Learning to fear novel stimuli by observing others in the social affordance framework

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ABSTRACT

Fear responses to novel stimuli can be learned directly, through personal experiences (Fear Conditioning, FC), or indirectly, by observing conspecific reactions to a stimulus (Social Fear Learning, SFL). Although substantial knowledge exists about FC and SFL in humans and other species, they are typically conceived as mechanisms that engage separate neural networks and operate at different levels of complexity. Here, we propose a broader framework that links these two fear learning modes by supporting the view that social signals may act as unconditioned stimuli during SFL. In this context, we highlight the potential role of subcortical structures of ancient evolutionary origin in encoding social signals and argue that they play a pivotal function in transforming observed emotional expressions into adaptive behavioural responses. This perspective extends the *social affordance hypothesis* to subcortical circuits underlying vicarious learning in social contexts. Recognising the interplay between these two modes of fear learning paves the way for new empirical studies focusing on interspecies comparisons and broadens the boundaries of our knowledge of fear acquisition.

1. Introduction

Learning to fear and avoid novel stimuli and events with potentially harmful consequences is evolutionarily advantageous, as it enhances an animal's defensive readiness in future encounters. Research on the neuronal mechanisms enabling rapid threat detection and response has revealed a variety of defensive circuits. Some of these circuits are phylogenetically ancient and shared across multiple species, while others are evolutionarily newer and vary in their degree of complexity (Chivers et al., 1996; Cooke and Graziano, 2004; Cooke et al., 2003; Graziano et al., 2002; Kobayakawa et al., 2007; Mathuru et al., 2012; Papes et al., 2010; Pereira and Moita, 2016; Stepniewska et al., 2005). But what is the contribution of these different defensive circuits to an animal's capacity to learn to fear new stimuli?

The fear response to unexperienced stimuli - here referred to as involuntary and non-conscious defensive response (LeDoux, 2014) - may

be acquired directly or indirectly (LeDoux, 2003). The Pavlovian fear conditioning (FC) paradigm is a simple yet effective experimental tool for studying the neuronal underpinnings of *direct* fear learning for novel stimuli (Pavlov, 1927) (Fig. 1a, b, c). In this paradigm, a neutral stimulus, such as a light or an object, is simultaneously paired with an aversive unconditioned stimulus (US), such as a noxious stimulus, that innately triggers fear responses (e.g., freeze or flight). Consequently, the originally neutral stimulus becomes a conditioned stimulus (CS), capable of eliciting behavioural and autonomic responses (e.g., changes in skin conductance) even in the absence of the US (Battaglia and Thayer, 2022; Lonsdorf et al., 2017). A crucial aspect of this process is the dependency of the US-CS association on their spatial and temporal co-occurrence during first-hand experience (Olsson et al., 2020).

Luckily, not all learning about threats requires direct and potentially dangerous experiences. Social animals can learn to fear novel stimuli *indirectly* by witnessing the conspecific reactions. This mechanism,

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known as Social Fear Learning (SFL), is typically studied using an observational fear learning paradigm (Debiec and Olsson, 2017; Olsson and Phelps, 2007) (Fig. 1d, e, f). For example, juvenile laboratory-reared monkeys, initially unafraid of snakes, rapidly develop an intense and persistent fear of them after watching wild-reared macaques reacting to snakes (Mineka et al., 1984). Consistent evidence supports the notion that social animals can learn the value of novel stimuli by observing conspecific reactions from early developmental stages (Bandura and Walters, 1977; Jeon et al., 2010; Olsson and Phelps, 2007). This spontaneous tuning is coherent with the innate ability of human newborns to process face-like stimuli (Goren et al., 1975), especially when they display negative emotions (Safar and Moulson, 2020). Likewise, monkeys prefer to look at faces rather than objects (Dal Monte et al., 2022), even if deprived of any previous visual experience with faces (Sugita, 2008). Notably, observational learning extends to various taxa, not just conspecifics (Avarguès-Weber et al., 2013), suggesting that some fearful bodily expressions are rooted in common mammalian ancestors and have been preserved along the evolution of the visual system. Over the past two decades, evidence indicates that facial and bodily cues are prime candidates for triggering defensive reactions (de Gelder and Poyo Solanas, 2021; Tamietto and de Gelder, 2010). Features such as eye whites, limb contraction, speed of movement, head orientation or gaze direction can be encoded automatically and non-consciously, underscoring their significance in initiating defensive responses (Burra et al., 2013; Poyo Solanas et al., 2020; Van den Stock et al., 2015; Whalen et al., 2004). All these findings indicate that social animals are endowed with the neurobiological machinery required to innately process others' bodily configurations that, according to Olsson and collaborators, can act as effective US, thus enabling animals to promptly respond to them (Debiec and Olsson, 2017; Olsson et al., 2020; Olsson and Phelps, 2007). Evidence suggests that seeing fearful signals induces analogous responses in observers, including autonomic changes (Haaker et al., 2017), rapid and specific behavioural reactions (Jeon and Shin, 2011), and automatic activation of the motor system (de Gelder et al., 2004;

Grèzes et al., 2014; Hortensius et al., 2016; Huis In 't Veld et al., 2014). Therefore, just as in classical FC - where an aversive physical stimulus, such as a foot shock, represents the US that innately elicits fear responses - in SFL the emotional display of others can act as a *social US* that triggers an adaptive fear response in the observer, preventing physical interaction with potentially harmful stimuli (CS). The primary difference between these two learning modes may lie in the nature of the US (nociceptive vs social) rather than in fundamental neural mechanisms, which likely involve largely shared neural substrates subserving both direct and indirect fear learning.

