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Human caregiving under safety and threat: The role of empathy and its endocrine regulation

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ABSTRACT

Empathy is a core motivational driver of human caregiving, shaped by evolution to ensure the survival of dependent others. Human caregiving consists of two complementary components that are each supported by distinct neuroendocrine systems: nurturance, which flourishes under safety, and protection, which is activated in the face of threat. This review synthesizes current evidence on how empathy operates within these components, focusing on the endocrine regulation of caregiving and the adaptive shifts that occur along the safety–threat continuum. We highlight how oxytocin, testosterone, cortisol, and opioids modulate empathic processes to promote either nurturing, soothing care or rapid, protective responses. While these shifts are essential for flexible caregiving, severe or prolonged activation of the stress system, particularly in contexts of chronic adversity, can impair sensitivity and compassion, leading to maladaptive outcomes. We also discuss individual differences, such as sex and early life experiences, that shape the regulation of empathy in caregiving contexts. Understanding these dynamic interactions can inform interventions aimed at strengthening the quality of care, with relevance extending beyond the parent–child relationship to other caregiving domains.

"Why do I say all human beings have a heart which cannot stand to see the suffering of others? Even nowadays, if an infant were about to fall into a well, anyone would be upset and concerned. This concern would not be due to the fact that the person wanted to get in good with the baby's parents, or because s/he wanted to improve his/her reputation among the community or among his/her circle of friends. Nor would it be because he/she was afraid of the criticism that might result from a show of non-concern."- Mencius 2 A 6.

Since the concept of empathy entered the academic discourse, it has inspired thousands of empirical and theoretical studies across disciplines such as philosophy, neuroscience, psychiatry, and psychology (e.g., Baron-Cohen, 2011; de Waal, 2010; Gallagher et al., 2024; Keysers, 2011; Maibom, 2022; Rijnders et al., 2021). Although a substantial body of research has examined the construct of empathy, there is still no clear consensus on its exact definition. Scholars continue to debate the core components and boundaries. Nevertheless, there is broad agreement on its critical role in human caregiving, particularly a caregiver's ability to attune to a child's internal states and to respond swiftly in situations of distress or danger

Currently however, an overall framework for the role of empathy in human caregiving is missing. This gap hampers our ability to systematically understand how empathy supports or obstructs adequate caregiving under varying conditions. In this theoretical review we provide such a framework, by bringing together the wealth of research on empathy - which generally focusses on nulliparous adults – with the research on parenting and childcare. Our goal is to offer a framework that captures how the components of empathy are dynamically and adaptively regulated dependent on the demands and safety of the caregiving environment.

We begin by tracing the evolutionary origins in the context of mammalian caregiving and describe how empathy developed as a key motivational driver of caregiving behavior. Central to our framework is a distinction between two components of caregiving: care directed at *nurturance* and at *protection*. This dissociation is crucial since each component relies on distinct neuroendocrine mechanisms, that regulate

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empathy under either safe or threatening conditions. We then explore individual differences in empathy regulation, shaped by factors such as sex, oxytocin sensitivity and early life experiences. Finally, we describe the conditions and risk factors under which these mechanisms falter under conditions of severe and persistent stress, with implications for caregiving quality.

By elucidating the dynamic regulation of empathy in caregiving and the impact of perceived environmental threat or safety, our framework offers a foundation for more targeted interventions and preventive strategies. We hope it will serve as a catalyst for future research aimed at enhancing caregiving outcomes across diverse contexts.

1. What is empathy?

A Pubmed search on the topic of empathy indicates a steeply increasing growth in publications which currently counts over 2500 papers annually, reflecting the lifetimes that have been spent on thinking about the concept. Despite this flowering field of research, it has not yet resulted in a broadly accepted definition on what empathy is, and what it is not. This reflects a point on which the extant literature agrees; that empathy is a broad and multifaceted concept not easily reduced to a concise definition.

The term empathy has a relatively recent origin. Derived from the German *Einfühlung* it has its roots in the early 20th century (Montag et al., 2008). Despite the 'vagaries' of the terminology used to describe empathy (Panksepp and Panksepp, 2013), it generally refers to a process by which organisms are able to incorporate or understand the emotions, feelings, and thoughts of others. We adopt the comprehensive definition from de Waal and Preston (2017), who use empathy as an *'umbrella term for all processes that emerge from the fact that observers understand others' states by activating their own personal, neural and mental representations of that state'*. This activation can occur unconsciously and without observable behavior, underscoring that empathy is a multi-level process that cannot be fully captured by behavior alone. This broad and integrative definition allows us to bridge the gap between neurobiological and caregiving research traditions. Building on this integrative definition, a better understanding of the biological and evolutionary foundations of empathy, will shed more light on its mechanisms, variability, and relevance in caregiving contexts.

