related words during emotional Stroop tasks [44]. Notably, scenes are necessarily
more ambiguous and complex than the word stimuli used in emotional-stroop tasks. In summary, scanpath studies show that deluded schizophrenia patients pay comparatively less attention to the salient features of threat-related faces [58], and to the threatening areas of social scenes [75,76].

2. ‘Vigilance-avoidance’ for threat and persecutory delusions?

Reduced foveal attention to threat-related faces suggests that individuals with persecutory delusions may be abnormally sensitive to threatening stimuli in the social environment. As such, the directed attentional bias away from threat-related material in these individuals may represent a strategy to reduce the unpleasant anxiety associated with the perception of a socially threatening stimulus. This hypothesis has been raised previously in cognitive models of the aetiology and maintenance of anxiety [77], in terms of a ‘vigilance-avoidance’ style of processing threat. In this context, an initial orienting of attention toward threat-related stimuli is argued to result from automatic information processing priorities which are biased toward the detection of threat, followed by active avoidance of threat (during later controlled stages of attention) to reduce the associated anxiety. Indeed, this pattern of attention for threat-related stimuli has been demonstrated in both cognitive and psychophysiological (visual scan path) investigations of attention to threat in clinically deluded and delusion-prone individuals. For example, the cognitive evidence reviewed in previous sections suggests the existence of both a pre-attentive orienting bias for threat-related information, as well as a difficulty disengaging threatening material from conscious awareness (such that threatening information is subject to further cognitive processing) operating in association with high levels of delusional ideation [16,44]. On the other hand, evidence from eye-movements to threat-related faces and social scenes converge in reflecting a later period of active avoidance of overtly threatening information. The role of anxiety in contributing to this pattern of attention to threat in deluded individuals has received relatively little attention to date, and thus requires further investigation.

One previous study tested the prediction that ‘hyper-vigilant’ scanning for social threat would be associated with higher anxiety levels in individuals with generalized anxiety disorder (GAD), in addition to schizophrenic patients with persecutory delusions [75]. In neither population was a pattern of hyper-vigilant visual scanning demonstrated, however. Deluded patients did exhibit reduced attention to potentially threatening areas of ambiguous scenes, while those with GAD showed no such pattern. Potential differences between the triggers of anxiety in deluded and anxiety disordered patients suggest that these associations deserve further attention—especially since preferential attention to threat-related faces has been associated with heightened levels of social anxiety in several studies [10–15]. Moreover, the role of anxiety in the formation of delusional beliefs may be such that anxiety in deluded individuals is generated from internal experiences (such as voices, perceptual anomalies, perceived significance) that are subsequently and erroneously attributed to potentially threatening information in the social environment (such as an ambiguous facial expression) [78]. In contrast, patients with GAD may be aware of their increased attention to internally-generated anxiety; avoidance of social cues that trigger this process may then be actively avoided. These issues require further clarification.

2.1. The neurobiology of threat processing

There is considerable evidence for the role of the amygdala in processing social threat (such as that perceived in facial expressions) from behavioural [79], lesion [80–85] and functional imaging studies [7,42,86,87]. The amygdala receives cortical input from sensory processing areas, and in turn provides feedback to these areas through reciprocal projections to the prefrontal cortex, as well as additional projections to other cortical areas [88]. The amygdala has also been implicated in the role of maintaining attention to emotionally relevant stimuli, through modulation of activity within the appropriate sensory cortex [1]. The salience or significance of the stimulus may then be determined by processing within sensory cortex and neural regions associated with attention and affect regulation, including dorsal regions of the anterior cingulate gyrus and prefrontal cortex [89–91].

Further data suggests that the amygdala contributes to the recognition of facial expressions of emotion beyond those of a threat-related nature [86,92]. For example, the amygdala has been associated with the retrieval of social information, and generation of social judgments (e.g. attributions regarding trustworthiness) about other people from their facial expressions [93], whilst other, ventrally-located prefrontal structures, including the orbitofrontal cortex, have been associated with the processing of socially relevant affective material per se [94,95].