While contemporary accounts on SFL highlight the involvement of cortical areas, including the anterior insula (AI), temporo-parietal junction (TPJ), and anterior cingulate cortex (ACC) (Debiec and Olsson, 2017), mounting evidence also points to the engagement of subcortical structures because of their role in encoding defensive behaviours, preceding the activity of higher-order visual structures for category perception (de Gelder et al., 2004; Grèzes et al., 2014; Haaker et al., 2017; Hortensius et al., 2016; Huis In 't Veld et al., 2014). Investigating core mechanisms common to both FC and SFL, particularly in the initial stages of social cue encoding, may reveal underlying principles of fear learning and transmission that diverge only in advanced ontogenetic and phylogenetic stages.

This review critically evaluates the pivotal role of the amygdala and thalamus in learning novel threats during both FC and SFL. We propose that visual subcortical structures, including the superior colliculus (SC) and the pulvinar, although poorly considered in the SFL literature, may provide a rapid and coarse route for conveying to the amygdala relevant social signals displayed by other individuals. Finally, we suggest that the *social affordance hypothesis* (Orban et al., 2021a), originally proposed to explain the cortical mechanisms of action selection in social contexts, can be used to frame the contribution of several subcortical nodes in triggering potential defensive reactions to fearful stimuli and acquiring novel fears during SFL.
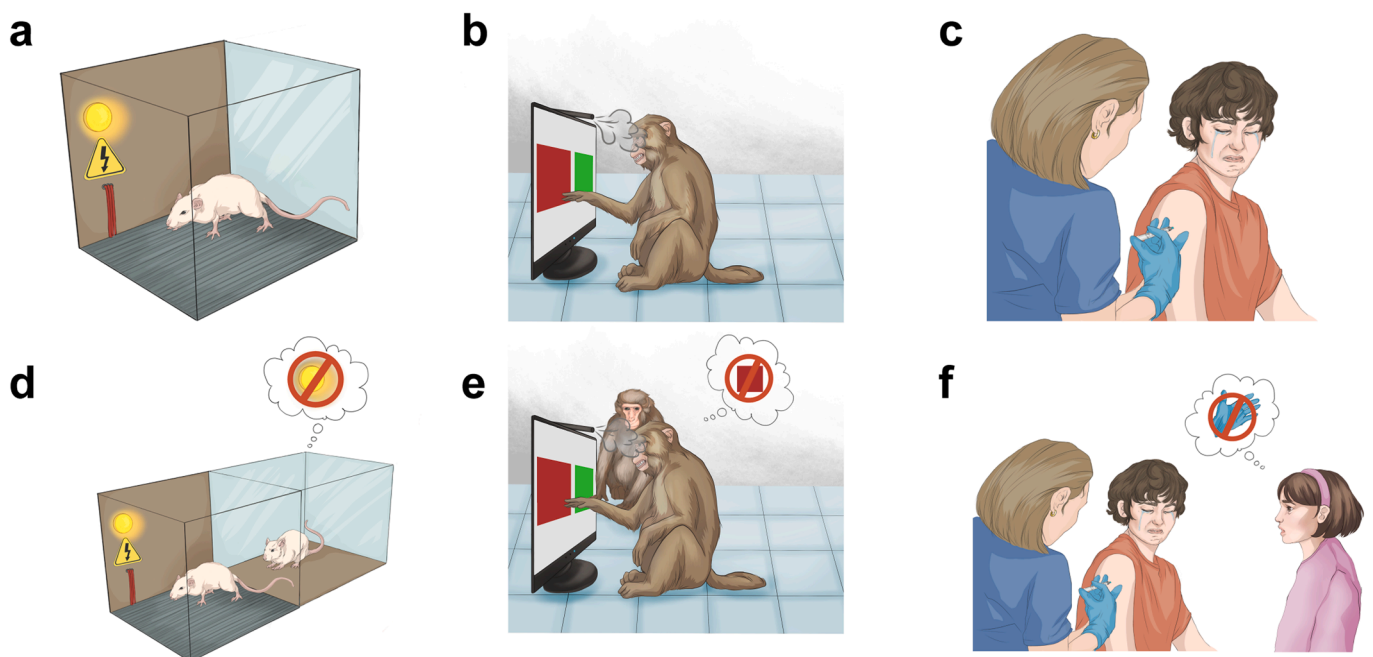
Fig. 1. Classical and Social Fear Learning in rodents, non-human primates, and humans. Representative scenarios of classical fear learning for a mouse (a), a rhesus macaque (b) and a human (c) (top illustrations). During classical fear learning, a mouse (a) can learn the association between a conditioned stimulus (CS), such as a light, and an unconditioned stimulus (US), such as a foot shock. A rhesus macaque (b) can learn the association between a red square stimulus (CS) and an air puff (US). A human can learn the association between a person wearing a blue glove (CS) and a syringe puncture (US). Representative scenarios of social fear learning in mice (d) macaques (e) and humans (f) (bottom illustrations). During social fear learning, mice (d), macaques (e) and humans (f) can learn to fear novel stimuli (CS, e.g., light, red square and a person wearing blue gloves) *indirectly* by simply witnessing the conspecific reactions to these stimuli, which serve as potentially effective US during social fear learning.

