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The human fear paradox: Affective origins of cooperative care

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Target Article

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Abstract

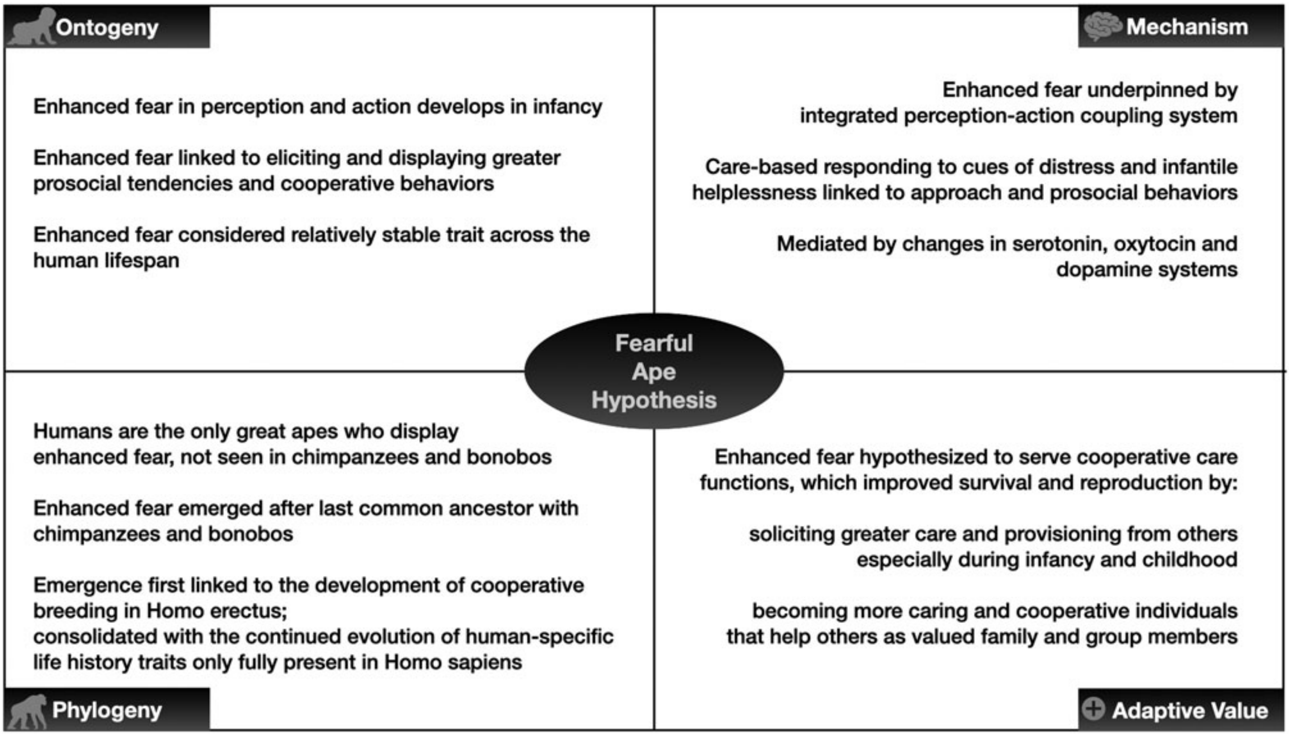
Already as infants humans are more fearful than our closest living primate relatives, the chimpanzees. Yet heightened fearfulness is mostly considered maladaptive, as it is thought to increase the risk of developing anxiety and depression. How can this human fear paradox be explained? The *fearful ape hypothesis* presented herein stipulates that, in the context of cooperative caregiving and provisioning unique to human great ape group life, heightened fearfulness was adaptive. This is because from early in ontogeny fearfulness expressed and perceived enhanced care-based responding and provisioning from, while concurrently increasing cooperation with, mothers and others. This explanation is based on a synthesis of existing research with human infants and children, demonstrating a link between fearfulness, greater sensitivity to and accuracy in detecting fear in others, and enhanced levels of cooperative behaviors. These insights critically advance current evolutionary theories of human cooperation by adding an early-developing affective component to the human cooperative makeup. Moreover, the current proposal has important cultural, societal, and health implications, as it challenges the predominant view in Western, educated, industrialized, rich, and democratic (WEIRD) societies that commonly construe fearfulness as a maladaptive trait, potentially ignoring its evolutionary adaptive functions.

1. Introduction

Adaptive behavior among great apes including humans is considered to be mediated by affective traits. Indeed, human-specific behavioral traits – especially our enhanced prosociality and cooperativeness – have been linked to affective traits such as reduced aggression and increased social tolerance (Hare, 2017). Research directly comparing affective traits between humans and other great apes has shown that already at the young age of 2.5 years, humans display significantly higher levels of fearfulness than chimpanzees, bonobos, and orangutans (Herrmann, Hare, Cissewski, & Tomasello, 2011). The current review is aimed at addressing the question, what are the origins for this human-specific enhancement of fearfulness traits?

The novel evolutionary framework presented here – the *fearful ape hypothesis* – proposes that, in the context of the strong interdependence reflected in cooperative caregiving and provisioning unique to human great ape group life (Hrdy & Burkart, 2020; Kramer, 2011; Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012), heightened fearfulness was adaptive. The central hypothesis put forth is that, starting early in human ontogeny, fearfulness traits facilitate care-based responding and provisioning from, while concurrently increasing cooperation with, mothers and others. Within this framework, enhanced fearfulness is assumed to be of adaptive value because of its functions in facilitating cooperative care across the lifespan, which improved survival and reproduction in human evolution (see Kramer [2019], for a review showing that human cooperative care supports survival and reproductive success).

In order to support this hypothesis, empirical work with human infants and children will be systematically reviewed, suggesting a link between fearfulness traits, parental care, greater sensitivity to detect fear in others, and enhanced levels of cooperative behavior. This synthesis of the research on this question points to the existence of a virtuous caring cycle that views fearfulness as a key adaptive affective trait supporting human-unique levels of cooperative concern and care. In light of this new evolutionary-developmental synthesis a major paradox emerges. Namely, in the existing clinical and psychological work, heightened fearfulness is predominately viewed as maladaptive, as it is associated with an increased risk of developing anxiety and depression. A further goal of this review is consequently to better understand, explain, and ultimately deconstruct this seeming human fear paradox. For this purpose, it will be important to acknowledge that construing fearfulness as a maladaptive trait is likely linked to the predominant research and cultural focus on large-scale Western, educated, industrialized, rich, and democratic (WEIRD) societies and their emphasis of independence (Henrich, Heine, & Norenzayan, 2010). Viewing fearfulness traits through this WEIRD lens is at odds with the presumed social environment of interdependence in which human



Enhanced fear in perception and action develops in infancy

Enhanced fear linked to eliciting and displaying greater prosocial tendencies and cooperative behaviors

Enhanced fear considered relatively stable trait across the human lifespan

Enhanced fear underpinned by integrated perception-action coupling system

Care-based responding to cues of distress and infantile helplessness linked to approach and prosocial behaviors

Mediated by changes in serotonin, oxytocin and dopamine systems

Humans are the only great apes who display enhanced fear, not seen in chimpanzees and bonobos

Enhanced fear emerged after last common ancestor with chimpanzees and bonobos

Emergence first linked to the development of cooperative breeding in Homo erectus;
consolidated with the continued evolution of human-specific life history traits only fully present in Homo sapiens

Enhanced fear hypothesized to serve cooperative care functions, which improved survival and reproduction by:

soliciting greater care and provisioning from others especially during infancy and childhood

becoming more caring and cooperative individuals that help others as valued family and group members

Figure 1. Overview of the arguments put forth in support of the *fearful ape hypothesis*, organized according to proximate (ontogeny and brain mechanisms) and ultimate (phylogeny and adaptive value) levels of explanation for humans' enhanced fearfulness traits.

group life evolved. Therefore, the exceedingly high rates of anxiety and depression seen in WEIRD societies (Chiao & Blizinsky, 2010) might need to be added to the list of potential evolutionary mismatch diseases (Kohrt, Ottman, Panter-Brick, Konner, & Patel, 2020). In other words, fearfulness is adaptive in small-scale, interdependent human societies primarily built on cooperative care and success, whereas fearfulness can become maladaptive in large-scale, independent human societies built more on individual success and less on cooperative care.

This review is aimed at providing a systematic analysis and synthesis across multiple levels, illuminating the ultimate (adaptive and phylogenetic level) and proximate mechanisms (ontogenetic and brain level) that account for the emergence of heightened fearfulness traits in human evolution (Tinbergen, 1963) (see Fig. 1). Section 2 outlines the novel evolutionary framework and provides arguments for the adaptive value (functions) of fearfulness in the context of human cooperative care. After laying out the foundation for the current proposal, Section 3 presents an analysis focused on reviewing and synthesizing research on phylogenetic, ontogenetic, and brain origins in which human fearfulness emerged. Section 4 discusses the emerging fear paradox and its cultural, societal, and health implications, while outlining specific predictions to be tested in future research.

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2. Rethinking fearfulness: The adaptive framework

The *fearful ape hypothesis* presents a novel evolutionary framework stipulating that heightened fearfulness was adaptive in the context of the strong interdependence unique to human cooperative caregiving systems (Hrdy, 2011; Hrdy & Burkart, 2020; Kramer, 2011; Tomasello et al., 2012). Humans are the only great apes that have evolved cooperative care, which is extremely rare among primates (Burkart, Hrdy, & Van Schaik, 2009; Hrdy, 2011; Hrdy & Burkart, 2020). Human cooperative care is considered special among great apes because human infants and children are cared and provided for not only by their mothers but also by many others, including other kin and even non-kin (Bogin, Bragg, & Kuzawa, 2014; Kramer, 2019; Kramer & Otárola-Castillo, 2015). This alloparental form of care and provisioning of the young only seen in humans has led to the notion that humans can be classified as cooperative breeders; however, human offspring care is considered distinct from other cooperative breeding species, in that alloparental behavior is defined culturally rather than by genetic kinship alone, allowing for care from unrelated individuals (see Bogin et al., 2014). Cooperative caregiving and provisioning are thought to have developed early in hominid evolution as a result of evolutionary pressures necessitating extra-maternal help with raising helpless and highly costly human infants (Hrdy, 2011; Kramer & Otárola-Castillo, 2015;

Rosenberg, 2021). Specifically, the evolutionary pressures at play have been identified as: ecological changes (drier and cooler climate), foraging in novel habitats (savanna), and increases in body and brain size, seen with the emergence of *Homo erectus* about 1.8 million years ago (Hrdy, 2011; Rosenberg, 2021; Vaesen, 2012). Modeling work suggests that human-specific life-history traits – characterized by much shorter inter-birth intervals, prolonged child dependence, and an extended life span – likely only emerged in their full-fledged form in *Homo sapiens* (Kramer, 2019; Kramer & Otárola-Castillo, 2015). Considering this evolutionary scenario, heightened fearfulness presumably emerged gradually over the last 1.8 million years, first in response to the emergence of infant helplessness and cooperative caregiving, and then became consolidated with the emergence of the above human-specific life-history traits.

According to what has become known as the cooperative breeding hypothesis, cooperative care as seen in humans is thought to have contributed critically to the evolution of human emotion, cognition, and behavior (Burkart et al., 2009, 2014; Hrdy, 2011). The cooperative breeding hypothesis has been criticized, however, because research with nonhuman primate cooperative breeders fails to provide clear evidence for human-like cognitive adaptations (Thornton et al., 2016; Thornton & McAuliffe, 2015). Notwithstanding this criticism regarding *cognitive* traits, a different aspect of the cooperative breeding hypothesis proposes that human infants possess critical *affective* features that are thought to “ingratiate” mothers and others into providing them with attention and care (Hrdy, 2011; Hrdy & Burkart, 2020). The current proposal builds on this line of theorizing and extends it into the specific domain of the emergence of heightened fearfulness as an affective trait and its potential adaptive significance for human cooperation. More explicitly, in the current proposal cooperative care is primarily viewed as a precondition (“breeding ground”) enabling heightened fearfulness to emerge and become adaptive in human infants and children through eliciting more care and provisioning from mothers and others. Yet the current proposal goes beyond this first step (fearful infants eliciting and benefitting from cooperative care). Specifically, in a second step, the emergence of heightened fearfulness traits within a context of cooperative care resulted in these infants growing up to become more caring and cooperative children, adolescents, adults, parents, and alloparents, in the long term. This proposal is largely based on work identifying intergenerational/cooperative childcare, including juvenile help, as a key adaptation, enabling human reproductive success (Kramer, 2011, 2019).

Put plainly, according to the hypothesized evolutionary scenario, infants and children displaying increased signals of fearfulness elicit greater cooperative care and provisioning from mothers and others. While parenting factors interact in complex ways with infant- and child-affective traits (Belsky, Rha, & Park, 2000; Kiff, Lengua, & Zalewski, 2011; Klein et al., 2018), there is evidence to show that greater displayed fearfulness among infants and children principally elicits caring and especially protective behaviors from parents (Kiel & Buss, 2011). Within the current framework, the assumed increase in care and provisioning during infancy – a developmental time of great dependence on others – is likely to have direct fitness and survival benefits as may be reflected in reduced mortality rates (Kramer, 2019). In fact, heightened fearfulness might at least partially account for the significantly increased survival rates (reduced mortality rates) seen in humans during early development when compared to other great apes (Kramer, 2019). The increased fearfulness traits, which are thought to be relatively stable across the human lifespan (see Kagan & Snidman, 2004), were likely associated with an enhancement of fearfulness among parents and alloparents. This enhanced fearfulness among (allo)parents would have been associated with a greater sensitivity to perceive fear and distress in others and thus in eliciting concern and care for others including infants and children (Grossmann, 2018; Hrdy & Burkart, 2020; Marsh, 2015; Warneken, 2015). In other words, in a developmental cascade, fearful infants growing up in a highly cooperative and supportive environment become more concerned, caring, and cooperative children, adolescents, alloparents, and parents. In this context, it is important to mention that cooperative caregiving among humans is characterized by what has been coined intergenerational care including juvenile help, whereby also children and adolescents, especially siblings and cousins, play a vital role in caring for infants and young children (Kramer, 2011, 2019). In fact, in traditional societies across various cultures, allomaternal care on average makes up about 43% of infant care, with juvenile help coming from siblings as the most common form of allomaternal care for infants (Kramer & Veile, 2018). More generally, intergenerational care has been argued to be the key adaptation that allowed for humans’ reproductive success by reducing inter-birth intervals and increasing child-survival rates (Kramer, 2019). Within the current proposal, humans’ unique life history, characterized by much prolonged early development, dependency, and reliance on alloparental care and sustenance, including juvenile help (Kramer, 2011, 2019), is considered another critical factor providing the ontogenetic conditions that contribute to and ultimately consolidate the adaptive benefits of enhanced fearfulness over the course of human evolution.

Notably, the current proposal further implies that, at a more mechanistic level, enhanced fearfulness displayed and perceived represents an integrated system that supports adaptive functioning in the context of cooperative care. More specifically, an essential part of the integrated system idea relies on the notion that a self-other link is established through some form of perception–action coupling, which is commonly seen in social cognition (Keysers & Gazzola, 2006; Knoblich & Sebanz, 2008; Preston & de Waal, 2002; Prinz, 1990) and is presumed to be elevated in the context of fear here. However, perception–action coupling alone, as it is present in other apes and primates (Preston & de Waal, 2002), is unlikely to account for the human-specific effects of perceived and displayed fear on cooperative behavior. Therefore, the current framework proposes a pivotal mediating mechanism that links fear to cooperation.

Before introducing the stipulated mechanism, it seems important to at least briefly contemplate the general experience of fear and the typically associated behaviors, which presumably exists in most mammals. One prominent line of thinking is that the experience of fear in light of a perceived threat in an animal leads to what has become commonly known as fight-or-flight (or freeze) responses (Adolphs, 2013). However, for highly social animals including humans there appears to be a further option, which is to approach and be approached by supportive conspecifics to help and be helped (“tend and befriend”). This response has received much less attention in both theory and research with humans (Sosna et al., 2019) but might perhaps represent the most effective and adaptive response in the face of fear, particularly in our ultrasocial species (Tomasello, 2014).

Returning to the hypothesized mechanism, the proposal is that it is motivational in nature and depends upon approach and reward systems previously shown to be involved in instantiating caring behaviors directed toward offspring in most mammals. In consequence, neither the perception–action coupling nor the caring behavior mechanism by itself is evolutionarily novel. What is presumed to constitute its novelty in human evolution is (1) a matter of degree – heightened fearfulness rather than fearfulness per se – and (2) the way in which these two mechanisms – perception–action coupling and caring – work in conjunction in a species with heightened fearfulness. Put succinctly, in addition to so-called fight and flight responses seen in many animals, among ultrasocial humans, heightened levels of fear when detected in self or in others is hypothesized to elicit motivational approach responses and may result in help, comfort, and support being provided. This response is thought to be adaptive because it allows for: (1) Potential threats or uncertainties in novel environments to be cooperatively managed and avoided, and (2) mutually beneficial cooperative relationships to be established, maintained, or strengthened. Moreover, the hypothesized approach response in the context of heightened fear may be particularly strong and beneficial for the youngest and most vulnerable members of our species. Indeed, there is a body of evidence from the area of attachment research, showing that infants and young children use parents as a secure base and safe haven, meaning that they approach them, seek protection and help when experiencing fear in the face of threat or uncertainty (Ainsworth, Blehar, Waters, & Wall, 2015; Bretherton, 2013; Cassidy et al., 2017; Cassidy, Ehrlich, & Sherman, 2014; Stern & Cassidy, 2018). Intriguingly, when considered in the context of alloparental care, as only seen among humans, this implies that there might not only be one safe haven, which is the primary caregiver but rather a multitude of safe havens beyond the primary caregiver including allomothers such as siblings, cousins, aunts, uncles, grandparents, and other genetically unrelated close group members (Howes & Spieker, 2008). This scenario further supports the presumed adaptiveness and uniqueness among great apes of enhanced fearfulness traits in humans, because we find ourselves surrounded by alloparents that provide safe havens.

Consequently, the hypothesized ontogenetic scenario also allows for interactions between mostly biologically determined individual fearfulness traits and the caregiving environment (Belsky et al., 2009; Belsky & van Ijzendoorn, 2017). In particular, more fearful infants and children may thrive in environments characterized by enhanced levels of cooperative care as evident in traditional hunter–gatherer societies, which are similar to our presumed ancestral caregiving environment (Kohrt et al., 2020; Konner, 2018). In this context, it is important to emphasize that, within the current proposal, heightened levels of interdependence and intergenerational cooperative child care (Hrdy & Burkart, 2020; Kohrt et al., 2020; Konner, 2018; Kramer, 2011, 2019; Tomasello et al., 2012) can be considered the experience–expectant social environment for human infants' and children's brains, bodies, and behavior to develop in (Greenough, Black, & Wallace, 1987; Konner, 2018). In other words, human infants and children expect to be cared for by others and in the process develop traits and competencies in caring for others.

Taken together, a framework emerges that views enhanced fearfulness – when embedded in human-specific cooperative care – as a key adaptive affective trait linked to cooperative cognition and behavior from early in ontogeny. After outlining the conceptual framework let us now turn to reviewing the existing evidence in support of this proposal in more detail. In particular, the next section will apply an evolutionary-developmental analysis focused on reviewing and synthesizing research on the phylogenetic, ontogenetic, brain, and cooperative origins in which human fearfulness evolved (the following sections address phylogeny at the ultimate level and ontogeny and [brain] mechanisms at the proximate level; see Fig. 1 for an overview).

3. The evidence

3.1. Phylogenetic origins

Adaptive behavior among primates, especially humans, is thought to be significantly impacted by affective traits that impact behavior (Hare, 2017; Hrdy, 2011; Hrdy & Burkart, 2020). An *affective trait* is an emotional tendency or characteristic, sometimes referred to as temperament, that is individually stable and seen across contexts, situations, and time (Davidson, 2003; Davidson & Irwin, 1999; Garstein & Rothbart, 2003; Gartstein et al., 2006; Kagan & Snidman, 2004). Fearfulness is one such affective trait characterized by enhanced reactivity to, and inhibited approach of, novel situations, objects, and people (Garstein & Rothbart, 2003; Kagan & Snidman, 2004). Human infants who display heightened reactivity to novelty as reflected in the first year have been shown to be more likely to become inhibited toddlers who are less likely to approach novelty in the second year (Kagan & Snidman, 2004). In humans, this pattern of fearfulness and behavioral inhibition is largely preserved into adolescence and associated with increased amygdala reactivity to novelty and heightened levels of anxiety in adulthood (Henderson, Pine, & Fox, 2015; Kagan & Snidman, 2004; Kagan, Snidman, Kahn, & Towsley, 2007; Schwartz, Wright, Shin, Kagan, & Rauch, 2003).

In the most comprehensive existing study, comparing between a large sample of human and nonhuman great apes, fearfulness was examined by measuring the reaction of bonobos, chimpanzees, orangutans, and 2.5-year-old human infants to novel objects and people (Herrmann et al., 2011). Human infants displayed much higher levels of fearfulness indexed by avoiding novelty in social and nonsocial contexts significantly more than the other great ape species tested in this study. In fact, this study showed that only human infants avoided novelty, whereas the other species of nonhuman great apes were either attracted (chimpanzees, orangutans) or indifferent (bonobos) to novelty.

One consideration offered by the authors of this comparative study is that the chimpanzees' and orangutans' reported boldness (attraction to novelty) may be attributed to their feeding ecologies characterized by much greater uncertainty than either the bonobos' or the humans' cousins, which would make chimpanzees' and orangutans' approach of novelty an adaptive strategy in their less predictable ecological context (Herrmann et al., 2011). While this proposal based on feeding ecology may account for the similarities between orangutans and chimpanzees and differences between chimpanzees and bonobos, it cannot explain the quantitatively and qualitatively distinct fear responses seen in human infants, especially as far as the differences between bonobos and human infants are concerned. Another consideration in regards to Herrmann et al.'s (2011) study is that the social novelty manipulations for the nonhuman great apes took place in response to familiar and unfamiliar humans, whereas the human infants in this study were responding to familiar and unfamiliar adult conspecifics, which represents a limitation of this study. Prior work employing conspecific tests indicates that, in contrast to human infants (who, as mentioned above, display fearful [xenophobic] behavior in the context of strangers [Herrmann et al., 2011]), bonobos have been shown to share food with conspecific strangers (Tan & Hare, 2013; Tan, Ariely, & Hare, 2017). This xenophilic behavior directed toward unfamiliar conspecifics appears to be contingent on the opportunity for social interaction, because bonobos do not share food when a social interaction with the unfamiliar conspecific is not possible (Tan & Hare, 2013). This tendency of bonobos to approach and engage with conspecifics in a xenophilic manner has been argued to have evolved as a function of specific ecological changes increasing the benefits of relationship formation as the risk of intergroup aggression dissolved (Tan et al., 2017). Returning to the only existing study systematically comparing fearfulness traits across great ape species (Herrmann et al., 2011), it is important to emphasize that human infants' enhanced fear responses were replicated in two different contexts, that is, absence of parents and removing physical barriers to increase comparability to nonhuman apes, attesting to the robustness of the displayed fearfulness behavior among humans (see Herrmann et al., 2011). This comparative study clearly represents a critical step in delineating heightened fearfulness as an essential affective feature of human psychology.

It has been also argued that the findings from Herrmann et al.'s (2011) study are in general agreement with the view articulated in the conceptual framework provided within the self-domestication hypothesis (see Hare, 2017). According to this view, human-specific behavioral traits – especially our enhanced prosocial tendencies – have been linked to a domestication syndrome seen in other domesticated animals, especially concerning affective traits linked to tameness such as reduced aggression and the concomitant increase in social tolerance (Hare, 2017). Yet again the reduction of aggression alone, presumably driven by negative selection against genes linked to aggression, is unlikely to account for the heightened fearfulness seen in humans, which rather indexes positive selection on genes linked to enhanced fearfulness. Moreover, enhanced fearfulness and increased reactivity to novelty are undesirable traits in domesticated animals, and selection against fearfulness is considered to represent a key component in the successful domestication of animals (Zeder, 2012). Consistent with this view, domesticated animals have generally been shown to display reduced fearfulness. For example, experimental studies measuring responses to novelty have demonstrated that dogs are less fearful than wolves (Hansen Wheat, van der Bijl, & Temrin, 2019), suggesting that self-domestication is an unlikely candidate to explain enhanced human fearfulness.

At the neurochemical level, reduced aggression and increased social tolerance have been attributed to reduced levels of acetylcholine and particularly to increased levels of serotonin (Hirter et al., 2021; Raghanti et al., 2018). With respect to species differences in serotonergic function, there is important evidence comparing humans' closest living ape relatives, the bonobos and chimpanzees, who are known to differ considerably from each other in terms of their social behavior. Specifically, bonobos are reported to be more socially tolerant of conspecifics, whereas chimpanzees more commonly engage in aggression with conspecifics (Hare, 2017; Tan et al., 2017; Tan & Hare, 2013; Wobber et al., 2010). When comparing between bonobos' and chimpanzees' brains, the amygdala of bonobos had more than twice the density of serotonergic axons than chimpanzees (Stimpson et al., 2016). Considering the role of serotonin in regulating amygdala function and fear reduction, the findings from this study suggest that the demonstrated variation in serotonergic innervation of the amygdala may contribute to the observed behavioral differences exhibited by bonobos and chimpanzees. This difference in serotonergic innervation of the amygdala may also account for the differences in fear behaviors seen between bonobos and chimpanzees discussed above (Herrmann et al., 2011). However, work assessing ape species comparisons including human amygdala serotonin innervation is currently lacking.

Directly assessing the neurochemical profile within the brain and comparing it between humans, chimpanzees, and different monkey species revealed that the human-unique profile is characterized by enhanced dopamine levels in addition to increased serotonin and reduced acetylcholine (Hirter et al., 2021; Raghanti et al., 2018). This human-specific neurotransmitter profile was obtained for the striatum, which is a subcortical brain structure, interconnected with the amygdala and prefrontal cortex (Raghanti et al., 2018). The striatum is crucially involved in a host of behavioral functions related to reward processing, decision making, and social appetitive behaviors (Bhanji & Delgado, 2014). Considering the importance of dopamine and the striatum in motivating and regulating social behavior and decision making in the context of reward and approach, this finding of enhanced dopamine in humans points to an additional neurochemical mechanism that goes beyond a reduction of aggression and increased tolerance. More specifically, it may indicate that human evolution was associated with an increase and extension of behaviors linked to the brain's reward and approach systems. With respect to this suggestion, it is critical to note that there is considerable evidence linking the brain's dopamine system and especially the striatum to parental care in humans and other mammalian species (Feldman, 2015, 2017; Preston, 2013; Rilling, 2013; Rilling & Young, 2014). In particular, it has been reported that viewing or listening to infant stimuli results in enhanced activation of the striatum in human parents and even in non-parents (Feldman, 2015, 2017; Rilling & Young, 2014). Moreover, in human parents including fathers, the strength of the striatum responses to infant stimuli predicted positive caring behaviors (Feldman, 2015, 2017; Rilling, 2013; Rilling & Young, 2014). Taken together, the brain's dopamine system with its human-unique elevated dopamine profile likely is a major player in caring behaviors that may contribute to enhanced parental and alloparental caring responses.

Another neurotransmitter system that has been identified as playing an important role in brain functions associated with mammalian parental caring behavior is the oxytocin system (Carter, 2014). Oxytocin administration in human adults has also been associated with a number of effects on social cognition and behavior, including greater attention to eyes (Guastella, Mitchell, & Dadds, 2008; Kemp & Guastella, 2011). Furthermore, meta-analyses of oxytocin administration studies showed that a single dose of intranasal oxytocin significantly improved the recognition of facial emotional expressions, particularly for fearful faces (Leppanen, Ng, Tchanturia, & Treasure, 2017; Shahrestani, Kemp, & Guastella, 2013). Considering that eye cues – widened eyes with large exposure of white sclera – play a critical role in detecting fear in others' faces, oxytocin may facilitate fearful face recognition through its effect on increasing attention to the eyes (see Grossmann [2017], for a review including an extensive discussion of the role of oxytocin in social perception and behavior). When comparing between chimpanzees and bonobos, oxytocin administration increased attention to the eye contact in bonobos, but not in chimpanzees (Brooks et al., 2021). The oxytocin administration effect seen in bonobos is similar to what has previously been shown in human adults (Guastella et al., 2008), suggesting a commonality in how oxytocin modulates face-to-face social interactions in humans and bonobos. However, similar to the work assessing amygdala serotonin innervation discussed above, a direct comparison with humans is currently lacking. The picture emerging from the existing work suggests greater similarities between humans and bonobos than humans and chimpanzees, particularly with regard to serotonin and oxytocin system functions linked to affect and behavior. Clearly, more research systematically comparing between humans', chimpanzees', and bonobos' brain, neurotransmitter, and behavioral systems, which include developmental data, is needed to provide a more comprehensive understanding of commonalities and differences between great apes.

Notwithstanding the mentioned similarities between bonobos and humans that have been discussed and analyzed in much greater details elsewhere (see Hare, 2017), the intriguing puzzle of what exactly accounts for the emergence of the documented heightened fearfulness (see Herrmann et al., 2011) in human evolution remains. The scenario presented herein favors an explanation based on a socioecological variable that sets humans apart from other great apes, which is our cooperative child-rearing practices (Hrdy & Burkart, 2020; Kramer, 2019). This phylogenetically novel feature within the hominoid clade likely provided a socio ecological context in which offspring that displayed, experienced, and processed fear more strongly than others, were cared for by mothers and others more effectively, which increased not only their survival rates but also their own cooperative tendencies. In this context, it is important to point out that displays of fearfulness are not limited to the face but are also expressed vocally. Crying during separation from the mother as a form of distress vocalization is seen among many animals including human infants, while producing tears that accompany crying events appears to represent a unique expression of distress in humans (Gračanin, Bylsma, & Vingerhoets, 2018). Particularly relevant to the current proposal, previous research shows that greater fearfulness traits in human infants are also associated with more frequent crying and may hence elicit more frequent caring behavior (Kagan & Snidman, 2004).