Recent advances in neuroscience, endocrinology, and evolutionary biology have given us a much better view on the distinct components, developmental trajectories, neural substrates, and evolutionary origin of empathy (de Waal and Preston, 2017; Decety, 2011; Decety and Svetlova, 2012; Gonzalez-Liencres et al., 2013; Panksepp and Panksepp, 2013; Preston and de Waal, 2002; Singer, 2006). In their influential evolutionary model of the proximate and ultimate causes of empathy—the perception-action model (PAM)—Preston and de Waal detail how early evolved automatic state matching mechanism formed the basis of more complex forms of empathy (de Waal, 2008, 2010; de Waal and Preston, 2017; Preston and de Waal, 2002). The view that we share the evolutionary basis of empathy with many other animals, concedes with other evolutionary accounts of empathy (Decety, 2011; Panksepp and Panksepp, 2013). The most fundamental form of automatic state matching mechanisms is rooted in automatic motor imitation (also known as mimicry) and later evolved emotional contagion. Well-known examples of these processes are contagious yawning, or contagious crying observed in infants exposed to other infants crying (Geangu et al., 2010; Prochazkova and Kret, 2017). Such automatic matching of emotional states are consistently demonstrated for a variety of processes, including the execution of facial expressions and the experience of physiological stress, pain, and disgust (Buchanan et al., 2012; Keysers and Gazzola, 2006; Kraaijenvanger et al., 2017). These vicarious processes are often referred to as affective empathy: the ability which allows us to feel what others feel. Whereas affective empathic processes generally occur automatic and instantaneously, they are sensitive to contextual and personal factors (e.g., Avenanti et al., 2010; Kraaijenvanger et al., 2017; Seibt et al., 2015). In relation to caregiving, adults' automatic facial imitation of children, for example, is dependent on information about children's background or behavior, with negatively behaving children eliciting stronger frowning responses (Bos et al., 2016).

A specific form of affective empathy, which holds strong relevance for the topic of caregiving, is *empathic distress*—also referred to as personal distress. Empathic distress represents our aversive emotional and physiological reactions while witnessing another's suffering, which can interfere with providing good care, as will be explained in more detail below.

Affective empathy interacts with later-evolving cognitive processes that are supported by the prefrontal cortex (Panksepp and Panksepp, 2013). The development of these cognitive abilities- subserved by a strong neocortical expansion in the human lineage- has resulted in our ability to reflect on the internal thoughts and motivations of others. This ability is often referred to as *mindreading, theory of mind,* or more broadly *cognitive empathy*, and emerges early in infancy but requires time to fully develop. It is strongly influenced by environmental factors and the maturation of other cognitive functions, such as language (Heyes and Frith, 2014; Slaughter, 2015).

The emergence of cognitive empathic abilities paved the way for more complex forms of empathy to develop, such as *empathic concern* (also termed *sympathy)* and *compassion.* Unlike affective empathy, these responses are other-directed: the observer recognizes that the emotional response is triggered by another's state, not their own (Decety and Svetlova, 2012). This requires a form of self-other distinction, in which the observer is aware of the source of such concern, which is not necessary for more automatic processes such as emotional contagion. See Fig. 1 for an overview of the specific components of empathy.

2. Empathy as grounded in caregiving

Empathy thus refers to a process that ranges from automatic matching of emotional and physiological states, to the deliberate and effortful ability to infer and understand the motivation of others, or even taking the perspective of another, respectively referred to as affective and cognitive aspects of empathy. Evolutionary accounts of empathy suggest that it most likely evolved in the context of maternal care in the first mammals (Brown et al., 2012; Decety et al., 2016; Panksepp, 1998; Preston, 2013). However, caregiving behaviors, and particularly protective responses, predate empathy and are observed in species without complex social cognition, such as fish and amphibians, and already existed in dinosaurs (Royle et al., 2012; Varricchio et al., 2008). Protection of infants has been a critical form of caregiving throughout human evolution, yet is often overseen in research on human caregiving (Bakermans-Kranenburg and van IJzendoorn, 2017b). Due to their dependence on mothers offering food, warmth and hygienic care, mammalian species extended their caregiving repertoire with nurturing care (Farmer, 2000). Throughout mammalian evolution, protective and nurturant caregiving behavior increased in complexity, for example including reduced avoidance of offspring and increased sensitivity towards infant cues (Preston, 2013). At the same time, infants co-evolved increased signals of distress, cuteness features, and the formation of an attachment-system (Glocker et al., 2009; MacLean, 1985; Panksepp et al., 1985). Extensive animal research examined these evolutionary developments in caregiving behavior, and laid the foundation for a neurobiological caregiving system in which empathy functions as a core motivational driver for both protective and nurturant caregiving behaviors (Brown and Brown, 2006; Brown et al., 2012; de Waal and Preston, 2017; Mayseless, 2015; Panksepp, 1998).