2. The amygdala and thalamic relaying in FC and SFL

2.1. Amygdala

The amygdala comprises a group of heterogeneous nuclei in the medial temporal lobe that are distinguishable based on cytoarchitectonic organisation and anatomical connectivity (Benarroch, 2015). This structure is central to the acquisition, storage, and expression of fear for new stimuli during FC (LeDoux, 2014). Specifically, the lateral nucleus (LA), which is the primary target of cortical and thalamic inputs (Aggleton et al., 1980), processes both the neutral (CS) and innately aversive stimuli (US). Initially, the activation of LA neurons is exclusive to the US, but following CS-US pairing during learning, synaptic changes potentiate the LA response to the CS, enabling CS alone to activate these neurons (Johansen et al., 2011). This activity propagates to the basal nucleus (BA) of the amygdala, an intermediate station projecting to the centromedial nuclear group (Ce) (Aggleton et al., 1980), which orchestrates autonomic fear responses through its downstream projections to various midbrain regions (Kalin et al., 2004). Nevertheless, recent evidence in rodents suggests a more complex function for Ce in FC (Duvarci et al., 2011; Ehrlich et al., 2009; Wilensky et al., 2006), as it receives also direct input from sensory areas (Paré et al., 2004). Indeed, optogenetic inactivation of the centrolateral portion in the Ce impedes fear acquisition in mice, while inactivation of its centromedial portion impairs fear expression, highlighting distinct functional roles within the Ce (Ciocchi et al., 2010).

Interestingly, recent studies in both human and non-human animals have shown that the amygdala plays also a key role in SFL (Debiec and Sullivan, 2014; Meffert et al., 2015; Olsson and Phelps, 2007). For example, disrupting the LA and medial amygdala nuclei in rats results in deficits in exploiting social cues to guide behaviour (Twining et al., 2017). Similarly, pharmacological inactivation of the basolateral complex in infant rodents hinders fear transmission from mother to pup (Debiec and Sullivan, 2014), suggesting that inactivation of this structure impairs both the acquisition and expression of new fear during SFL.

However, the amygdala involvement in SFL might also stem from its role in processing the emotional content of social signals. Evidence from human neuroimaging demonstrates significant amygdala activation in response to fearful facial expressions (Calder et al., 2001) or whole-body postures (de Gelder et al., 2004; Grèzes et al., 2007; Hadjikhani and de Gelder, 2003; Poyo Solanas et al., 2018), with consistent encoding patterns across developmental stages (Ross et al., 2019). Accordingly, single neuron recordings in humans indicate that the amygdala encodes not only facial features (Rutishauser et al., 2011) but also their emotional valence and intensity (Wang et al., 2017). Similarly, neurons in the macaque amygdala exhibit selectivity for facial expressions and identities (Gothard et al., 2007) and their activity is modulated by visual attention, with stronger responses when social stimuli are attentively fixated than when they are freely and rapidly viewed (Minxha et al., 2017). Causal evidence from amygdala damage further supports its crucial role in recognizing and detecting facial expressions in both humans (Adolphs et al., 1994; Young et al., 1996) and non-human primates (Dal Monte et al., 2015).

Notably, amygdala response to emotional facial or bodily expressions can persist even when visual awareness is lacking. This has been observed both settings where visual awareness is experimentally manipulated (e.g., masking, flash suppressions) (Whalen et al., 1998) and in cases of brain damage affecting the visual cortex or the attentional systems, as reported in patients with "blindsight" or hemispatial neglect, respectively (Anders et al., 2004, 2009; Celeghin et al., 2019; de Gelder et al., 2015; Tamietto et al., 2005; Van den Stock et al., 2015, 2011).

In summary, current results underscore the amygdala's crucial role in both fear acquisition and expression, whether through classical FC or SFL. It responds to a wide range of stimuli, from simple physical triggers like electric shock to complex social cues such as bodily configurations, all serving as effective US.

2.2. Thalamus

In addition to the role of the amygdala in FC and SFL, evidence highlights significant contribution of the thalamus in relaying sensory information, both directly and rapidly to the amygdala via its sensory nuclei, and indirectly via the polysynaptic thalamocortical pathways (LeDoux et al., 1984; LeDoux, 1994), thereby potentially influencing both FC and SFL.

Indirect thalamocortical pathways have been shown to be crucial for memory dynamics involving threatening stimuli, such as consolidation, retrieval, and extinction (Cambiaghi et al., 2016; Dalmay et al., 2019). Recent evidence also suggests their involvement in forming CS-US associations (Battaglia et al., 2020, 2022). Conversely, direct thalamo-amygdala pathways are pivotal for establishing novel CS-US associations. For example, auditory FC remains unaffected by lesions to the primary auditory cortex but is significantly impaired by damage to the bilateral medial geniculate nucleus, underscoring the importance of the auditory thalamus in FC (Romanski and LeDoux, 1992). The sensory specificity of thalamic nuclei is further demonstrated as bilateral lesions of the posterior intralaminar complex of the thalamus selectively disrupt FC to a tone (CS) paired with a foot shock (US), but not to a loud sound used as US (Lanuza et al., 2004). In the visual domain, patients with lesions confined to primary visual cortex (V1) still exhibit intact FC to a visual cue of which they are unaware (Hamm et al., 2003). In contrast, combined lesions of the lateral geniculate nucleus (LGN) and the lateral posterior nucleus - the rodent homolog of the primate pulvinar (Zhou et al., 2017) - fully block the fear-potentiated startle response to a visual CS, but not when damage involves either structures individually (Shi and Davis, 2001).