Recent studies (Kret, Prochazkova, Sterck, & Clay, 2020) also show that, in contrast to humans who display an attentional bias toward fearful (and other negative) facial expressions, chimpanzees and bonobos fail to show such a bias in their attention when viewing conspecific distress displays (Kret, Jaasma, Bionda, & Wijnen, 2016; Kret, Muramatsu, & Matsuzawa, 2018). Specifically, across two experiments chimpanzees did not show an emotional bias toward conspecific and human distress displays (Kret et al., 2018). Furthermore, bonobos do show an attentional bias to sexual, grooming, and yawning displays, attesting to the fact that they possess attentional biases to other emotionally charged stimuli, but critically this bias does not extend to distress (fear) displays (Kret et al., 2016). Interestingly, humans' biased attention to fear displays is even seen in response to bonobo displays of distress (Kret & van Berlo, 2021), suggesting that it generalizes from humans to other apes and might at least partly rely on expressive features shared among apes.

Taken together, while the phylogenetic comparisons based on the existing work are still rather sparse, there is clear evidence that, humans when compared to our closest living primate relatives possess what can be considered heightened fearfulness traits that might be linked to a unique neurochemical profile characterized by heightened serotonin, dopamine, and oxytocin levels in the brain. Furthermore, the reviewed evidence suggests that humans differ from their closest living primate relatives with regard to not only how they *express* fear themselves (Herrmann et al., 2011) but also in how they *perceive* fear/distress in others (Kret et al., 2016, 2018, 2020). Humans are the only great apes showing enhanced fear in expression and perception, supporting the hypothesized notion that enhanced fearfulness emerged as an integrated (perception–action coupling) system during human evolution. This raises the question of when in human evolution this affective trait emerged. The bioanthropological work hints at a scenario whereby cooperative caregiving and infant helplessness emerged early in hominid evolution and likely already existed in *H. erectus*, whereas the characteristic traits of human life history – including shorter inter-birth intervals, prolonged child dependence, and intergenerational cooperative care – only emerged in their full-fledged form with the arrival of *H. sapiens* (Hrdy, 2011; Kramer, 2019; Kramer & Otárola-Castillo, 2015; Rosenberg, 2021; Vaesen, 2012). Considering this scenario, human fearfulness may have emerged gradually over the last 1.8 million years, first in response to the emergence of infant helplessness and cooperative caregiving, and might then have been consolidated with the evolution of human life-history traits (see Fig. 1).

3.2. Ontogenetic origins

There is now a body of work showing that among human adults, responses vary markedly when viewing others in fear and that heightened sensitivity to fearful faces is associated with enhanced cooperative behavior (Marsh, 2015). One prominent line of work concerned with capturing and examining this intra-species variability in responding to fear has shown that highly cooperative anonymous kidney donors show heightened sensitivity, whereas highly antisocial psychopaths show hampered sensitivity when viewing fearful faces (Marsh et al., 2014; Marsh & Blair, 2008). Notably, enhanced recognition of fearful faces has also been linked with higher levels of cooperative behavior among neurotypical adults (Marsh & Ambady, 2007; Marsh, Kozak, & Ambady, 2007). These findings stress the importance of examining intra-species variability in fear responding in order to understand its origins, mechanisms, and adaptive functions, supporting the view that a caring continuum exists along which individual humans differ in their propensity to display sensitive responses to others' fear that motivate cooperative behavior (Grossmann, 2018; Marsh, 2015).

Previous work with adults also shows that fearful facial expressions predominantly evoke behavioral approach tendencies in the onlooker. There is work to support the hypothesis that this approach effect relies upon fearful facial expressions' resemblance to helpless, vulnerable infantile faces (Hammer & Marsh, 2015). In this study, adults demonstrated an implicit association between fearful facial expressions and infant faces; the study also showed that both fearful expressions and infant faces predominantly elicit behavioral approach tendencies. Furthermore, this study reports that approach responses to both fearful and infant faces were diminished as psychopathic personality traits increased. The pattern of results from this study suggests that fearful faces through their association with infantile faces might be viewed as social signals that convey vulnerability and a need for help. These findings from adults, in conjunction with the research discussed above (see Marsh, 2015), imply that the link between responses to fearful faces and cooperative behavior observed across these various studies might originate from this association with infantile faces and its effect on approach. Taken together, this line of research with adults demonstrates that variability in responding to fearful faces is linked to variability in cooperative behavior, raising the question of when this link emerges in human development.

Heightened sensitivity to fearful faces has also been found to be linked to enhanced cooperative behavior in preschool children across two different cultures (Rajhans, Altvater-Mackensen, Vaish, & Grossmann, 2016). In this study, children in India and Germany who were faster to orient to fearful faces displayed greater cooperative behavior – sharing of a valued resource – in a dictator game. Consequently, the essential link between variability in responding to fearful faces and cooperative behavior already exists in preschool-aged children. It is vital to emphasize that the ability to detect and differentiate between various emotional facial expressions including fear emerges during the first year of life (Grossmann, 2012). This is much before the age of 14 months at which cooperative behavior has first been described to be exhibited by infants in experimental contexts (Warneken & Tomasello, 2007). By 7 months of age, but not younger, human infants show increased neural and attentional responses to fearful faces and distinguish them from other positive and negative facial expressions (Grossmann & Jessen, 2017; Jessen & Grossmann, 2014, 2016; Krol, Monakhov, Lai, Ebstein, & Grossmann, 2015; Peltola, Leppänen, Mäki, & Hietanen, 2009). Given this evidence from behavioral and neuroscience research, infancy can be considered a sensitive developmental period during which fear-processing skills come online. Prominently, this is around the same time in early human ontogeny when infants first begin to experience and display fear themselves (Brand, Escobar, & Patrick, 2020; Gaensbauer, Emde, & Campos, 1976; Sroufe, 1977). This raises the possibility that there is a connection between the ability to experience and display fear in self and the ability to detect fear in others. In congruence with this kind of perception–action coupling account of the emergence of fear systems in human infancy, recent neuroimaging data show that variability in fearfulness traits among 7-month-old infants maps onto differences in the neural processing of others' fearful faces in brain regions implicated in perception–action coupling (Krol, Puglia, Morris, Connelly, & Grossmann, 2019).

With respect to the question of when the link between fearful face processing and cooperative behavior emerges in development, it is important to look at research that has investigated this link in early human ontogeny at a time when fear processing and cooperative behavior first come online. A recent longitudinal developmental study reported that variability in brain responses measured by functional near-infrared spectroscopy (fNIRS) and attentional responses to fearful faces at 7 months of age measured by eye tracking (using a visual-paired comparison task) predict cooperative behavior – instrumental helping at 14 months of age (Grossmann, Missana, & Krol, 2018). This finding establishes a clear link to existing work with adults summarized above (Marsh, 2015) and thus demonstrates that heightened fear processing is associated with enhanced cooperative behavior from early in ontogeny.

Furthermore, variability in infants' attention to fearful faces in the first year measured by eye tracking (using a gap task) has been linked to attachment quality in the second year (Peltola, Forssman, van Puura, & Leppänen, 2015). Specifically, this study shows that enhanced biased attention to fearful faces at 7 months of age predicts secure attachment at 14 months of age, whereas the absence of biased attention to fear was associated with disorganized attachment (Peltola et al., 2015). With regard to this finding it is important to point out that secure attachment in 3- to 5-year-old children has recently been shown to be associated with greater levels of cooperativeness seen across various prosocial behavioral tasks involving helping, sharing, and comforting (Beier et al., 2019). However, employing the same eye-tracking paradigm using a gap task as in prior work (Peltola et al., 2015) failed to show a direct association between biased attention to fearful faces at 7 months of age and spontaneous helping behavior at 24 months of age (Peltola, Yrttiaho, & Leppänen, 2018). These studies thus hint at a developmental trajectory, whereby secure attachment, presumably as a reflection of early supportive caregiving experiences (Ainsworth et al., 2015), mediates the link between fearful face processing in infancy and cooperative behavior in childhood. In this context, it is also critical to acknowledge that, while there is inter-individual variability, the great majority of infants and children show: (1) biased attention to fear, (2) secure attachment, and (3) robust cooperative behavioral tendencies (Ainsworth et al., 2015; Krol et al., 2015; Peltola et al., 2018; Tomasello, 2019), supporting the notion that this represents the developmentally normative pattern of social functioning.

Another line of developmental research relevant to the ontogenetic origins of heightened fearfulness and its adaptive significance in the context of human cooperative behavior comes from work on children's moral emotions and behavior. For example, children from 2 to 4 years of age who displayed more fearfulness in fear-inducing experimental paradigms also showed more guilt in an experiment where they caused harm to others (Kochanska, Gross, Lin, & Nichols, 2002). Furthermore, in this study, children who displayed more guilt were reported to be less likely to violate rules of conduct at 5–6 years of age. These findings are in support of a mediation model whereby heightened fearfulness enhanced guilt proneness, which in turn served to reduce children's tendency to violate social rules. This points to an additional or interrelated pathway through which heightened fearfulness may serve adaptive cooperative functions, namely, through its effects on enhancing harm aversion in the form of experiencing guilt. However, while fearfulness may also function as a deterrent to wrongdoing (misbehavior) as suggested by this line of work, harm avoidance effects cannot directly explain why enhanced sensitivity to fear in others, as shown in the work discussed above (see Grossmann et al., 2018), promotes cooperative behavior in the form of instrumental helping.

Furthermore, as argued in much more detail elsewhere (Hare, 2017), affective and motivational traits may have directly or indirectly impacted the evolution of human social-cognitive capacities. In regards to this notion, it is important to mention work demonstrating that heightened fearfulness among human children is systematically linked to enhanced social-cognitive competencies, especially theory-of-mind skills (Wellman, Lane, LaBounty, & Olson, 2011). This points to the possibility that human-specific affective traits – such as heightened fearfulness – facilitate adaptive perspective taking skills, likely in the service of cooperative behavior (Tomasello, Carpenter, Call, Behne, & Moll, 2005).

The proposal here is that in early human ontogeny heightened fearfulness leads to enhanced pursuit of eliciting cooperative concern and care from mothers and others. In the context of highly interdependent group life characterized by intergenerational cooperative care (Kramer, 2019), this fear-guided pursuit is hypothesized to result in fearful infants receiving greater care, attention, and provision, which in turn not only increases survival and reduces childhood mortality but also increases cooperative tendencies among fearful children who benefitted from heightened cooperative care. This hypothesized ontogenetic scenario also allows for developmental epigenetic effects, whereby biologically determined individual fearfulness traits interact with caregiving environments (Belsky & Pluess, 2009; Belsky & van Ijzendoorn, 2017). In other words, highly fearful infants may thrive in rearing environments characterized by enhanced levels of cooperative care as seen in traditional hunter–gatherer groups, which may serve as a model for our ancestral caregiving environment (Kohrt et al., 2020; Konner, 2018). Conversely, highly fearful infants may suffer the most in rearing environments characterized by much reduced levels of cooperative care as seen in many modern, anonymous, urban environments (Lederbogen et al., 2011). Furthermore, the hypothesized ontogenetic scenario is presumed to play out in the context of a unique human life history characterized by much prolonged early development, dependency, and reliance on alloparental care and sustenance (Hrdy, 2011; Hrdy & Burkart, 2020; Kohrt et al., 2020; Konner, 2018; Kramer, 2011, 2019). This prolonged, increased dependency on others' cooperative care not seen among our great ape cousins may have critically contributed to the adaptive benefits of enhanced fearfulness among infants and children.

3.3. Brain (mechanistic) origins

At the brain level, detecting, processing, and expressing fear has been linked to inter-connected brain systems centered on the amygdala and various prefrontal brain regions (Adolphs, 2013; Adolphs, Tranel, Damasio, & Damasio, 1995; Ochsner & Gross, 2005; Ochsner, Silvers, & Buhle, 2012). Lateral prefrontal brain regions primarily serve regulatory functions and have been shown to be inversely related to amygdala responses (Ochsner et al., 2012; Ochsner & Gross, 2005). There exists an immense amount of work on the brain circuits involved in fear, which is well beyond the scope of the current article to review. Thus, here the focus is on research that has assessed the link of fear detection to cooperative behavior, which is relatively sparse even in adults. The most prominent line of work with adults reports that amygdala shows diminished responding to fearful faces in highly antisocial psychopaths and enhanced responding in highly cooperative anonymous kidney donors (Marsh, 2015). This study further showed that heightened amygdala response to fearful faces was associated with enhanced recognition rates of fearful faces in a behavioral experiment. Importantly, from a developmental perspective, similar effects particularly between regarding amygdala responses and fearful faces and its link to caring behaviors have also been obtained in 10- to 17-year-old children and adolescents (Lozier, Cardinale, VanMeter, & Marsh, 2014). Together, this indicates that enhanced amygdala responses when viewing others in fear are associated with greater cooperative tendencies.

Most neuroimaging research with human infants has used fNIRS, which due to methodological constrains, is limited to mapping variability in cortical brain regions in response to viewing fearful faces and does not allow to directly measure amygdala responses (Grossmann, 2008; Lloyd-Fox, Blasi, & Elwell, 2010). This work shows that infants who display reduced lateral prefrontal cortex involvement during fear processing behave more cooperatively (Grossmann et al., 2018). As outlined above, in adults, greater amygdala responses to fearful faces is linked with greater levels of cooperative behavior (Marsh et al., 2014). Moreover, previous work shows that greater lateral prefrontal cortex involvement is linked to reduced amygdala activity (Ochsner et al., 2012; Ochsner & Gross, 2005). The neuroimaging findings suggest that infants who display reduced lateral prefrontal cortex involvement during fear processing behave more cooperatively raising the possibility that a similar inverse functional relation between lateral prefrontal cortex and amygdala may exist in them. However, inverse coupling between prefrontal cortex and amygdala is not thought to mature until adolescence, according to previous work (Gee et al., 2013). In this context, it is important to mention the eye-tracking findings also obtained in this neuroimaging study with infants (Grossmann et al., 2018). Specifically, this study showed that lateral prefrontal responses, while predicting reduced sustained attention to fearful faces, did not predict initial heightened attention to fearful eyes, measured as the duration of infants' first look. One possible interpretation of these findings is that reduced engagement of lateral prefrontal cortex represents more effective cognitive control (disengagement) when responding to fear in others, which might be required in order to initiate helping actions when seeing others in distress. This interpretation is in agreement with work suggesting that emotion regulation and control play a key role in enabling prosocial responding and cooperative behavior (Cowell & Decety, 2015; Eisenberg et al., 1989; Steinbeis, Bernhardt, & Singer, 2012).

Another recent fNIRS study with 7-month-old infants demonstrates that fearful face processing engages inferior frontal brain system implicated in perception–action coupling (Krol et al., 2019). As already mentioned above, this study further showed that variability in fearfulness traits among these 7-month-old infants maps onto differences in the neural processing of others' fearful faces in these inferior frontal brain regions. The emerging picture from the neuroimaging work with infants suggests that by around 7 months of age, infants differentially engage various prefrontal brain systems when processing fearful faces. Tentatively, there appears to be an association between displayed fearful behavioral traits for the self and how this accounts for variability in processing fear displays in others, with greater engagement of inferior frontal brain systems among infants with greater fearfulness (Krol et al., 2019).

In addition, there is a host of research using event-related brain potentials (ERPs) to examine the neural correlates of emotional face processing in infants (see Grossmann [2012] for a review). This line of work further supports the notion that by around 7 months of age human infants begin to distinguish fearful from non-fearful faces and typically show an enhanced negative component in response to fearful faces (Peltola et al., 2009). This ERP response has been linked to attention allocation and is thought to be generated in prefrontal cortex, especially medial prefrontal cortex (Johnson et al., 2005; Reynolds & Richards, 2005). Medial prefrontal cortex is a key brain region involved in social cognition and behavior, particularly theory of mind, that is, attributing emotional and mental state to others (Amodio & Frith, 2006; Grossmann, 2013). Together with previous behavioral work (Krol et al., 2015) showing increased looking time to fearful faces when compared to other positive and negative facial expressions, neuroimaging work suggests that infants show what has also been called a fear bias reflected in heightened attention and neural processing when viewing others' facial expressions of fear (Grossmann & Jessen, 2017).

Strikingly, as shown in another line of ERP studies, by 7 months of age, infants display the ability to detect fearful faces independent of conscious perception (Jessen & Grossmann, 2015). This subliminal detection of fearful faces appears to be underpinned by infants' sensitivity to eyes, especially the white sclera of the eyes, which is unique to humans (Grossmann, 2017). Specifically, prior work shows that 7-month-old infants, when presented with eye stimuli below their visibility threshold, still can distinguish between fearful and non-fearful eyes as shown in their ERP responses (Jessen & Grossmann, 2014, 2020). In previous work with adults, the human brain's capacity to detect fearful eyes has been shown to be linked to the amygdala (Whalen et al., 2004). This may indicate that infants, similar to adults, recruit the amygdala when processing fear. A recent prospective longitudinal study provides evidence that the amygdala indeed plays a role in the developmental emergence of the fear bias (Tuulari et al., 2020). This study showed that at 8 months infants displayed a fear bias, that is, they were less likely to disengage from fearful than from happy or neutral faces. This study further showed that amygdala volume (corrected for intracranial volume) measured when the same infants were neonates was positively associated with the displayed fear bias. These findings are the first to directly implicate the amygdala in the emergence of heightened attention to fear during infancy.

In summary, the existing ERP research further bolsters the neuroimaging work based on fNIRS reviewed above and points to the emergence of fear-processing systems in the human brain during the second half of the first year of postnatal life. The question of why this development takes place during that time in human ontogeny has not been explicitly assessed. One possibility is that this is when infants first begin to experience fear themselves, which then enables them to relate to, detect and identify others in fear. There certainly is correlational evidence suggestive of this possibility, especially when referring to developmental work identifying the emergence of "stranger anxiety" as a form of fear, which substantially increases by this time in human infancy (Brand et al., 2020; Gaensbauer et al., 1976; Sroufe, 1977). There might also be maturational brain changes that take place during this time in early development. Specifically, prior work measuring functional connectivity from the amygdala indicates that during the second half of the first year there are significant changes in functional connectivity centered on the amygdala (Ulfig, Setzer, & Bohl, 2003). Ultimately, experiential and maturational changes may go hand in hand during the second half of the first year, particularly as the developing infant begins to more independently locomote through its physical and social environments using reaching, crawling, and walking as means to approach, explore, and withdraw (Brand et al., 2020; Campos et al., 2000).

Another insight gleaned from the host of infant neuroscience studies concerned with fearful face processing is that there is considerable variability in infants' processing of fearful faces (see, e.g., Grossmann et al., 2018). In particular, genetic variability in the dopamine system has been shown to be linked to systematic differences in infants' brain responses to fearful faces (Grossmann et al., 2011). In this study, infants with a genetic variant associated with higher levels of dopamine in the prefrontal cortex displayed greater Negative component (Nc) responses to fearful faces than infants with a genetic variant associated with lower levels of dopamine. Intriguingly, the gene variant linked to heightened brain sensitivity to fear in others is novel among humans and does not exist in other great apes such as chimpanzees, who only have the ancestral gene, which in human infants is linked to reduced fear sensitivity (Palmatier, Kang, & Kidd, 1999). In this context, it is important to mention that adults with this novel gene variant have been shown to display greater levels of fearfulness, specifically, anxiety symptoms (Heinz & Smolka, 2006; Smolka et al., 2005). Considering the general role of the dopamine system in guiding behavior and decision making (Bromberg-Martin, Matsumoto, & Hikosaka, 2010; Schultz, 2007a, 2007b), this finding may be seen as tentative support for the hypothesized mechanism regarding fear processing and its link to brain systems involved in reward and approach behaviors. The aforementioned enhanced looking time seen in 7-month-old infants while viewing fearful faces when interpreted as a sign of approach or preference may further support this viewpoint (Krol et al., 2015; Peltola et al., 2009). Furthermore, prior work examining variability in ERP responses of 8-month-old infants' viewing fearful body expressions indicates that the Nc to fearful bodies is enhanced among infants with greater approach tendencies (Rajhans, Missana, Krol, & Grossmann, 2015). While the existing evidence is certainly rather limited at this stage, the prior work reviewed above hints at the possibility that from early in human ontogeny there is systematic variability in brain systems linked to approach and reward that may support the adaptive responding scenario to fear laid out herein.

When considering the brain level findings reviewed in this section it becomes evident that from early in human ontogeny viewing fearful faces engages key social-cognitive brain processes linked to: (a) perception–action coupling in inferior frontal cortex, (b) cognitive control and emotion regulation in lateral prefrontal cortex, and (c) social attention and theory of mind in medial prefrontal cortex (Grossmann et al., 2011, 2018; Johnson et al., 2005; Krol et al., 2019; Peltola et al., 2009). This engagement appears to develop around 7 months of age, occurs at least partly without conscious perception and varies as a function of individual differences in infants' fearfulness traits, genetic differences in the dopamine system, and behavioral approach tendencies (Grossmann et al., 2011; Krol et al., 2019; Rajhans et al., 2015). Together, these neuroscience findings begin to shed light on the neurocognitive underpinnings of enhanced fear processing, confirming the hypotheses that: (a) processing fear in self and others is intricately linked, (b) fear processing elicits cognitive control and regulation processes, and (c) seeing others in fear taps into motivational systems related to approach.

4. Discussion and implications

As laid out in the previous sections, the reviewed evidence principally supports the *fearful ape hypothesis* as a novel evolutionary-developmental framework arguing that, in the context of the strong interdependence present in cooperative caregiving and provisioning unique to human great ape group life (Hrdy, 2011; Konner, 2018; Kramer, 2019; Tomasello et al., 2012), heightened fearfulness and sensitivity to fear in others emerged as an adaptive trait. A host of studies with human infants and children favor the main hypothesis that from early in human ontogeny fearfulness traits enhanced care-based responding, social-cognitive brain processes, and cooperative behaviors. Together, the synthesis of the reviewed research points to the existence of a virtuous caring cycle that understands fearfulness as a key adaptive affective trait supporting human-unique levels of cooperative concern and care.

In light of the insights gleaned about fearfulness within this new evolutionary-developmental synthesis, a major paradox emerges. Specifically, when examining most of the existing clinical psychological and psychiatric work, heightened fearfulness is predominately viewed as maladaptive, as it has been shown to be linked with an increased risk of developing anxiety and depression

(Fox et al., 2021; Sandstrom, Uher, & Pavlova, 2020). This view of heightened fearfulness as a risk factor for developing anxiety and depression ignores the reviewed comparative, developmental, and neuroscience work, indicating that fearfulness is uniquely elevated in humans and linked to cooperative mind reading and behavior from early in ontogeny.

How can this seeming *human fear paradox* be explained? In order to tackle this question, it is critical to first recognize that construing fearfulness as a maladaptive trait is likely also rooted in cultural biases and the fact that most research has been focused on large-scale Western, educated, industrialized, rich, and democratic (WEIRD) societies (Henrich et al., 2010). This has been identified as a general problem plaguing much of research in the psychological, brain and behavioral sciences (Henrich et al., 2010). In addition to the obvious issues concerning representativeness of existing research, which also apply here, perhaps more problematic might be that within WEIRD societies there is a great emphasis on independence of the individual as a culturally highly regarded value that drives socialization goals, education, and clinical practice in mental health (Chiao & Blizinsky, 2010; Tsai, 2017). In other words, what psychological traits are viewed as adaptive and healthy critically depend on cultural values and norms. With respect to the heightened fearfulness traits under examination here, fearfulness might be considered adaptive in small-scale, interdependent human societies primarily build on cooperative care and success, whereas fearfulness has become maladaptive in large-scale, independent human societies build more strongly on individual success and less so on cooperative care. It is thus possible that the exceedingly high rates of anxiety and depression seen in WEIRD societies and anonymous urban centers across the world might need to be added to the list of potential evolutionary mismatch diseases (Chiao & Blizinsky, 2010; Gluckman, Hanson, & Low, 2019). In this context, it is also important to stress that the argument here is not to undermine the clinical relevance and individual suffering associated with extremely enhanced fearfulness traits in the etiology of anxiety and depression particularly among WEIRD samples (Henderson et al., 2015; Sandstrom et al., 2020), but rather to point to the importance of evolutionary, developmental, and cultural considerations when dealing with fear, anxiety, and depression.

In addition to supporting efforts in conducting cross-cultural research on fearfulness in non-WEIRD cultures, it seems critical to foster an interdisciplinary discourse that brings clinically orientated and evolutionarily orientated approaches together when studying fearfulness. For example, a recent behavioral study with children showed that greater anxiety was associated with greater accuracy when processing fearful faces (Thompson & Steinbeis, 2021). The authors interpret their findings as indicating greater threat bias in childhood anxiety and go on to make recommendations as to how their findings inform treatment using threat bias modification. When taking into account the body of research reviewed here, a considerably different interpretation emerges. Specifically, fearful faces, rather than communicating direct threat, more likely reflect signs of distress and helplessness (Hammer & Marsh, 2015; Marsh, 2015), which changes the interpretation of children with greater anxiety from showing a threat bias to children who show an enhanced sensitivity to others in distress. Moreover, considering previous work demonstrating that more sensitive responding and enhanced recognition of fearful faces is linked to greater cooperative behavior, this raises the possibility that children with anxiety may even be more inclined to behave cooperatively. This speculative interpretation is supported by the reviewed research showing greater levels of moral emotion and behavior among more fearful children (Kochanska et al., 2002). Therefore, when considering this specific example, a dramatically different picture emerges depending on whether the same data are interpreted in a clinically orientated threat bias anxiety framework or in an evolutionarily orientated fear bias and cooperation framework.

Perhaps even more important from a societal perspective than the conceptual issues and interpretations, which are the heart of the current proposal, applying these two different views radically changes how we tend to treat and deal with fearfulness-related symptoms. Within the clinically orientated threat bias and anxiety framework the focus appears to be on treating an individual's disordered mental functioning through psychopharmacological and cognitive-behavioral therapeutic interventions designed to reduce fearfulness. In contrast, an evolutionarily orientated fear bias and cooperation framework, which identifies the issue as arising out of a presumed mismatch between heightened fearfulness characteristics and the social environment, allows for a more systems- and community-based interventions that could help improve outcomes, especially if interventions foster greater supportive caregiving opportunities during sensitive periods of early human development (Gluckman et al., 2019). Again, this is not meant to undermine existing clinical work demonstrating an association between extreme forms of fearful temperament among children and its role in the etiology of anxiety and depression (Henderson et al., 2015; Sandstrom et al., 2020), but rather to offer a different level of analysis from a fundamentally evolutionary perspective that takes cultural factors relating to the social and caregiving environment into account.

In this context it is important to emphasize that a more extensive and comprehensive discussion of the potentially far-reaching clinical and societal implications of rethinking fearfulness in evolutionary terms while warranted and important is beyond the scope of this article (and the primary expertise of the author). Nonetheless, it appears worthwhile to more closely examine the hypothesized ontogenetic scenario and its potential relations to existing developmental theories. Specifically, a main takeaway from the current proposal was the argument that highly fearful infants may thrive in rearing environments characterized by enhanced levels of cooperative care as seen in traditional hunter–gatherer groups, whereas highly fearful infants may suffer the most in rearing environments characterized by much reduced levels of cooperative care as seen in many modern, anonymous, urban environments. To a certain extent this idea connects to and may be seen as an extension of the differential susceptibility model (Belsky & Pluess, 2009; Belsky & van Ijzendoorn, 2017). According to this model, individuals differ in their developmental plasticity, such that some children may be more susceptible than others to environmental influences than others and over the course of development this may play out in a for-better-and-for-worse manner. When applied to the current framework, fearfulness may be seen as a sign of heightened developmental susceptibility to the cooperative caregiving environment, whereby fearful children are more likely to benefit and thrive under supportive caregiving conditions and be detrimentally impacted under suboptimal caregiving conditions. In fact, there is evidence suggesting that individuals who have a genetic variant of the serotonin transporter gene (5-HTTLPR) linked to fearfulness are impacted in this for-better-and-for-worse way as a function of their childhood caregiving experience (Belsky & van Ijzendoorn, 2017; Canli & Lesch, 2007; Lesch et al., 1996; van Ijzendoorn, Belsky, & Bakermans-Kranenburg, 2012).

Importantly, the frequency of this genetic variant of the serotonin transporter gene and fearfulness has been shown to vary as a function of cultural characteristics. Specifically, there is work to show that there is an association between cultural values of individualism–collectivism and genetic frequency of 5-HTTLPR, which in turn explains global variability in the prevalence of anxiety and mood disorders (Chiao & Blizinsky, 2010). In this study, comparing across 29 nations, it was shown that collectivistic cultures were significantly more likely to include individuals carrying the variant of the serotonin transporter gene (short allele) also linked to fearfulness. Furthermore, this study indicates that collectivistic cultural norms and values interact with the variant of the serotonin transporter gene linked to fearfulness to negatively predict global prevalence of anxiety and mood disorders. This has been taken to suggest that some form of culture–gene coevolution with cultural values buffering genetically susceptible populations from increased prevalence of affective disorders. The current proposal, while acknowledging the likely importance of culture–gene coevolutionary processes at play here, offers a different interpretation of these observations, leading to novel predictions. Namely, according to the *fearful ape hypothesis*, rather than a buffering against susceptibility, cultural values, and norms characteristic of collectivism through its effects on increasing interdependence and cooperative care might in fact have benefitted fearful individuals' development the most.