The importance of empathic resonance with emotional states of infants in eliciting protection and nurturing behavior directed at their basic needs—such as soothing or feeding—is clear, and might take 'its most poignant form' in the response of mothers to infant vocalizations of distress (p. 493: Panksepp and Panksepp, 2013). This aligns with the

Fig. 1. Components of empathy, This figure provides a non-exhaustive overview of the specific components of empathy discussed in this review. The components are arranged on a continuum from affective to cognitive forms of empathy.

impact of infant cry sounds on human adults, which yield strong neurophysiological, endocrine and subjective responses in both men and women (Crouch et al., 2008; Fleming et al., 2002; Witteman et al., 2019). But in contrast to such reactive forms of caregiving, many forms of caregiving toward infants are proactive, and stem from the parental motivation to nurture or interact with children (Mayseless, 2015). Much less a matter of investigation, affective empathy also plays an important role in nurturing care, in a way that matching of *positive states* or sharing the joy and wellbeing of others can motivate parental behavior. Yet as any parent knows, nurturing care can at times be far from rewarding in itself (Baumeister et al., 2016). However, the deeply gratifying and meaningful feelings when experiencing the happiness, flourishing or tranquility of the child you care and carry responsibility for, are the real reward for a parent. This might be the reason why for many parents it is difficult to take their eyes of their sleeping child. Although affective empathy is far from a sufficient explanation for feelings and motivations such as these, it would be impossible to experience such an impact of another's state on one's own wellbeing without empathic resonance of affective and mental states. Feelings such as these probably evolved in the context of what Brown and Brown define as a state of *fitness interdependence*, referring to a state in which the reproductive success of individuals is linked, and the wellbeing of another becomes shared with that of your own (Brown and Brown, 2006, 2015).

On the other side of the empathic continuum lie our mindreading or cognitive empathic abilities, which are neither sufficient for caregiving behavior, since this capacity can equally be used to deceive and manipulate others (Baron-Cohen, 2011; Rijnders et al., 2021). The seminal work of Daniel Batson demonstrates that for altruistic and prosocial behavior, such as targeted helping, *empathic concern* is the most important motivational driver (Batson, 2010, 2014). This, however, does not imply that other aspects of empathy besides *empathic concern* are irrelevant or redundant. Especially in the dynamic context of human caregiving, it is the whole repertoire of empathic components that has a role to play (Mayseless, 2015), as will be further illustrated below. Empathic abilities thus are a prerequisite – but not a guarantee – for adequate caregiving. And some aspects can even be problematic. This integrative view is comparable to a neuropsychiatric model of empathy presented by Rijnders et al. (2021), in which the integration of affective and cognitive empathic abilities into 'mature' empathy is a necessity for healthy social functioning.

In sum, with its evolutionary roots grounded in the mother-infant caregiving relation, empathy has a crucial function in the motivation to elicit both protective and nurturant aspect of human caregiving. To fully understand how empathy shapes caregiving behavior, it is essential to move beyond its conceptual definitions and examine the underlying neurobiological mechanisms. In the following sections, we explore how distinct hormonal systems regulate empathic processes, and how these systems adaptively shift in response to safety and threat. As will become clear, the unprecedented importance of empathy for caregiving does not guarantee the quality of care, and certainly not in the face of long-term stress.

3. Caregiving behavioral systems: protection and nurturance

Research on the human caregiving system has recently found empirical support for a conceptual distinction between nurturing and protective tendencies, that predict unique variation in attitudes and judgements towards parenting, mating and children's behavior (Schaller, 2018). These components of caregiving rely on distinct neuroendocrine pathways, with evolutionary antecedents of protection predating nurturance (Hahn-Holbrook et al., 2011a). We here provide a concise overview of these pathways, for an extensive overview of the neuroendocrine factors relevant for human caregiving behavior see Bos (2017).