Emerging evidence suggests the involvement of thalamic nuclei also in modulating SFL. In mice, inactivating the parafascicular or mediodorsal thalamic nuclei diminishes fear responses in observational settings when the animals watch conspecifics receiving repetitive foot shocks (Jeon et al., 2010). In rodents, pharmacological inactivation of the medial geniculate nucleus blocks the auditory social transmission of fear by impairing the receiver's ability to process ultrasonic distress calls from conspecifics (Kim et al., 2010). Similarly, the inactivation of either the left or right anteromedial thalamic nucleus impairs SFL in mice (Kim et al., 2012), indicating that social fear transmission requires intact thalamic nuclei, at least in rodent models.

Among the various thalamic nuclei, evidence from human lesion studies highlights the pulvinar contribution in processing socially relevant stimuli. For example, one patient with complete unilateral loss of the pulvinar was incapable of recognizing fearful expressions in his contralesional field (Ward et al., 2007). The authors suggested that the cortex, in isolation from the entire pulvinar, is unable to recognize fearful expressions (Ward et al., 2007). Likewise, pulvinar lesions disrupt non-conscious processing of fearful stimuli in hemianopic patients with V1 damage, possibly because the relaying of fear-related information from the SC to the amygdala is interrupted (Bertini et al., 2018). This is consistent with neuroimaging findings showing that fearful facial expressions (Kragel et al., 2021; McFadyen et al., 2019) and whole-body postures (Hadjikhani and de Gelder, 2003) activate a subcortical network involving the SC, the pulvinar, and the amygdala, even after cortical damage to V1 (Van den Stock et al., 2015, 2011). Collectively, current evidence suggests a crucial contribution of the pulvinar in processing fearful signals from conspecifics, which should pave the way for future investigations into its possible involvement in SFL.

3. An ancient subcortical pathway conveying social US to the amygdala

Primates possess a more complex repertoire of social behaviours

compared to other animals (Zych and Gogolla, 2021). Facial and bodily expressions of basic emotions are innate in both humans and non-human primates (Kret et al., 2020; Matsumoto and Willingham, 2009; Celeghin et al., 2017), are universal across cultures (Ekman, 1989; Tracy and Matsumoto, 2008), and are crucial for vicarious learning to fear novel stimuli by observing others' reactions. But how does this social information reach the neural circuits responsible for defensive fear responses?

Based on pioneering evidence in rodents (LeDoux, 1996; Phelps and LeDoux, 2005), research over the past two decades has shown that also in primates the amygdala receives visual information about threatening stimuli through two parallel yet interconnected pathways (Garrido et al., 2012) (Fig. 2). The cortical pathway originates in V1, proceeds to inferotemporal areas, and then reaches the amygdala (Freese and Amaral, 2005). In contrast, the subcortical pathway, essential for the rapid and coarse processing of innately threatening stimuli, relays visual information from retino-recipient structures such as the SC to the amygdala via the pulvinar (McFadyen, 2019; Morris et al., 2001; Tamietto and Morrone, 2016; Tamietto et al., 2012).

3.1. Anatomo-functional evidence for a visual subcortical pathway

Several anatomo-functional approaches have provided converging evidence for the ancient and common phylogenetic origin of the visual subcortical pathway in mammals (Kragel et al., 2021; Stepniewska et al., 2000; Zhou et al., 2017). Anatomical studies using the injection of retrograde tracers into the amygdala have labelled sectors of the medial, anterior, and inferior pulvinar that are also labelled by anterograde tracers injected into the SC. This demonstrates that the same pulvinar sectors that receive input from the SC also send efferents to the amygdala (Elorette et al., 2018). Tractography-based diffusion imaging in

Fig. 2. The major cortical and subcortical neural pathways for processing complex visual information. The subcortical pathway is depicted in red, while the cortical pathway is in black. In the cortical pathway, visual information travels from the retina to the lateral geniculate nucleus (LGN) of the thalamus and then to the primary visual cortex (V1) in the occipital lobe. From V1, visual information reaches the extrastriate cortices (V2 and V3) and then flows along two parallel but interconnected streams, one ventral and one dorsal. The ventral stream (V4-IT) projects to the amygdala (Amy) for the processing of salient visual information. The subcortical pathway originates in the retina and reaches the superior colliculus (SC), which in turn projects to the Pulvinar. This latter region projects to the Amy, which sends direct efferents to several deep nuclei, including the hypothalamic paraventricular nucleus (PVN), lateral hypothalamus (LH), periaqueductal grey (PAG), rostral ventrolateral medulla (RVLM), and nucleus tractus solitarii (NTS).