To return to the proposed ontogenetic scenario, this research on gene–culture coevolution (Chiao & Blizinsky, 2010) may be viewed in support of the prediction that more fearful infants and children thrive more in rearing environments characterized by enhanced levels of cooperative care as seen in collectivistic societies, whereas they may suffer more in rearing environments characterized by much reduced levels of cooperative care as seen in highly individualistic environments. Indeed, there is evidence from cross-cultural research showing that fearfulness among infants and young children is more common in Eastern-collectivistic societies than in Western-individualistic societies (Gartstein et al., 2006; Slobodskaya, Gartstein, Nakagawa, & Putnam, 2012). More importantly, longitudinal work attests that, fearfulness in infancy, which in WEIRD individualistic contexts has been associated with a heightened risk for maladaptive developmental outcomes (Henderson et al., 2015; Sandstrom et al., 2020), predicted largely positive developmental outcomes including greater cooperative behavior and better peer relationships in a sample of Chinese children (Chen, Chen, Li, & Wang, 2009). Clearly, more work that directly assesses the predicted relation between fearfulness and the social and cultural environment by bridging between genes, brain, behavior, and culture is needed to explicitly investigate this theoretical claim.

To conclude, the empirical work reviewed and synthesized here advances the *fearful ape hypothesis* by demonstrating a link between human fearfulness traits and enhanced levels of cooperative behavior. The pattern of findings supports the notion of a virtuous caring cycle that views enhanced fearfulness as a key adaptive affective trait, enabling human-unique levels of cooperative concern and care. This new synthesis based on *the fearful ape hypothesis* stands in contrast to existing clinical work relying on WEIRD samples, conceptualizing heightened fearfulness as a predominately maladaptive trait increasing the risk of developing anxiety and depression. Viewing fearfulness traits through a WEIRD lens focused on risk conflicts with the presumed social environment that interdependent human group life evolved in and is adapted to (Hrdy, 2011; Hrdy & Burkart, 2020; Konner, 2018; Kramer, 2019; Tomasello et al., 2012). In contrast, according to the *fearful ape hypothesis*, fearfulness is considered an evolved adaptive trait that enhances cooperative care and success, which emerged in and is maintained by highly interdependent and supportive human societies. When viewed through this evolutionary lens, novel predictions are generated (see Fig. 1) and a radically different picture arises, painting an image of humans as fearful apes, trading off a risk for anxiety and depression with the affective foundations for cooperative care.

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Open Peer Commentary

Fearful apes or emotional cooperative breeders?

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Abstract

The "fearful ape hypothesis" is interesting but is currently underspecified. We need more research on whether it is specific to fear, specific to humans (or even cooperative breeders in general), what is included in "fear," and whether these patterns would indeed evolve despite arms races to extract help from audiences. Specifying these will result in a more testable hypothesis.

Grossmann argues that humans display unusually high levels of fear compared to other apes, and that we do so because heightened fear allowed our ancestors to acquire extra help from others, especially within the small-scale cooperative societies in which humans evolved. This "fearful ape" hypothesis is intriguing, but is currently underspecified. There are a number of issues that need to be addressed to flesh out the hypothesis and to increase its usefulness and its ability to generate novel predictions.

First, it is unclear whether the hypothesis should apply only to fear. There are many emotions or affective responses that elicit caring responses from parents or alloparents, including fear, hunger, discomfort, cold, sickness, and so on. If humans are more fearful because this elicits help from others, then all emotions that garner sympathy and assistance (henceforth "care-eliciting emotions") should be heightened in humans as well. To say that there's something special about fear, we would need much more research comparing parental responses to infant fear with other affective states, and how the heightened levels of fear in humans compare with other care-eliciting emotions.

Furthermore, if one's ability to detect fear is linked to increased helpfulness, then people's ability to detect other care-eliciting emotions (i.e., not just fear) should also lead to increased helpfulness. For example, prosocial behavior has been robustly linked to trait empathy, including the ability to accurately detect *all* emotions in others (Kim & Kou, 2014; Smith, Norman, & Decety, 2020). Although there are several studies showing enhanced cooperative behavior among children and adults who had heightened sensitivity to fearful faces (e.g., Kiel & Buss, 2011; Marsh & Ambady, 2007; Marsh & Blair, 2008; Marsh et al., 2014; Rajhans, Altvater-Mackensen, Vaish, & Grossmann, 2016), those studies either did not compare fearful faces with faces displaying other care-eliciting emotions, or found little difference. Other papers argue for the link between perceiving general emotions of distress and cooperation, rather than a specific link with fear (e.g., Warneken, 2015). To make the "fearful ape hypothesis" stronger and more specific, we need stronger evidence of fear being unique to other aversive states, and why. Without such evidence, it seems that instead of the "fearful ape hypothesis," a better term might be the "emotional ape hypothesis."

Second, it is unclear whether this hypothesis is specific to humans. Cooperative breeding is rare in primates, but is not unique to humans (reviewed by Hrdy, 2011). If the "fearful ape hypothesis" is true, then we should observe higher levels of fearfulness in callitrichid monkeys (e.g., marmosets, tamarins), as well as other cooperatively or communally breeding mammals (e.g., meerkats, naked mole rats, wild dogs, spotted hyenas, lions) and birds (e.g., scrub jays, groove-billed anis). If this heightened fearfulness is not observed in these species (relative to similar non-cooperatively breeding species), then this would rebut the "fearful ape hypothesis." There is evidence that both human children and (non-cooperatively breeding) orangutans attend preferentially to fearful faces (Pritsch, Telkemeyer, Mühlenbeck, & Liebal, 2017), which suggests that attention to fear is not limited to humans or other cooperative breeders.

Third, the target article characterizes fearfulness as an enhanced reactivity to, and avoidance of, novelty. It is unclear why this avoidance would elicit aid from others. Dangerous stimuli – whether novel or not – should trigger fear and elicit emergency aid to overcome that danger. Novel stimuli should not trigger emergency aid in the same way, although it is possible that they should trigger teaching. Framed in this manner, avoidance of novelty may be more indicative of anxiety or uncertainty rather than fear. Research on chimpanzees indicates that fear and anxiety result in different facial expressions (Parr, Waller, Vick, & Bard, 2007). However, anxious facial expressions in other great apes and their responsiveness to them are currently an underexplored topic (Kret, Prochazkova, Sterck, & Clay, 2020). Investigating whether there are cross-species differences in the detection of anxious faces rather than fearful ones may provide more relevant results to support the hypothesis.

Fourth, it is currently unclear why one's own expressed fear should be positively related to one's ability to detect fear in others (and respond with help). One might even predict the opposite relationship, given the potential arms race between individuals exaggerating their fear to extract more aid than they need versus audience members lowering their response threshold to avoid such exploitation. Young in other species do exaggerate their need (reviewed by Caro, West, & Griffin, 2016a), especially when other dependent siblings are present or when those siblings are only half-siblings because of remarriage, both of which occur regularly in humans (e.g., Daly & Wilson, 1999; Hrdy, 2011). These exaggerated reactions should then lead to lowered response thresholds. In fact, parents in poor and unpredictable environments respond less to signals of need, and rely more on signals of offspring quality (Caro, Griffin, Hinde, & West, 2016b). It is currently unclear how such arms races and lowering response thresholds would apply to cooperatively breeding species like humans, and whether this would cause an escalation of care-eliciting emotions. However, it does mean this part of the "fearful ape hypothesis" requires further specification, to understand how one's own fear levels are related to the ability to detect fear in others and respond with the appropriate help.

Overall, the "fearful ape hypothesis" is an intriguing idea, but several aspects are currently underspecified. By highlighting these aspects, we hope to advance the "fearful ape hypothesis" into a testable idea that can be supported or rebutted.

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The power of the weak: When altruism is the equilibrium

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Abstract

A rational economic analysis complements Grossmann's fearful ape hypothesis. Two examples of mixed-motive games with strong inter-dependence (i.e., weak chirping nestling, boxed pigs) demonstrate that signaling weakness is a dominant strategy. Weakness elicits cooperative, caring response, comprising the equilibrium of the game. In extensive form, a reliable reputation of weakness elicits caring as a sequential equilibrium.

Grossmann offers the *fearful ape hypothesis*: "… in the context of the strong interdependence … heightened fearfulness was adaptive… facilitate care-based responding … increasing cooperation with mothers and others" (target article, sect. 1 [Introduction], para. 2). Grossmann presents behavioral level and neuro-chemical brain responses to signals of fear. Phylogenetic research and ontogenetic research support the notion of heightened sensitivity to fear signals and the association to caring or cooperative responses.

This commentary offers a complementing game-theory rationale that supports Grossmann's fearful ape hypothesis. We present two famous examples of mixed-motive games with strong interdependence between asymmetric players. In both examples, a strong player's caring response for a weak player is economically rational, establishing the equilibrium of the game.

Example 1: The weak chirping nestling

This example is discussed in the Selfish Gene (Dawkins, 1976, 1989, Ch. 8). Referring to siblings' competition over parental investment, Dawkins first notes that being strong is an advantage. But what about the weak? Considering a bird feeding its nestlings, Dawkins notes that the weakest nestling sometimes chirps the loudest to get more than its fair share of food (see Fig. 1). Zahavi (1987) speculated that because loud chirps could attract predators to the nest, the mother's best response is to care for the loud chirper first to make it quiet and protect the nest. In terms of economic rationality, chirping loud is a dominant

Figure 1 (Barkan and Lahav). Feeding the weak first.

strategy for the weakest nestling, and feeding the weak nestling first is the stable solution of the game. According to Nash equilibrium, no player (i.e., the bird, weakest nestling, other nestlings) can gain more by unilaterally changing their behavior.

Example 2: The boxed pigs

A second example refers to "the Boxed Pigs" game (Baldwin & Meese, 1979). A big (strong) pig and a small (weak) pig are put in a box. Pressing a lever on one end of the box dispenses food at the other end of the box. Each pig has to choose between "wait" or "press." The food equals 10 utility units. Pressing the lever (and running to the other end of the box) costs two utility units (−2 for Press choice). If the weak pig presses the lever and the strong pig waits, the strong pig gets to the food first and consumes nine units, leaving only one unit for the weak pig. If the strong pig presses the lever and the weak pig waits, it gets to the food first and consumes four units of the food. If both press the lever and arrive at the same time, the strong pig will consume seven units and the weak pig will consume three units of the food. Recall that whoever presses the lever loses two utility units. Table 1 summarizes the outcomes for each pig in the four choice combinations of the game. In the lower-right cell both pigs wait and get nothing. In the upper-left cell both pigs press, arrive together to the food, and both pay the cost of pressing. In the lower-left cell the strong pig gains at the expense of the weak pig (selfish outcome). In the upper-right cell the small pig gains at the expense of the strong pig (caring outcome).

Table 1 (Barkan and Lahav). Outcomes in the Boxed Pigs game

		Small/weak pig	
		Press	Wait
Big/Strong Pig	Press	5, $\underline{1}$	4, $\underline{4}$
	Wait	9, $\underline{-1}$	0, $\underline{0}$

Note. Underlined values indicate food units for the small/weak pig.

Note that regardless of the choice of the strong pig, the weak pig is always better off waiting (than pressing). Thus, "wait" is the dominant strategy for the weak pig. The strong pig does not have a dominant strategy, but given that the small pig waits, the strong pig must press the lever or it will end up with nothing. The stable solution of the game is the caring outcome. The small pig gets all the four units of food it can consume, and the strong pig is left with just four units (i.e., 10 units, minus the "press" cost of two, minus four units consumed by the weak pig). This is a Nash equilibrium and neither the small nor the big pig can gain more by unilaterally changing their behavior.

Consistent with Grossmann's proposal, both examples demonstrate "the power of the weak" in eliciting a caring response. An economical rational analysis indicates that weakness can be a dominant strategy, leading to an equilibrium, where a strong player "cares" for a weak player (the bird feeds the weakest nestling first, the strong pig "sacrifices" its needs to provide for the weak pig).

We need to bridge the gap between these one-shot games and Grossmann's perspective of evolutionary based, brain-wired caring response to fear signals. We thus consider the above examples in extensive form where they are repeated over and over. Will the bird continue to feed the weak nestling? Will the strong pig keep pressing the lever?

In extensive form games, we consider sequential equilibrium and the effect of reputation. Reputation of a player is built through the history of their choices in former interactions (i.e., sub-games). Reliable reputations raise expectations for the player's future choices and guide the behavior of other players. If the equilibrium of the sub-game becomes the stable solution of the long, repeating game, it presents sequential equilibrium (e.g., Camerer & Weigelt, 1988; Kreps & Wilson, 1982). If the weak nestling establishes a reliable reputation of chirping, the bird will repeatedly feed it first. If the small pig consistently waits in each (or most) sub-games, the big pig will continue to provide the food. Beyond the above examples, economists consistently document prosocial altruistic behavior in a range of one-shot and repeated games (e.g., Camerer & Fehr, 2006; Henrich et al., 2005; Levitt & List, 2007; Smith, 2003). Complementing Grossmann's review, a rational economic analysis of strong asymmetric interdependence supports the notion that signaling fear and weakness can effectively elicit a cooperative, caring response.

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The human fear paradox turns out to be less paradoxical when global changes in human aggression and language evolution are considered

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Abstract

Our commentary focuses on the interaction between Grossmann's fearful ape hypothesis (FAH) and the human self-domestication hypothesis (HSDH), also taking into account language acquisition and evolution. Although there is considerable overlap between the two hypotheses, there are also some discrepancies, and our goal is to consider the extent to which HSDH can explain the phenomena identified by FAH without invoking fearfulness as directly adaptive.

Our commentary addresses the discrepancies pointed out by Grossmann between his fearful ape hypothesis (FAH) and the human self-domestication hypothesis (HSDH). In brief, according to FAH, fearfulness itself was adaptive in the context of cooperative caregiving unique to human group life, resulting in increased caregiving by adults, and ultimately, in increased cooperation with others. On the other hand, according to HSDH, increased cooperation in humans resulted from (sexual) selection for less aggressive partners (e.g., Hare, 2017; Hare & Woods, 2020), rather than for fearfulness per se. Grossmann concludes that HSDH is not well-positioned to explain what he identifies as the phenomenon of "increased fearfulness" in humans, given that successful animal domestication leads to a reduction in fearfulness, rather than an increase (Zeder, 2012). Our contention is that certain aspects of FAH may prove incompatible with some features of the human phenotype, which are better accommodated under HSDH, while at the same time, much of FAH, including cautiousness, can actually be accommodated under HSDH. The evidence we use to support these claims includes research on language acquisition and language evolution, as well as neurobiological considerations.

First, FAH relies, to a great extent, on research suggesting that human infants exhibit increased fearful responses to strangers, particularly Herrmann, Hare, Cissewski, and Tomasello's (2011) study. Notably, however, these authors also found that human children behave like bonobos in this respect. But bonobos have been claimed to have gone through a self-domestication process (Hare, Wobber, & Wrangham, 2012). Also, in the experiment by Herrmann et al., "strangers" are people totally unknown to children. But humans do exhibit reduced fearfulness toward more individuals than, for example, chimps, as our kinship systems go far beyond parent–child ties (Gowlett, 2018). Chimps contrast with bonobos in the fact that they have not been self-domesticated. In this sense, it is also noteworthy that hospitality codes, as found in present-day hunter–gatherers, which entail tolerance (i.e., reduced fearfulness) toward strangers, became generalized in our species during Upper Paleolithic (see Nikolsky & Benítez-Burraco, 2022, for discussion), in parallel with an increase in self-domestication features, as attested by the anthropological record (Cieri et al., 2014). It thus seems to us that FAH is not well-positioned to accommodate some unique elements that characterize humans, which are better accommodated under HSDH, the argument which we will further develop below.

Focusing on language, in particular, research suggests that shyness can impact negatively on language acquisition. For instance, shyer children tend to perform worse on measures of word learning (Hilton, Twomey, & Westermann, 2019), seemingly because of a less-efficient formation and retention of novel word–object mappings (Hilton & Westermann, 2017). Clinical conditions featuring abnormally high fearfulness and avoidance behaviors result in inadequate language acquisition, as is the case with Reactive attachment disorder (Raaska et al., 2012). Accordingly, it might be difficult to reconcile any trend toward increased fearfulness, as claimed by the FAH, with how human children acquire language. More specifically, at the age of 2.5 when children's fearfulness of novelty was compared to that of other primates in Herrmann et al.'s (2011) study, children have already experienced contact with a variety of cultural objects, some dangerous for them, and have already mastered a great deal of language, including being exposed to many warnings of dangers around them. This element in itself, unique to humans, may be contributing to the state of enhanced cautiousness/fearfulness in children, rather than selection for fearfulness itself.

With respect to language evolution, there is extensive research supporting the view that increased self-domestication in humans favoured the potentiation of many of the traits that make language more complex through a cultural mechanism, specifically, learning and shared intentionality (Thomas & Kirby, 2018). In our own work, we have emphasized the role of management of aggression in language evolution, in particular reactive aggression, which is a crucial ingredient of HSDH. In this respect, we have proposed that self-domestication favoured the emergence of early grammars, especially suitable for verbal aggression (insult), which in turn contributed to a gradual replacement of reactive physical aggression with verbal/cognitive contest, so that language complexity and self-domestication processes were engaged in a mutually reinforcing feedback loop (Benítez-Burraco & Progovac, 2020; Progovac & Benítez-Burraco, 2019). In comparison, it is not clear how increased fearfulness in humans would have resulted in the evolution of sophisticated languages.

Furthermore, we find that other outcomes of HSDH can account for the increased protective behavior toward children by adults, which is at the core of FAH, without a need to invoke selection for fearfulness. One such outcome is prolonged childhood/juvenile period, that is, helplessness, which, in itself, can be the cause of more adult caring and attention, including enhanced co-parenting, as children would have demanded more attention during longer periods and from more people (Bogins, 1999). Moreover, HSDH is associated with a reduction in sexual dimorphism, which in humans manifests itself as males becoming more like females (Gleeson & Kushnick, 2018). If females on average are more cautious, that is, less bold or reckless than males (e.g., McLean & Anderson, 2009), and if fearfulness responses are also inversely correlated to physical strength (e.g., Manson et al., 2022), then this feminization brought about by self-domestication could by itself have contributed to the human fearfulness (or cautiousness) phenotype, without a need to invoke any direct selection for fearfulness.

Finally, we wish also to note that most if not all the neurobiological mechanisms involved in fearful responses and invoked to provide support for FAH are indeed impacted by (self-)domestication, from the dopamine system to the oxytocin system. Accordingly, changes in the dopamine system have been extensively documented in domesticated animals (e.g., Komiyama et al., 2014; Sato et al., 2020). Likewise, in humans, oxytocin has been identified as a target of sexual selection contributing to a reduction in physically aggressive behavior (Hare, 2017). In our opinion, this further reinforces our argument that HSDH can account for many aspects of the human distinctive phenotype, including fearfulness/cautiousness, weakening the case for FAH.

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Heightened fearfulness as a developmental adaptation

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Abstract

Although we find many merits to Grossmann’s fearful ape hypothesis, unlike Grossmann, we see heightened fearfulness as an ontogenetic adaptation, signaling helplessness and fostering caregiving during infancy, which subsequently became exapted to promote cooperation. We also argue that, rather than being the “breeding ground” for enhanced infant fearfulness, cooperative care is more likely the evolved product of enhanced fearfulness.

Grossmann’s *fearful ape hypothesis* stipulates that heightened fearfulness is an adaptation, first seen in infancy, to solve the problem of cooperation in *Homo sapiens*, mostly mediated by cooperative care. Grossmann documents powerful links between heightened fearfulness traits and enhanced levels of cooperation in humans, based on a comprehensive approach to fearfulness and grounded in the four ethological questions proposed by Tinbergen. Grossmann's approach also demonstrates the merit of an evolutionary-developmental framework to better understand both the potential adaptive and maladaptive effects of a trait (here, heightened fearfulness), depending on the type of human society (small-scale vs. large-scale), culture (Western-individualistic vs. Eastern-collectivist), and rearing environments (harsh and unpredictable vs. easy and predictable), where both child and adult life takes place. In our commentary, we focus on two issues: (1) The conceptualization of the adaptive nature of heightened fearfulness from an evolutionary-developmental psychological perspective, and (2) the assumption that cooperative breeding is a precondition (or "breeding ground") for the adaptive role of heightened fearfulness in infancy.

Grossmann essentially conceptualizes heightened infant fearfulness as an isolated adaptation associated with enhanced cooperation. We argue instead that heightened fearfulness is better viewed as part of a suite of evolved features that serve to signal, in a reflex-like way, adults' caregiving motivations and actions toward helpless babies, increasing the chances that infants will be attended to, cared for, form attachments, and survive. Other infantile adaptations that foster infant attention and attachment, including neotenous facial features (Lorenz's kindchenschema, or baby schema), smiles, laughs, and vocal behaviors such as coos and cries (e.g., Bründl et al., 2021; Hrdy & Burkart, 2022), decline in influence with time. In contrast, Grossmann's view of humans' heightened fearfulness is best conceptualized as a *deferred adaptation* (an evolutionary solution to a problem beginning early in life and serving the same or similar function later in development, Hernández Blasi & Bjorklund, 2003), having both an immediate function in infancy (increasing the chances of adult caregiving) and a deferred one later in life (contributing to older humans' enhanced ability to cooperate, including in childcare). Although this is a reasonable proposal, an alternative, and we argue a more likely possibility, is that heightened fearfulness first stabilized as an *ontogenetic adaptation* (Bjorklund, 1997; Oppenheim, 1981), serving to promote infant attachment and survival at a particular time in development, and that its subsequent role in promoting cooperation can be better thought of as an *exaptation*, or spandrel (Gould, 1991), a feature whose final function is quite different to the one originally shaped by natural selection. Rather than heightened fearfulness being directly selected because of its benefits to cooperation, cooperation was, in part, a gradually evolving byproduct of a developmentally stable fearful temperament, with ancestral fearful infants growing up to become cooperative (and cooperative-caring) adults.

Central to Grossmann's thesis is that *cooperative breeding* (Hrdy, 1999; Kramer, 2019) was a precondition for fearfulness to develop and stabilize as an adaptation over the last 1.8 million years or so of *Homo* phylogeny. We concur with theorists who argue that cognitive and affective changes in *Homo sapiens* resulted in increased abilities to cooperate and are substantially responsible for humans' current ecological dominance (e.g., Hare, 2017; Tomasello, 2019), and that cooperative childcare was an important component in this evolution. However, we question whether cooperative childcare was a precondition for the emergence of an adaptation of infant fearfulness and its later impact on adult cooperation. It is more parsimonious, we believe, that increased infant fearfulness arose over humans' biological history along with other "psychological weapons" (Trivers, 1974) infants evolved to compete with their parents (mainly their mothers) for investment, independent of any cooperative-caregiving practices. Although infants' fearful responses might be signals of helplessness and dependence to unrelated adults, infants' wariness of strangers might actually make it less likely (not more so) for a nonparent to form attachments to them. All primate infants display fear of loud noises, abandonment, and falling, and human babies' greater fearfulness relative to chimpanzees might instead be a neotenous feature, maintaining and extending fearfulness into later development. Rather than being the "breeding ground" for enhanced infant fearfulness, we argue that cooperative care is more likely the evolved product of enhanced fearfulness, along with other adaptations (e.g., increased inhibition, tolerance for conspecifics, friendliness, Hare, 2017) that led to *Homo sapiens*' remarkable degree of cooperation, including cooperative care.

The fearful ape hypothesis has much to offer. Regardless of whether greater human fearfulness is an adaptation selected primarily to make babies more attractive to adults and used as a byproduct for adult cooperation, or a full-fledged adaptation derived from cooperative care, it identifies heightened fearfulness as an evolved feature of *Homo sapiens*, adds to the list of infantile features that promote caregiving, and generates discussion about the entwined relations between evolution, development, and culture.

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Is there a human fear paradox? A more thorough use of comparative data to test the fearful ape hypothesis

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Abstract

Grossmann's intriguing proposal can benefit from a more thorough integration of the primate literature, particularly on neophobia. Moreover, it directly leads to strong predictions in callitrichids, the only other cooperatively breeding primates beyond humans, which may indeed be met: Being more likely to signal distress than independently breeding monkeys, and responding to such signals with approach and affiliation.

Grossmann proposes that humans are particularly fearful apes, and more likely to react to signals of fearfulness in others not only with fight and flight reactions, but also with approaching distressed individuals which can result in providing comfort, support, or even help. The hypothesis that this may be linked to our reliance on allomaternal care fits well with the cooperative breeding model of human evolution (Burkart, Hrdy, & van Schaik, 2009; Hrdy, 2009; Hrdy & Burkart, 2020), and is carefully elaborated regarding the ontogenetic patterns in humans and underlying brain mechanisms.

Grossmann's comparative evidence is taken from Herrmann, Hare, Cissewski, and Tomasello (2011), who showed that 2.5-year-old human toddlers indeed have a more fearful temperament than adult orangutans, bonobos, and chimpanzees. However, because fearfulness (i.e., enhanced reactivity to, and inhibited approach of, novel situations, objects and people; target article, sect. 2, para. 1) is well known to change dramatically during ontogeny in primates, as well as with settings (wild vs. zoo), the conclusion that humans are more fearful than other apes requires further evidence. Immature primates are remarkably neophobic. For instance, Forss, Motes-Rodrigo, Hrubesch, and Tennie (2019) report higher neophobia in immature nonhuman apes than adults in captivity. Unfortunately, the younger age classes directly comparable to the 2.5-year-old human toddlers from Herrmann et al. (2011) were not part of this sample. Immatures are also more neophobic in the wild (e.g., orangutans: van Schaik et al., 2016; capuchin monkeys: Perry, 2020) and some, including the marmoset monkeys, who notably are cooperative breeders like humans, are so neophobic as young immatures that they may not even touch novel food unless they can first observe that adult group members are accepting it (Voelkl, Schrauf, & Huber, 2006). By adolescence, however, the pattern changes and individuals go through a period of low neophobia and high risk-taking (Taylor et al., 2022; van Schaik et al., 2016), which likewise resembles human developmental patterns. Without taking this systematic age-based trajectory into account and thus only comparing subjects at the same developmental stage, a meaningful comparison of fearfulness in humans and other primates is impossible. This comparison is further hampered by captivity effects which can remarkably decrease neophobia, for instance in orangutans who even as adults will avoid novel objects in the wild for months, but happily interact with the same novel objects in captivity immediately (Forss, Schuppli, Haiden, Zweifel, & van Schaik, 2015; van Schaik et al., 2016; see Forss, Motes-Rodrigo, Dongre, Mohr, & van de Waal [2021] for vervet monkeys). These setting effects strongly suggest that also for humans, fearfulness needs to be assessed cross-culturally, and not only based on Western, educated, industrialized, rich, and democratic (WEIRD) populations. The jury for whether humans, and in particular human infants, are indeed more fearful may thus still be out.

Grossmann's proposal directly leads to additional evolutionary predictions. First, the comparative evidence does not have to be restricted to comparing human and nonhuman apes. Through broad phylogenetic analyses, we can test in a wider range of species whether interspecific variation in fearfulness is indeed correlated with variation in allomaternal care. Phylogenetic tests can also be more targeted (MacLean, 2016) and focus on specific contrasts, in this case not only the contrast between humans and other apes, but also the one between callitrichid monkeys (i.e., marmosets and tamarins), which are the only cooperatively breeding primates beyond humans, and their closest, but independently breeding sister taxa, the cebids (capuchin monkeys and squirrel monkeys). Additional contrasts targeting the role of cooperative breeding can be found outside primates, for instance in voles (see below).

Second, evolutionary predictions can be made not only for fearfulness. Signaling fearfulness may well be only part of a larger package in cooperative breeders to more readily signal affective states to others (Burkart et al., 2022), because in tightly knit interdependent groups, this will facilitate behavioral coordination, and immatures are under selection pressure to attract helpers, for example, by signaling their neediness. A comparative analysis of relative neuropil fraction of the facial nucleus indeed suggests a link between allomaternal care and facial dexterity which can facilitate communication and coordination (Cerrito & DeCasien, 2021). Moreover and in line with this comparative evidence, when callitrichids ingest non-palatable food, they often produce gag faces that group members can use to learn to avoid this type of food (Snowdon & Boe, 2003). Perhaps most impressively, immature callitrichids engage in conspicuous babbling behavior, loudly announcing their neediness and vigor (Snowdon, 2001). These behaviors appear shared between humans and callitrichid monkeys, but have not been reported in other primates.

But do callitrichid monkeys also react with approach when group members signal their affective states? Some evidence suggests they do. When infants are babbling, adults are more likely to approach and interact with them, highlighting that one function of babbling is indeed the attraction of caregivers (Snowdon, 2001). When adults can observe how infants unsuccessfully struggle to open a specific apparatus to reach the food inside, they are more likely to share food that they have to extract from this apparatus than food that is freely handed over, suggesting some flexible adjustment to infant need (Martins & Burkart, 2013; Sehner & Burkart, 2022). Among adults, marmosets observing the fear-related signal "piloerection of the tip of the tail" in others showed higher rates of affiliative behaviors (de Boer, Overduin-de Vries, Louwerse, & Sterck, 2013). In a follow-up study, de Oliveira Terceiro, Willems, Araújo, and Burkart (2021) found that naïve marmosets who encountered a group member displaying this fear signal preferentially approached this distressed individual even when not aroused themselves. Intriguingly, a similar pattern was also found in voles and could directly be linked to cooperative breeding and oxytocin. Burkett et al. (2016) reported that within pairs of the cooperatively breeding prairie voles (*Microtus ochrogaster*), an unstressed partner increased its grooming of a stressed partner; an oxytocin receptor antagonist infused into the anterior cingulate cortex abolished this partner-directed response. In contrast, the closely related, independently breeding meadow voles (*M. pennsylvanicus*) did not show this consolation behavior at all.

In line with Grossmann's proposal, these results suggest that in cooperative breeders, internal affective states may be more readily signaled to group members, and perceiving others in distress may indeed elicit affiliative approach. However, to what extent the fearful ape hypothesis, or which elements of it, will stand the test of time has to await more systematic comparisons of directly comparable data, in the context of broader phylogenetic analyses or targeted comparisons (MacLean, 2016).