2.2. The neurobiology of abnormal threat perception in schizophrenia

Studies employing neuroimaging techniques have demonstrated in schizophrenic patients structural and functional abnormalities within ventral and dorsal neural systems important for emotion processing, although inconsistent findings have been noted. An absence of the normal amygdalar response to fearful facial expressions [42,87,96], and aversive scenes [97] has been reported in deluded schizophrenia patients. In schizophrenia patients with prominent persecutory delusions, however, preliminary data shows amygdalar activation to ambiguous but not overtly fearful stimuli (faces and sounds) [98] and a more
transient response of both amygdalae to fearful faces [99]. These findings suggest an attenuated response of the amygdala to overt displays of threat-related emotion in schizophrenia, particularly fear, although this requires further study. One possibility is that impaired recognition of negative (e.g. threat-related) emotions in schizophrenia may result from dysfunction in the neural system for processing facial emotion per se [100]. Aberrant connectivity within a more generalised network subserving facial emotion recognition may produce an overall decrease in the discriminant capacity of the network, such that the most prominent recognition deficits in schizophrenia are observed for expressions which are the most difficult to recognise (i.e. fear and disgust). In schizophrenia patients with persecutory delusions, additional information processing abnormalities (such as an automatic propensity for threatening material to engage attention, and the continual expectation of social threat) may lead to the misperception of ambiguous facial expressions as threatening.

One recent neuroimaging study has attempted to localize the functional disturbances associated with a generalised facial affect recognition deficit in schizophrenia [101]. This magnetoencephalographic study reported decreased activity in the orbito-frontal cortex in schizophrenia subjects [102], and decreased activity in other brain areas implicated in face processing (e.g. visual processing regions: precuneus, fusiform gyrus, hippocampus) [103] in association with facial affect recognition deficits in schizophrenia. The latter areas have also been associated with reduced cerebral blood flow during a face identity recognition task in schizophrenia [104], and thus suggest that emotion-recognition impairments in schizophrenia may reflect aberrant neural circuitry in a wider distribution of brain regions implicated in face perception more generally. However, evidence for a double dissociation between the neural networks for processing facial expressions and face identity recognition [79, 105–107] suggests that facial recognition impairments in schizophrenia are unrelated to difficulties in processing facial identity. It is, of course, possible that cortico-limbic dysfunction schizophrenia could account for disturbances in both of these independent cognitive processes. In this way, the neural correlates of affect recognition deficits in schizophrenia may be one instance of a wider distribution of abnormalities within a broader ‘social brain’ neural network [94].

Aberrant responses in these neural systems have been associated with mentalising deficits and other social-cognitive biases in schizophrenia. For example, mentalising (theory-of-mind) abilities have been most consistently associated with neural responses in the right medial prefrontal cortex, superior temporal sulcus, and temporo-parietal junction in normal individuals [108], while schizophrenia patients demonstrate hypoactivity in the left inferior frontal cortex during mental state attribution [109]. Another study shows that hyperactivity in the lateral inferior frontal cortex corresponds with attention to self-referent threatening stimuli [110]. Collectively, these data suggest that abnormal social cognition in schizophrenia may be associated with dysconnectivity within and/or between temporo-limbic regions and the pre-frontal cortex.

Abnormal neural circuitry in schizophrenia, involving dysfunctional prefrontal-thalamic and temporo-limbic or cerebellar connections, has been emphasised by previous authors [111,112]. For example, a disruption in connectivity between nodes in prefrontal cortex, the thalamus and the cerebellum has been associated with ‘cognitive dysmetria’, a difficulty in prioritizing, processing, coordinating, and responding to information, which may account for many of the diverse symptoms of schizophrenia [111]. Furthermore, temporo-limbic structures (e.g. amygdala, thalamus, hippocampus, parahippocampal gyri) and the orbito-frontal cortex (projecting to the anterior cingulate) have been consistently implicated in the aetiology of positive symptoms such as delusions [113–123].