healthy humans (Koller et al., 2019; Kragel et al., 2021) and patients with V1 lesions (Tamietto et al., 2012) have confirmed these findings, suggesting a role for the SC-pulvinar-amygdala pathway in processing salient social stimuli. Similarly, probabilistic tractography studies have shown that the fibre density of this pathway in healthy individuals reliably predicts accuracy in detecting fearful faces during a fast emotion recognition test (McFadyen et al., 2019) and correlates with the tendency to orient towards a threatening stimulus during saccade decision tasks (Koller et al., 2019).
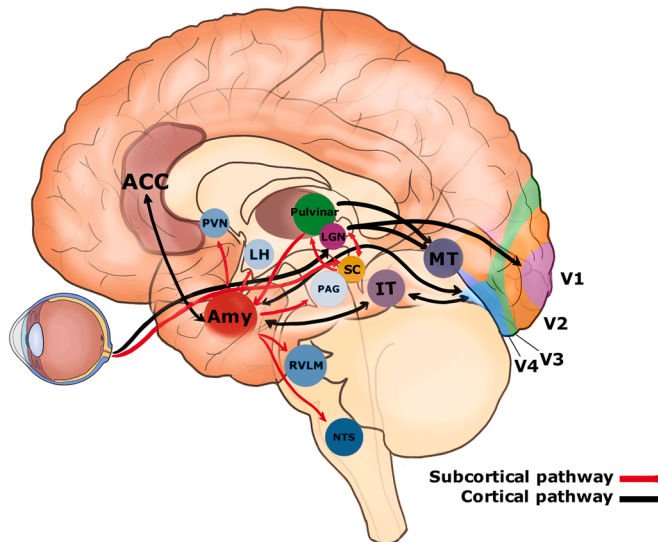
Functional neuroimaging in humans has further characterized the involvement of this subcortical pathway in processing emotional signals, identifying stimulus features and the behavioural outcomes that best activate it. For example, facial expressions in low spatial frequencies selectively engage this pathway, but not the face-selective cortical regions in the fusiform gyrus, consistent with the magnocellular input to the amygdala (Vuilleumier et al., 2003). Magnetoencephalography (MEG) studies have identified a dissociation in amygdala responses to fearful faces. Early amygdala responses ($\sim$ 60 ms post-stimulus onset) occur automatically, independent of conscious attention, while later responses ($\sim$ 280 ms) are modulated by voluntary attention (Luo et al., 2007). More conclusively, human intracranial electrophysiology found rapid responses ($\sim$ 70 ms) in the lateral amygdala specifically to fearful facial expressions, which occur much earlier than similar fear responses in the visual cortex, typically emerging in the temporal regions around 170 ms post-stimulus (Méndez-Bértolo et al., 2016).

Studies on patients with "affective blindsight", who retain non-conscious emotion discrimination despite cortical blindness, demonstrate that activity in the subcortical pathway to the amygdala persists for both facial (de Gelder et al., 2005; Morris et al., 2001) and bodily expressions (de Gelder and Hadjikhani, 2006). Moreover, non-conscious decoding of facial or bodily expressions in these patients induces emotional contagion, as revealed by spontaneous facial mimicry in the unaware observer and pupil dilation reflecting physiologic arousal (Tamietto et al., 2009). This suggests that socially salient visual signals initially processed through this subcortical pathway are integrated with corresponding motor and psychophysiological responses.

3.2. Beyond passive relaying: the superior colliculus and pulvinar in direct emotional computation

The SC is crucial to visuomotor transformation, especially in orienting behaviour and oculomotor control, while the pulvinar is traditionally associated with attentional functions and multisensory integration. Recent studies, however, have expanded our understanding of these structures, revealing their ability to innately encode emotionally relevant stimuli based on direct retinal inputs (Isa et al., 2021; McFadyen et al., 2019). For example, the SC and pulvinar exhibit response selectivity to face-like patterns and evolutionarily relevant stimuli, such as prey, predators, or food, as early as 50 ms after stimulus onset (Le et al., 2020; Nguyen et al., 2013, 2014; Nishijo and Ono, 2021). Additionally, a recent *in silico* study using a Convolutional Neural Network (CNN) model that mirrors the physiological, anatomical, and connectional properties of the SC closely matched the error patterns and classification accuracy of patients with V1 damage and "affective blindsight" (Méndez et al., 2022). This model also spontaneously tuned to low spatial frequencies, consistent with human fMRI data, and generated saliency maps that directed attention to specific facial features depending on their emotional expressions (Celeghin et al., 2023).

Neurons in the monkey pulvinar encode emotional expressions of human faces (Maior et al., 2010), displaying shorter response latencies to face-like stimuli compared to non-face configurations (Nguyen et al., 2013). Interestingly, neurons in the macaque medial and dorsolateral pulvinar selectively respond to images of snakes and angry faces, with their activity unaffected by low spatial filtering (Van Le et al., 2013). Human neuroimaging on face and body perception indicates that these subcortical structures may underlie fear contagion (de Gelder et al.,

2004) and prime the observer for action in response to fear stimuli (de Gelder et al., 2004; Grèzes et al., 2014).

In summary, current anatomical and functional evidence suggests the existence of distinct, yet interacting, networks that relay social information to the amygdala. These networks exploit the different computational properties of subcortical and cortical routes, supporting amygdala functions at different stages of emotion processing and reflecting various modes of social fear transmission. These findings challenge the cortico-centric view of visual functions, highlighting the roles of the SC and pulvinar in the early stages of encoding emotional information. This early encoding may be crucial in initiating SFL, where an observer learns to fear a novel, potentially harmful stimulus (CS) by witnessing a conspecific fearful reaction (social US) to that stimulus without having directly experienced it.