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The adaptiveness of fear (and other emotions) considered more broadly: Missed literature on the nature of emotions and its functions

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Abstract

We agree with Grossmann that fear often builds cooperative relationships. Yet he neglects much extant literature. Prior researchers have discussed how fear (and other emotions) build cooperative relationships, have questioned whether fear per se evolved to serve this purpose, and have emphasized that human cooperation takes many forms. Grossmann's theory would benefit from a wider consideration of this work.

We agree with Grossmann that experiencing and expressing anxiety/fear can signal support is needed (Clark & Taraban, 1991) and can elicit support (Graham, Huang, Clark, & Helgeson, 2008; Simpson, Rholes, & Nelligan, 1992). Expressing fear also serves a social referencing function by allowing observers to use others' fear expressions to evaluate situations for themselves (Klinnert, Emde, Butterfield, & Campos, 1986; Schachter, 1959).

Yet, we disagree that psychologists, to date, have *mostly* considered fear and its expression to be dysfunctional and also with the implication readers may draw from Grossman's article that fear is "the" one emotion that promotes cooperative relationships. We also question the idea that infants are evolutionarily prepared at birth to feel and to express fear per se and that caretakers are evolutionarily prepared to respond to fear per se with care. Finally, in analyzing how emotions can underlie human cooperation we think it is important to recognize that human cooperation assumes more than one form and that the form or combination of forms it takes will vary with relationship type (Bugental, 2000; Clark & Mills, 1979, 2012). This means the functionality or dysfunctionality of expressing fear will be dependent upon the type relationship under consideration.

Is the idea that fear builds cooperative relationships novel?

No. Grossmann suggests that psychologists predominantly view heightened experience and expression of fear and anxiety to be dysfunctional. However, large, long-standing, literatures on social referencing and social support show that feeling and expressing fear is often supportive of human cooperation.

Included in this literature are studies by developmentalists showing that very young children interpret their caretakers' and even a familiar experimenters' expressions of fear as signals that they ought not cross a visual cliff (Klinnert et al., 1986; Sorce, Emde, Campos, & Klinnert, 1985). Moreover, both classic (Schachter, 1959) and recent (Scarantino, Hareli, & Hess, 2021) research shows another's fear serves social referencing functions for adults. Extant work also shows expressing fear signals a desire for support (Scarantino et al., 2021), that humans selectively express fear (and other emotions) to potentially trusted-caring others (Clark & Finkel, 2005; Von Culin, Hirsch, & Clark, 2017) and that doing so often elicits support (Graham et al., 2008; Simpson et al., 1992). Simpson et al. (1992), for instance, brought dating couples into a laboratory. The female member was subjected to a fear induction and then the couple was left alone. Results showed that the more anxiety/fear securely attached women displayed, the more they sought support and the more care that securely attached male partners provided. To give another example, in study 1 of a paper published by Graham et al. (2008), participants read vignettes about a person who needed help. In the condition where this person was described as expressing fear/anxiety, participants said they would provide the person with more help. In study 2 of the same paper, when a confederate in a laboratory study looked fearful and verbally expressed fear that confederate received more help than the same confederate who did not behave in these ways. In a fourth and final study, self-reports of willingness to express negative emotions (including fear/anxiety) prior to college arrival predicted forming more relationships, achieving greater intimacy in the closest of those relationships, and receiving more support from roommates across their first semester of college.

Psychologists do not view fear as "mostly" dysfunctional

As just noted, many psychologists recognize adaptive functions of fear. They also know that fear *can* be dysfunctional when it is disproportionate to the fearful person's needs (Lemay & Dudley, 2011), prevents engagement in normal activities (National Institute of Mental Health, 2022), is expressed to insecure partners (Simpson et al., 1992), or is expressed in non-communal relationships wherein it may invite exploitation. There is no paradox. There simply exist social bounds within which feeling and expressing fear is and is not adaptive and it is also the case that some people do persistently experience clinically debilitating levels of fear.

Have humans evolved to feel and to express fear per se at birth?

Is fear "the" emotion that has evolved to be expressed and to promote human cooperation? We think not. Rather we and many others (e.g., Barrett & Campos, 1987; Stroufe, 1996) believe human infants are prepared to feel and express distress at birth (which is negatively valenced and associated with arousal) when they have a variety of needs. Parents appear to be prepared to respond with care. When this adaptive pairing occurs again and again it builds trust and cooperative bonds (Leerkes, Blankson, & O'Brien, 2009). Later, as social and conceptual learning and language develop, children differentiate distress into more granular conceptual categories such as fear, sadness, anger, embarrassment, and disgust (Hoemann, Xu, & Barrett, 2019; Holodynski & Seeger, 2019). The expression of these negative emotions (and positive emotions too) conveys valuable information about the welfare of the expresser. Their expression, when appropriate to the relational context, supports human cooperation in nuanced ways that have been documented (e.g., Algoe, Fredrickson, & Gable, 2013; Clark, Ouellette, Powell, & Milberg, 1987; Donato, Pagani, Parise, Bertoni, & IaFrate, 2014; Feinberg, Willer, & Keltner, 2011; Gable & Reis, 2010; Semin & Manstead, 1982). There certainly exists broad theoretical disagreement on the nature of emotion among psychologists, but currently insufficient evidence that feeling and expressing heightened fear per se (rather than general distress) is evolutionarily determined and present at birth.

More than one type of cooperative relationship exists

Human cooperation takes many forms (Bugental, 2000; Clark, Earp, & Crockett, 2020). Cooperation in parent/infant relationships, friendships and romantic relationships, business relationships, and in leader–follower relationships differs in form and function (Earp, McLoughlan, Monrad, Clark, & Crockett, 2021). Grossmann appears to write about just one type of cooperative relationship, which aligns with what Clark and Mills (1979, 2012) would call an asymmetrical communal relationship and which Bugental (2000) would call an attachment relationship. In such a relationship a child expresses needs to which caretakers typically respond with non-contingent given care. Yet, cooperation (and caring about treating partners well) takes a very different form in, for example, exchange/transactional relationships. In these relationships, benefits are provided with the expectation of receiving comparable benefits in exchange or in repayment of these provisions (Clark, 1984; Clark & Mills, 1979, 2012). Expressions of emotion are less likely to occur within these relationships (Von Culin et al., 2017). Indeed, doing so can make a person appear especially dependent (Clark & Taraban, 1991), making them vulnerable to exploitation. In exchange relationships partners can be unresponsive to expressions of emotions (Clark et al., 1987). To understand how fear and other emotions and their expression subserve cooperation, we must specify the type of cooperative or non-cooperative relationship about which we are talking.

Summary

Emotions and their expression, fear included, subserve cooperative relationships. Yet to understand how, when, and why this develops (and sometimes goes awry) more attention to and integration with extant work on the nature of emotion, the social function of emotions, and the cooperative (or lack thereof) nature of social relationships is needed.

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More than fear: Contributions of biobehavioral synchrony and infants' reactivity to cooperative care

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Abstract

We present two challenges to the *fearful ape hypothesis*: (1) biobehavioral synchrony precedes and moderates the effects of fear on cooperative care, and (2) cooperative care emerges in a more bidirectional manner than Grossmann acknowledges. We present evidence demonstrating how dyadic differences in co-regulation and individual differences in infants' reactivity shape caregivers' responses to infant affect.

Expressing and recognizing fear in conspecifics is critical to survival. In the *fearful ape hypothesis*, Grossmann thoughtfully integrates evidence from comparative, developmental, and neuroscience research to explain how fear developed differently in humans compared to our primate relatives. By focusing exclusively on fear, however, some of the most complex dynamic factors contributing to the development of cooperative care are neglected. We present two challenges to the *fearful ape hypothesis*: (1) biobehavioral synchrony is a precursor to cooperative care that precedes the development of fear and varies as a function of a multitude of factors, and (2) cooperative care emerges in a more bidirectional manner than implied by this target article.

First, most accounts, including Grossmann's, suggest that fear does not develop until the latter half of the first year. Yet, infants are already engaging in biobehavioral synchrony with their caregivers in the first few months of life (e.g., Feldman, 2007). Synchrony is highly associated with early cooperative behavior and contributes to the development of infants' emotion regulation (Feldman, Greenbaum, & Yirmiya, 1999), including their negative affect in novel or stressful situations such as the still-face paradigm (Tronick, Als, Adamson, Wise, & Brazelton, 1978). For example, infants often exhibit distress when mothers withdraw interactive cues during the still-face episode because it violates their expectations about parental responsiveness (Jones-Mason, Alkon, Coccia, & Bush, 2018). Critically, synchrony is not present all the time even when the mother is contingently responsive, because successful affective communication between mother and infant involves a series of mismatched states that are repeatedly repaired through the dynamic and reciprocal interaction of the mother and child (Tronick & Beeghly, 2011). Recent work from our laboratory points to physiological synchrony as a key moderator of infants' affect regulation. We found that once mothers resume engagement following the still-face stressor, there is a significant reduction of negative affect for those infants who displayed positive physiological synchrony with their mothers during the initial face-to-face episode, but only among infants with less developed autonomic nervous systems (Abney, DaSilva, & Bertenthal, 2021). Mothers also dynamically alter their behaviors, including their gaze, facial expressions, vocalizations, and movements, to match those of their infants (e.g., Chong, Werker, Russell, & Carroll, 2003; MacLean et al., 2014). Moreover, high values on a composite measure of maternal prosody are associated with a reduction of infant negative affect following the still face, with larger reductions observed among infants with lower capacity for self-regulation (Kolacz, DaSilva, Lewis, Bertenthal, & Porges, 2022). These results are important because they demonstrate that biobehavioral synchrony changes as a function of the characteristics of the dyad as well as infants' developmental status.

The *fearful ape hypothesis* focuses too narrowly on fear as a trigger of cooperative care without sufficient acknowledgement of the many other affective factors that contribute to effective parenting. Over time, repeated interactions with responsive caregivers provide predictability and safety for the infant, which in turn fosters the development of secure attachment with caregivers (Gee & Cohodes, 2021). Importantly, good parenting develops both through responding to infants' distress, but also through responding to other emotions, including positive emotions such as joy (Leerkes, Blankson, & O'Brien, 2009; Lohaus, Keller, Ball, Elben, & Voelker, 2001) and interest (Hammond & Drummond, 2019). The sharing of positive experiences is foundational to healthy caregiver–child interactions (e.g., Brown & Fredrickson, 2021; Ramsey & Gentzler, 2015). By focusing exclusively on fear, Grossmann overlooks how maternal responsiveness to other emotions, and early, recurring experiences with parental co-regulation more broadly, lead to positive socioemotional development and cooperative care.

Second, the *fearful ape hypothesis* presents fearfulness as a state of helplessness that the caregiver must respond to without considering bidirectional pathways through which the infant has the agency to dynamically influence the interaction. In three well-known paradigms for infant research – still face, strange situation, and visual cliff – infants are faced with a challenge that violates their expectations. Yet, it is not the case that all infants exhibit negative affect and wait for their caregivers to soothe them. Rather, many infants actively solicit responses from their caregivers or look for cues signaling how to behave. For example, some infants as young as 2–3 months will attempt to re-engage their still-faced mother through social bids – looking at her while smiling or vocalizing (Bigelow & Power, 2016). Infants will also use social referencing by attending to adults' facial expressions to gauge how to respond to their uncertain situation, such as whether to traverse the deep side of the visual cliff (Sorce, Emde, Campos, & Klinnert, 1985), or what to do when presented with an unfamiliar toy (Klinnert, Emde, Butterfield, & Campos, 1986). Over the course of the first year, infant–caregiver interactions become more interactive and bidirectional, such that infants initiate and actively elicit responses from their caregivers just as caregivers are responding to their infants (Beebe et al., 2016; Chow, Haltigan, & Messinger, 2010; Tronick & Gianino, 1986). These changes in communicative pathways are further influenced by infants' temperament because differences in reactivity interact with maternal sensitivity and responsiveness to the child's needs. Notably, infants with negative temperaments receive less responsive parenting, including reduced parental co-regulation, compared to their less fussy peers (Bridgett et al., 2009; Mills-Koonce et al., 2007). In sum, infants' own behaviors influence and elicit responses from their caregivers, suggesting that cooperative care involves more than the caregivers' response to the child.

In conclusion, the relation between the emergence of fear and cooperative care is more complex and multifaceted than implied by the *fearful ape hypothesis*. The reviewed evidence supporting how fear contributes to cooperative care is incomplete because it neglects the emergence of cooperative care in the broader context of infant–parent affect regulation, particularly early experiences with caregivers co-regulating both negative and positive emotions. Children's fearful responses may be adaptive in eliciting cooperative care, but not all the time and not for all individuals. This hypothesis overlooks many of the complex interactions between emotion, temperament, and biobehavioral synchrony that shape good parenting and cooperative care. As we discussed, cooperative care emerges from co-regulation, and as such it is a co-created experience that depends jointly on the caregiver as well as the child.

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We aren't especially fearful apes, and fearful apes aren't especially prosocial

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Abstract

Grossmann posits that heightened fearfulness in humans evolved to facilitate cooperative caregiving. We argue that three of his claims – that children express more fear than other apes, that they are uniquely responsive to fearful expressions, and that expression and perception of fear are linked with prosocial behaviors – are inconsistent with existing literature or require additional supporting evidence.

Are we really fearful apes, and are fearful apes more prosocial?

Grossmann proposes that humans are both more likely to express fear than other ape species and particularly sensitive to conspecifics' fear. This heightened fearfulness and fear detection, then, serves to elicit approach from caregivers, and increases one's own tendency to approach needy conspecifics. These tendencies ultimately ensure that humans receive, and deliver, the nurturance that uniquely characterizes our species. In what follows, we argue that these claims, although interesting and provocative, are currently unsupported by the broader literature in at least three ways. First, the assertion that humans are particularly fearful requires further evidence. Second, infants' sensitivity to fear ("fear bias") may not actually reflect responsiveness to fear specifically, but rather to a broad range of distress signals. Finally, associations between both the expression and perception of fear and children's own prosocial behaviors are empirically tenuous. We detail our concerns below, ultimately concluding that the "fearful ape" may not be a useful description of the human species.

One aspect of Grossmann's hypothesis is that humans experience and express higher levels of fear than do other nonhuman primates. Support for this assertion comes from a single study (Herrmann, Hare, Cissewski, & Tomasello, 2011) in which human infants demonstrated relatively more avoidance toward novel objects and people than did nonhuman ape species. These findings, however, suffer from some important confounds. First, there were significant age differences between the human (2.5 years) and nonhuman (6.4, 6.5, and 6.8 years) primate participants, a difference exacerbated by the faster rate of maturation in nonhumans. These age differences resulted in significant body size differences between participants and experimenters across species. That is, compared with 6.5-year-old nonhuman apes, 2.5-year-old children are much smaller than an adult experimenter, and might have displayed more fear because of the vulnerabilities this size difference entailed. Indeed, although this condition was not without interpretive difficulties, a control condition in which the experimenter was absent from the scene revealed no increased avoidance in humans. Thus, claiming that heightened fearfulness is an essential feature of the human species may be premature.

Another facet of Grossmann's hypothesis posits that infants are particularly sensitive to others' fear. We propose, instead, that the literature is more consistent with a general sensitivity to distress (Decety et al., 2016; de Waal & Preston, 2017). While human infants do demonstrate sensitivity to fear (Leppänen & Nelson, 2012), they are also highly receptive to distress signals, including pain and sadness (Addabbo, Bolognini, & Turati, 2021; Davidov et al., 2021; Dondi, Simion, & Caltran, 1999). The fear bias literature typically compares infants' responses to fear solely with anger and happiness (Grossmann, Missana, & Krol, 2018; Peltola, Leppänen, Mäki, & Hietanen, 2009; Xie, McCormick, Westerlund, Bowman, & Nelson, 2019); these comparisons do not distinguish the "fearful ape" from the "distressed ape." Indeed, some studies have shown that infants respond comparably and/or inconsistently to any arousing and/or threatening emotions (fear, anger, pain) relative to happy/neutral stimuli (Cheng, Lee, Chen, Wang, & Decety, 2012; Hunnius, de Wit, Vrins, & von Hofsten, 2011; Vanderwert et al., 2015). Thus, more evidence is required to show that infants are uniquely sensitive to fear.

Further, Grossmann suggests that the enhanced experience and privileged perception of fear make humans more caring and cooperative. To support the link between heightened fearfulness and prosociality, he draws from evidence suggestive that heightened fearfulness enhances children's guilt proneness, which in turn reduces rule violation (Kochanska, Gross, Lin, & Nichols, 2002). He also cites research showing that heightened fearfulness in children is associated with enhanced theory-of-mind skills (Wellman, Lane, LaBounty, & Olson, 2011), thought to be important for cooperation (Tomasello, Carpenter, Call, Behne, & Moll, 2005). Although guilt proneness and social-cognitive competencies are clearly relevant to prosociality, they are at best indirect measures. Further, direct evidence seems to contradict Grossmann's claims. For example, shyness is a core dimension of fearfulness traits (Henderson, 2010; Poole, Tang, & Schmidt, 2018). Many studies have shown that higher levels of shyness is associated with reduced, rather than enhanced, prosocial behavior (Beier, Terrizzi, Woodward, & Larson, 2017; Eisenberg et al., 1996; Karasewich, Kuhlmeier, Beier, & Dunfield, 2019; Tan, Mikami, Luzhanska, & Hamlin, 2021; Young, Fox, & Zahn-Waxler, 1999), presumably because prosocial behavior requires social interaction with unfamiliar others. In addition, exhibiting fearfulness and inhibited responses early in life has consistently been associated with less adaptive social functioning (e.g., fewer close friends, higher loneliness, less prosocial behavior) and greater risk for developing social anxiety later in life (Clauss & Blackford, 2012; Eisenberg, Spinrad, Taylor, & Liew, 2019; Liew et al., 2011; Sandstrom, Uher, & Pavlova, 2020; Tang et al., 2020). Thus, rather than promoting prosociality, enhanced fearfulness appears to have a negative impact on prosocial behavior specifically and social functioning broadly.

To support the assertion that sensitivity to fear facilitates children's prosociality, Grossmann offers limited evidence that children who exhibit a fear bias are more helpful and generous (Grossmann et al., 2018; Rajhans, Altvater-Mackensen, Vaish, & Grossmann, 2016). However, different means of measuring fear bias across these studies (e.g., latency to fixate, duration of first look) make this argument less convincing. Further, it seems that responsiveness to distress signals generally, not fear specifically, elicits caring behavior (Davidov, Zahn-Waxler, Roth-Hanania, & Knafo, 2013; Decety, 2016). For instance, individual differences in 3–10-month-olds' empathic concern for peers and adults feigning injury (i.e., pained, not fearful) predicts caring responses at 12–18 months (Davidov et al., 2021; Roth-Hanania, Davidov, & Zahn-Waxler, 2011), suggesting a role for processing others' pain in facilitating prosocial responses. Even past work from Grossmann's own lab suggests that viewing painful (vs. angry) expressions activates approach mechanisms during infancy (i.e., left hemisphere activation; Missana, Grigutsch, & Grossmann, 2014). Thus, evidence supporting a unique relationship between responsiveness to fear and caring behaviors appears tenuous at best.

Although Grossmann's hypothesis is intriguing, it contradicts existing work or requires further evidence to support three of its major claims: That humans are particularly fearful, highly receptive to fear, and that these tendencies promote prosociality. Instead, it is more likely that human caregiving and prosocial behavior result from the expression of, and sensitivity to, a broad range of distress cues.

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Conceptualization, context, and comparison are key to understanding the evolution of fear

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Abstract

The fearful ape hypothesis proposes that heightened fearfulness in humans is adaptive. However, despite its attractive anthropocentric narrative, the evidence presented for greater fearfulness in humans versus other apes is not sufficient to support this claim. Conceptualization, context, and comparison are strongly lacking in Grossmann's proposal, but are key to understanding variation in the fear response among individuals and species.

Grossmann presents the fearful ape hypothesis, claiming that from infancy humans are more fearful than other apes, and that "in the context of cooperative caregiving and provisioning unique to human great ape group life, heightened fearfulness was adaptive" (target article, abstract). We consider Grossmann's hypothesis to represent a false premise. We question the evidence provided to demonstrate heightened fearfulness in humans, which is critical to the author's argument. In the absence of such evidence, the proposed hypothesis does not take us beyond adaptationist storytelling (Gould & Lewontin, 1979) and we believe it should currently be treated as such. We argue that conceptualization, context, and comparison are strongly lacking in Grossmann's proposal, but are key to understanding variation in the fear response among individuals and species.

Grossmann discusses heightened fearfulness in humans without any explicit conceptualization or definition of how we should measure this multifaceted and complex emotional state (Boissy, 1995). While subjective conscious experience of emotion may be asked verbally of humans, this is not possible in pre-verbal infants, humans without language, or other animal species. Therefore, proxy measurements of emotional processes (including fear) have been used, including behavioural, neurobiological, physiological, and cognitive responses of individuals to a variety of different stimuli (Paul, Harding, & Mendl, 2005). Such methods offer important insights into the evolution of emotion. However, the results can be very difficult to interpret and judgements concerning affective states are stronger if based on multiple techniques and/or correlated measures, with appropriate controls (Miller, Garner, & Mench, 2006; Safryghin, Hebesberger, & Wascher, 2019). Grossmann cites a single study (Herrmann, Hare, Cissewski, & Tomasello, 2011) as evidence for heightened fearfulness in humans. However, that study (Herrmann et al., 2011) uniquely examines the behavioural responses of infant humans and apes to specific novel objects as a measure of temperament (shyness–boldness, or neophobia). Interpretation of this methodological paradigm has recently been criticized (Takola, Krause, Müller, & Schielzeth, 2021), and the inference that affective states such as fear may be judged by the behavioural response to novel objects alone is not supported by the current literature (Crane, Brown, Chivers, & Ferrari, 2020; Greggor, Thornton, & Clayton, 2015). A single study, based on a small number of "WEIRD" (Henrich, Heine, & Norenzayan, 2010) and "STRANGE" (Webster & Rutz, 2020) subjects (24 bonobos, 24 chimpanzees, 24 orangutans, and 14 German children), and which uses a single behavioural measure, is simply not sufficient to establish the key evidence for Grossmann's claim.

Grossmann also characterizes fearfulness (measured as neophobia) as a species-level trait, which does not vary across individuals or contexts. However, responses to novelty are known to be highly context dependent, varying with a range of social, cultural, environmental, and developmental factors (Coleman & Mellgren, 1994; Forss, Koski, & van Schaik, 2017; Greggor, Clayton, Fulford, & Thornton, 2016; Miller, Bugnyar, Pölzl, & Schwab, 2015; Moretti, Hentrup, Kotrschal, & Range, 2015; Webster & Lefebvre, 2000). For example, food neophobia in children varies considerably across differing cultural environments (Birch, 1995). Furthermore, some species show high individual repeatability in their responses over time, and to different types of novelty, whereas other species are seemingly more flexible (Miller et al., 2022; Vernouillet & Kelly, 2020). More broadly, ecological factors such as resource availability (Greggor et al., 2016) and, in particular, predation pressure (Isbell, 2006; Kawai & Koda, 2016; Öhman, 2009) are known to play a significant role in both intra- and inter-specific variation in fear responses (Mobbs, Hagan, Dalgleish, Silston, & Prévost, 2015; Pellman &

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Kim, 2016); often conceptualized as "the ecology of fear" (e.g., Laundre, Hernandez, & Ripple, 2010). Context can define whether neophobia is adaptive for an individual in the evolutionary sense. For instance, fear responses stemming from animals' encounters with predators can be beneficial to an individual in terms of increasing its survival (Mobbs et al., 2015; Pellman & Kim, 2016), or may influence adaptive evolutionary phenomena such as the development of enhanced visual systems (Isbell, 2006). On the other hand, fear responses can also be costly in terms of leading to poor innovation, competitive ability, or increased stress-related mortality (Crane et al., 2020). We therefore consider that the links between socioecological context and fear response behaviours, and their (mal)adaptive effects on free-living animals, are key considerations before any conclusions about the adaptiveness of fearfulness can be drawn.

Finally, although Grossmann places a strong emphasis on "phylogenetic origins" as evidence to support the fearful ape hypothesis, the evidence presented is highly hominoid-centric and no formal comparative analyses are conducted. There is no reference to non-ape species, despite the large literature on neophobia and fear responses in many other clades (Crane et al., 2020; Laundre et al., 2010). As behavioural ecologists, we find this disappointing, as neither fearfulness, nor cooperative care (which is distinct from cooperative breeding, as Grossmann points out; Clutton-Brock, 2006; König, 1997), are unique to humans. There are many examples of fear (as measured by neophobia, shyness) and recognition of emotions, for example, in response to predators, in several other primate species. Likewise, there is a large body of evidence for cooperative care, sometimes even independently of kinship (Clutton-Brock, 2006; Koenig & Dickinson, 2016). The socioecological drivers of neophobia and the role of individual differences have also been well studied in corvids (Miller et al., 2022; Vernouillet & Kelly, 2020). Indeed, some species show high levels of both neophobia and cooperative care (Horn et al., 2020), which would seem to be highly relevant to the proposed hypothesis. Comparative analyses have also been reported for other families of birds, as well as for ungulates (Blumstein, 2006; Mettke-Hofmann, Winkler, & Leisler, 2002; Schaffer et al., 2021), but are not considered in Grossmann's review. There is a growing corpus of data on this topic from which to develop more robust hypotheses and more formal empirical analyses. Therefore, a broader comparative analysis, controlling for phylogenetic relatedness, would surely provide much greater insight into the evolution of fear responses.

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Fearfulness: An important addition to the starter kit for distinctively human minds

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Abstract

Grossmann's impressive article indicates that – along with attentional biases, expansion of domain-general processes of learning and memory, and other temperamental tweaks – heightened fearfulness is part of the genetic starter kit for distinctively human minds. The learned matching account of emotional contagion explains how heightened fearfulness could have promoted the development of caring and cooperation in our species.

Grossmann makes a compelling case that heightened fearfulness is a component of the genetic starter kit for distinctively human minds (Frith, 2001). Mother Nature tweaked hominin minds – not only to increase our social tolerance, enhance our attention to faces and voices, and expand our capacities for learning and memory (Heyes, 2018a, 2019; Heyes, Chater, & Dwyer, 2020) – but also to make us more fearful. By giving us unprecedented access to care and information from others, the small, quantitative changes in the starter kit had huge downstream consequences. Like sticks and tinder, they ignited a fire of change in our minds and in our lives. Grossmann argues convincingly that heightened fearfulness contributed to the fire by making human infants better able to elicit care, and more likely to develop into caring and cooperative members of their social group.

We are particularly interested in Grossmann's account of how heightened fearfulness promoted the development of caring and cooperation. He suggests that, in the context of heightened fearfulness, the integration of a "perception–action coupling" mechanism with a "caring behaviour" mechanism increased the motivation to help (sect. 2, paras. 6–8). This is plausible but programmatic. More details are needed to avoid a hint of alchemy – the impression that two mysterious elements conjoined under the stars of fearfulness to create something precious. Grossmann's hypothesis can be developed, and the relationship between fearfulness and cooperation elucidated, by looking inside the black box of his perception–action coupling mechanism.

In a wide range of animals, observation of emotional gestures and vocalisations (e.g., wincing, shrieking, laughter) triggers a rapid, matching emotional response (de Waal & Preston, 2017). In humans, this automatic form of empathy, or "emotional contagion," is a major driver of controlled judgements about the plight of others and ultimately of helping behaviour (e.g., Decety & Cowell, 2014; Gonzalez-Liencres, Shamay-Tsoory, & Brune, 2013). Emotional contagion is often called "perception–action matching" and attributed to an unspecified, genetically inherited mechanism – a set of pre-wired connections between emotional stimuli and responses, or an obscure currency converter that can take any emotional input from others and produce matching emotional output. However, there is now a substantial body of evidence – from nonhuman animals, infants, adults, and robots – that emotional contagion is made possible by learned associations, each connecting a distal sensory cue (e.g., an emotional gesture or vocalisation) with a motoric or somatic response belonging to the same emotional category (Heyes, 2018b). According to this learned matching account of emotional contagion, these connections are formed in three situations where the experience of a particular emotion "from the outside" is correlated with observation of the same emotion "from the outside": (1) *Self-stimulation* – such as when an infant hears her own cries while feeling distress; (2) *affective mirroring* – when a caregiver imitates an infant's facial and/or vocal emotional displays; and (3) *synchronous emotion* – when two or more individuals react to some event in the same way at the same time and observe the emotional reactions of others while experiencing their own.

Heightened fear would multiply and intensify the opportunities for learning in all three of these situations. A more fearful infant would produce more frequent and intense emotional displays (e.g., crying) co-occurring with the internal experience of fear, and thereby promote learning via self-stimulation. The increased frequency of emotional displays resulting from heightened fear would provide greater opportunities for caregiver imitation – promoting learning in the context of affective mirroring. Finally, heightened fear in infants and adults would increase the frequency with which multiple individuals (including the target infant) react in similar ways to an external fear-inducing event – promoting learning through synchronous emotion. Thus, the learned matching account of emotional contagion identifies three ways in which heightened fear could supercharge the development of the "perception–action coupling mechanism," and thereby the "caring behaviour mechanism" responsible for controlled helping behaviour, to make more caring and cooperative adults. It suggests that heightened fear changes the relationship between the two mechanisms ontogenetically rather than phylogenetically, and that there is nothing mysterious about their "integration." Via learned matching, heightened fear produces a more comprehensive coupling mechanism at an earlier stage of development. Consequently, the coupling mechanism provides earlier, more powerful input to the caring mechanism – coupling gives caring a bigger push.