3.1. Protection

Infant protection has its roots in the neuroendocrine mechanisms of self-defense, with a critical role of the periaqueductal gray (PAG) and the amygdala in the detection and reactivity to threat and the initiation of freezing and fight behavior (Fanselow, 1994; Panksepp, 1998; Vieira and Olsson, 2023). In response to threat, activation of the locus coeruleus (part of the brainstem) activates the endocrine stress response. This leads to excretion of (nor)adrenaline, shifting neural activation from regions involved in executive control to salience networks, which enables fast responding and emotionally reactive behavior (Hermans et al., 2014). It results in activation of the insula, cingulate gyrus and the hypothalamus; regions that are also activated in response to signals of infant distress such a crying (Numan, 2006; Witteman et al., 2019). Besides involvement of the endocrine stress response, the sex steroid testosterone is also involved in parental caregiving behavior in both men and women (Glasper et al., 2019; Gordon et al., 2017; Horrell et al., 2019; Luberti and Carre, 2024). Generally, parental status has a down-regulating effect on testosterone levels in both mother and fathers (Barrett et al., 2013; Meijer et al., 2019). However, testosterone reactivity can be beneficial in challenging situations by promoting care responses, for example towards an infant exposed to threat (Bos, 2017). For example, exposure to infant crying results in testosterone increases in fathers (Fleming et al., 2002; Storey et al., 2000), and administration of testosterone in women increases neural responsiveness to infant

crying (Bos et al., 2010). A recent study further demonstrated that administration of testosterone in young women also resulted in stronger empathic responses towards children in a distressing situation, suggesting that testosterone may particularly promote infant protection (Bos et al., 2021). Such an effect of testosterone might, however, suppress the nurturing component of caregiving (Rilling, 2013). Indeed, another study showed that higher levels of testosterone, combined with higher levels of cortisol in response to infant crying, predicted lower levels of sensitivity towards one's own child (Bos et al., 2018). A final hormonal factor examined in relation to offspring protection is the neuropeptide oxytocin, which in rodent mothers increases defensive aggression towards intruders (Bosch and Neumann, 2012). Interestingly, the effects of oxytocin show strong context dependency, as another function of this neuropeptide entails the facilitation of nurturing behavior.

3.2. Nurturance

The neural circuitry that brings forth nurturant behavior consists of subcortical structures that are primarily involved in reward processing, such as the ventral tegmental area in the brainstem, and its efferent projection site of the striatum and orbitofrontal cortex (Rilling, 2013). These regions are sensitive to the distinctive features of children, and critical for motivating caregiving behavior. These networks are strongly intertwined with endocrine pathways of the neuropeptides oxytocin and endogenous opioids. Human nurturance further depends on cortical regions involved in understanding the feelings and motivations of others, such as the anterior insula, ventromedial prefrontal cortex, and the temporoparietal junction (TPJ). But also lateral prefrontal regions are important for emotion regulation (for an overview see Feldman, 2017).

Oxytocin is a uniquely mammalian neuropeptide with a primordial function to promote parturition and lactation. From there it developed a more encompassing role in maternal caregiving, extending to mother-infant attachment (Carter, 2022; Feldman, 2017; Rilling and Young, 2014). Research in humans confirms this extended role of oxytocin in parental behavior, demonstrating its positive associations with neural reward-related responses towards own infants, and increased positive interactions during play behavior (Bakermans-Kranenburg and van IJzendoorn, 2017a; Bos, 2017). As such, oxytocin plays a key role in the nurturing component of human caregiving behavior, facilitating soothing and sensitive responding. Oxytocin administration studies in humans have demonstrated stress reducing effects, which are stronger during social interaction (Heinrichs et al., 2003; Taylor, 2006). Oxytocin has further been shown to reduce amygdala and insula activation in response to emotional faces or aversive stimuli (Bethlehem et al., 2013; Bos et al., 2015). Such reduced activation can induce a shift in neural processing towards regions that facilitate emotion regulation, and cognitive empathic abilities (Feldman, 2015). These findings match with studies showing that oxytocin administration increases emotion recognition and empathic responses, and facilitates approach motivation behavior (Bartz et al., 2010; Leppanen et al., 2017).

The nurturing component of caregiving is further supported by actions of prolactin and endogenous opioids, yet less data is available in humans (Bos, 2017; Nelson and Panksepp, 1998). Especially opioids might play a crucial role in the formation and maintenance of human social bonds, through its facilitating effects on the neural reward system (Inagaki, 2018; Meier et al., 2021).

4. Adaptive regulation of empathy in the context of care

The question of what constitutes high quality care has as many answers as there are parents (Koops, 2016). Nonetheless, the concept of *sensitivity* in parents—which refers to caregivers' ability to detect and correctly interpret signals of children and provide appropriate responses promptly (Ainsworth et al., 2015)—is generally considered an important aspect of high quality care, especially with regard to infants (Cooke et al., 2022). Empathy is strongly intertwined with the concept of sensitivity and an important prerequisite for sensitive responding (see Box 1). However, the function of empathy is different for the protective and nurturing components of the caregiving system.