4. Are subcortical structures sufficient to support SFL in primates?

The full implications and limitations of relying on a subcortical network for SFL are still poorly investigated. Studies in rodents have shown that selective pharmacological inactivation of the ACC, or bilateral optogenetic inhibition of ACC-amygdala projections, specifically impairs SFL without affecting FC (Allsop et al., 2018; Jeon et al., 2010). In mice, neurochemical inactivation or electrical stimulation of the ACC impairs SFL (Kim et al., 2012), suggesting that subcortical structures alone may not suffice for accomplishing SFL. Notably, ACC neurons in rats respond to both direct experiences of foot shocks and the observation of conspecifics undergoing similar shocks (Carrillo et al., 2019). Interestingly, these neurons are also correlated with distressed vocalisations of conspecifics and their behaviours, such as jumping, but do not respond to a simple fear-conditioned tone (CS). Temporary deactivation of this region significantly impairs the social transmission of distress, indicating its crucial role in mediating socially induced fear responses (Carrillo et al., 2019).

In primates, the ACC, alongside the amygdala, is involved in encoding conspecific facial expressions as well as pictures of snakes (Konoike et al., 2020; Schaeffer et al., 2020) with relatively short response latencies (<113 ms) (Konoike et al., 2020). Notably, research involving macaques and humans has demonstrated that the functions of the ACC (Caruana et al., 2020, 2018; Livneh et al., 2012) and amygdala (Livneh et al., 2012) extend beyond mere encoding of others' facial expressions. Instead, they are integral in the automatic regulation of one's facial expressions in response to emotional cues of others. This sensory-motor transformation may have important advantages in promoting behavioural coordination or synchronization with conspecifics (de Waal and Preston, 2017). The neural pathway involving the ACC and amygdala is thought to be a primary conduit for transmitting visual signals related to others' emotional displays to the brainstem nuclei, including the facial nucleus, to facilitate automatic somatic mimicry (Gothard, 2014). This pathway potentially aligns individual facial expressions with those of others, a synchronization that can occur even in the absence of conscious awareness (Dimberg et al., 2000; Tamietto and de Gelder, 2008; Tamietto et al., 2009).

Typically, the expressive and physiological outcomes of nonconscious emotion processing are quantitatively and qualitatively different from those occurring during conscious perception, as they tend to be stronger and faster when awareness is lacking (Williams et al., 2004; Tamietto et al., 2009, Tamietto et al., 2015). This suggests a distinct processing mode for non-conscious emotional stimuli characterized by enhanced physiological responses such as skin conductance, eye blink magnitude, stress hormone levels, pupil dilation, and heart rate changes (Esteves et al., 1994; Gläscher and Adolphs, 2003; Hamm et al., 2003; Tamietto et al., 2009, 2015; Ruiz-Padial et al., 2011; van Honk et al., 1998).

Further evidence of the immediate impact of emotion on motor response comes from transcranial magnetic stimulation (TMS) studies

(Borgomaneri et al., 2015a, 2015b), which reveal extremely rapid sensory-motor modulation in response to fearful bodily expressions, likely involved in freezing. Since these effects are related to changes in the excitability of cortico-spinal downstream projections rather than cortical excitatory mechanisms, the authors propose that fast and automatic amygdala responses modulate cortico-subcortical interactions before the visual stimuli are consciously processed (Grèzes et al., 2014; Huis In 't Veld et al., 2014).

In summary, while subcortical structures enable rapid and automatic responses to social signals indispensable for developing SFL, their inherent limitations in processing complex social cues devoid of cortical contribution are yet to be established. The complexity of human social interactions likely requires cortical areas to interpret subtle signals, understand intentions, and modulate social behavior based on past experiences and cultural contexts; tasks that may be beyond subcortical processing alone.

5. The social affordance hypothesis: a possible theoretical framework for SFL

The concept of US, which triggers motor responses automatically without prior learning, showcases the brain innate capacity for sensory-motor transformation. Indeed, the primate brain extracts behaviourally relevant information from the environment, crucial for planning and executing motor behaviours, often independently of perceptual awareness. For instance, patients with visual form agnosia, caused by a lesion of the ventral visual pathway, can reach for and grasp objects they cannot recognize (James et al., 2003; Karnath et al., 2009; Milner and Goodale, 2012). Notably, neurons in parietal and frontal areas encode various potential motor plans triggered by observed objects (Maranesi et al., 2014), and competition among these concurrent motor plans guides action selection (Cisek, 2007). Therefore, converging evidence suggests that the neural substrates underlying the planning and execution of one's object-directed actions can also encode bodily actions of the onlooker, treating the latter as *dynamic biological objects* that afford various behavioural reactions contingent on the context (Bonini et al., 2022; Orban et al., 2021a). This theoretical framework, namely the *social affordance hypothesis* (Orban et al., 2021a), has been inspired by evidence that parietal neurons of both humans (Aflalo et al., 2020) and monkeys (Lanzilotto et al., 2019, 2020) stably encode the identity of observed actions, while also responding during the execution of manual actions that are not strictly congruent with the observed ones. This hypothesis suggests that bodily actions (Orban et al., 2021a, 2021b), such as manipulative or defensive movements, are mapped onto neural substrates in the observer's brain responsible for action planning and motor execution. This mapping may ultimately translate into corresponding behavioural responses, which can be congruent or incongruent with the observed actions.