Learned matching comes with two bonuses for the fearful ape, one specific and the other general. On the specific side, it provides yet further impetus for Grossmann's fascinating proposal that the norms and values of collectivist cultures, rather than buffering against susceptibility, make these societies better able to benefit from heightened fearfulness. Learned matching is consistent with this proposal because it suggests that the power and efficiency of the perception–action coupling mechanism depends on three sets of conditions – relating to self-stimulation, affective mirroring, and synchronous emotion – that vary across cultures with child-rearing practices and social rituals.

More generally, by underlining the importance of simple learning mechanisms in human development, learned matching reminds us that the adaptive consequences of heightened fearfulness could include faster direct and observational conditioning of object avoidance (Mineka, Davidson, Cook, & Keir, 1984). It has long been recognised that conditioning is faster and more complete when the event being predicted is highly salient (e.g., Rescorla & Wagner, 1972). Consequently, enhanced fear may make a moderately threatening stimulus, such as a poisonous spider seen from a distance, more salient, and thereby support good avoidance learning without getting close to a dangerous object. The risk that this learning will result in avoidance of benign stimuli is reduced in the case of observational conditioning. After a lifetime of experience, an adult who shows fear of an object is likely to be providing a signal that the object is truly dangerous. Therefore, an infant who learns faster from the adult's reaction – for whom that reaction is, because of heightened fearfulness, a more salient predicted event – rapidly absorbs genuinely useful information about the world.

Competing interest. None.

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Fear can promote competition, defensive aggression, and dominance complementarity

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Abstract

Fear can undermine cooperation. It may discourage individuals from collaborating with others because of concerns about potential exploitation; prompt them to engage in defensive aggression by launching a preemptive strike; and propel power-seeking individuals to act dominantly rather than compassionately. Therefore, accumulated evidence requires a more contextualized consideration of the link between fear and cooperation in adults.

The target article proposes that expressions of heightened fearfulness by infants facilitate care-based responding from mothers and others. It also stipulates that the emergence of stable fearfulness traits facilitates cooperation across the lifespan. I am making no claims about caregiving in response to heightened fearfulness in infants. Rather, this commentary draws on three literatures to claim that experienced, expressed, and perceived fear is often associated with lower levels of cooperation in adults. Taken together, the empirical evidence coming from research on social decision making, defensive aggression, and social hierarchy suggests that heightened fearfulness may promote competitive behavior in social interactions.

Consider first a broad class of social decision-making situations in which mutual trust is required to achieve a shared goal, such as the successful completion of a joint project (Skyrms, 2004). To the extent that experiencing heightened fearfulness is associated with distrust of others and concerns about the possibility of being exploited (i.e., worrying that others may shirk, defect, or free-ride one's efforts), it may undermine cooperation with others (Kramer, 1998; Wildschut, Pinter, Vevea, Insko, & Schopler, 2003). Fear of the other's fearfulness, in turn, may result in mutual defection as partners timidly choose a risk-averse strategy to avoid unilateral exploitation (i.e., choosing to work alone on a small challenge rather than collaborating with others to tackle a great challenge together; Halevy & Katz, 2013; Kuwabara, 2005). Hence, experiencing fear and perceiving fear in another may result in interaction partners settling for a suboptimal equilibrium attained through mutual defection in situations that require high levels of reciprocal trust to achieve the optimal equilibrium.

Consider next the particular case of preemptive strikes, a form of fear-based aggression (Simunovic, Mifune, & Yamagishi, 2013). A preemptive strike occurs when an individual attacks another in an attempt to eliminate or disable a perceived threat (Halevy, 2017). Schelling (1980) provides the example of an interaction between an armed burglar and an armed homeowner. Fear that the other person may use their gun can propel the burglar, the homeowner, or both of them to shoot even if everyone prefers the burglar to leave quietly. This form of aggression is motivated by self-defense, and is particularly likely to emerge when interaction partners experience a "reciprocal fear of a surprise attack" (Schelling, 1980, p. 207). Heightened fearfulness can promote preemptive strikes through the personal experience of fear as well as through the perception of fear in another. The fearful person may choose to launch a preemptive strike to eliminate or disable a perceived threat. Additionally, observing heightened fearfulness in another person may promote a preemptive strike when the perceiver worries that the fearful person may attack them. Hence, both experienced fear and perceived fear may increase the likelihood of defensive aggression.

Finally, consider situations that involve one or more individuals who seek to gain or maintain power by dominating others. Ruling by dominance (e.g., by using intimidation or coercion) means feeding off others' fear (Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013; Maner & Case, 2016). Perceiving heightened fearfulness in others may reinforce power-seeking individuals' tendencies to use dominance strategies as means to gain or maintain an elevated social rank. The expression of fear signals to the power-seeking individual that the fearful individual perceives their own level of power to be substantially lower than that of the power-seeking individual (Balliet, Tybur, & Van Lange, 2017, p. 373). This signal, in turn, propels the power-seeking individual to seize the opportunity to gain or maintain their power by acting dominantly. Research also suggests that dominant leaders' competitive behavior is often fueled by fear of losing their (unstable or illegitimate) position of power (Maner & Case, 2016). Therefore, experiencing fear as well as perceiving fear in others may increase dominant behavior by power-seeking individuals.

The idea that power-seeking individuals who encounter heightened fearfulness in others are likely to dominate and subjugate them rather than treat them with compassion and care recurs across two distinct literatures. First, research on dominance complementarity shows that people typically behave in a way that contrasts with the behavior of their counterparts on the dimension of interpersonal control. Hence, individuals tend to respond to submission with dominance and to dominance with submission (Tiedens & Fragale, 2003; Tiedens & Jimenez, 2003). Second, analyses of social behavior in brinkmanship situations, such as those modeled with the risky game of chicken (Halevy & Phillips, 2015; Schelling, 1980), suggest that power-seeking individuals are likely to compete with a timid counterpart. The expressed fearfulness of the timid counterpart leads power-seeking individuals to conclude that they can safely keep course and count on the timid counterpart to change course as a means to avoid the disastrous outcomes associated with a head-on collision (Halevy, Chou, & Murnighan, 2012; Rapoport & Chammah, 1966). Both of these literatures suggest that, upon encountering an individual showing heightened fearfulness, a power-seeking individual is likely to respond with self-serving dominance rather than with prosocial care.

In sum, accumulated evidence across multiple streams of research on social decision making, defensive aggression, and social hierarchy suggests that experienced, expressed, and perceived fear is often associated with lower levels of cooperation in adults. This evidence requires a thoughtful consideration of potential boundary conditions to the target article's claim for "a link between human fearfulness traits and enhanced levels of cooperative behavior" (target article, sect. 4, para. 9) in adults.

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How "peer-fear" of others' evaluations can regulate young children's cooperation

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Abstract

Children's cooperation with peers undergoes substantial developmental changes between 3 and 10 years of age. Here we stipulate that young children's initial fearfulness of peers' behaviour develops into older children's fearfulness of peers' evaluations of their own behaviour. Cooperation may constitute an adaptive environment in which the expressions of fear and self-conscious emotions regulate the quality of children's peer relationships.

Emotions are commitment devices that play a crucial role in regulating children's social interactions with peers towards shared, cooperative goals. In the context of cooperation, emotions motivate one's own behaviour to help and care for others and regulate others' behaviour in response to one's emotional expression (Frank, 1988; Keltner, Kogan, Piff, & Saturn, 2014; Parkinson, 1996; Vaish & Hepach, 2020). From early in ontogeny, emotions underlie the two-step process involved in cooperation: generating benefits and distributing benefits (Warneken, 2018). Grossmann presents an intriguing developmental account of how children's fear expression, typically classified as a negative emotion, has in fact positive outcomes because it motivates cooperation from caregivers. But there is no reason to assume that children's expression of fear and attention to fear in others is limited to regulating cooperation between infants and adult caretakers. Here we offer a critical reflection on how children's fear proneness may regulate their cooperative interactions – specifically their helping and concern for fairness towards peers – beyond provisioning help from caretakers.

In the first years of life, children's interactions are not exclusively cooperative and include bouts of mild aggression accompanied by negative emotions such as frustration and anger (Dahl, 2016; Hay & Ross, 1982). Such negative interactions are not so much driven by antisocial motivations but can rather arise from children's curiosity and interest in their peers. Should such "exchanges" of toys or "explorations" of personal space escalate, caretakers offer help and resolve such conflicts which is, to some extent, motivated by children's fearful expression. Despite the temperamental volatility evident in young children's peer interactions, children do help and share with peers and their ability to coordinate joint actions develops into cooperative activities by the end of the second year of life (Brownell, Ramani, & Zerwas, 2006; Eckerman, Davis, & Didow, 1989; Hepach, Kante, & Tomasello, 2017). Cooperation with peers thus presents a scaffold for children's interactions and mutual expectations. Children's expressed fearfulness, moreover, can elicit cooperation from peers and children's attention to fear in their peers may predict their own cooperation. Indeed, Grossmann cites evidence, much from his own pioneering work, to demonstrate a link between children's attention to fear in others and their own helping and sharing behaviour (Grossmann et al., 2018; Rajhans, Jessen, Missana, & Grossmann, 2016).

The widening of children's social circle, the increased complexity in their peer interactions, and their elevated cognitive capacity for reputation management (see Engelmann & Rapp, 2018, for a review) all increase children's concern for or even fear of others' evaluations. Emotions such as shame are elicited when children think that they have failed to meet a (social) standard, especially if such failures are observed by others. By contrast, pride is elicited when children feel that they have met or even exceeded a social standard (e.g., Lewis et al., 1992; Stipek, Recchia, McClintic, & Lewis, 1992). Self-conscious emotions may thus offer a means for children to express how much they value cooperative relationships with peers starting during the preschool years. The nature and development of such emotions can be examined when presenting children with situations in which they receive undeserving help, unfair distributions of resources, or make unjustified requests.

At 4 years of age, children express less positive emotions, a reduction in upper-body posture, when they were helped but a more needy peer was not (Hepach & Tomasello, 2020). Five-year-old children showed more negative emotions – through a lowered-body posture – compared to 4-year-olds when they failed to complete tasks both for themselves and for others (Gerdemann, Tippmann, Dietrich, Engelmann, & Hepach, 2022c). In addition to expressing negative emotions in response to unsuccessful helping and receiving undeserving help, 5- but not 3-year-old children's posture is lowered when making justified requests, that is, asking someone for a tool if that person needs the tool more than the child (Waddington, Hepach, Jackson, & Köymen, 2022). The most systematic investigation to date of changes in children's body posture in the context of (un)fairness demonstrated that between 4 and 10 years of age, children's emotions expressed in response to receiving more of a reward than a peer (i.e., advantageously unequal outcomes) became more negative with increasing age. Conversely, children's emotions became more positive with age following equal distributions of resources (Gerdemann, McAuliffe, Blake, Haun, & Hepach, 2022a). Together, these findings suggest that emotions can regulate children's cooperative interactions although more research is needed to specify this relation. Receiving help or resources may be beneficial for the individual child but if the outcome is undeserving or unfair, then this may strain the cooperative relationship with peers. Children may risk being viewed as more concerned for their own gains even if it comes at a cost to others. In the context of cooperation, signalling one's fear of a peers' evaluation and rejection, for example, through lowered-body posture, may have an adaptive value for children who aspire to good terms with their peers (see also Gerdemann, Büchner, & Hepach, 2022b).

In summary, one direction for future research could be to test the implications of the *fearful ape hypothesis* in the context of children's peer interactions. In addition to soliciting help from caretakers, peer cooperation may constitute a setting in which children respond to each other's expression of fear to solicit mutual aid. Cooperation may even reduce fear much like it increases positive emotions and sharing (Hamann, Bender, & Tomasello, 2014; Lennon & Eisenberg, 1987; Stengelin, Hepach, & Haun, 2020). The emergence of self-conscious emotions such as shame in early childhood may build on children's fear expression observed in infancy yet may arguably constitute a qualitatively more complex emotional experience. One way of testing the hypothesized developmental relation between these two kinds of emotions would be to relate the early expression of fear – assessed using methods pioneered by Grossmann and colleagues – to children's social emotions expressed in the context of children's peer cooperation. This would be one way to assert whether the expression of shame, in middle childhood, elicits cooperation from peers in the same way that the expression of fear in early childhood elicits caretaking from adults.

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Infants aren't biased toward fearful faces

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Abstract

Grossmann's argument for the "fearful ape hypothesis" rests on an incomplete review of infant responses to emotional faces. An alternate interpretation of the literature argues the opposite, that an early preference for happy faces predicts cooperative learning. Questions remain as to whether infants can interpret affect from faces, limiting the conclusion that any "fear bias" means the infant is fearful.

Human responses to positively and negatively valenced stimuli have been examined for years. Many believe that negative stimuli are most salient (recognized faster and more accurately) so that threats can be avoided. Grossmann reviews a variety of evidence leading to the conclusion that human infant displays of fearfulness lead to more care and investment from parents and others.

However, the summary of fear perception and responsiveness through human maturation is incomplete. Infant and toddler responses to emotional faces are not unequivocal. Grossmann's own research shows this (Jessen & Grossmann, 2015), where brief presentations of fear and happy expressions were compared, with event-related brain potentials (ERPs) larger for happy faces than fear in some cases and not others. These inconsistent results match those reported in extensive reviews of the literature on infant expression recognition (Quinn et al., 2011; Ruba & Repacholi, 2020; Walker-Andrews, 1997). The infant expression discrimination and recognition literature shows: (1) Significant variability in the behavioral response to emotional faces before 1 year of age (using measures like categorization and matching; e.g., Kotsoni, de Haan, & Johnson, 2001; Peltola, Leppänen, Palokangas, & Hietanen, 2008; Serrano, Iglesias, & Loeches, 1992); (2) a happy face bias in early infancy (e.g., Barrera & Maurer, 1981; Farroni, Menon, Rigato, & Johnson, 2007; Field, Woodson, Greenberg, & Cohen, 1982; Kotsoni et al., 2001); and, (3) a fear (or angry) face bias that emerges at 7 months, but then diminishes by age 11–12 months (e.g., Peltola, Hietanen, Forssman, & Leppänen, 2013; Serrano et al., 1992; Xie, McCormick, Westerlund, Bowman, & Nelson, 2019). Many articles cited here report inconsistent results across multiple experiments, highlighting the uncertainty about infant and toddler facial expression responses. One could easily argue that cooperative care evolved because of a happy face bias by citing different articles on infant and toddler expression recognition. In short, the literature review is incomplete, and does not reflect the complexity of interpreting infant responses to emotional stimuli (notably facial expressions) across all ages.

In addition to the lack of clear "fearfulness" bias in perceiving or discriminating among emotion faces in human infants, there are questions about whether infants under 1 year of age are extracting affect information from faces unless there are multimodal stimuli (Kotsoni et al., 2001; Quinn et al., 2011; Walker-Andrews, 1997). Conservative interpretations of the results across a myriad of studies suggest high contrast features drive the effects observed (like eye whites or toothy smiles, e.g., Whalen et al., 2004). Just because an infant looks longer at a stimulus it does not mean affect, or the possible consequences of that stimulus, are understood by the child (Quinn et al., 2011; Walker-Andrews, 1997). Research on older children shows significant developmental changes in successfully categorizing facial emotions as generally positive or negative (Gao & Maurer, 2009, 2010; Vesker, Bahn, Degé, Kauschke, & Schwarzer, 2018).

In older children and adults, happy faces are processed faster and more accurately than other emotional facial expressions when artifacts are eliminated and stimuli are equated for salience (Beall & Herbert, 2008; Calvo & Lundqvist, 2008; Durand, Gallay, Seigneuric, Robichon, & Baudouin, 2007; Gao & Maurer, 2010). The relative salience of negative (usually angry) and positive (happy) faces has been tested using visual search or attentional blink (reviewed by Brosch, Pourtois, & Sander, 2010; Yiend, 2010); Stroop-type tasks (Beall & Herbert, 2008; Williams, Mathews, & MacLeod, 1996; Yiend, 2010); the Simon task (e.g., Altarriba & Basnight-Brown, 2010); as well as lexical or semantic decision-type tasks (Brosch et al., 2010; Yiend, 2010); and dot-probe tasks (Sutton & Lutz, 2019). Across a myriad of studies one finds evidence for a positivity or negativity bias in the perception of facial expressions across age, although studies on children demonstrate a consistent positive emotion bias (Gao & Maurer, 2009, 2010; Kauschke, Bahn, Vesker, & Schwarzer, 2019).

The argument that speeded perception of negative faces may confer an evolutionary advantage has rested on pop-out of emotional faces (the *anger superiority effect*, Öhman, Lundqvist, & Esteves, 2001). This *face in the crowd* effect was likely driven by a contrast artifact (Purcell & Stewart, 2010; Purcell, Stewart, & Skov, 1996). Savage, Lipp, Craig, Becker, and Horstmann (2013) demonstrated an anger superiority effect with some faces, and not others. Overall, pop-out of facial expressions does not occur without the presence of low-level stimulus differences, and the anger superiority effect is inconsistent (Calvo & Nummenmaa, 2008; Coelho, Cloete, & Wallis, 2010; Purcell & Stewart, 2010; Purcell et al., 1996; Yiend, 2010). A happiness superiority effect obtains when carefully controlled stimuli are used (Craig, Becker, & Lipp, 2014).

Based on his review of emotional expression perception by infants Grossmann develops a tenuous line of reasoning that increased attention to fear faces at 7 months can be considered a sign of increased fearfulness among humans, which can then be correlated with later behavioral cooperation in childhood. An unbiased review of the current perspective on infant facial emotion perception at the neural and behavioral levels indicates that any "fearfulness" bias is short-lived, and is bookended by a bias toward perceiving happy faces more quickly and more accurately. Recent attempts to identify individual infants who have heightened fear bias have produced inconsistent results, even when focusing on a narrow age range (5–8-month-olds) using a matching task involving visual disengagement from fearful (compared to other emotional) faces (Kataja et al., 2020). While longitudinal studies may clarify whether individual differences in facial emotion expression are predictive of later behavioral effects (e.g., Wagner, Keehn, Tager-Flusberg, & Nelson, 2020), the idea that a general fear bias drives cooperation among humans is unsupported. Many researchers have suggested that familiarity with emotional expressions drives the effects, rather than infants understanding fearful expressions to convey fear (e.g., Walker-Andrews, 1997). The link between an infants' changing preferences for particular facial expressions, their understanding of affect, and how these influence cooperative skills demands direct longitudinal research.

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A novel(ty) perspective of fear bias

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Abstract

Grossmann presents an exciting and interesting theory on the function of fearfulness. In this commentary it is argued that fearfulness may be a byproduct of a larger executive functioning network and these early regulatory skills considered more broadly may be key building blocks for later cooperative behaviors.

Grossmann introduces the "fearful ape hypothesis," an exciting perspective on the function and evolution of fearfulness. The author outlines associations between maternal sensitivity, early recognition and response to fearful expressions, and later prosocial outcomes. However, there may be a more comprehensive explanation, as a heightened response to fearfulness in infancy is not conclusive evidence for a highly specialized and evolved fear system. Here, we put forth an alternative perspective following three levels of evidence outlined in the target article: ontogeny, adaptive value, and mechanism. We argue that fearfulness in infancy may not be the root of future cooperation but rather fearfulness is a byproduct of a larger executive functioning/regulatory network (i.e., cognitive processes [e.g., visual working memory, inhibitory control] that aid in the regulation of thoughts, actions, and emotions).

The *ontogeny* of executive functioning abilities begins in infancy and one aspect of executive functioning development that is nicely outlined in the target article is fear bias (Blankenship et al., 2019). Fearful faces are less common in positive emoting moms, and thus infants would obtain less exposure to fearful faces compared to other emotions such as happiness (Downes, Bathelt, & De Haan, 2017; Ruba & Repacholi, 2020). Given the relatively minimal exposure to fear, the assessment of fear bias, or the enhanced attention to fearful compared to happy (and sometimes other target faces) indexed from emotion discrimination tasks (e.g., habituation and preferential looking), is thought to index novelty detection, a key precursor for executive functioning. Moreover, positive associations exist between infant fear bias and maternal positive emotionality providing further evidence for fear bias indexing novelty detection (de Haan, Belsky, Reid, Volein, & Johnson, 2004). Critically, attentional biases to fearful faces, novel objects, and other social stimuli are all linked to executive functioning outcomes, providing evidence for fear bias being just one behavior of a larger suite of behaviors encompassed in executive functioning (Blankenship et al., 2019).

One of the key brain regions introduced in the target article as *mechanistic* evidence for the fearful ape hypothesis is the dorsolateral prefrontal cortex. The dorsolateral prefrontal cortex is not typically considered in emotion perception, but rather experimental and correlational evidence has characterized the dorsolateral prefrontal cortex in supporting executive functions (Kelsey, Krol, Kret, & Grossmann, 2019; Nejati, Salehinejad, & Nitsche, 2018; Panikratova et al., 2020). Remarkably, these associations between dorsolateral prefrontal cortex connectivity and regulatory behaviors, such as increased orienting to stimuli, are seen very early in development (Kelsey, Farris, & Grossmann, 2021). In the target article, key mechanistic evidence for the fearful ape hypothesis is derived from a study finding a negative association between dorsolateral prefrontal cortex response to fearful faces at 7 months and instrumental helping at 14 months (Grossmann, Missana, & Krol, 2018). Here, it is important to note that this study also found an association between dorsolateral prefrontal cortex response and fear bias (an approximation for novelty), but not fearful behaviors assessed using a temperament questionnaire. This hints at the possibility that the dorsolateral prefrontal cortex response to fear may be an index of general executive functioning rather than a specific marker for fearful emotions and behaviors.

In support of the alternative hypothesis for a larger executive functioning network being the root of cooperation and the *adaptive value* of executive functioning, mothers with a high level of executive functioning are more responsive caregivers and raise children with greater executive functioning abilities, likely because of both genetic and environmental contributions (Ribner, Devine, Blair, Hughes, & Investigators, 2022). Critically, young children with greater executive functioning abilities go on to be more prosocial humans (Aguilar-Pardo, Martínez-Arias, & Colmenares, 2013; Traverso, Viterbori, & Usai, 2020).

Given the confounding between fearfulness and executive functioning, it is essential for future work to better isolate the unique contributions of fearfulness. More specifically, work testing components of the fearful ape hypothesis should include measures of executive functioning (e.g., visual working memory task, effortful control temperament assessments, etc.) to better understand the unique contributions. In addition, when assessing links between attentional and neural responses to fear similar to Grossmann et al. (2018), it is imperative to include a nonsocial novelty control condition. These additions will allow for a richer understanding of how fearfulness and general executive functioning abilities contribute to later prosocial development.

Overall, Grossmann presents exciting and innovative ideas that I think raise critical questions for the field. This commentary offers an alternative explanation for the ontogenetic and brain evidence of the "fearful ape hypothesis" in hopes of providing a roadmap for future research needed to disentangle these two accounts.

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Cultural evolution needed to complete the Grossmann theory

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Abstract

Grossmann used evolutionary analysis to argue for the adaptive nature of fearfulness. This analysis, however, falls short of addressing why negative affectivity is maladaptive in contemporary Western societies. Here, we fill the gap by documenting the implied cultural variation and considering cultural (rather than biological) evolution over the last 10,000 years to explain the observed cultural variation.

Grossmann argues that fearfulness was adaptive in ancestral interdependent social environments. His treatise is commendably thorough. However, it invites an important paradox. Why is negative affectivity (which undergirds fearfulness) maladaptive today? He may be right that this paradox does not apply to "small-scale, interdependent human societies primarily built on cooperative care and success" (target article, sect. 1, para. 3). He notes that Western norms of independence conflict with cooperative care. However, why might such norms exist, and more importantly, why might they make fearfulness problematic? Until he could fully address these questions, his analysis would remain incomplete. Here, we will outline a way to fill this gap.

Negative affectivity and biological health in Japan and the United States

We start with recent evidence documenting a relevant cultural variation. This evidence focuses on neuroticism – a global personality trait defined by negative affectivity. Although this trait is widely regarded as maladaptive in the current literature (Friedman & Kern, 2014), this consensus may be premature. Neuroticism may be adaptive or maladaptive, depending on how readily people are willing and able to adjust their behaviors and preempt the existing threat, which this personality trait highlights and thus amplifies (Kitayama et al., 2018). If people are relatively high in behavioral adjustment, they can change their behaviors to cope with the threat. Hence, the sensitivity to the threat, enhanced by neuroticism, can be adaptive. However, if they are unable or unwilling to adjust their behaviors, they may be overwhelmed by the threat, especially if it is magnified by high neuroticism. In a recent study, Kitayama et al. (2018) tested how neuroticism might be associated with a biological health risk in a large sample of adults in interdependent and independent countries (Japan vs. the United States) while assessing this risk with biomarkers of inflammation and cardiovascular malfunctioning. They also measured behavioral adjustment with a rating scale.

This study found a significant behavioral adjustment × neuroticism interaction, which indicates that neuroticism is adaptive for those relatively high in behavioral adjustment. However, the effect of neuroticism was reversed for those low in behavioral adjustment. Moreover, consistent with the proposition that Japanese culture values interdependence with others and thereby positively sanctions behavioral adjustment, but American culture does not (Markus & Kitayama, 1991), Japanese were significantly higher in behavioral adjustment than Americans. Correspondingly, neuroticism was associated with a decreasing biological health risk among Japanese. However, this effect disappeared for Americans. Importantly, among a subset of Americans who were particularly low in behavioral adjustment, neuroticism was associated with a significant increase in biological health risk. The conclusion that negative affect can be adaptive in an interdependent society has been corroborated in other studies (Kitayama et al., 2015; Miyamoto et al., 2013; Park, Kitayama, Miyamoto, & Coe, 2020). Contrary to Grossmann's speculation, the putative adaptiveness of negative affectivity (and thus fearfulness) is not limited to small-scale societies.

Cultural evolution

To fully understand the above evidence, we must consider how culture has evolved over the last 10,000 years. Grossmann is perhaps right that hunting-and-gathering small-scale societies were closely knit and centered around kinship. That is, they were interdependent. The emphasis on interdependence, however, continued even after humans began sedentary living aided by farming and herding approximately 10,000 years ago. Since then, larger communities emerged as farming became supportive of larger populations. Such communities turned into big cities and kingdoms. Along the way, different regions developed strikingly different forms of interdependence. For example, interdependence can be supported by self-effacement, as in East Asia, where the hegemonic culture was supported by rice farming (Talhelm et al., 2014). It can also be supported by self-assertiveness, as in Arab regions, where the hegemonic culture recognizes a dire need to protect ingroups against outgroups (San Martin et al., 2018). Although these two cultures seem diametrically different at first glance, they are similar in one respect. Both cultures share a strong commitment to interdependence within ingroups.

All of this began to change in the Western corner of the Eurasian continent over the last 1,000 years, with a radical change occurring in how people understood themselves and their world (Kitayama et al., in press). This change, perspectival in nature, was precipitated by numerous historical happenstances and developments, including the reformation and enlightenment (Taylor, 1989; see also Schulz, Bahrami-Rad, Beauchamp, & Henrich, 2019). It has gradually defined the Modern West – a cultural tradition organized by the model of the self as an agent independent from others. Perhaps for the first time in human history, the independent model of the self became hegemonic, linked to wealth and power. This trend may still be underway (Varnum & Grossmann, 2017).

Before the Modern West, people defined themselves while referring to the group they were part of. They saw themselves and understood the world while taking the group's perspective. Consequently, it was satisfying to "be appreciated" or "honored" by others. Adjustment and conformity to group norms were the default. However, people in the Modern Western traditions began understanding the self and the world from their perspective. Consequently, social acknowledgments, such as appreciation and honor, while desirable, were no longer fully satisfying. Instead, it became imperative for people to affirm their positive selves, which, in turn, commanded others' respect and admiration. One consequence was a strong insistence on holding fast to the self's values and goals at the expense of social expectations. Freedom became valued and prioritized over conformity, which explains why the behavioral adjustment is lower (which rendered negative affectivity a major health risk) among European Americans today compared to Asians and perhaps other non-Westerners (Schulz et al., 2019).

Conclusion

Altogether, theories of the affective dynamic surrounding negative affectivity (including the one on fearfulness by Grossmann) cannot be complete without cultural considerations. Here, we showed how culture moderated the adaptiveness of neuroticism and sketched how one might go around and explain this variation. It is imperative to examine cultural evolution as the primary causal factor in shaping, in a historical timescale, all psychological processes, including negative affectivity and all other cognitive, emotional, and motivational processes.

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Fearful apes or nervous goats? Another look at functions of dispositions or traits

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Abstract

In his article, Grossmann argues that, in the context of human cooperative caregiving, heightened fearfulness in children and human sensitivity to fear in others are adaptive traits. I offer and briefly defend a rival hypothesis: Heightened fearfulness among infants and young children is a maladaptive trait that did not get deselected in the process of evolution *because* human sensitivity to fear in others mitigates its disadvantageous effects to a sufficient extent.

My main argument is rather simple. I challenge Grossmann's claim (target article, sect. 2, para. 1) that heightened fearfulness among young children is an adaptive trait in the context of the human cooperative caregiving system. I do not deny that human sensitivity to fear in others is an adaptive trait. Rather, I argue that, because humans are ultrasocial, the adaptive nature of human sensitivity to fear in others in the context of their joint caregiving mitigates sufficiently (or even completely neutralizes) the negative effects of maladaptive heightened fearfulness in human children. The function of heightened fearfulness is gaining attention rather than leading to being helped and protected.

Grossmann's main argument can be deconstructed in the following way:

(1) The experience of fear in light of a threat in animals leads to fight-or-flight (or avoid being detected) responses.
(2) (However,) humans have an additional "tend and befriend" response.
(3) Arguably, this response is the most effective response in the face of fear in ultrasocial species because (*inter alia*):
    (a) it allows for potential threats or uncertainties to be cooperatively managed and avoided, and
    (b) in the context of heightened fear, the approach response may be particularly beneficial for the youngest and most vulnerable members of the species (i.e., the heightened fear increases the effectiveness of "tending").