Based on the extant literature, we can distill a tradeoff in caregiving behavior, where in a safe situation oxytocin and opioids together can facilitate nurturing and sensitive responses by inducing a positive mood state, allowing the focus on the other instead of the self, and improve cognitive empathic abilities. In a threatening situation, under influence of (nor)adrenalin, cortisol, oxytocin and testosterone, there is down-regulation of sensitivity and a shift to immediate protective action. Stress can induce this shift from proactive caregiving to more reactive caregiving such as protection by lowering the threshold for affective empathic resonance with others, although the extent to which this occurs will depend on the relation with this other, and more specifically; the extent to which the image of the self overlaps with the other (Lamm et al., 2016). In the following paragraphs we describe these mechanisms in more detail.

4.1. Strategic regulation and integration of empathy

Affective empathy is of paramount importance for the quick detection of infant signals of distress or discomfort (Bos et al., 2021; Witteman et al., 2019). Yet, it depends on the context whether this detection requires protection or nurturance. Enhanced reactive responding under the influence of the endocrine stress response and testosterone, which is typical for protection, does not guarantee appropriate care and may even result in dismissive care. For example, when a parent supports a frightened child during a vaccination or dentist appointment, the parent's initial impulse might be to protect the child and walk away, or avoid the visit altogether: both resulting in dismissive care. Thus, besides the reactive aspect of empathic responding, which can motivate protective and nurturant responses, proactive and deliberate reflection is also needed to meet the needs of those who depend on care of others (Bornstein et al., 2008). As such, cognitive aspects of empathy, including empathic concern and compassion, are more strongly associated with the nurturing component of the caregiving system. Also, when parents consistently ignore the child's perspective, this can result in a controlling parenting style with negative developmental outcomes. Such a parenting style relates to the concept of intrusiveness, which is central in attachment theory, and refers to a caregiver's tendency to override a child's autonomy (Barber, 1996). The fundamental role of cognitive empathy in human (parental) caregiving is further illustrated by research on mind-mindedness and reflective functioning. In the first year of life, parents with higher levels of mind-mindedness—a concept referring to appropriately commenting on, and not misreading, infant's mental states—promote their child's secure attachment, mindreading abilities, and emotion regulation (McMahon and Bernier, 2017). The strongly related concept of reflective functioning—which refers to the ability to see one's own and others' behavior as expressions of mental states— is positively associated with parent and child attachment, (Fonagy and Target, 1997; Katznelson, 2014).

Adequate caregiving thus depends on adaptive integration of affective and cognitive components of empathy. This integration, importantly, requires strategic regulation of empathic processes (Weisz and Cikara, 2021). Emotion regulation is a an important parental quality, which affects the development of emotion regulation abilities in children (Morris et al., 2017). A recent meta-analysis further showed that emotion regulation in parents predicted more overall positive parenting behavior and lower internalizing symptoms in their children (Zimmer-Gembeck et al., 2021). These effects may be supported by an adequate integration of empathic processes: the 'zipping up' of cognitive and affective abilities (Rijnders et al., 2021). Such integration and strategic regulation is however strongly context dependent. Depending on situational demands, substantial cognitive regulation is required to

Box 1
Empathy and attachment: overlapping yet distinct frameworks.

The concepts of empathy and attachment are strongly related in understanding parent–child relationships, yet they represent different vantage points. Philosophical writing on the manifestation of empathic behavior has a long tradition, going back hundreds of years before the term empathy was first coined (Maibom, 2022). Attachment theory was however formulated in the sixties and seventies of previous century by Bowlby, inspired by psychoanalytic theories and Harlow's studies on maternal separation (Bowlby, 1983; Harlow et al., 1965).

Attachment theory focuses on the quality of the affective bond, emphasizing the maintenance of proximity and the regulation of stress in the child (Ainsworth, 1978; De Wolff and van IJzendoorn, 1997). Sensitivity, mind-mindedness, and co-regulation—constructs predictive of secure attachment—are also manifestations of empathic processes (Fonagy and Target, 1997; Meins et al., 2003). Empathy research, however, places greater emphasis on the underlying neurobiological and psychological mechanisms and the context-dependent regulation of affective and cognitive empathy, including individual variation in hormonal and genetic sensitivity (Bos, 2017; Decety and Svetlova, 2012). Whereas attachment theory primarily describes *what* characterizes secure relationships and *which* developmental outcomes they predict, empathy research explains *how* caregiving behavior is motivated and regulated at behavioral and physiological levels. Integrating these perspectives offers a richer explanatory framework for the interplay between stress, neurobiology, and care quality, and can inform interventions that are both relationally and biologically grounded.

facilitate either protective or nurturant responses, which is based on efferent prefrontal cortical control over subcortical structures (Wager et al., 2008). Moreover, this adaptive regulation is partly under endocrine control, with a key role of oxytocin, which also plays an important role in facilitating caregiving behavior.