While the social affordance hypothesis was originally formulated to elucidate the cortical mechanisms for selecting bodily actions in response to observed movements, it also provides a framework for understanding how emotional stimuli are remapped onto emotional responses within subcortical structures. Indeed, in the context of SFL, bodily signals conveying fear expressions can act as social US, eliciting a range of somato- and viscero-motor responses in the observer. When these signals are spatially and temporally associated with a neutral stimulus (CS), they can facilitate SFL. Conceiving others' emotional displays as social stimuli that trigger a range of potential behavioural responses suggests that also the physical and social context in which fear-related cues are observed could significantly impact the learning process. This opens avenues for novel hypotheses in future SFL research (Fig. 3). Factors such as familiarity (Allsop et al., 2018; Jeon et al., 2010) and sex differences (Pisansky et al., 2017) may significantly influence SFL, reflecting gender-specific brain activations during the processing of threatening faces and bodies (Kret et al., 2011).

Contextual factors also seem to play a crucial role in modulating fear
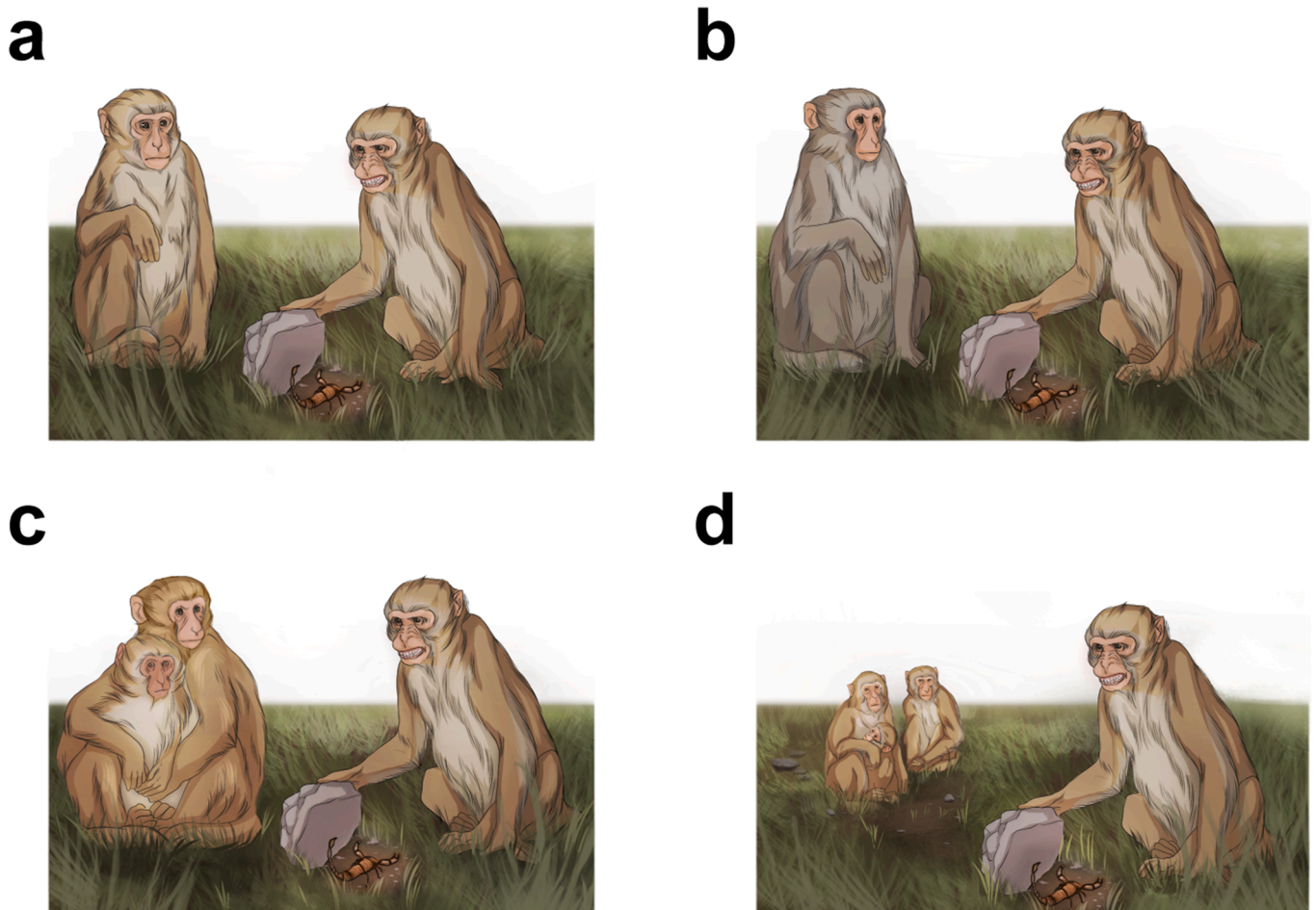
Fig. 3. Social and physical factors that can modulate social fear learning. The influence of familiarity on SFL (a, b). A rhesus macaque may indirectly learn that moving a rock can be dangerous because it could hide a scorpion underneath. This may be learned more quickly and effectively if displayed by a familiar conspecific (a) rather than by a stranger (b). The influence of physical distance between conspecifics on SFL (c, d). SFL may be quicker and more effective if the event occurs nearby (c) rather than at a far distance (d) from the observer.

