the reciprocal exchange of resources instead of mutual care), rather than the communal close relationships that seem to benefit from supplication emotions (Batson, 1993; van Kleef & Côté, 2022). More specifically, appeasement emotions are particularly functional by virtue of their impact on individuals' tendency to follow social norms and meet obligations (Beall & Tracy, 2020). For example, when individuals commit a social transgression, they risk being perceived as untrustworthy, selfish, and unfit for future relationships (Gilbert, 2007). Displaying shame or embarrassment in these situations can appease onlookers by demonstrating awareness of social norms and acknowledgment that they were violated, thereby helping the transgressor maintain their relationships by conveying one's motivation to behave prosocially moving forward (Feinberg, Willer, & Keltner, 2012; Keltner & Buswell, 1997; Martens, Tracy, & Shariff, 2012).

In fact, this appeasement function extends beyond existing relationships; studies have found that individuals choose more lenient penalties for unacquainted transgressors (e.g., CEOs making public apologies) who express shame and embarrassment, compared to those who express no emotion (Giner-Sorolla, Castano, Espinosa, & Brown, 2008; Keltner & Buswell, 1997). Appeasement emotions thus help individuals form and maintain cooperative exchange relationships by reducing the consequences of social transgressions and preventing relationship dissolution, which benefit both parties' long-term fitness, and may explain the evolution of these emotions (Barkow, 1989; Gilbert, 1997; Leary & Baumeister, 2000). In this way, appeasement emotions serve a function very similar to that of fear, proposed in the fearful ape hypothesis, but more narrowly in exchange relationships.

In closing, we commend Grossmann's review and strong support for the fearful ape hypothesis, while also recommending that it be expanded to include supplication and appeasement emotions. Both classes of emotions are associated with signals and behaviors that underlie humans' desire and ability to cooperate in specific moments, as well as to form and maintain long-standing cooperative relationships. Nonetheless, questions remain for future research. To our knowledge, the primate research that Grossmann describes has yet to be conducted for other supplication emotions like sadness, leaving it unclear whether humans are uniquely prone to experiencing sadness and recognizing it in others in the way they appear to be for fear. We look forward to research in this vein, and thank Grossmann for bringing these important questions to light with his novel and thought-provoking hypothesis.

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# Heightened fearfulness in infants is not adaptive

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**Abstract**

Grossmann proposes the "fearful ape hypothesis," suggesting that heightened fearfulness in early life is evolutionarily adaptive. We question this claim with evidence that (1) perceived fearfulness in children is associated with negative, not positive long-term outcomes; (2) caregivers are responsive to *all* affective behaviors, not just those perceived as fearful; and (3) caregiver responsiveness serves to *reduce* perceived fearfulness.

As affective scientists, we appreciate the target article's focus on how emotions emerge within early social development and are influenced by aspects of social functioning, including cooperation. The basic premise of the article should be called into question, however, when viewed through the lens of published, empirical evidence that was underemphasized, overlooked, or misinterpreted in the article's discussion of fearfulness in early childhood.

First, there is a robust and growing literature demonstrating that heightened fearfulness in children is not an adaptive trait, and is instead an important predictor of negative behavioral outcomes. The abundance of research on the relation between fearful behavior and mental health problems was greatly minimized in the target article, even though some of it was mentioned (e.g., Fox et al., 2021; Sandstrom, Uher, & Pavlova, 2020). In fact, a large body of research indicates that perceived fearfulness in children is associated with a variety of long-term negative outcomes (e.g., Buss & McDoniel, 2016; Coplan, Wilson, Frohlick, & Zelenski, 2006; Van Brakel, Muris, Bogels, & Thomassen, 2006), contrary to the author's claims regarding the benefits of early fearfulness. It has been known for some time that the extent to which infants and young children demonstrate a fearful temperament (commonly defined as behavioral inhibition, or children's tendency to excessively avoid or withdraw from novel situations) prospectively predicts internalizing behaviors and adverse social and mental health outcomes (e.g., Chronis-Tuscano et al., 2009; Williams et al., 2009). In fact, fearful temperament is the *strongest predictor of social anxiety* in later childhood, with approximately 40% of behaviorally inhibited children going on to develop anxiety disorders compared to roughly 12% in children with other temperaments (Clauss & Blackford, 2012; Fox, Barker, White, Suway, & Pine, 2013). Importantly, the link between fearful temperament and anxiety disorders has also been documented cross-culturally (Howard, Muris, Loxton, & Wege, 2017; Vreeke, Muris, Mayer, Huijding, & Rapee, 2013), suggesting that this relation is unlikely to be the function of an evolutionary mismatch with Western culture as suggested by the author.