4.2. Endocrine regulation of empathy under safety of threat

In a relatively safe environment oxytocin can reduce stress, increase emotion recognition, cognitive empathy, compassion, and rewarding responses to one's infant and partner (Bos, 2017; De Dreu and Kret, 2016). It may do so by shifting neural activation to prefrontal regions to accommodate cognitive empathy and emotional regulation. The role of oxytocin in affective empathy is less clear. Some studies have indicated that oxytocin elicits stronger subjective and objective responses to stimuli eliciting empathy (Abu-Akel et al., 2015; Hurlemann et al., 2010; Shamay-Tsoory et al., 2013; Spencer et al., 2022). For example, Shamay-Tsoory (2013) reported that administered oxytocin increased empathy, but only towards outgroup members, in seeming contrast to previously reported effects on ingroup favoritism (De Dreu and Kret, 2016). These effects of oxytocin are perhaps mediated by altered perception of self-other distinction, as Abu-Akel (2015) demonstrated that oxytocin increased empathy for pain in others, but only in a condition where they were instructed to empathize with others instead of empathizing with oneself. Conversely, Bos et al. (2015) reported reduced neural responses to others' pain (videos of a needle penetrating a hand) following oxytocin administration, possibly reflecting its analgesic properties. Similar effects have been observed with acetaminophen, which dampens empathy for pain and social rejection (Dewall et al., 2010; Mischkowski et al., 2016). Oxytocin thus appears to play a critical role in adaptively shifting empathic processes for the benefit of others. It remains uncertain, however, if this shifting is included by a blurring of sharpening of self-other boundaries. In an unsafe and threatening environment, oxytocin has – at least in rodent studies – demonstrated to increase aggression towards unfamiliar others, especially in mothers (Bosch and Neumann, 2012). Parental aggression in humans has not been studied in the context of oxytocin, but administration studies do suggest that oxytocin increases in-group favoritism or 'in-group love' at the expense of 'outsiders' (De Dreu and Kret, 2016). In addition, circumstantial evidence in humans for a link between maternal aggression and oxytocin comes from a study in which aggression to unfamiliar adults was measured in mothers that where either breastfeeding bottle feeding, or nulliparous women (Hahn-Holbrook et al., 2011b). The result showed that aggression wat highest in breastfeeding mothers, who simultaneously had the lowest levels of physiological stress. This may be attributable to effects of oxytocin, since these findings are in line with the animal work on oxytocin that indicate stress reducing properties combined with increased maternal aggression. However, other hormones involved in breastfeeding, such as prolactin, could also be involved (Sanson and Bosch, 2022).

Other hormones that may play a key role in modulating empathic processes relevant to caregiving, are testosterone and cortisol. Whereas testosterone, at least in women, downregulates cognitive empathy and trust, it does not seem to downregulate affective empathy towards pain in others (Boksem et al., 2013; Bos et al., 2010; Heany et al., 2020; van Honk et al., 2011). Yet as described above, testosterone increases neural responses to infant cry sounds and enhances empathic facial responses towards children in difficult situations (Bos et al., 2010; Bos et al., 2021). Cortisol can also affect empathic processing. Administration studies on cortisol are scarce, but previous work has demonstrated that cortisol increased neural responding to infant cry sounds (Bos et al., 2014), and improved empathic concern for emotional states of others, indicating enhanced affective empathy (Wingenfeld et al., 2014).

Together, this hormonal regulation of empathic responses might account for some of the effects of acute stress on empathy that have been reported. For example, in a study by Wolf et al. (2015) participants subjected to acute stress reported stronger affective (but not cognitive) empathic reactions towards others. Another study showed stronger neural responses towards pain in others under stress, as well as increased prosocial behavior in an economic game (Tomova et al., 2017). However, Nitschke et al. (2020) show that acute stress reduced positive facial communication to others in the form of smiling, an important reinforcer of positive communication (Kraaijenvanger et al., 2017). In line with this finding, a recent overview of the literature concludes that stress can also lead to blocking empathic contagion with others. This may result from stress-induced shifting of attention to the self instead of to others, a situation that results in empathic distress instead of empathic concern (Nitschke and Bartz, 2022). Effects of stress on cognitive empathic abilities are less convincing compared to the effect of affective empathy (Nitschke and Bartz, 2022). Interestingly, the overall view is that effects of stress have only been observed in more sensitive empirical tasks, such as those measuring the accuracy of empathic reactions, indicating that existent effects are subtle. Furthermore, a meta-analysis on prosocial behavior, for which empathy is an important motivation drive, recently concluded no clear effects of stress (Nitschke, Forbes, et al., 2022).