A comprehensive review of the structural and functional abnormalities in schizophrenia within regions important for emotion processing and social cognition, including subcortical regions, the amygdala, anterior insula and ventral striatum, hippocampus, and dorsal prefrontal cortical regions has recently been provided elsewhere [124]. Essentially, findings indicate structural and functional abnormalities in regions important for the appraisal and identification of positive and negative emotional stimuli and production of affective states in this patient population. This may result in a restriction of the range of positive and negative emotions able to be identified by these patients, which may be associated with a tendency for ambiguous stimuli to be misinterpreted as threatening, particularly in patients with prominent persecutory delusions. Structural and functional abnormalities in the hippocampus and dorsal prefrontal cortical regions, resulting in impairments in reasoning, contextual processing and effortful regulation of affective states, may perpetuate these abnormalities in threat perception, and exacerbate paranoid ideation.

Consistent with this proposal, the evidence for visuo-cognitive abnormalities for threat-related expressions in deluded schizophrenia point toward a dysfunction in the connectivity between prefrontal regions involved in ocular-motor control (e.g. frontal eye fields; [125]) and in the limbic circuitry relevant to the perception of threat-related facial expressions [7,42,86]. The frontal eye field and supplementary eye field located in the prefrontal cortex have been implicated in controlling voluntary shifts of attention to visual locations across a wide variety of visual tasks [126–129].

How can these neurobiological findings be interpreted in relation to findings from visual scanpath and cognitive studies? One possibility is that reduced visual attention to threat-related faces may result from decreased amygdalar activity to these stimuli, resulting in dysfunctional
amygdala-prefrontal cortical projections [130]. A second possibility is the presence of an inhibitory influence of prefrontal cortical regions upon the amygdala, which serves to disengage attention to threat-related stimuli in order to reduce anxiety due to perceived threat. The decreased activity within sub-cortical limbic regions associated with the efficient and rapid response to threat-related stimuli, but more sustained activity within prefrontal cortical regions during threat-perception may be associated with a delayed processing of these stimuli in deluded schizophrenic patients, and the adoption of controlled, serial-based visual processing strategies for threat-related faces in this population. Alternatively, functional abnormalities in prefrontal cortical regions could result in impairments in reasoning, contextual processing, and/or effortful regulation of attention to affective material, thus perpetuating aberrant processing of threat-related stimuli [124]. Hypotheses regarding cause and effect relationships between the prefrontal cortex and the amygdala are difficult to disentangle because of the reciprocal connections between these areas [88]. The employment of concurrent electrophysiological and neuroimaging techniques may be useful to establish the timing of proposed dysfunctions in the connectivity between these regions in schizophrenia.

3. Conclusion

Accurate and rapid detection of social threat is critical for species survival. In subjects experiencing inappropriately high levels of social anxiety and perceived threat, including schizophrenic patients with persecutory delusions, there is accumulating evidence for an initial automatic attentional bias towards threatening material, but a subsequent controlled attentional bias away from threat. This apparent inconsistency does not support the conceptualisation of persecutory delusions as involving increased attention to threat. Instead, the pattern of findings from pre-attentive and visual processing paradigms suggests that the direction of threat-bias in individuals with persecutory delusions may vary across early and late stages of information processing. Delusional information processing may thus involve an initial ‘vigilance’ for threat followed by active ‘avoidance’ of threat during later, controlled stages of information processing [60], as has been suggested as a possible explanation for attentional biases in socially anxious individuals [77]. Attentional vigilance according to the continual expectance of threat in individuals with persecutory delusions could feasibly lead to the misperception of threat in ambiguous or inappropriate places, followed by an active avoidance of the perceived threat, in order to reduce anxiety. Further investigation of the neurobiology involved in social-cognitive aberrations in delusions might aim to clarify the neural basis of the proposed pattern of vigilance-avoidance for threat-related information. The use of integrative brain imaging techniques in further investigations of social perceptual abnormalities associated with persecutory delusions will help to clarify the neural basis of the proposed pattern of vigilance-avoidance for threat-related information in this socially-dysfunctional population.

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