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Emotional Contagion – Improve survival by preparing for socially sensed threats. Christian Keysers^{1,2} and Valeria Gazzola^{1,2}

Rats respond to the emotions of others. A new study reveals how their central amygdala uses such social information to selfishly trigger defences that adapt to the nature of the danger with all the hallmarks of true emotional contagion

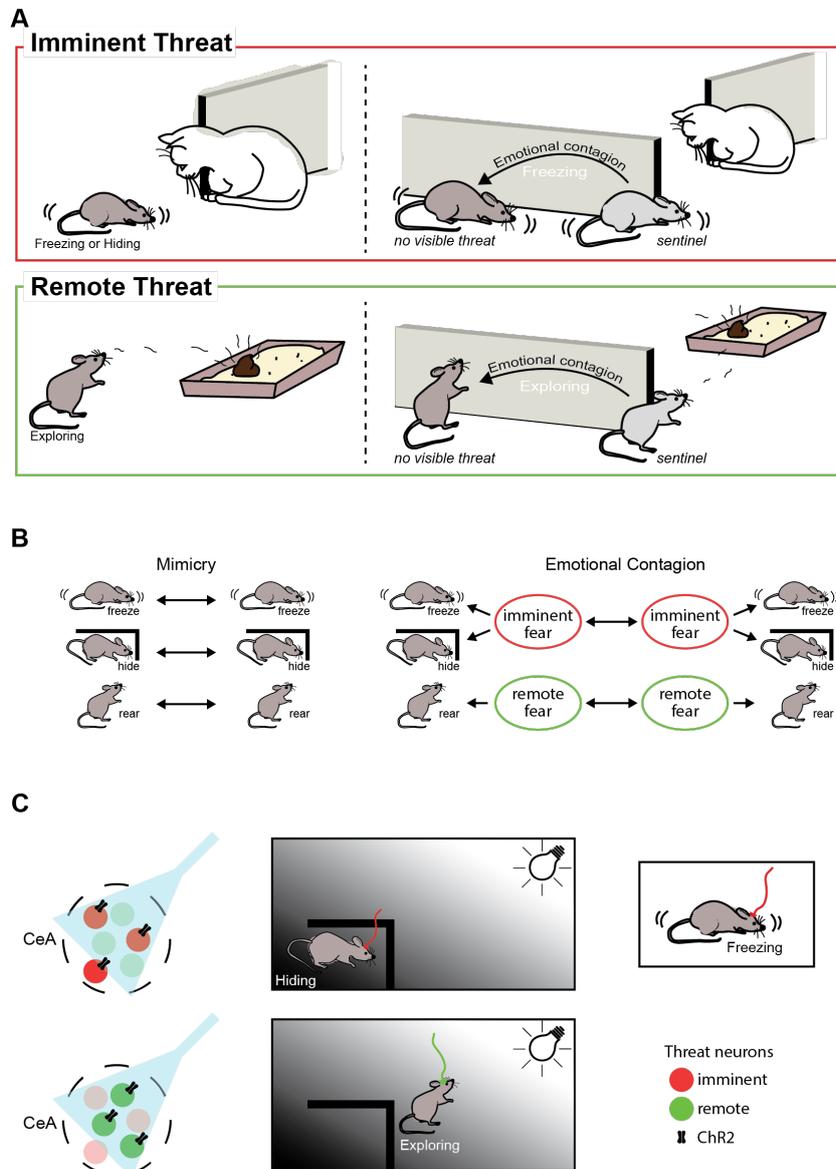


Figure 1 | Fine grained emotional contagion of fear in the central amygdala:

(A) Left: When alone, rats respond to imminent danger with freezing or hiding, and with exploration to stimuli suggesting a remote threat. Right: Andraka et al. show emotional contagion empowers rats to deploy appropriate defensive reactions even when they are deprived of first-hand threat evidence, by harnessing better informed conspecifics as sentinels. (B) Mimicry and emotional contagion both explain how the behaviour of two rats come to resemble each other. While mimicry predicts that a behaviour directly triggers the same in another animal, emotional contagion posits a particular emotional state triggers a similar state in the other. In the latter account, behaviour across animals may align through these resonating emotional states, but freezing in one animal could also trigger hiding in another, and the temporal alignment of behaviour is less direct. (C) C-Fos-ChR2 viruses were injected in the central amygdala (CeA) before animals underwent the imminent threat paradigm (top) or remote threat paradigm (bottom), leading to the expression of an excitatory opsin (ChR2) in imminent or remote threat neurons in the CeA, respectively. Photostimulation of imminent threat neurons (red) in a novel environment leads to hiding if a shelter is available (middle) or freezing if it is not (right). Photostimulation of remote threat neurons (green) leads to exploration of brighter areas of the arena (bottom).

Fear, a powerful emotional state triggered by the detection of threat, is a key adaptive response that aids survival by triggering flexible behaviours that depend on the imminence of danger. We share this emotion with many other mammals and it has been studied richly in rats¹. If danger is imminent, for instance if a rat is staring into a feline's eyes, the rat will hide if it can or freeze if it cannot (Figure 1A). If danger is remote, e.g. a suspicious smell, the rat will assess the risk by rearing and scanning its environment. In their recent paper, Andraka et al.² shed the limelight on the fact that rats do not have to wait to witness danger first-hand: they can use other rats to sense the presence and remoteness of danger, and prepare by deploying appropriate responses before they sense the danger directly (Figure 1A, right column). Their study shows that the central amygdala, previously known to orchestrate defensive reactions to directly perceived threats³, also orchestrates these socially triggered

defensive reactions. That rats react to the fear of another with fear-typical behaviours has been interpreted as empathy⁴. This work invites us to consider whether the evolutionary roots of sharing the distress of others may be found in the selfish motivation to sense and prepare for dangers^{5,6}.

Rodents are sensitive to the emotional states of others. They freeze when they witness another freeze⁵ or if they witness another receive shocks^{4,6}. Because freezing is a gold-standard indicator of fear, and socially triggered freezing has become a powerful paradigm to study the transmission of fear in animals. In the human literature, when the emotion of one triggers a similar emotion in another, we speak of emotional contagion, and this is seen as a precursor of empathy – the ability to feel and understand the emotions of others while attributing that state to the other individual⁷. Empathy, in turn, is seen as a door to the inner states of others⁸, with some suggesting that it evolved to generate caring in maternity and prosocial behaviour^{7,9}. Some findings however question whether in rats sharing of emotions really means caring: socially triggered freezing does not depend strongly on familiarity⁶; is not stronger in females¹⁰; and recordings suggest neural activity while witnessing the distress of others is stronger when the witness is at risk¹¹. Together, these findings feed a different narrative that sharing fear may serve a more self-serving function: improving preparedness by using others as sentinels^{5,6,12}.

To refine our understanding of how well, and through what neural mechanisms, rodents tune into others as danger antennae, Andraka et al. took the distinction between imminent vs. remote threat, well established when rats face danger alone, to the social domain. They compared the behaviour of witness rats that themselves experience no danger, but that are paired with a demonstrator that experiences either imminent or remote threats. In the imminent threat paradigm, the demonstrator received footshocks while the witness observed the demonstrator's distress through a transparent perforated divider. In the remote threat paradigm, the demonstrator had received footshocks elsewhere, then returned to its homecage where it interacted with the witness. The golden question was of course: what reaction would the witnesses display? Electroshocks are invisible and inaudible, so witnesses had no direct evidence for the presence or distance of shocks in either paradigms. Nevertheless, they responded as if they had. In the imminent threat condition, witnesses froze as if they were being exposed to shocks themselves. In the remote threat, witnesses explored the environment and reared, as if they sensed a remote threat. Rats show behaviour appropriate to the imminence of danger simply by sensing the affective state of their conspecific.