Clearly, a better understanding of the dynamic interactions between empathy, threat-induced stress and its endocrine regulation is needed. However, this overview provides clear indications that different aspects of empathy are under endocrine regulation which is dependent on safe or threatening contexts (see Fig. 2). The biggest caveat is knowledge on how these interactions play out in the context of parenting and other forms of caregiving. So far the literature is mostly confined to

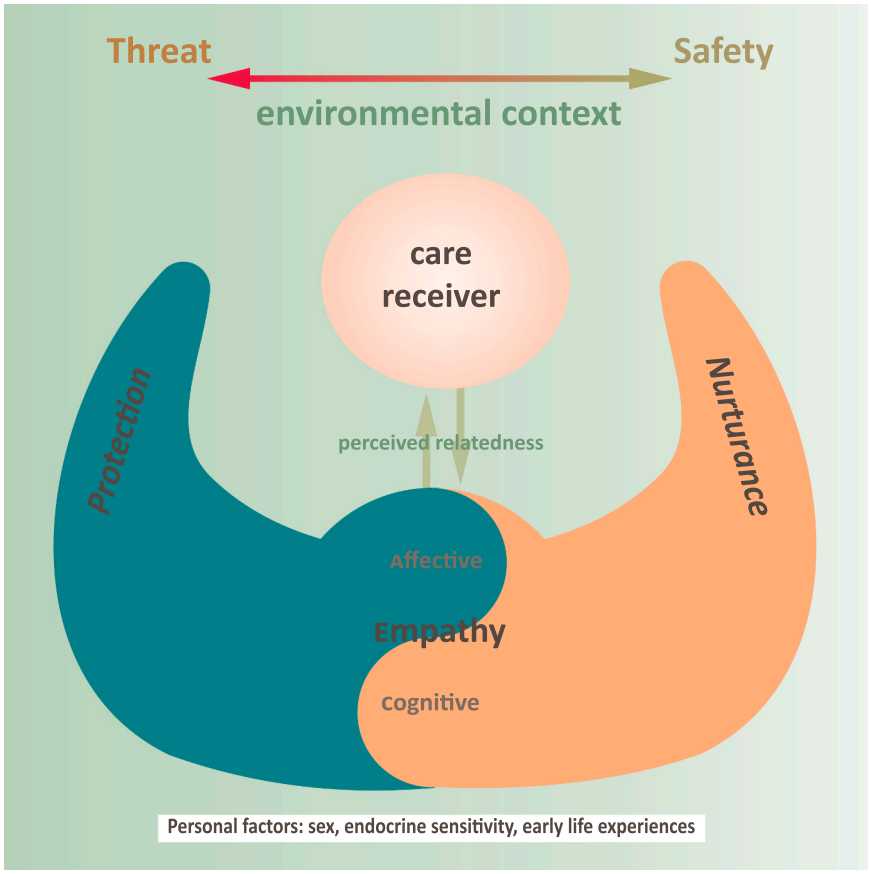

Fig. 2. A model for the role of empathy in human caregiving, This figure presents a visual display of the dynamic interactions between a caregiver and care receiver. The distinct components of empathy motivate the two aspects of human caregiving: nurturance and protection. This system functions adaptively depending on the safety-threat continuum of the environment. Caregiving behavior is further dependent on personal characteristics of the caregiver, as well as of the perceived relatedness the caregiver has to the care receiver. The neuroendocrine systems that facilitates caregiving behavior are described in the text.

nulliparous adults tested in a lab-setting (Nitschke and Bartz, 2022). Our hope is that the current review can contribute to a theoretical foundation supporting future research on this important topic. Another open road in the research on caregiving is improvement of our understanding of individual variation in caregiving behavior.

5. Individual variation

There might be some truth in Tolstoy's famous phrase that 'every unhappy family is unhappy in its own way', compared to the over-generalization that 'all happy families are alike' (Tolstoy, 2016). In a system as complex as the family, the stability that 'happiness' warrants is easily lost in the face of inevitable challenges. Individual variation in caregiving responses while dealing with these challenges arises from multiple sources. Two prominent domains are (1) sex differences in neuroendocrine stress reactivity and caregiving behavior, and (2) individual sensitivity of the oxytocin system, shaped by genetic and environmental factors in early life. These forms of variation influence how caregivers respond to stress and empathic demands, and may interact with contextual factors to shape caregiving quality.