Conclusion: (Therefore,) heightened fearfulness and sensitivity to fear in others are adaptive, interconnected traits (they generate direct fitness and survival benefits).

I challenge premise 3b. This premise assumes that the function of heightened fear is to lead to being helped and protected (target article, sect. 3.2, para. 8) but, given that the fear is exaggerated, even when there is a need to respond, the intensity of the response will not be proportionate to the real need for help: That is because the fearfulness is exaggerated, the reaction will be exaggerated as well. Because exaggerated reactions require using unnecessary resources, this response would lead to resource depletion (individuals that really need help would not be helped) if it weren't the case that humans are ultrasocial and the social structure can afford to allocate unnecessary resources in these circumstances. Therefore, heightened fear in children seems to be a consequence of a lucky circumstance; specifically, the fact that humans live in intense cooperation.

In this context, then, heightened fearfulness is a flaw but, given the nature of human cooperation, it is not a *debilitating* flaw. The disposition is disadvantageous, that is, but human social cooperation is capable of sufficiently mitigating its negative effects. If this hypothesis is correct, then heightened fear does not lead to being helped; rather being surrounded by many alloparents capable of providing more attention leads to human children exhibiting heightened fear. The heightened fear is a mechanism of getting additional attention rather than seeking help: The more attention children get as a response to exhibiting fear, the stronger and more frequent their display of fear becomes.

The fact that a disposition, trait, or behaviour is not adaptive does not entail that it will disappear. The evolutionary processes may just need some time to deselect it. Also, some relevant historical circumstances may facilitate or tolerate it: As an example, consider the example of the so-called "nervous" or "fainting" goats (e.g., Lush, 1930; White & Plaskett, 1909). When "nervous" goats are suddenly surprised or startled, they become perfectly rigid. Typically, this condition lasts only 10–20 seconds but it is still not adaptive for these goats to freeze in the face of danger; because this is not a strategy for avoiding detection. Interestingly, farmers find this behaviour useful because the goats cannot jump over fences: They freeze if they try. What this means is that farmers gave a function to the goats' functionless, maladaptive disposition thereby transforming it into an adaptive disposition. Also, some pointer dogs exhibit sudden immobility in the presence of humans (Reese, Newton, & Angel, 1982, p. 611). Unlike the above farmers, owners of these dogs do not find the behaviour useful but they do not see it as a reason not to have these dogs. The dogs' disposition is neither adaptive nor debilitating.

Similarly to the sudden immobility of these pointer dogs, many human traits and dispositions are not adaptive but human society is capable of mitigating, neutralizing, or simply tolerating their negative effects. My suggestion is that heightened fearfulness among infants and young children is a trait of this kind. Likewise, self-inflation bias does not seem to be adaptive but contemporary society tolerates it to an extent (see, Funkhouser, 2019, sect. 7) and many cases of self-deception are also not adaptive but are tolerated or facilitated by the relevant historic circumstances (see, Krstić, 2020).

In conclusion, the *fearful ape hypothesis* assumes that the function of heightened fearfulness is to lead to being helped and protected. This hypothesis sits uneasily with the fact that the degree of the response does not correspond to the degree of the real need for help (the fear is exaggerated). Thus, the function of this trait does not seem to be leading to being helped and protected; rather, getting attention may be the real function. According to the rival, *nervous goat hypothesis*, this trait is not adaptive but it still exists because humans are capable of developing a relevant response and the response is owed to our adaptive sensitivity to fear in others. Perhaps, one beneficial side-effect of this overall situation is that these infants grow up to become more caring and cooperative human beings in the long term but it does not follow that this is a function of heightened fearfulness.

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Are we virtuously caring or just anxious?

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Abstract

According to Grossmann, the high levels of cooperation seen in humans are the result of a "virtuous caring cycle" on which the increased care that more fearful children receive brings increased cooperative tendencies in those children. But this proposal overlooks an equally well supported alternative on which children's anxiety – not a virtuous caring cycle – explains the cooperative tendencies of humans.

Grossmann's target article posits a novel "virtuous caring cycle" on which the increased care that is received by more fearful children begets increased cooperative tendencies in those children (target article, sect. 1, para. 3). While this proposal is insightful in many ways, it may overlook an alternative, and potentially complementary, explanation of the unique level of cooperativeness that we find in humans. More specifically, for all that's been said, *anxiety* remains an equally plausible driver of the ontogenetic changes that Grossmann's proposal aims to explain.

The starting place for an anxiety-focused alternative is the observation that human social life is structured by norms whose complexity and vagueness often leave individuals uncertain about how they ought to behave (Kitcher, 2011; Sterelny, 2013). Anxiety, as an emotion triggered by problematic uncertainty of this sort, would then be a predictable and prudent response (Hookway, 1998; Kurth, 2015). More specifically, we should expect that through the course of human history, there was a tendency for some individuals to experience increased anxiety as they struggled to navigate these complex and uncertain social norms (Kurth, 2016). Moreover, this anxiety would have brought the emotion's characteristic response: increased risk assessment and risk minimization behaviors (Davis, Walker, Miles, & Grillon, 2010; Kurth, 2018; Öhman, 2008). In the context of alloparenting, when these anxiety-driven behaviors were experienced by children, they would likely have manifested as, for example, cautious approach, reassurance seeking, and greater deference toward authority figures – behaviors, that is, that could have worked to enhance the cooperative tendencies of children, especially in the more anxious ones. But, contra Grossmann's picture, these enhanced cooperative tendencies would not be the upshot of a virtuous caring cycle. Rather, they would be the upshot of anxiety.

To draw out the plausibility of this alternative explanation, we can move in two steps. First, notice that there's an important ambiguity in Grossmann's rendering of the "fear" that he takes to underwrite the virtuous caring cycle. In particular, his distinction between *general fear* and the distinct *fearfulness of social animals* (target article, sect. 3.1, para. 9) mirrors the standard ways that fear and anxiety are often distinguished in emotion science: Fear engages a fight/flight/freeze response in the face of imminent dangers, while anxiety prompts cautious approach in the face of uncertain threats (e.g., Davis et al., 2010; Kurth, 2016, 2018; Öhman, 2008). But while this common understanding of anxiety is functionally similar to Grossmann's notion of the fearfulness of social animals, the two responses are underwritten by distinct motivations: Risk assessment/minimization motives in the case of anxiety, care/affiliation seeking for Grossmann's fearfulness. Recognizing this suggests that two different mechanisms may underlie the enhanced cooperation seen in "fearful" children.

Second, much of the evidence that Grossmann marshals in defense of his virtuous caring cycle is compatible with an anxiety-focused alternative, thus frustrating our ability to determine which of these two mechanisms (or both) underlies humans' distinctive tendency toward cooperation. Three examples will help draw this out.

1. The paper makes extensive appeal to research using emotional facial expressions, and it does this both as a way of measuring relative "fearfulness" levels and as a way of inducing "fear" so that the resulting neuro/chemical changes and behaviors (e.g., cooperativeness) can be assessed. But using emotional facial expressions in these ways is highly controversial (e.g., Barrett, 2006). Moreover, even if we set these general worries aside, a deeper problem remains: In Grossmann's use of this research, what counts as a "fearful" facial expression is understood so broadly that we cannot say which emotion is actually in play. For instance, in some of Grossmann's appeals to the facial expression research, "fear" is understood expansively so as to include general distress displays (target article, sect. 3.1, para. 9). Moreover, where a more narrow rendering is sought by way of contrasting "fearful" faces with other negative emotion facial expressions, the work typically just compares "fear" and "anger" faces (e.g., Grossmann & Jessen, 2017; Krol, Monakhov, Lai, Ebstein, & Grossmann, 2015). Thus, we do not have evidence that allows us to tease apart our competing fear- and anxiety-based hypotheses. In fact, to the extent that the experiments that Grossmann's argument builds from make use of just still images (thus leaving test participants without contextual cues about what the emotional expression is a response to), they're arguably more likely to cue anxiety (a sensitivity to *uncertain* threats) than fear (a sensitivity to imminent dangers).
2. The article points to imaging work indicating that neural structures like the amygdala and striatum are engaged in "fear" responses. But because these structures have also been shown to be engaged as part of anxiety responses (e.g., Davis et al., 2010; Kurth, 2018; Lago, Davis, Grillon, & Ernst, 2017), we do not have findings that provide unique support for Grossmann's fearfulness model. Similarly, the paper cites the longitudinal study of Tuulari et al. (2020) in support of the amygdala's role in the development of fear biases. But it's unclear how much support this work provides for favoring a fear-based mechanism because the Tuulari's study did not test for activity in "anxiety" brain regions like the base nucleus of the stria terminalis (BNST).
3. The research Grossmann cites in support of a connection between fear detection and increased cooperation also fails to be dispositive (target article, sect. 3.2, paras. 1–6): Much of this work implicates not just fear and its neural correlates (e.g., the amygdala), but also anxiety and its neural correlates (e.g., the BNST) (Bosch, 2011; Insel, 1990; Marsh, 2015).

In sum, Grossmann is correct to focus on the role that affective traits might play in fostering cooperation; and in looking beyond the usual suspects like empathy, his work advances our understanding of the complex mechanisms that are likely to underlie these ontogenetic changes. That said, it appears that he has not (yet) succeeded in identifying a virtuous cycle of caring as the central driver of the enhanced cooperation that we see in "fearful" children.

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Developmental and evolutionary models of social fear can address "the human fear paradox"

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In this commentary, we synthesize existing models of *social* fear that address within-species variability, a topic that we believe is underacknowledged in Grossmann's model. These developmental and evolutionary models address (1) why there are individual differences in social fear, and (2) the varying, adaptive outcomes of social fear, which can include cooperative behavior as Grossmann proposes, but also withdrawal.

Grossmann posits that the species-unique fearfulness of human infants is adaptive because it promotes a cascade of parental and alloparental cooperative responses that, in turn, seemingly promote and sustain cooperative behavior across generations. But does this model fully address the "paradox" of human fearfulness?

Grossmann's arguments are built primarily from between-species comparisons of fear, with minimal incorporation of within-species variability. The cost of this approach is the omission of *developmental* consideration regarding (1) why there are individual differences in fearful profiles within our species, and (2) the variety of adaptive outcomes of certain fear-related behaviors, which can include cooperation, as Grossmann proposes, but also withdrawal, as we will argue.

We believe that Grossmann's arguments can be improved by considering existing developmental models that have addressed a similar paradox in relation to *social* fear (also referred to as shyness or social anxiety), which can have detrimental health effects and yet is still common in our species.

If there is indeed an "optimal" amount of fear as Grossmann argues, why then, is there such a range of fear within our species? How do infants come to display the local optima of fear for their environment? Similar questions have been asked in relation to social anxiety. Karasewich and Kuhlmeier (2020) proposed that trait social anxiety is a conditional adaptation, such that individual variation results from a developmental system that is predisposed to process cues of social threat within the environment during infancy. For individuals with inhibited temperaments, experiencing cues of social threat, such as controlling parenting, rejection, or neglect in early development, can entrain development on a path to social anxiety, in preparation for a socially threatening future. In contrast, inhibited children who are exposed to supportive parenting and general feelings of social and physical safety are less likely to be socially anxious as an adolescent or adult. Thus, social anxiety can be viewed as an adaptive response to the local social environment, which explains why we observe individual differences in this trait within the human species.

Further, several groups have proposed diverse evolutionary timelines and functions of various shyness subtypes (Hassan, MacGowan, Poole, & Schmidt, 2021; Schmidt & Poole, 2019) and shy expressions (Colonnesi, Nikolić, & Bögels, 2020). For example, Schmidt and Poole (2019) draw from Buss's (1986) argument that some shy individuals predominantly experience *fear* in novel social situations. This temperamental profile is thought to have been adaptive in our ancestral past because it limited exposure to potentially dangerous individuals. They further argue that this "fearful shyness," which is conserved across many primate and non-primate species, is evolutionarily older than a primarily *self-conscious* shyness subtype specific to humans. "Self-conscious shyness" is purportedly more adaptive than "fearful shyness" in our contemporary world, in which ensuring one's safety through appeasement or avoidance of social blunders is arguably more pertinent than concerns about potential physical threat.

Similarly, there is evidence for heterogeneity in the expression of shyness. Shy behaviors can be accompanied by either positive (approach-motivated) or non-positive (avoidance-motivated) facial expressions (Colonnesi, Nikolić, de Vente, & Bögels, 2017, 2020; Susa-Erdogan, Benga, & Colonnesi, 2022).

Indeed, some expressions of shyness lead to approach, and associated cooperative behaviors or sociocognitive correlates like theory of mind (MacGowan, Colonnesi, Nikolic, & Schmidt, 2022a), but other manifestations of shyness can lead to avoidance, and therefore *reduced* cooperative behavior (Karasewich, Kuhlmeier, Beier, & Dunfield, 2019; MacGowan & Schmidt, 2021a, 2021b). In fact, both temperamental shyness and fearfulness have been associated with lower instances of helping and comforting from toddlerhood to middle childhood (Beier, Terrizzi, Woodward, & Larson, 2017; Eisenberg, Spinrad, Taylor, & Liew, 2017; Findlay, Girardi, & Coplan, 2006; Karasewich et al., 2019; MacGowan & Schmidt, 2021a, 2021b; Young, Fox, & Zahn-Waxler, 1999).

Although avoidant shy behaviors can be costly (e.g., reduced cooperation), withdrawing can be adaptive in some social situations and for some individuals. For example, for some people, it may be adaptive to engage in avoidance of certain cooperative opportunities to protect their physiological vulnerability (e.g., low physiological regulatory capacity, high physiological reactivity; MacGowan & Schmidt, 2021a; Thompson & Calkins, 1996) or to avoid the possibility of performing a risky social blunder in the presence of high-status group members. In support of this notion, there has been some evidence to suggest that withdrawn behavior in early childhood and adulthood can result in social-cognitive strengths that appear to have evolved for the purpose of remaining vigilant of possible social threat (Brunet, Heisz, Mondloch, Shore, & Schmidt, 2009; LoBue & Perez-Edgar, 2014; MacGowan, Mirabelli, Obhi, & Schmidt, 2022b; Matsuda, Okanoya, & Myowa-Yamakoshi, 2013) and for blending in with the social environment (MacGowan et al., 2022b). Of course, we acknowledge that some expressions and manifestations of shyness may not be adaptive at all, and result in rejection and exclusion, such as when an adult's environment does not match what they experienced in childhood (Karasewich & Kuhlmeier, 2020).

In sum, we believe that existing lines of developmental research – and related evolutionary arguments – that exist in the context of social fear can be used to incorporate within-species nuance into Grossmann's model. Specifically, we presume that delineating social from nonsocial fear may be warranted. In addition, considering the many subtypes and expressions of social fear that have been well-documented in the developmental and evolutionary literature (Colonnesi et al., 2017, 2020; Hassan et al., 2021; Schmidt & Poole, 2019) would allow for more nuanced interpretations of when and how these behavioral profiles have been adaptive for our ancestors. Finally, we propose that, based on reasoning from Karasewich and Kuhlmeier (2020), fearfulness, more broadly than social anxiety, may also be considered a conditional adaptation such that existing individual differences in temperamental fearfulness would likely interact with early information from the child's environment, resulting in behavioral outcomes that are suited to that environment.

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Fear signals vulnerability and appeasement, not threat

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Abstract

Humans are not only fearful apes, but we also communicate our fear using social cues. Social fear displays typically elicit care and assistance in the real world and the lab. But in the psychology and neuroscience literature fearful expressions are commonly interpreted as "threat cues." The fearful ape hypothesis suggests that fearful expressions should be instead considered appeasement and vulnerability cues.

Social displays of fearfulness – that is, fearful facial, vocal, or body expressions – are commonly interpreted by psychologists and neuroscientists as "threat cues"; that is, cues that primarily serve to signal that the perceiver may be in danger. Fearful expressions have been variously described as cues that "trigger an automatic response to potential danger" (Morris et al., 1996), "implicit signals of broad environmental threat" (e.g., Farber, Kim, Knodt, & Hariri, 2019), a "cue of potential threat" (Powers & Casey, 2015), and, "threatening" (Imbriano, Sussman, Jin, & Mohanty, 2020).

Grossmann's compelling synthesis of the social functions of fear in humans may fundamentally change this practice.

The idea that decontextualized fearful expressions primarily represent threat cues can be traced back at least to the early days of human functional brain imaging research, when several seminal studies investigated patterns of brain activation when participants viewed various types of facial expressions (Breiter et al., 1996; Morris et al., 1996; Phillips et al., 1997). All found increased recruitment of the amygdala when participants saw faces expressing fear relative to other emotions (happiness, disgust, or anger) or no emotion (neutral expressions) – a pattern that largely held up in subsequent research (Fusar-Poli et al., 2009).

The interpretation of these effects was strongly influenced by Morris et al. (1996), who surmised that, because "integrated responses to threat or danger … can be mediated by the amygdala," one could infer that, "perceiving an expression of fear in a conspecific may trigger an automatic response to potential danger that accounts for the observed amygdala activation in response to fearful faces" (p. 814). But problems soon became apparent with the reverse inference that an amygdala response to a face means the face signals threat. For example, it was discovered that the amygdala responds more strongly to fearful expressions than to angry expressions (Fusar-Poli et al., 2009; Whalen et al., 2001), the latter of which clearly signal a direct interpersonal threat (Blair, 2012). In an effort to resolve this discrepancy, it was suggested that perhaps fear is the most alarming expression of all because it represents an *ambiguous* threat (Whalen et al., 2001) – that is, the expresser is not themselves the threat but is responding to an unspecified threat elsewhere in the environment. This remains a common interpretation of the social function of fear in psychology and neuroscience to this day (e.g., Farber et al., 2019; Imbriano et al., 2020).

But this interpretation has flaws. One is that if someone is looking at you in fear, an obvious potential reason – absent any other contextual cues – is that they are afraid *of you* (Rhoads et al., 2020). Another is that, as Grossmann's review makes clear, the "threat cue" interpretation of fear does not account for how perceivers actually respond to others' fear in the social world, which is often with care and the inhibition of aggression.

The care-eliciting effects of fear have been observed both in various social settings, as Grossmann describes, and in the laboratory. For example, even subliminally presented fearful expressions reliably elicit increased self-reported care and concern (Brethel-Haurwitz et al., 2017; Marsh & Ambady, 2007). Consistent with this, expressions of fear also reliably elicit behavioral approach in perceivers, as measured using a lever task (Hammer & Marsh, 2015; Marsh, Ambady, & Kleck, 2005b). This is the opposite response one would expect if perceivers primarily interpreted fearful expressions as threats. Thus, it appears that fear functions more reliably as a cue that conveys vulnerability and appeasement, similar to the bared-teeth displays other primates use to signal submission and appeasement (Vlaeyen et al., 2022), and to the submission and fear displays used in other alloparenting mammals like wolves (Schenkel, 1967). Human fearful expressions may elicit caring responses particularly effectively when displayed by children, consistent with Grossmann's hypothesis. But they may also succeed in eliciting care among adults in part because the components of a fearful expression – widened eyes, raised brows, and a rounded lower face – cause the expresser's face to appear more babyish (Marsh, Adams, & Kleck, 2005a) – which may stimulate human adults' alloparental tendencies.

How, then, should observed neural responses to fear cues be understood? Why *does* the amygdala respond so robustly to fearful expressions? One logical conclusion stemming from Grossmann's hypothesis is that amygdala responses to others' fear are empathic (Marsh, 2016). Just as the regions involved in coordinating the personal experience of pain are recruited when observing another's pain in order to interpret their experience and respond to them adaptively (Lamm et al., 2019), so the regions involved in coordinating the personal experience of fear (including the amygdala) may be recruited in response to others' fear in order to interpret their experience and respond adaptively. In many cases, the appropriate response to another's fear is protection and care. That unusually caring adults recruit the amygdala more than typical adults when viewing others' fear supports this conclusion (Marsh et al., 2014). Of course, in some contexts the most appropriate response to others' fear might be social fear learning (Olsson & Phelps, 2007) or marshaling one's own fearful response.

But fundamentally, if humans are indeed not only fearful apes, but apes endowed with a multitude of social cues to convey our fear to each other, it supports the idea that we are also caring apes who can generally be trusted to respond to others' displays of fear with the help they are seeking rather than selfishly fleeing or exploiting their vulnerability.

Both our fearfulness and our readiness to signal fear to one another can thus be interpreted as evidence of our species' prosocial nature.

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Beyond the fearful ape hypothesis: Humans are also supplicating and appeasing apes

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Abstract

We review research suggesting that several of the functions attributed to fear, in the target article's fearful ape hypothesis, also apply to supplication and appeasement emotions. These emotions facilitate support provisioning from others and the formation and maintenance of cooperative relationships. We therefore propose that the fearful ape hypothesis be expanded to include several other distinctively human emotional tendencies.

As reviewed in Grossmann's target article, research indicates that humans experience fear more often and intensely, and are more attuned to conspecifics' fear expressions, compared to other primates. To account for this between-species difference, Grossmann proposes (and marshals a compelling body of evidence in support of) *the fearful ape hypothesis*, positing that humans' heightened fearfulness emerged out of its adaptive benefits, namely: (1) Eliciting support from others in response to specific, momentary threats, and (2) promoting and maintaining long-term cooperative relationships that are crucial for survival and reproduction. We agree with Grossmann's synopsis, but contend that its scope may be too narrow. Emotions beyond fear – notably, *supplication* emotions (i.e., a group of emotions that includes fear but also sadness, disappointment, distress, and worry) and *appeasement* emotions (i.e., shame, guilt, regret, and embarrassment; van Kleef & Côté, 2022) – likely facilitate the same adaptive ends as those proposed for fear. As a result, several additional distinct emotions may also underlie and shape humans' unique capacity for cooperation (see Keltner & Shiota [2021] for a broad review of the cooperative functions of emotions).

According to van Kleef and Côté (2022), supplication emotions are those that occur when one's expectations or desires go unfulfilled. Similar to fear, the experience and expression of other supplication emotions elicit support from others. For example, like nonverbal expressions of fear (e.g., Hammer & Marsh, 2015; Marsh & Ambady, 2007), nonverbal expressions of sadness and disappointment elicit emotional and financial support from observers (Hendriks & Vingerhoets, 2006; Small & Verrochi, 2009; van Doorn, van Kleef, & van der Pligt, 2015). Furthermore, just as heightened fearfulness promotes cooperative tendencies across contexts (per the target article), individuals who are generally prone to sadness and distress are also generally prone to sympathy (Eisenberg, 2000), which increases caring behavioral tendencies toward others (Weidman & Tracy, 2020). Thus, stable tendencies to feel multiple supplication emotions may underpin the same set of cooperative behaviors as does fearfulness.

Expressing supplication emotions also has been shown to facilitate relationship formation and maintenance. One study found that individuals were more willing to help a person expressing sadness than they were a person expressing no emotion, but only when they believed the expressor was open to meeting new people (Clark, Oullette, Powell, & Milberg, 1987). Similarly, a willingness to express emotions like distress, nervousness, and anxiety is associated with the formation of intimate friendships (Graham, Huang, Clark, & Helgeson, 2008). Further supporting the role of supplication emotions in maintaining close relationships, Parkinson, Simons, and Niven (2016) found that expressions of worry lead expressors' romantic partners to attempt to calm them, suggesting that these emotions elicit needed emotional support within existing relationships.

Unsurprisingly, given the positive relationship effects of expressing supplication emotions, suppressing these emotions can, conversely, impede relationship formation and damage existing relationships. In one study, suppressing sadness led unacquainted conversation partners to feel less rapport and a weaker desire to affiliate with the suppressor (Butler et al., 2003). Suppression of these emotions in romantic relationships is associated with greater conflict, as well as suppressors' partners feeling greater negative emotions and lower relationship satisfaction (Impett et al., 2012). Overall, research on supplication emotions complements research consistent with the fearful ape hypothesis, suggesting that the hypothesis might be fruitfully broadened to include this entire family of emotions.

Appeasement emotions occur when a person who has committed a social transgression or failed to meet others' expectations anticipates reactive physical or relational aggression. These emotions serve similar social functions to supplication emotions, but they are more specialized to facilitate exchange relationships (i.e., relationships based on 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).

Empirical and theoretical work on social learning has revealed processes that adaptively guide learning behavior and facilitate cultural transmission and development (Rendell et al., 2011). Such processes are proposed to be key to understanding the sophisticated forms of group coordination and culture found in humans.

Social learning is especially important within the aversive domain, where learning (asocially) from one's own experiences can be dangerous (Lindström, Selbing, & Olsson, 2016). Social pathways are believed to contribute greatly to the acquisition of fear reactions and avoidance behavior (Debiec & Olsson, 2017; Rachman, 1977). Social fear learning depends on human transmission of threat-related information, for instance through facial expressions, body posture, or verbal communication (Lebowitz, Shic, Campbell, MacLeod, & Silverman, 2015; Mertens, Boddez, Sevenster, Engelhard, & De Houwer, 2018), making our ability to express and perceive fear crucial for social fear learning.

At its simplest level, perceiving fear reactions in others notifies us of the (possible) presence of a threat, making us more alert and attentive (Azarian, Esser, & Peterson, 2016; Lee, Susskind, & Anderson, 2013). By observing others' aversive reactions, we can acquire fear vicariously (Olsson & Phelps, 2007). Observational fear learning has also been demonstrated in nonhuman animals (Mineka, Davidsson, Cook, & Keir, 1984), and is likely a common pathway through which humans learn fear (Askew & Field, 2008). It is generally believed that observational learning hinges on similar associative learning mechanisms as nonsocial learning (Heyes, 2016; Olsson & Phelps, 2007). Further, anxious individuals have stronger fear learning responses, possibly driven by an increased sensitivity and attention toward threat-related stimuli such as facial expressions of fear (Reynolds, Field, & Askew, 2014).

Research also shows that humans can, unlike nonhuman animals, acquire fear through verbal instructions (Mertens et al., 2018). Instructed fear learning appears to be similar in nature to observational or direct learning (Mertens et al., 2018) and possibly similarly modulated by trait anxiety (Grillon, Ameli, Merikangas, Woods, & Davis, 1993). The importance of verbal transmission of threat-related information is also evident in the negativity bias seen in social transmission of information, for example, in storytelling and social media (Bebbington, MacLeod, Ellison, & Fay, 2017; Tsugawa & Ohsaki, 2017). Along the same line we also see that anxious individuals pay more attention to threatening or negative information such as news stories (Gadarian & Albertson, 2014)

Moreover, it is relevant to note that *expressing* fear is also believed to be a way to show submissiveness and accept the dominance of someone else (Öhman, 1985) which means that we can learn something about a group's social structure by observing others' expressions of fearfulness (Jones, DeBruine, Little, Watkins, & Feinberg, 2011). Learning about social structures around us can help us predict and avoid social threats, either direct threats such as attacks, or more indirect threats such as loss of support, status, or one's social group.

However, some aspects of social fear learning are likely nonadaptive. Research indicates that social forms of fear learning are important pathways in the development of clinical fears such as post-traumatic stress disorder (PTSD), phobias, or anxiety disorders (Askew & Field, 2008; Öst & Hugdahl, 1981), for example, through observation of violence or accidents. There are also studies demonstrating transmission of anxiety between individuals, typically from parent to child (Aktar, Nikolić, & Bögels, 2022; Eley et al., 2015). This is possibly driven by transmission of beliefs that the world is unsafe or through transmission of coping strategies such as avoidance and worrying, although the exact mechanisms are unknown. It further appears as if anxious parents are worse at responding caringly and supportive to negative emotional reactions in their children (Creswell, Apetroaia, Murray, & Cooper, 2012) which would, at least partly, contradict Grossmann's arguments. However, typically anxious behavior does not appear to be transmitted to healthy adults (Selbing & Olsson, 2019).

Taken together, a large body of research from the perspective of social learning suggests that our ability to express and perceive fearfulness is adaptive, as it helps us predict and handle potential threats while decreasing our own exposure to danger. In the fearful ape hypothesis, Grossmann builds his argument for the adaptiveness of heightened fear around the adaptiveness of our ability to *express* and *perceive* fearfulness, given that it promotes helping behavior and increases cooperation. We agree that observation of fearfulness in another individual can elicit helping or caring, even though helping also can be triggered by perceiving a threat toward other individuals without those individuals expressing fearfulness (Vieira, Schellhaas, Enström, & Olsson, 2020). However, given the fundamental and ubiquitous role of adaptive social learning across the human lifespan, we suggest that the fearful ape hypothesis needs to consider social learning as an alternative candidate explanation for why the expression and perception of fearfulness is adaptive.

According to Grossmann, cooperative care is the primary precondition which enables the emergence of heightened fearfulness. However, if we consider social learning as the fundamental precondition and primary mechanism, then care-based cooperation can be seen as an adaptive byproduct of more domain-general social learning capacities. In either case, we argue that any theory that builds on the adaptiveness of a (human) social signal should, for theoretical and explanatory adequacy, consider the competing or contributing role of social learning.

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The dark side of fear expression: Infant crying as a trigger for maladaptive parental responses

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Abstract

While infant fearfulness, and its expression via crying, may have been adaptive in our evolutionary history, for modern parents, crying can be challenging to respond to. We discuss how and why prolonged crying can raise the risk for difficulties with adult care. Given that crying is the most-reported trigger for shaking, its potential to elicit maladaptive responses should not be overlooked.