Second, research suggests that parents are unlikely to differentiate between negative emotions in their infants, and contrary to the author's claim that parental responses to fear are uniquely beneficial, parents are responsive to the intensity of both positive and negative affective behaviors. Many (if not all) evocative behaviors in infants capture caregiver attention, regardless of valence or perceived emotion category (e.g., Thompson-Booth et al., 2013). For example, caregivers are highly sensitive to behaviors that suggest positive affect in infants (Kivijarvi et al., 2001). Additionally, caregiver sensitivity to infant distress relies more on integrating information about context and the intensity of infant distress than on making inferences about whether an infant is fearful, sad, angry, and so on (Mesman, Oster, & Camras, 2012). This makes sense given evidence that, across both Western and non-Western cultures, infants do not show distinct facial configurations in fear- and anger-eliciting situations (Camras et al., 2007) and that caregivers respond similarly to bouts of child distress cross-culturally (Bornstein et al., 1992, 2017). More generally, many of the arguments offered in the target article about the adaptiveness of fear in infants and young children would also hold for caregivers' perceptions of other emotions, such as sadness or happiness, or intense affective experiences.

Further, throughout the target article, the description of infant behavior is not clearly distinguished from inferences about its cause. Infant behaviors were frequently described as "fearful" without clearly demonstrating that the situations were reasonably likely to evoke fear. Indeed, instances of a given emotion category are situationally expressed with a variety of facial configurations and behaviors (e.g., in anger, infants and adults furrow their brows in a scowl less than 30% of the time; Barrett, Adolphs, Marsella, Martinez, & Pollak, 2019; Bennett, Bendersky, & Lewis, 2002; Sears, Repetti, Reynolds, & Sperling, 2014). Given this situated variation in expressive behaviors, some infant behaviors (such as crying) will be interpreted by adults in more than one way, depending on the context (Chóliz, Fernández-Abascal, & Martínez-Sánchez, 2013). Scientists must take care to separate their descriptions of physical actions (e.g., facial movements such as widened eyes and gasping mouth) from their inferences about the causes of such actions (such as an inference that the movements are an expression of emotion, or an expression of fear more specifically). Thus, in line with our second point it is more scientifically accurate to conclude that intense or affectively evocative behaviors, rather than fearful behaviors per se, elicit caregiving responses.

Third, parental presence reduces perceived fearfulness early in life at both the behavioral and neural levels; it does not support perceived fearfulness as one would expect if this were, indeed, adaptive. Recent developmental research suggests that a caregiver's presence *reduces* the development of behaviors commonly associated with perceived fearfulness, such as startle responses (e.g., Van Rooij et al., 2017). There is also evidence in both human and nonhuman animals that the presence of a caregiver promotes exploration and learning in children, buffering *against* behaviors that are perceived as fearful (e.g., Callaghan et al., 2019). Although the original article proposes the role of amygdala activity in supporting fearfulness, caregiver presence typically functions to buffer rapid amygdala development and premature amygdala engagement (Tottenham, 2012). Further, maternal presence allows child amygdala-prefrontal circuitry to function more similarly to adolescent connectivity, thereby allowing for more mature regulatory behavior (Gee et al., 2014). These findings suggest that exploration, and not fearful behavior, is what is most adaptive for infants.

In our view, the target article falls short of demonstrating that heightened fearfulness in infants and young children is evolutionarily adaptive. This hypothesis is called into serious doubt by several hidden inferences that are not supported by existing research, specifically that which demonstrates long-term mental health outcomes of perceived fearfulness as well as parental buffering. Instead, intense affect more generally elicits responses from caregivers. These affective behaviors, and not fearfulness per se, may be what elicits responsive caregiving, ultimately leading to improved functionality within the lifespan of an individual human and improved adaptation of the species.

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# Social learning and the adaptiveness of expressing and perceiving fearfulness

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**Abstract**

The fearful ape hypothesis revolves around our ability to express and perceive fearfulness. Here, we address these abilities from a social learning perspective which casts fearfulness in a slightly different light. Our commentary argues that any theory that characterizes a (human) social signal as being adaptive, needs to address the role of social learning as an alternative candidate explanation.

We agree with many of the author's interesting and intriguing ideas, but in this commentary we suggest that in order to substantiate the fearful ape hypothesis, it should directly address alternative candidate explanations which emerge from the uniquely human abilities of social learning and interaction. In stating our case, we present a broad literature indicating that our ability to express and perceive fearfulness is adaptive in the context of social fear learning, which could potentially account, at least in part, for the emergence of heightened fearfulness.

Social learning is a fundamental and crucial ability that enables us to acquire behaviors, skills, and knowledge efficiently (Boyd & Richerson, 1985; Hoppitt & Laland, 2013). Although social learning is ubiquitous among human and nonhuman animals, humans have unique abilities in this domain, for example, in mechanisms such as imitation and teaching (Kendal et al., 2018; Kline, 2015).