Psychologists distinguish two processes that could underpin such social transmission (Figure 1B). Mimicry entails that a particular behaviour *directly*, rigidly, and rapidly triggers the same behaviour in the other – just as watching someone yawn can make you yawn, or seeing a smile can activate your zygomatic muscles¹³. Emotional contagion, in contrast, entails that the emotional state of a person triggers a similar emotional state in another and behaviours aligns only *indirectly*, because people in similar states act somewhat similarly. Already at the behavioural level, Andraka et al.'s findings favour emotional contagion as the driving mechanism: dyads with high-freezing demonstrators had high-freezing witnesses, suggesting the quantitative transmission of fear that emotional contagion predicts, but the tight second-to-second relationship in when animals froze or reared, characteristic of mimicry, was missing.

At the neural level, we may wonder what computational principle accounts for this contagion. Simulation theory proposes that emotional contagion occurs when watching the state of others reactivates neural substrates also involved in experiencing a similar state first-hand^{8,14,15}. Recent work confirmed that in the cingulate cortex, witnessing the pain of another rodent indeed triggers activity in a significant proportion of the neurons recruited by first-hand experience of pain^{14,16}. Here, the authors shed fresh light on simulation theory by asking whether the central amygdala (CeA), critical for deciding between freezing, hiding, and risk assessment when animals face danger alone, is also important when threat is sensed socially. They injected a virus in the CeA that was engineered to express an excitatory opsin selectively in recently activated neurons using a c-Fos promoter. They then photo-stimulated CeA

neurons that were active during the imminent or remote threat paradigm while the witness animals were placed in a new arena (Figure 1C). This arena contained a place to hide and a bright place to explore. Stimulating imminent CeA neurons made the animals hide, while triggering remote CeA neurons made them explore. Moving the animals into yet another, small environment devoid of hiding options, changed the behavioural manifestation: now imminent threat CeA neurons triggered freezing instead of hiding. This context dependent selection of hiding vs. freezing is further evidence, that the internal state triggered by witnessing the demonstrator is not a specific motor program, as mimicry would suggest, but an emotion that triggers defensive behaviours appropriate to the environment. That this occurs in the CeA, supports simulation theory as it reveals yet another overlap between first hand experiences of fear and witnessing those of others, with the CeA probably involved in selecting the most appropriate response to fear independently of whether a threat is sensed directly, or socially, through a sentinel³.

Together, these experiments refine our thinking. First, it provides compelling evidence that rats show true, fine-grained emotional contagion of fear rather than simple motor mimicry. Second, fear evolved to trigger self-preserving behaviours. That emotional contagion triggers the same behaviours begs us to consider that emotional contagion could have evolved for the same, self-preserving purpose. Indeed, simulations confirm that aligning levels of fear across neighbours – be it by becoming more scared close to scared individuals or less scared close to relaxed animals – improves the ability to adapt to the level of danger⁶, and even flies use others as danger signals¹⁷. Embracing this self-preserving perspective does not negate the possibility that emotional contagion could also trigger behaviours that benefit others^{7,18}, but it suggests that self-preservation, a mighty evolutionary force, is likely to have encouraged its evolution. Third, that the CeA is involved in fear and in its emotional contagion adds to evidence that the anterior cingulate, thalamus, and basolateral amygdala are recruited by an animal's own distress and that of others¹⁹, to provide further evidence for simulation theory.

In the debate about whether emotional contagion serves selfish or altruistic purposes, this study illustrates a powerful way forward. Rather than arguing whether an entire animal cares about self-preservation or benefiting others, a more dialectic approach is perhaps to delineate brain networks that trigger behaviours that favour self-preservation and networks that trigger behaviours that benefit others such as harm aversion¹⁸ or liberation²⁰. It has recently been shown that some nodes, such as the cingulate, are involved in both^{18,20}, and tagging neural populations involved in witnessing the distress of others in candidate brain regions, and reactivating them in situations that assess self-preservation or other-regarding behaviours could pave the way to a more mechanistic understand of the interplay and balance across these two motives – and perhaps also individual differences relevant to psychiatric disorders. Where in the brain human emotional contagion serves to harness others as sentinels or to benefit them is then perhaps the next frontier.

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