Central to the *fearful ape hypothesis* is the notion that infants expressing heightened fearfulness traits received increased care from mothers and others in our evolutionary history. Crying is conceptualized by Grossmann as a vocal expression of infant fear, and more frequent crying is argued to "elicit more caring behavior." We agree with the contention that infant crying typically elicits adaptive caregiving and is powerful in securing attention over the protracted period of human infant dependency. However, we would add the caveat that, in modern times, crying is also the most commonly cited trigger for physical abuse in the first months of life. Even if we believe that fearful crying has been broadly adaptive in human evolution, we should not overlook the role of infant crying in maladaptive responses in modern parents. Although Grossmann does discuss how fearful infants may be differentially susceptible to environmental influences, there is no discussion of how adults may be differentially susceptible to infant crying. For many modern parents, crying is commonly perceived as excessive. Prolonged and extended crying is difficult to cope with and is one of the most common reasons for help-seeking from healthcare professionals (St James-Roberts, Hurry, & Bowyer, 1993). Crying has been identified as a major risk factor for infant shaking or inappropriate physical actions. In a landmark study of parents in the Netherlands, nearly 6% reported having smothered, slapped, or shaken their infants to stop their crying (Reijneveld, van der Wal, Brugman, Sing, & Verloove-Vanhorick, 2004). Actual rates of shaking may be even higher because of parental underreporting (Reijneveld, 2007).

Although physical abuse may be at the extreme end of negative outcomes, other non-optimal associations between crying and caregiving have been reported. When caregivers perceive crying as excessive, it can lead to early termination of breastfeeding (e.g., Howard, Lanphear, Lanphear, Eberly, & Lawrence, 2006) and it can predict the subsequent onset of maternal depression (Petzoldt, 2018). Mothers who report that their infants cry a lot also tend to score high on parental stress indices and report less positive reinforcement from their infants (Beebe, Casey, & Pinto-Martin, 1993).

Why might crying elicit approach and caregiving behaviour in most adults, but precipitate abuse or maladaptive responses in some? The impact of infant crying, or vocal fear expression, may depend on parents' own health, vulnerabilities, prior family history, and current family circumstances. For example, adults at risk for harsh parenting have been shown to be less likely to habituate in response to repeated cry sounds compared to other adults (Out, Bakermans-Kranenburg, van Pelt, & Van Ijzendoorn, 2012). Mothers with mood disorders show blunted reactivity to infant crying, as measured by eye-tracking indices and galvanic skin response, compared to mothers with no mood disorder (Bjertrup et al., 2021). Limited social support for the parent is also suggested to increase the negative effects of crying on the parent and infant (St James-Roberts et al., 2019).

A number of the characteristic properties of infant crying have the potential to increase maladaptive responding, together or in isolation. First, crying, as with other forms of fear expression, is an ambiguous signal, and many cry bouts begin and end for no clear reason (Barr, 2014). Second, the acoustic properties of crying mean that it is typically perceived as aversive, with its high pitch, unpredictability (Young et al., 2019), and "roughness." Crying can be especially aversive, or frustrating to caregivers when it is prolonged and difficult to soothe (Fujiwara, Barr, Brant, & Barr, 2011). If we consider crying not just as a one-off alarm signal, the complexity of the cry–caregiving association becomes clear.

Indeed, crying is a communicative signal that parents must repeatedly respond to over a lengthy developmental period. Meta-analytic evidence from parent reports of crying across countries shows that parents deal with substantial durations of crying over the first 12 months post-birth. Cry duration does not drop off as markedly from its initial peak at 6–8 weeks as earlier described in the classic "cry curve," whereby crying duration shows a clear and steady decline (Vermillet, Tølbøll, Litsis Mizan, Skewes, & Parsons, 2022). Although data on what constitutes typical or normal cry behaviour is still sparse, crying for long periods beyond 6 months of age has been shown to predict later childhood regulatory difficulties (von Kries, Kalies, & Papoušek, 2006). What is appropriate fear expression at one age may signal developmental difficulties, problems in parent–infant interactions, or physical health issues, at a later age.

Whether high infant fearfulness, and crying as we have focused on here, elicits enhanced caregiving, depends on the context in which it occurs, and in particular, on the capacities of nearby adults. Taking our broader evolutionary context, as the *fearful ape hypothesis* does, fearful crying is understood as a stimulus for cooperative caregiving by a familial group. However, a mother in a modern single-family home, deprived of sleep, with limited social support might have different capacities to respond to a high-fear infant than a mother living communally with none of these risk factors. While overarchingly, fear expression and crying might function to promote cooperative group caregiving by adults, if perceived as excessive by the individual listener, it can precede, in the most unfortunate cases, physical abuse.

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Fearful apes, happy apes: Is fearfulness associated with uniquely human cooperation?

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Abstract

In the fearful ape hypothesis, Grossmann argues that heightened fearfulness increases human-unique cooperation. We suggest that this conclusion, however, may be premature. In particular, we question Grossmann's singling out of fear as *the* affective trait that enhances cooperative care. Additionally, we problematize the extent to which heightened fearfulness in humans, and its association with human-unique cooperation, are supported empirically.

Grossmann's fearful ape hypothesis provides a novel and compelling account for the supposed link between heightened fearfulness and enhanced cooperation in humans. We appreciate the author's re-conceptualization of fear as a potentially adaptive response in some contexts, which in previous clinical works has largely been viewed as maladaptive. Despite its novelty, however, we argue that, at present, there is insufficient evidence to conclude that: (1) it is specifically heightened fearfulness (and not other affective traits or emotions in general) that enhances cooperation and (2) that heightened fearfulness is related to enhanced, “uniquely human,” cooperation.

Grossmann singles out fearfulness as the key affective trait that evolved to support “human-unique” levels of cooperation. He suggests that fearful infants evoke more (allo)parental care and, by receiving more care, become more cooperative children, adults, and parents themselves. We argue, however, that the influence of affective states on cooperative behaviour may not be bound to fearfulness alone. Other affective states may also be associated with – or even evoke more – cooperation.

Similarly to fear, from early in human ontogeny, infants experience and display positive affect (Messinger, 2002; Messinger & Fogel, 2007) and can distinguish positive from other facial expressions (de Haan & Nelson, 1998). Furthermore, although results are mixed, there is some evidence that humans also display a perceptual sensitivity bias towards happy faces (Wirth & Wentura, 2020; Zsido et al., 2021). Crucially, although Grossmann and others failed to find an association between sensitivity to happy faces and infants’ prosociality (Grossmann, Missana, & Krol, 2018; Rajhans, Altvater-Mackensen, Vaish, & Grossmann, 2016), there is robust evidence that experienced and displayed positive affect results in more cooperation in child and adult actors (e.g., Aknin, Van de Vondervoort, & Hamlin, 2018; Centorrino, Djemai, Hopfensitz, Milinski, & Seabright, 2015; Isen & Levin, 1972; Kushlev, Radosic, & Diener, 2022; Moore, Underwood, & Rosenhan, 1973; Rosenhan, Salovey, & Hargis, 1981), as well as observers (including in cooperative parental-care contexts) (e.g., Centorrino et al., 2015; Danvers & Shiota, 2018; Lengua & Kovacs, 2005; Scharlemann, Eckel, Kacelnik, & Wilson, 2001). Therefore, it is not only fearful infants, but also happy infants, who may evoke cooperation in others, and may, by receiving more care, themselves become more cooperative adults. The putative effect of fearfulness on cooperation is therefore not necessarily unique in this regard – and it may also be that happiness, or emotional expressivity more generally, foster cooperation.

Grossmann also argues that humans display and perceive more fearfulness in comparison to other great ape species, and that this heightened fearfulness evokes increased levels of “human-unique” cooperation (i.e., alloparental care). However, there is not enough evidence that: (1) fearfulness is heightened in humans compared to other great apes; and that (2) heightened fearfulness is associated with enhanced “human-unique” cooperation.

Although some studies found that great apes do not show attentional bias to fear specifically (Kret, Jaasma, Bionda, & Wijnen, 2016; Kret, Muramatsu, & Matsuzawa, 2018), other work has found heightened attention towards fear (Pritsch, Telkemeyer, Mühlenbeck, & Liebal, 2017), and towards emotions in general (Wilson & Tomonaga, 2018, 2021; for a review, see Kret, Prochazkova, Sterck, & Clay, 2020). Furthermore, the claim that human infants *express* more fearfulness than other great apes is based on one empirical study (Herrmann, Hare, Cissewski, & Tomasello, 2011). This study, however, used a human-centred paradigm (sensitivity to novel humans and objects) to contrast the reactions of human children to adult great apes. Herrmann et al. (2011) assumed that showing an unfamiliar human is similarly relevant and meaningful for a captive adult ape (who is likely exposed to unfamiliar humans many times on a daily basis) and a human child (for whom this context may be drastically different). As such, this study might have or might have not captured the full extent of the fear response in other primates, calling to question Grossmann’s claims about uniquely human heightened fear production.

Even if displaying and perceiving fear is, on average, heightened in humans, this does not mean that it necessarily evolved for “human-unique” cooperative care purposes (i.e., alloparental care). First, whether alloparental care is uniquely human is questionable considering some evidence for such forms of cooperation in other primate species (Boesch, Bole, Eckhardt, & Boesch, 2010; Fairbanks, 1990; Samuni, Wittig, & Crockford, 2019; Tokuyama et al., 2021). Second, to support the association between fearfulness and “human-unique” cooperation, Grossmann cites research showing associations between enhanced fearfulness sensitivity and cooperation in non-alloparental care contexts, such as parental care of own children (e.g., Kiel & Buss, 2011), and helping/sharing in infants, children, and adults (e.g., Grossmann et al., 2018; Marsh & Ambady, 2007; Rajhans et al., 2016) that are, importantly, not unique to humans. Given that such forms of cooperation exist also in other species (for a review, see de Waal & Suchak, 2010), evidence is lacking that heightened fearfulness is associated with “human-unique” cooperation.

Grossmann further argues that, next to the fight-or-flight response seen in many animals, heightened displayed and detected fearfulness elicits approach behaviours (tend and befriend) in humans in particular. However, the groundwork for a link between fearfulness and cooperation also exists in nonhuman animals. For example, newborn chimpanzees and bonobos are known to express fearfulness and distress through pout moans and whimpers in the context of maternal care (De Waal, 1988), and adult caregivers comfort offspring who show such signs by embracing and kissing them, similarly to humans (de Waal & Preston, 2017). Furthermore, offspring displaying distress provoke parental cooperative care in other species, including rodents and birds (de Waal & Preston, 2017). Even outside of infant–parent relationships, nonhuman animals, such as rodents, react to conspecifics displaying fear by engaging in prosocial behaviours (Keysers, Knapska, Moita, & Gazzola, 2022). Therefore, it seems highly unlikely that heightened fearfulness elicits approach behaviours exclusively in humans.

In sum, singling out fearfulness as *the* affective trait that evolved specifically for cooperative purposes in humans seems premature. Additionally, there is insufficient evidence to conclude that human fear perception and production is significantly increased compared to other nonhuman animals. Finally, the link between heightened fearfulness and alloparental care awaits first empirical support. To truly examine these facets, it will be critical for future work to take the sensitivities and milieu of both human and nonhuman animals into account.

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Under greater cooperative care, childhood fear is more accommodated, but less warranted

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Abstract

The target article posits that caregiver cooperation rendered heightened expression of childhood fear an adaptive response to threat. I argue that caregiver cooperation rendered childhood fear expression less accurate as a signal of actual threat, and hence less effective for harm avoidance. Further, other emotional expressions that avoid unwarranted caregiver stress may be more likely to evoke needed care.

At its core, the fearful ape hypothesis posits that vulnerable humans under perceived threat started signaling for help (expressed fear) in environments where help was likely to be given (alloparental care). The notion of emotions as a social influence tactic is well accepted (Crivelli & Fridlund, 2018), and the author argues that fear signaling as a threat response is more adaptive in cooperative care environments, where help is more abundant. Neglected, however, is the parallel notion that in environments where help is more abundant, fearfulness may be less indicative of actual threat. In cooperative care environments, expressions of fear may be more noticed and attended to, *but less accurate*. Why? In environments with more abundant cooperative care, most threats are anticipated and addressed, rendering persistent childhood fear unnecessary. For instance, the dark is very unlikely to present any danger when one sleeps in a caregiver-protected dwelling, in the vicinity of a large extended family, under the protection of the entire community. The real threats that remain require enculturation to comprehend.

It follows that under cooperative care, the expression of heightened childhood fear is an unlikely adaptive solution to staving off immediate danger as it is a poor indicator of actual threat.

Consider an environment replete with ultrasociality, wherein adults at the apex of their intellectual and physical capacities form groups within which they cooperate to feed, protect, and educate their children. Let's assume that in such groups, individuals value common knowledge (Lewis, 1969; Shteynberg, Hirsh, Bentley, & Garthoff, 2020) – that is, they prioritize information known to be known. In such groups, historic, present, and would-be threats under shared attention (Shteynberg, 2010, 2015) are emphasized, collective attitudes toward those threats (Hardin & Higgins, 1996; Pinel, Long, Landau, Alexander, & Pyszczynski, 2006) are felt deeply, shared intentions (Tomasello, 1995) and a division of labor (Wegner, 1987) govern threat prevention and threat response. These collective notions of environmental threats, appropriate safeguards, and contingent responses are codified into a cognitive representation of the group itself – a part and parcel of a collective identity schema (Brewer & Gardner, 1996). In short, group members define themselves, in part, by the means they undertake to protect the group. In addition, "in situ" responses can be formulated "on-the-fly" based on in-the-moment sharedness of objective, affective, motivational states, wherein individuals represent themselves as non-specific collective agents – experienced as a knowing, feeling, and pursuing "we" in the moment (Shteynberg, Hirsh, Garthoff, & Bentley, 2022). That is, group members can engage in an improvised, yet organized, collaborative defense of the group.

One task of a child born into such a social soup is to learn its ways, a protracted process that culminates in adolescence. Heightened childhood fear is unlikely to be indicative of actual threat as it precedes rather than follows enculturation. It is therefore an open question of whether heightened childhood fear can help caregivers protect the child from danger; it may even distract caregivers from noticing such danger.

After all, when caregivers are more responsive, children are less fearful, not more (Ainsworth, 1979). These securely attached children rely more on their caregivers to keep them safe than their personal capacity to detect threats. In societies with greater wealth and thus lower childhood mortality, childhood fear expression is even less indicative of actual threat because there is less threat. Childhood fear in such societies may not be less accommodated, but less warranted.

Perhaps heightened childhood fear is adaptive – but not because it helps human adults respond to a child in real danger, but rather, as the target article also suggests, because it increases affective bonding and caregiver investment (Hrdy, 2016; Tomasello, 2020). How would a heightened expression of fear help such a child?

Perhaps by evoking empathy. When it comes to the provision of altruistic care to progeny, a significant amount of scholarship suggests that empathic concern, worry about the welfare of another, is an essential ingredient (Batson, 2009, 2011). Let us assume that the expression of fear is particularly powerful is soliciting feelings of empathic concern from would-be caregivers, yielding greater affective bonding, and caregiver investment in the child. However, this sword is double-edged. To the extent that the child's expressions of fear are not well calibrated to actual threats in the environment, a-child-who-cried-wolf dilemma emerges: Heightened, but "baseless," expressions of fear are likely to tax the emotional, cognitive, and behavioral resources of caregivers – especially in ultrasocial contexts where the few threats that do remain are already under cooperative surveillance and care.

Humans may express more fear than apes. The adaptive, or otherwise, reasons for heightened fear expressiveness are worth exploring. The target article raises one definite possibility: cooperative care. However, under cooperative care, children's fear as a signal of threat is both more noticed, and less accurate. This implies that as an affective bonding strategy, emotional expressions that avoid unwarranted caregiver stress may be more adaptive.

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The suffering ape hypothesis

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Abstract

The "fearful ape hypothesis" could be regarded as one aspect of a more general "suffering ape hypothesis": Humans are more likely to experience negative emotions (e.g., fear, sadness), aversive symptoms (e.g., pain, fever), and to engage in self-harming behavior (e.g., cutting, suicide attempts) because these might motivate affiliative, consolatory, and supportive behavior from their prosocial environment thereby enhancing evolutionary fitness.

Humans are a highly prosocial species, which does not only mean that they cooperate in good times but also that they – under certain conditions – support each other in need (Fabrega, 1997; Gurven, Stieglitz, Hooper, Gomes, & Kaplan, 2012; Kessler, 2020; Spikins et al., 2019; Steinkopf, 2017a, in press; Sugiyama, 2004; Tilley, 2015). That is why expressions of weakness, incapacity, despair, vulnerability, and neediness may benefit the individual that depicts them, for example in terms of being absolved from duties, receiving assistance and material support, or motivating affiliation and integration attempts from others (Finlay & Syal, 2014; Hagen, Watson, & Hammerstein, 2008; Nock, 2008; Steinkopf, 2015). In the target article, Grossmann presents the "fearful ape hypothesis" which states that humans are more fearful than other apes because of potential affiliative responses of their particularly prosocial environment to expressions of fear. This hypothesis is in line with several similar hypothesis regarding emotions, conditions, or behaviors like pain in general (de Williams & Kappesser, 2018; Steinkopf, 2015; Wall, 1999), labor pain in particular (Finlay & Syal, 2014), signs of depression (Hagen, 2003; Henderson, 1974; Watson & Andrews, 2002), self-harm (Nock, 2008), suicidal behavior (Syme, Garfield, & Hagen, 2016) as well as sickness behavior and other symptoms of sickness (Steinkopf, 2015, in press). Grossmann's "fearful ape hypothesis" could therefore be regarded as one aspect of a more general "suffering ape hypothesis." From this perspective, pain, sickness behavior, depression, anxiety, and so on are just different channels through which need is communicated (Steinkopf, 2017b, in press). As Grossmann gives a great overview and argument for the case of fear, this commentary will give a very short overview of the other aforementioned cases.

The great pain researcher Patrick Wall (1999) regarded pain not as an emotion or a sensation, but as a motivation or need state. That is the need to withdraw from a harmful situation, the need to spare the injured body part, and – most importantly – the need to seek care and treatment. Thereby, the often loud, pervasive, and specific expressions of pain (de Williams, 2002) not only serve as a warning to other, but also as a signal that help is needed (Finlay & Syal, 2014; Steinkopf, 2015, 2016). This is very well illustrated by the case of labor pain as presented by Finlay and Syal (2014). They hypothesize that the extraordinary pain of childbirth that women experience and express in comparison to females of other species is not exclusively based on the particular difficulties of human birth (obstetric dilemma), but connected to the fact that midwifery is a human universal. In this critical situation, when two lives are at stake, having assistance may heighten the chance of survival for the mother as well as for the child. Therefore, natural selection should have favored expressive and unbearable labor pain that mobilizes support over stoic childbirth.

The same might be true for symptoms of sickness and sickness behavior. Certainly, the primary function of these bodily reactions to infection is to fight an infectious agent and create circumstances advantageous for this immune response (Aubert, 1999; Dantzer & Kelley, 2007; Schrock, Snodgrass, & Sugiyama, 2020). However, symptoms like social withdrawal, lack of motivation, and fever are easily discernible for others and may motivate certain behaviors, for example avoidance but also affiliation and support. Therefore, symptoms of sickness might not only be shaped for optimal immune effectiveness, but also for their communicative and social impact, that is the prevention of infection among kin and community through triggering avoidance responses as well as care and support (Kessler, 2020; Kessler, Bonnell, Byrne, & Chapman, 2017; Shakhar & Shakhar, 2015; Steinkopf, 2015, 2017b, in press; Tiokhin, 2016). Thereby, symptoms and sickness behaviors might be exaggerated above the intensity level that is optimal for immune function to optimize the mobilization of social support (Steinkopf, 2015).

In a similar way, suicidal behavior can be explained through its high-communicative value as a signal of need (Hagen, 2003; Syme et al., 2016). From this evolutionary perspective, it is not the aim to complete the suicide but to send a credible signal that one's life has become worthless and, in this way, motivate support and reintegration. Through the risk of death, the cry for help becomes pervasive and persuasive. Noteworthily, this explains why natural selection did not sort out suicidal behavior, it does not mean that suicidal individuals act consciously and strategically to extract support from others. The argument for non-suicidal self-harm is similar. From the individual, subjective perspective, self-harm helps regulating aversive emotions but, from a social perspective, self-harm is a convincing signal of neediness (Nock, 2008). Conversely, self-harm and suicidal behavior could only evolve in a highly prosocial environment. Symptoms of depression such as social withdrawal, anhedonia, or loss of motivation are less pervasive but they may also signal surrender and need for help (Henderson, 1974; Price, Sloman, Gardner, Gilbert, & Rohde, 1994; Watson & Andrews, 2002).

When emphasizing the benefits of suffering it is important not to forget about the obvious downsides. There are direct costs to suffering such as the energy expenditure of high fever, the risk of becoming victimized because of displayed weakness (de Williams, Gallagher, Fidalgo, & Bentley, 2016), or the reputational damage of "cowardice" (see Ackerman & Kenrick, 2008). Also, there are opportunity costs such as a lowered chance of mating because of social withdrawal, lost opportunities for social bonding because of debilitating pain, and missed out food because of appetite loss (see Lopes, 2014). However, these downsides also serve an important function: They make suffering expensive and thereby credible – it is a signal that is not cheap to fake and therefore convincing (Hagen et al., 2008; Steinkopf, 2016).

To sum up, it is not only fear and anxiety but probably all kinds of aversive states that might be more pronounced in humans because of their high prosociality. Helpfulness and suffering are two sides of the same coin. In the end, it is not even necessary to limit the hypothesis to emotions and conditions with negative valence. Not only suffering but also feelings of joy, gratitude, and love might be more pronounced in humans.

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Hominin life history, pathological complexity, and the evolution of anxiety

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Abstract

In order to address why the number of patients suffering from anxiety and depression are seemingly exploding in Western, educated, industrialized, rich, and democratic (WEIRD) countries, it is sensible to look at the evolution of human fearfulness responses. Here, we draw on Veit's *pathological complexity framework* to advance Grossmann's goal of re-characterizing human fearfulness as an adaptive trait.

Grossmann elegantly reviews and synthesizes evidence from a variety of different disciplines to defend what he calls the *fearful ape hypothesis*, that is, the view that the apparently excessive fearfulness traits observed in humans as compared to other great apes should not be seen as pathological, but rather as an old adaptive strategy of our hominid ancestors. What makes it beneficial, however, is not – as one might assume – a greater level of danger experienced by human infants, but rather its effects through enhancing cooperative care and subsequent success in the highly interconnected societies of the human species. Grossmann argues that in early ontogeny, expression of fearfulness can enhance affective attention and caregiving from mothers and others in their proximity, which also leads to increased future cooperation. Rather than just being a maladaptive pathology, enhanced fearfulness should be seen as the outcome of natural selection having led to a design optimum where a risk for anxiety and depression is traded off against the role of fearfulness as an affective foundation for cooperative care in humans.

Here, we aim to strengthen Grossmann's fearful ape hypothesis by placing it in the context of Veit's (2022a, 2022b, 2022c) pathological complexity framework for the evaluation of life-history tradeoffs in evolution and the classification of disorders of consciousness. Pathological complexity refers to the complexity of the fitness challenges faced by an organism. It can be operationalized as the number of parameters and constraints in the Darwinian optimization problem of fitness, studied by modern state-based behavioural and life-history theory. It thus enables us to assess the difficulty faced by different life-history strategies in the pursuit of fitness maximization. The prefix "pathological" is here not meant to indicate that this complexity is inherently pathological, but rather that it is only within life-history theory that we can distinguish pathological from adaptive traits.

Grossmann has argued that despite the increased risk for anxiety, the social benefits of heightened fearfulness will outweigh this drawback and make the trait one worth having within the types of human society in which we evolved, that is, small, cooperative groups. If he is right, then there will also be a point at which further increases in fearfulness will no longer be beneficial, and instead should be seen as pathological. While it may be common that we (or at least Western, educated, industrialized, rich, and democratic [WEIRD] societies) treat even low levels of fearfulness as maladaptive precursors of anxiety and depression, through this framework we can see that this attribution may be wrong in some settings, while appropriate in others. Grossmann's hypothesis can assist through pushing the boundaries of what is seen as part of normal human variation and thus help us to better understand and diagnose when and how anxiety occurs as a distinctly pathological state.

One potential application is in understanding differences between the sexes. Previously, we have used the pathological complexity framework to argue that greater self-protection in human females should be seen as an adaptive, rather than pathological, trait that evolved as an optimal life-history strategy for females (Veit & Browning, 2022). This has direct links to Grossmann's proposal, because it could potentially be used to explain differences in "fearfulness" between human males and females, as its role in infant care could be especially important to mothers.

Nevertheless, despite its initial appeal we think that to advance it further, Grossmann's hypothesis should be linked to the employment of life-history theory in psychology and anthropology. After all, it is precisely the fact that humans at the age of 2.5 years show more fearfulness than other great apes (Herrmann, Hare, Cissewski, & Tomasello, 2011), that calls for a comparative approach to resolve what Grossmann calls the *human fear paradox*. Like Grossmann, we think that the exploding number of cases of depression and anxiety in WEIRD countries could be because of an evolutionary mismatch. Rather than thinking of these as "flaws" within the individual, it is instead the restructuring of our modern Western individualized societies where these traits are considered pathological. Returning to the idea of a tradeoff between the cooperative benefits of fearfulness and the risks of poor mental health, this will strongly depend on the socioecological context – what is beneficial within one type of social world.

In thinking about these changes in human life histories from small cooperative hunter–gatherer communities towards large-scale societies, it will hardly be surprising that an evolved fearfulness response to novelty could lead to severe cases of depression and anxiety in our modern ever-changing environments. The adaptive pressures have changed such as to now make excessive fear an obstacle to thriving in these environments, and the increase in independent living and concurrent decline in cooperative care shift the balance of the tradeoff. Modern humans in WEIRD societies face vastly different pathological complexity challenges in their life histories than our hominid ancestors. In order to more fully gauge the strength of Grossmann's proposal, we require a more detailed comparison of hominin life histories, including different great apes, our own ancestors, and cross-cultural studies of modern societies. This would allow a full assessment of the benefits and drawbacks of higher levels of fearfulness in different forms of hominin life; an assessment of the pathological complexity of these different life histories with regards to the fearfulness trait. While Grossmann has made a good start in drawing from a wide range of literature, future work will have to try to operationalize and measure the adaptive value of fearfulness, which will enable us to make sense of the evolution of anxiety and derive further testable predictions regarding its distribution.

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Cooperative care as origins of the "happy ape"?

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Abstract

Grossmann proposes an interesting framework to explain how heightened fearfulness among humans could be evolutionarily adaptive in the context of cooperative care. I would like to propose that cooperative care may also be a potential mechanism promoting *enhanced happiness expression* among humans, shedding light on questions about the scope and boundary of the fearful ape hypothesis.

Grossmann proposes that heightened fearfulness could be evolutionarily adaptive in the context of human cooperative care, which explains why humans display enhanced fearfulness compared to other apes. I would like to propose that the central mechanisms stipulated may also be potentially applied to explain the evolution of enhanced *happiness expression* among humans, which may shed light on questions about the scope and boundary of the framework.

The target article first presents evidence showing that humans are "fearful apes" who display heightened fearfulness compared to chimpanzees. In fact, humans may also experience and display more enhanced happiness than chimpanzees do. Humans are a particularly happy species, evolved to experience positive feelings not only to positive stimuli but also to even neutral stimuli

(Diener, Kanazawa, Suh, & Oishi, 2015). People around the world have been found to be generally in positive moods most of the time, even including those living under difficult circumstances (Diener & Diener, 1996). In terms of happiness expressions, chimpanzees *laugh* in response to playful stimuli (e.g., a good tickle) similar to how humans do (Kret, Prochazkova, Sterck, & Clay, 2020). But only humans display *smiles* when experiencing inner enjoyment. The "Duchenne smile" – the authentic smile that engages muscles around the eyes – enables human happiness to be more obviously and frequently observed, which has no known correspondence among nonhuman primates (Parr & Waller, 2006). It has been theorized that ubiquitous happiness among humans may have evolved to motivate behaviors (e.g., sociality, creativity, and planning) that increase one's own survival and reproductive fitness (Diener et al., 2015). But is it possible that human cooperative care also plays a role in the evolution of happiness expression among humans?

Grossmann has provided evidence that human children and adults are highly sensitive to fearful faces, which is necessary to support the view that enhanced fearfulness is an adaptive trait linked to cooperative cognition. In the same vein, it has been shown that humans are highly sensitive to happy faces. Happy faces are *vivid* to humans: They are more discriminable at a distance than other emotional expressions, and they automatically engage processing even at the earliest stages of perception (Becker & Srinivasan, 2014). The ability to perceive happiness expressions is so deeply rooted among humans that even 3-month-old infants are able to discriminate happiness expressions from other expressions (e.g., Barrera & Maurer, 1981; Kuchuk, Vibbert, & Bornstein, 1986; Young-Browne, Rosenfeld, & Horowitz, 1977). Directly relevant to caregiving behaviors, human adults are found to be able to detect even subtle features and changes in happiness expressions of infants and children (Bolzani Dinehart et al., 2005; Lobmaier, Sprengelmeyer, Wiffen, & Perrett, 2010).

Crucial to establishing an evolutionary link between cooperative care and happiness expressions, human adults are known to display positive and caring responses when perceiving happy expressions of infants and children (see review by Franklin & Volk, 2018). Human adults respond to happy infant and child faces with strong interests and nurturing motivation (Aradhye, Vonk, & Arida, 2015; Parsons et al., 2014). Happy (but not sad or neutral) infant faces activate reward-related brain regions in mothers (Strathearn, Li, Fonagy, & Montague, 2008). Happier infants also receive higher levels of parental care and play behaviors (Braungart-Rieker, Garwood, Powers, & Wang, 2001). Therefore, similar to the possibility that fearful expression stimulates care and approach responses, happiness expression also seems to elicit positive and caring responses from others.

To establish the existence of a virtuous caring cycle, Grossmann also presents evidence that fearfulness is associated with *cooperative* tendencies among fearful children and adults, supporting the possibility that fearful children may grow up to be cooperative people who are caring toward younger generations. Similar (and even stronger) associations have been found between happiness and cooperation. Happy adults and adolescents are more motivated to perform prosocial and kind behaviors (e.g., Aknin, Dunn, & Norton, 2012; Erreygers, Vandebosch, Vranjes, Baillien, & De Witte, 2019; Isen & Levin, 1972; Otake, Shimai, Tanaka-Matsumi, Otsui, & Fredrickson, 2006). Children who display higher levels of happiness are rated by their peers as being more prosocial and cooperative even 1 year later (Yu, Chen, Li, Liu, & Yang, 2022). Contributing to the virtuous caring cycle, happiness early in life is predictive of happiness levels across the life span (e.g., Coffey, Warren, & Gottfried, 2015), and it has been shown that happier adults are more likely to be nurturing parents and raise happy children (Douglas, 2019).