responses, with changes in the amygdala responsivity in different situations (Alvarez et al., 2008; de Borst and de Gelder, 2022; de Rosnay et al., 2006). For instance, the spatial distance between the observer and demonstrator (Fig. 3c, d) affects physiological and neural responses to emotion (Ellena et al., 2020). Increased proximity to fearful stimuli shifts neural processing from prefrontal regions, including the subgenual ACC, to midbrain structures like the periaqueductal grey (PAG) in both rodents (McNaughton and Corr, 2004) and humans (Mobbs et al., 2007). This dynamic shift between prefrontal regions and phylogenetically older midbrain regions may reflect a transition from voluntarily planned avoidance strategies to automatic behavioural reactions (e.g., fight, flight, or freeze), when the threat is too close to the body and constitutes an emergency requiring an immediate response (Bufacchi and Iannetti, 2018; de Borst and de Gelder, 2022; Graziano et al., 2006). Coherently, amygdala activation scales with proximity to a person (Kennedy et al., 2009) or predator (Mobbs et al., 2007), and complete bilateral damage to this structure can alter personal spatial boundaries and reduce interpersonal distance preferences (Kennedy et al., 2009). Approaching harmful stimuli also engages the SC and pulvinar, along with cortical regions associated with motor preparation (Billington et al., 2011; Vagnoni et al., 2015).

Incorporating the *social affordance hypothesis* into the study of SFL may provide deeper insights into how observing fear or distress in others influences learning processes. Social signals are not simply visually encoded but also internally mapped onto the observer's action repertoire, depending on both social and physical context. Such integration

highlights the complexity of the neural mechanisms underlying SFL, emphasizing the interplay between observed actions, spatial context, and potential behavioural responses. By understanding these dynamics, researchers can better grasp how SFL is shaped and expressed, revealing how observed emotional cues and contextual factors together influence learning and behavior.

6. Concluding remarks and future directions

Understanding the mechanisms behind learning to fear novel stimuli, as seen in FC, is crucial for adapting to potential threats. SFL extends this concept by assuming that emotional expressions of conspecifics enable animals to form associations with potentially harmful stimuli they have not directly experienced. We have argued that this learning begins with the processing of pre-categorical or mid-level features of salient visual stimuli (de Gelder and Poyo Solanas, 2021), leading to automatic motor and autonomic responses during social interactions (Bonini et al., 2023). Behavioural, anatomical, and functional evidence supports a model where fear-inducing facial configurations or bodily postures act as US, innately triggering implicit responses and forming new fear associations with a CS. This perspective bridges the theoretical frameworks of FC and SFL closer, emphasizing the innate and automatic aspects of SFL alongside its foundations classically traceable in social cognition (Conte et al., 2001; Debiec and Olsson, 2017; Olsson and Phelps, 2007).

The visual subcortical pathway, which includes thalamic and midbrain structures, serves as a crucial channel for rapidly transmitting

coarse emotional information to the amygdala (Tamietto and de Gelder, 2010), enabling the formation of novel and vicarious fear associations. Integrating insights from various research fields, we propose that emotional displays of others act as social affordances, triggering a range of behavioural responses that support social interactions and may underpin SFL functions. However, the exact influence of this framework on SFL remains to be fully explored. Future research, particularly studies combining single-neuron recordings with ethological approaches, holds the potential to deepen our understanding of the neurobiological underpinnings of SFL.

A critical area of inquiry concerns the interplay of biological, environmental, and cultural factors in SFL expression. Conceiving the emotional displays of conspecifics as social US implies that they can shape avoidance behaviours in various contexts, such as food preferences and anxiety transmission. For instance, adults' facial expressions can influence children's food choices (Barthomeuf et al., 2012, 2009) and their reactions to unfamiliar situations associated with fearful faces (Askew and Field, 2007). This implies that witnessing fearful behaviors can become associated with various conditioned stimuli, potentially contributing to the spread of maladaptive fears and anxieties, including phobias and post-traumatic stress disorders (Debiec and Olsson, 2017). Gender-specific differences in the neural and behavioral responses to social fear signals are well-documented (Bagnis et al., 2020, 2019) Yet, how these encoding differences impact social learning has been investigated only marginally. For instance, one study using virtual reality found that women report higher fear ratings than men in socially anxious situations, and socially anxious women maintain greater distances from male agents compared to female ones (Reichenberger et al., 2019). Other evidence reported that social buffering of human fear varies significantly by gender and is influenced by social concern and the presence of real versus virtual agents (Qi et al., 2021). These findings highlight the need for more in-depth research into gender-specific responses in SFL, which may be crucial for developing tailored therapeutic interventions for anxiety disorders.

In conclusion, future research should prioritise the understanding of how cortico-subcortical dynamics interact in SFL processes, particularly examining its developmental trajectory, impact on clinical conditions like social anxiety, and how individual experiences and societal norms influence this learning process.

Acknowledgements

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