Therefore, the above analysis shows that just as cooperative care could lead to enhanced fearfulness among humans, cooperative care may also promote enhanced happiness expressions among humans. Two interesting questions remain unanswered: (1) The virtuous cycle involving cooperative care might predict that humans would be selected to engage in increasingly higher levels of fear (and happiness), which may not be optimal or evolutionarily adaptive. High intensity of happiness has been shown to lead to overwhelmingness and negative adjustment outcomes (Aragón, Clark, Dyer, & Bargh, 2015; Gruber, Mauss, & Tamir, 2011). Might there be some built-in mechanism for cooperative care to promote *optimal* rather than excessive levels of emotions? (2) Relatedly, the framework is currently silent about whether cooperative care may play a role in the evolution of some emotional expressions (e.g., fear and happiness) but not others. Nonhuman primates and humans share many emotions (De Waal, 2019), but some emotional expressions (such as those associated with surprise) appear to be visibly present only in our own species (Kret et al., 2020). Might cooperative care also have influenced the evolution of these emotional expressions? To answer these questions, the framework may have to go beyond explaining how cooperative care could amplify a displayed emotion during evolution, but it also has to explain why and how the virtuous cycle is established in the first place.

In conclusion, I propose that similar to its role in promoting enhanced fearfulness among humans, cooperative care may also be a key mechanism leading to enhanced happiness expressions among humans. It will be important to further theorize why certain emotional expressions are more likely to elicit caring responses from others, which may help illuminate the scope of the theory as well as the origins of our emotional nature, such as the fearful ape or happy ape.

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Author's Response

Extending and refining the fearful ape hypothesis

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Abstract

The fearful ape hypothesis (FAH) presents an evolutionary-developmental framework stipulating that in the context of cooperative caregiving, unique to human great ape group life, heightened fearfulness was adaptive. This is because from early in human ontogeny fearfulness expressed and perceived enhanced care-based responding and cooperation with mothers and others. This response extends and refines the FAH by incorporating the commentaries' suggestions and additional lines of empirical work, providing a more comprehensive and nuanced version of the FAH. Specifically, it encourages and hopes to inspire cross-species and cross-cultural, longitudinal work elucidating evolutionary and developmental functions of fear in context. Beyond fear, it can be seen as a call for an evolutionary-developmental approach to affective science.

R1. Introduction

The novel evolutionary-developmental framework presented herein – the *fearful ape hypothesis* (FAH) – suggests that, in the context of the strong interdependence reflected in cooperative caregiving and provisioning unique to human great ape group life, enhanced fearfulness traits serve adaptive functions. The central hypothesis supported by the reviewed body of empirical research is that, starting early in human ontogeny, fearfulness traits facilitate care-based responding and provisioning from, while concurrently increasing cooperation with, mothers and others. Within this framework, enhanced fearfulness is assumed to be of adaptive value because of its functions in facilitating cooperative care across the lifespan, improving survival and reproduction in human evolution.

From a cultural perspective, enhanced fearfulness traits can thus be considered adaptive in *interdependent* human societies primarily build on cooperative care and success, whereas enhanced fearfulness has become maladaptive in *independent* human societies build more strongly on individual success and less so on cooperative care. The new synthesis based on *the fearful ape hypothesis*, stands in contrast to existing clinical work relying on Western, educated, industrialized, rich, and democratic (WEIRD) samples, conceptualizing heightened fearfulness as a predominately maladaptive trait increasing the risk of developing anxiety and depression. Viewing fearfulness traits through a WEIRD lens focused on risk conflicts with the presumed social environment that interdependent human group life evolved in and is adapted to. According to the *fearful ape hypothesis*, enhanced fear is considered an evolved adaptive trait that enhances cooperative care and success, which emerged in and is maintained by highly interdependent and supportive human societies. When viewed through this evolutionary lens, a radically different picture arises, painting an image of humans as fearful apes, trading off a risk for anxiety and depression with the affective foundations for cooperative care.

This response extends and refines the FAH by incorporating the conceptual and empirical points brought forward in the commentaries. Specifically, this response will address the following issues in turn. First, what kind of adaptation does the FAH invoke? Second, how can the FAH be extended by considering the roles of development, context, and learning? Third, how specific is the proposed affective/emotional adaptation to fear or may it extend more generally to suffering, distress, and anxiety? Fourth, how can the FAH be reconciled with research linking positive emotion to cooperation? Fifth, does responding to novelty (and cognitive control) rather than responding to fear account for the link between fear processing and cooperation? Sixth, what role does culture and caregiving play in what makes enhanced fear (mal)adaptive? Finally, this response discusses previously overlooked research indicating that enhanced fear may have direct adaptive benefits as it is linked to reproductive success. Together, this is aimed at providing a more comprehensive and nuanced version of the FAH in the hope to inspire cross-species and cross-cultural, longitudinal approaches to studying the evolutionary and developmental functions of fear in context.

R2. Enhanced fear: What kind of adaptation is it?

Before delving into the specific points made regarding the ontogenetic and phylogenetic evidence and reasoning behind the fearful ape hypothesis (FAH), it appears critical to address the important conceptual question raised by **Bjorklund & Hernández Blasi**, namely, what kind of adaptation is purported in the FAH? Specifically, Bjorklund & Hernández Blasi emphasize that one needs to distinguish between ontogenetic adaptations and deferred adaptations. According to Bjorklund & Hernández Blasi, ontogenetic adaptations are evolutionary solutions to specific problems with an immediate function in early development, whereas deferred adaptations represent an evolutionary solution to a problem beginning early in life and serving the same or at least a similar function later in development. Bjorklund & Hernández Blasi then argue that the adaptation invoked by the FAH likely represents an ontogenetic adaptation and is as such similar to other ontogenetic adaptations such as other evolved infantile traits that elicit care such as neotenous facial features (Kindchenschema), smiles and laughs, coos and cries, which do not play a role beyond early ontogeny/infancy. However, the notion that the FAH may represent an ontogenetic adaptation is at odds with a body of research attesting to the important role that enhanced fear continues to play in adolescence and adulthood (Marsh, 2015). In fact, in their commentary, **Marsh** presents a strong case based on research with adults to conclude that humans are not only fearful apes but also caring apes endowed with a multitude of social cues to convey our fear to concerned others providing help. In this context, it is important to mention that human infants, similar to adults, have been shown to detect not only facial expression of fear but also bodily expressions of fear and vocal signals of distress (Missana, Altvater-Mackensen, & Grossmann, 2017; Missana, Atkinson, & Grossmann, 2015; Missana, Rajhans, Atkinson, & Grossmann, 2014; Rajhans, Jessen, Missana, & Grossmann, 2016), supporting Marsh's point regarding the multitude of social cues used to express and respond to fear.

Intriguingly, a newly published study relying on longitudinal data from the Finn Brain Birth Cohort study (Kataja et al., 2022) lends some credence to **Bjorklund & Hernández Blasi**'s ontogenetic adaptation point, as this study shows that fear bias decreases (linearly) with age from 8 months to 60 months (5 years). Therefore, based on these novel insights, not available at the time the target article was written, enhanced fear might be most pronounced in early ontogeny. It is worth noting, however, that even though the fear bias was found to decrease with age, there still is a fear bias at 5 years of age. It is also important to mention that this study assessed the fear bias by measuring the disengagement probability when presenting an emotional face in the center of a screen and by assessing how quickly they disengage from the center image to a (non-emotional) distractor image located at the flanks of the screen (Kataja et al., 2022). This form of disengagement likely requires attentional processes related to cognitive control, which show a protracted development beyond infancy associated with the maturation of lateral prefrontal cortex (Holmboe, Bonneville-Roussy, Csibra, & Johnson, 2018). In any case, as summarized in the target article, the fear bias (in perception) does not exist among great apes (Kret, Jaasma, Bionda, & Wijnen, 2016; Kret, Muramatsu, & Matsuzawa, 2018), therefore, the species-level differences remain. It will also be important to see whether the decline in fear bias during early development observed in the Finnish sample generalizes across cultures. More specifically, enhanced fear might be tolerated less in Western (individualistic) societies but may even be promoted in Eastern (collectivistic) societies and cultural learning may play an important role in the developmental trajectory characteristics of the fear bias (see also, **Kitayama & Rossmaier**).

R3. Extending the FAH by considering development, context, and learning

From an ontogenetic perspective, **Hepach & Gerdemann** extend the FAH by proposing that enhanced fear may continue to play a critical role in regulating cooperation beyond infancy. Specifically, they suggest that with the widening of the children's social networks and relationships during preschool years, the increased complexity of peer interactions and the emergence of the capacity for reputation management, social emotions such as shame emerge that reflect children's concern for and perhaps even a fear of others' evaluation. Within this proposal the stipulated continued (adaptive) influence of enhanced fear beyond infancy stands in contrast to **Bjorklund & Hernández Blasi**'s critique and classification of enhanced fear as an ontogenetic adaptation limited to infancy. Evidence that enhanced fearful temperament is linked to greater expression of social emotions – especially – guilt was already included and discussed by us in the target article (Kochanska, Gross, Lin, & Nichols, 2002). This might be seen as tentatively supporting Hepach & Gerdemann's proposal. Nonetheless, as proposed by Hepach & Gerdemann, future work adopting a longitudinal approach mapping human fear and its effects on social emotions and cooperation is needed to directly test this developmental extension of the FAH.

Related to **Hepach & Gerdemann**'s suggestions, **MacGowan, Karasewich, & Kuhlmeier** stress that it is important to differentiate between social and nonsocial fears. However, as clearly outlined in the target article, enhanced fear among humans was seen across social and nonsocial contexts (Herrmann, Hare, Cissewski, & Tomasello, 2011). Therefore, the species-comparison and phylogenetic argument was based on fear across contexts. There obviously is much need for additional research especially at the phylogenetic level which examines fearfulness across species in nonsocial and social contexts. Regarding enhanced fearful behavior in social contexts or shyness, it is important to acknowledge research suggesting an adaptive subtype of shyness referred to as positive shyness, which is characterized by the expression of shy behavior in social interactions (e.g., gaze aversion, avoidance) in combination with positive affect (e.g., smiling) (Poole & Schmidt, 2020). Positive shyness is argued to be an adaptive phenotype that helps the shy individual modulate arousal in social contexts, which may protect the shy individual from maladjustment. Moreover, cultural context may play an important role in determining whether shyness among children is considered adaptive. In societies that endorse collectivistic values and norms, shyness in children and adolescents is viewed favorable by parents and others (Gurr et al., 2020; Yiu, Choi, & Chen, 2020). These suggestions and considerations can be seen as largely in agreement with the view put forward within the FAH as they also point to the potential adaptive and culture-sensitive nature of enhanced fearfulness.

Dwyer & Heyes see enhanced fearfulness as an important addition to what they call the "starter kit" for distinctively human minds and demand to further explicate the role that learning (and perception–action coupling) may play in the development of enhanced fearfulness during infancy. More specifically, within their framework, heightened fear is argued to provide critical learning opportunities by enhancing (a) emotional displays of fear co-occurring with the internal emotional experience of fear, (b) caregiver imitation and mirroring of fear, and (c) alignment of fear responses to external stimuli or events with others. Fear enhanced perception–action coupling and learning clearly plays an important role in the acquisition of fearful behavior in the developing individual and should thus be seen as a critical proximate mechanism within the FAH. However, as acknowledged by Dwyer & Heyes, heightened fearfulness is a part of the foundational "starter kit" and is thus needed to get learning off the ground rather than learning being the ultimate origin of the evolutionary trait itself.

Olsen & Selbing also stress the importance of social learning and mention a host of studies supporting the notion of vicarious social learning of fears including work with children, which might indeed represent another facet of the adaptive value of enhanced fearfulness in humans. However, Olsen & Selbing propose that social (observational) learning itself serves as the primary (ultimate) mechanism and care-based cooperation is only a byproduct of domain-general social learning capacities. Similar to the notion put forward in **Dwyer & Heyes**' commentary, we agree that (social) learning likely plays an important role in understanding enhanced fearfulness and the FAH needs to be extended by incorporating social learning as a critical proximate mechanism, yet it is not clear how this general social learning mechanism can explain the fear-specific effects seen in the phylogenetic and ontogenetic empirical evidence reviewed to support the FAH.

R4. Evolutionary test and behavioral economic extension of the FAH

In their commentary, **Burkart & de Oliveira Terceiro** point out that the FAH leads to strong predictions in callitrichids, who are the only other cooperative breeding primates. They then present work that may indeed support the FAH by showing that callitrichids display more distress than independently breeding monkeys and are also more likely to respond to distress signals with approach and affiliation. Similarly, **Dunn, Miller, Balasubramaniam, Akçay, & Wascher** point to research with corvids showing that enhanced fearfulness, especially neophobia, tracks with levels of cooperative care (Horn et al., 2020; Miller et al., 2022). These findings from cooperative breeders provide further evidence for the notion that cooperative breeding may have indeed provided a precondition, which allowed for the emergence of enhanced fearfulness in humans, who are the only cooperatively breeding great apes. Nonetheless, a much broader and systematic comparative analysis is needed to better characterize and understand the evolution of enhanced fearfulness traits and the role of socioecological variables more generally.

Barkan & Lahav present a rational behavioral economic analysis from two mixed-motive games with strong interdependence, which support and complement the FAH. More specifically, their game theoretical analysis shows that weakness elicits cooperative, caring responses from a stronger player leading to an equilibrium, even in sequential games. This is an important extension into the realm of behavioral economics and presents a critical test of a novel prediction generated based on the FAH.

Halevy points out that research on social decision-making with adults shows that states of fear can also be associated with aggressive or competitive behavior, which seemingly undermines the FAH. Regarding this criticism, it is important to re-emphasize something already stressed in the target article. Namely, the FAH stipulates that a human-specific link between heightened fear and cooperation exists in addition to fight (and flight) responses shared with many other animals when experiencing fear. Moreover, the FAH explicitly refers to fearfulness as an affective trait and thereby distinguishes it from affective state as used in the social decision-making research mentioned by Halevy. Therefore, Halevy's criticism does not directly undermine the FAH but rightly alerts us to a need for more systematic decision-making and behavior economics research including measures of affective traits to test the FAH.

R5. Beyond fear: Humans as suffering, distressed, or anxious apes?

Steinkopf argues that the FAH should be considered as only one facet of a more general "suffering ape hypothesis" (see **Barclay, Yerman, & Twardus**; **Clark, Adkins, Hirsch, Elizbeth, and Reed**, for similar argument), suggesting that humans are more likely to experience all sorts of negative emotions, aversive symptoms, and self-harming behavior, because they elicit caring which then provides fitness benefits. In response to this comment, it is important to clarify and stress that the FAH never claimed that fear is the only emotion enhanced or changed over the course of human evolution. For example, we already discussed the self-domestication hypothesis (Hare, 2017) at length, which shows that other affective traits such as social tolerance and aggression have changed during human evolution. More specifically, with respect to Steinkopf's specific suggestions, it might well be the case that other facets of human affective life are different from other great apes, however, to our knowledge, there currently is no direct evidence from comparative (phylogenetic) work supporting the notion of human-specific suffering responses as outlined by Steinkopf. Therefore, a more general human suffering hypothesis currently lacks empirical support.

Similar to **Steinkopf**'s criticism, **Drew, Tan, Yuen, & Hamlin (Drew et al.)** suggest that humans, rather than being uniquely fearful apes, might instead be more generally "distressed apes." This argument is based on research showing that responsiveness to distress signals generally, not fear specifically, elicits caring behavior (Davidov et al., 2021; Davidov, Zahn-Waxler, Roth-Hanania, & Knafo, 2013; Roth-Hanania, Davidov, & Zahn-Waxler, 2011). In response to this comment, it is important to note that we already emphasize that within the FAH framework, expression of fear is thought to convey distress rather than threat as has often been claimed (see also **Marsh**'s commentary). We also previously acknowledged work linking increased levels of fearfulness to greater levels of crying as a vocal signal of distress (Kagan & Snidman, 2004). In fact, Davidov et al.'s (2021) most recent study and prior work from this group (Roth-Hanania et al., 2011) explicitly used a video stimulus of an infant peer crying (when separated from her mother during the strange situation) when measuring infants' concern, which is linked to emotional helping behavior in these longitudinal studies. Therefore, Drew et al.'s comment implies a narrowness of the FAH that is not at all intended by the theoretical proposal put forward, which explicitly assigns a role to distress signaling in accounting for enhanced fearfulness in humans.

Relatedly, **Mercadante, Witkower, Hohm, & Tracy (Mercadante et al.)** suggest extending the FAH by including additional emotions beyond fear. Specifically, they argue for the FAH to be extended by including so-called supplication emotions, referring to a group of emotions that comprises not only fear but also sadness, disappointment, distress, and worry and appeasement emotions such as shame, guilt, and regret, which are all presumed to serve cooperative functions in human interactions and relationships. As noted above, the FAH is already explicit about the inclusion of distress and may have room to accommodate other supplication emotions in the framework. However, as noted by Mercadante et al., species comparisons are currently lacking, and it remains to be seen whether the human-specific effects obtained for fear (and distress) extend to other supplication emotions. With respect to the appeasement emotions mentioned, they all fall within the category of moral or social emotions, which since Darwin have been argued to be specific to humans (Darwin, 1872). Critically, these moral emotions have been shown to display relatively distinct comparative, developmental, cognitive, and brain characteristics from the supplication emotions (Tomasello & Vaish, 2013; Zahn, de Oliveira-Souza, & Moll, 2020), rendering it unlikely that they emerged through similar processes in human evolution as enhanced fearfulness. Nonetheless, it should be noted that we already explicitly mention work by Kochanska et al. (2002), showing that children who are more fearful in temperament are more likely to experience guilt listed as one of the appeasement emotions by Mercadante et al.

Kurth argues that a distinction should be drawn between fear as a reaction to immediate danger or threat resulting in freeze, fight, or flight responses, and anxiety as reflecting a distinct set of processes seen when facing uncertain threats. Kurth further suggests that anxiety rather than fear is at play in the FAH. To clarify, fear rather than anxiety was explicitly chosen in the FAH framework because it: (1) stands in contrast to the clinical, pathological, diagnostic meaning often associated with anxiety, (2) draws attention to natural variability on a dimension of fearfulness rather than a categorical difference (fear vs. anxiety), and (3) allows for continuity between species, whereby fear is shared with other apes and enhanced fear in humans represents a quantitative, gradual difference, and evolutionary modification. To further clarify, it is also important to stress that enhanced fear within the FAH refers to an evolved trait, which is linked to but not the same as the state of fear in the moment.

R6. Beyond fear continued: Humans as happy apes?

Another criticism put forward across several commentaries was based on evidence linking positive affect, smiling, and laughing with human cooperation (see **daSilva & Bertenthal**; **Drew et al.**; **Herbert, Condry, & Sutton**; **Riddell, Kret, Zijlstra, & Nikolic [Riddell et al.]**; **Yang**). This evidence is then used to argue that, in contrast to the FAH, humans are instead happy apes (Yang) and fear is not "human-unique" (Riddell et al.). In this context, it is important to reiterate that the FAH did not claim that fear is the only emotion changed/modified over the course of human evolution and further the FAH never suggested that fear is the only route to human cooperation. Importantly, human cooperation is highly complex and multi-determined (Rand & Nowak, 2013; Tomasello & Vaish, 2013), allowing for several psychological processes to be (simultaneously) linked to cooperation. In other words, links between enhanced fear and cooperation and increased happiness/positive affect and cooperation are not mutually exclusive. Nonetheless, it is critical to emphasize that empirical evidence discussed in the FAH review clearly demonstrates that, in human infancy, brain and attentional responses to fear, but not happiness, are linked to cooperative behavior. Specifically, in a longitudinal study, brain and attentional responses to fearful faces, but not to angry or happy faces, at 7 months of age predicted helping behavior at 14 months of age (Grossmann, Missana, & Krol, 2018). Another longitudinal study with infants at similar ages also failed to find evidence that infant positive emotion was linked to cooperative helping behavior (Davidov et al., 2021). Moreover, positive emotion has been shown to be the result of and hence follows rather than precedes cooperative behavior in toddlers, whereas concern for others precedes and more directly motivates cooperative behavior (Grossmann, 2018). For example, in a series of studies, concern for others, as reflected in sympathetic arousal, preceded helping behavior in toddlers, whereas elevated body posture, as an index of positive affect, followed helping behavior (Hepach, Vaish, Muller, & Tomasello, 2019; Hepach, Vaish, & Tomasello, 2012, 2017).

Relatedly, **daSilva & Bertenthal** raised the issue that biobehavioral synchrony and positive dyadic engagement with the caregiver rather than fear is at the origin of human cooperative care. Again, the FAH did not claim that fear is exclusive in this sense and that other factors cannot play a role in the emergence of human cooperative care. From an empirical perspective, however, it is important to mention that infants' responding to fearful faces selectively predicted their cooperative behavior even when controlling for positive maternal engagement measured during dyadic interactions (Grossmann et al., 2018), suggesting that the link between fearful face processing and cooperative behavior exists independent of positive maternal engagement. In fact, recent research suggests that positive maternal engagement only affects infants' brain responses to angry facial expressions, signaling direct threat, but did not affect infants' responses to fearful or happy facial expressions (Thrasher, Krol, & Grossmann, 2021).

R7. Novelty versus fear

Kelsey proposes an alternative explanation by arguing that rather than being specific to fear, infant responses to fear are driven by novelty and links between fear processing and cooperation may thus be mediated by greater cognitive control processes when facing novelty. Regarding this point, it is critical to mention that novelty is unlikely to account for the experimentally observed effects, because the study Kelsey is pointing to also used angry facial expressions, which are equally novel to infants, but did not predict cooperative behavior longitudinally (Grossmann et al., 2018). Moreover, in this study, when processing fear greater engagement of dorso-lateral prefrontal cortex, as one of the key brain regions implicated in cognitive control, was associated with reduced rather than enhanced levels of cooperative behavior. This is in line with other work showing that: (1) fear processing is automatic and occurs without conscious perception (Jessen & Grossmann, 2014, 2015, 2020) and (2) enhanced cognitive control (inhibitory control) is associated with reduced levels of cooperative behavior in infants (Grossmann, Missana, & Vaish, 2020). Therefore, cognitive control is an unlikely candidate for explaining early cooperative behavior. Similarly, research with adults also suggests that at least some cooperative behaviors are intuitive (implicit) rather than deliberative (explicit) in nature (Rand, 2016; Zaki & Mitchell, 2013) and that the link between fear and cooperative behavior is underpinned by implicit processes as it is seen during subliminal priming with fearful faces and linked to subcortical (amygdala) processes (Marsh, 2015).

R8. Culture matters

Ogren, Barrett, Hoemann, & LoBue (Ogren et al.) make the point that fearfulness is associated with negative long-term outcomes (see also **Krstić** for another commentary suggesting that fear is maladaptive). This is correct but exclusively based on data from WEIRD cultures. Even the cross-cultural work referred to by Ogren et al. as indicating negative developmental outcomes stems from WEIRD samples, Netherlands, and South Africa (Howard, Muris, Loxton, & Wege, 2017; Vreeke, Muris, Mayer, Huijding, & Rapee, 2013). Here it is important to reiterate that the FAH does not deny that extreme fearfulness is associated with negative outcomes (primarily in WEIRD samples), but rather tries to draw attention to the possibility that enhanced fearfulness evolved in the context of inter-dependent (collectivistic) group life. The FAH thus generates the proposal that it is important to study effects of cultural context, especially with respect to differences between cultures emphasizing collectivistic (interdependent) values and practices, and cultures emphasizing individualistic (independent) values and practices.

Indeed, **Kitayama & Rossmaier** present a whole line of research indicating that in collectivistic cultures but not in individualistic cultures, increased neuroticism, which links to the enhanced fearfulness traits invoked by the FAH, is associated with a whole host of positive (adaptive) outcomes. Kitayama & Rossmaier's commentary thus largely provides additional support for the ideas put forward in the FAH. However, Kitayama & Rossmaier also raised the criticism that the FAH falsely points to small-scale societies as the cultural context matching the enhanced fearfulness profile, because enhanced fearfulness (or more specifically neuroticism) is still adaptive in current large-scale societies characterized by collectivism/interdependence. In response to this point, we would like to clarify that the proposal was that enhanced fearfulness likely first evolved in small-scale groups of ancestral humans characterized by interdependence, but FAH never entailed that it is not adaptive (or cannot be associated with positive outcomes) in current large-scale societies, which also rely on interdependence (collectivism). In fact, when discussing the implications of the FAH, we explicitly refer to work from Eastern (collectivistic) countries showing that developmental outcomes are largely positive in this cultural context. We also raise the possibility that increased rates of anxiety and depression in WEIRD societies may represent a mismatch disease. Regarding the potential mismatch, Kitayama & Rossmaier present an important factor interacting with neuroticism, which is behavioral adjustment. Neuroticism is argued to be adaptive in the context of high behavioral adjustment in interdependent cultures, which positively sanction behavioral adjustment. Behavioral adjustment and social/cultural learning thus appear to represent an important proximate mechanism that may help explain the effects of enhanced fearfulness in varying cultural contexts.

R9. Caregiving matters

Another issue raised by **Ogren et al.** is that caregivers respond to all affective behaviors not just those perceived as fearful. Regarding this point, it seems critical to stress that the FAH never made any claims as to how fearful behavior is the only way to elicit care, but rather intends to put enhanced fearfulness "on the map" as a potential early-developing affective trait that serves such functions. In fact, other commentaries acknowledge this contribution of the FAH by noting that enhanced fearfulness may be added to other adaptations to elicit care. A further criticism is based on work showing that caregiver responsiveness reduces fear in the infant/child (see also **Shteynberg**). In fact, we explicitly mention research along these lines, in order to support our argument that displays of fear elicit care and protection, which makes it a functional adaptation. Within the FAH, reducing infant fear in any given instance through caregiver responsiveness is seen as a functional outcome rather than evidence undermining the notion that human infants and children display enhanced fear. Relatedly, the FAH conceives of enhanced fearfulness as a trait, whereas the reduction of fear as a function of caregiver responsiveness focuses on the state. Concerning caregiver responding, **Parsons & Skewes** point out that excessive infant crying has also been associated with maladaptive responses in caregivers, specifically shaking and in severe instances of physical abuse. The existence of extreme parental responses such as physical abuse being associated with excessive crying is important to acknowledge, but does not directly undermine the FAH, whereby fearfulness traits – enhanced in comparison to our closest living primate relatives – are thought to elicit increased caring behavior. Within any of these species, there is a range of infant fearfulness and a range of parental/caregiver responsiveness that at the extreme ends of the distribution may then be related to maladaptive behaviors and outcomes.

R10. Sex differences may exist

Veit & Browning see the FAH largely in agreement with their own theoretical framework (Veit & Browning, 2022) and suggest that one potential application or extension may be the consideration of sex differences in affective traits (see also **Benítez-Burraco and Progovac**). Specifically, they make the argument that greater self-protection among human females should be considered as an adaptive rather than pathological trait that evolved as an optimal life-history strategy. Therefore, greater fearfulness, depression, and anxiety among human females than human males as is commonly reported across studies, may represent one manifestation of this greater self-protection strategy in human female life history. This notion is compatible with the FAH and further strengthened by taking into account cross-cultural evidence showing greater involvement of mothers than fathers in cooperative child care (Kramer, 2019). Studying and understanding sex differences in fearfulness can thus be seen as an important extension of the FAH.

R11. Does enhanced fear have direct adaptive benefits?

Regarding the issue concerning enhanced fear's adaptiveness, there exists evidence that enhanced fearfulness is associated with higher rates of reproductive success. Specifically, a large three-generational analysis ($N = 2{,}657$), previously not mentioned in the target article, shows that heightened levels of anxiety when assessed along a continuum is associated with greater reproductive success across three generations as indexed by a significantly greater number of children, grandchildren, and great-grandchildren (Jacobson & Roche, 2018). This raises the possibility that, rather than through or in addition to cooperative care as stipulated in the FAH, enhanced fearfulness may even have direct fitness benefits. This possibility and extension of the FAH requires explicit examination and close attention in future research.

R12. Conclusion

To conclude, the thoughtful commentaries have provided the platform to further refine, specify, test, and extend the FAH. We have seen that enhanced fear in humans possesses characteristics that speak for it being a developmental adaptation with deferred or better continued adaptive benefits. Evidence from cooperative breeders and from employing formal behavioral economic analysis support the notion that enhanced fearfulness may have emerged as a function of cooperative care. Whether or not other emotions signaling suffering, distress, and/or positive emotion have undergone similar changes over the course of human evolution remains to be seen. The extension of the FAH outlined herein has particularly benefitted from research evidence on neuroticism and its adaptive versus maladaptive effects as a function of cultural context. This line of evidence not only further stresses the importance of culture when studying enhanced fear in humans but also suggests that enhanced fear, which is thought to have evolved in small-scale *interdependent* group life, may continue to serve adaptive functions in concurrent large-scale *interdependent* societies. In turn, maladaptive effects of enhanced fear may indeed represent a mismatch resulting from *independent* societal structures in WEIRD cultures.

In summary, incorporating the suggestions from the numerous commentaries, this response provides an extended and refined picture of the FAH and its complexity. As with any novel theoretical framework many of the predictions generated by the FAH need to be explicitly tested. There is a strong need for cross-species and cross-cultural, longitudinal approaches to study the evolutionary and developmental functions of fear in context. More broadly, the time is ripe for a comprehensive evolutionary-developmental approach to human affective science.

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