5.1. Sex differences in neuroendocrine regulation of caregiving

The overview above shows that human caregiving can be characterized by activation of a neuroendocrine caregiving system that comprises a protective and a nurturing component. Both components can be activated by empathic processes, which have evolved to tailor the needs of dependent others in both safe and threatening environments. Importantly, these components may function differently in males and females, reflecting evolved sex differences linked to reproductive roles.

The 'Tend and befriend' hypothesis by Taylor et al. (2006); (2000) proposes a framework for a sex specific stress-response which in males is characterized by a fight or flight response, but in women is directed at soothing and nurturing behavior (*tending*), and an inclination to seek social support (*befriending*). Empirical evidence supports sex differences in responses to psycho-social stressors. For example, a meta-analysis on studies that used the 'golden standard' of acute stress induction, the Tries Social Stress task (TSST), revealed that men overall have higher cortisol and testosterone levels during the procedure compared to women (Liu et al., 2017). Recent work suggests that the differences in cortisol are partly explained by dominance-motives, which makes men and women experience a social stressor differently. More specifically, the setup of the TSST might be more distressing for those prone to ego threat, pointing at a potential role of socialization in these differences between genders (Schüler et al., 2025). However, fundamental neuroendocrine differences between men and women could also account for these variable responses on the stress task (Ter Horst et al., 2009). Testosterone, in particular, has been linked to emotional reactivity and reduced empathic accuracy (Bos et al., 2012; Nitschke and Bartz, 2020). For example, in a study where men cared for an infant simulator in a non-challenging or challenging condition (during persistent crying), higher testosterone levels in the challenging condition was related to less sensitive care (Roellke et al., 2019). Similarly, while investigating prosociality, Wang et al. (2022) found that acute stress results in stronger punishment (vs helping) in men with higher testosterone levels, suggesting a broader link between testosterone and reduced prosociality under stress. In another study investigating the effect of acute stress, men showed reduced self-other distinction resulting in more ego-centric

reactions, whereas women display an opposite pattern (Tomova et al., 2014). Higher levels or stronger reactivity of testosterone in men may therefore particularly explain sex-dependent responses in threatening contexts, which can negatively affect nurturing care responses. Nonetheless, much remains unclear, especially with regard to the interactive effect of different hormones, as another study revealed a sex-specific effect in which stress improved accuracy selectively in men, potentially caused by cortisol (Nitschke et al., 2022). This finding links to the literature on the dual-hormone hypothesis, which posits that effects of testosterone are dependent on cortisol (Mehta and Prasad, 2015). Indeed, in fathers a negative relation between testosterone and sensitivity in interaction with their own child, was strongest in fathers high in cortisol, an effect that was absent in mothers (Bos et al., 2018).

Besides cortisol and testosterone, also the oxytocin system could account for stress-induced sex-differences, as neuroimaging studies reveal relatively consistent sex-specific effects of oxytocin on neural regions such as the amygdala, critical in stress responding (Procyshyn et al., 2024). Nonetheless, the literature in humans on these differences is inconclusive. A study that directly investigated the role of oxytocin in relation to the Tend and befriend hypothesis found that following stress, oxytocin was related to more frequent support seeking, as the theory predicts (Sunahara et al., 2022). The effect was, however, similar for both sexes.

Overall, these findings offer partial support for the tend-and-befriend hypothesis but also highlight the complexity of sex differences in stress responses. Notably, the original model contrasts fight-flight behavior with caregiving and helping. Yet, when protection is viewed as a core aspect of caregiving, this dichotomy becomes conceptually flawed. Recent empirical work in rodents and humans indeed demonstrates that the motivation for helping and care behavior rely, to a certain extent, on the same neural circuitry as self-defense (Vieira and Olsson, 2023). Nonetheless, sex differences in human parental care and extended forms of care, such as altruism and helping behavior do exist, perhaps due to sexual variation in the neuroendocrine mechanisms of protection and nurturance. Overall, male caregiving seems more reactive instead of proactive, and more directed at protection and helping that requires action (e.g. heroic helping behavior). In the domain of parenting, male care is characterized by more challenging play behavior and less nurturant care (Majdandžić et al., 2016; Mayseless, 2015). Males also tend to focus more on practical caregiving behaviors, but take much less 'process responsibility': the mental load involved in organizing the care around a child (Pleck, 2012).

Based on an extensive overview of sex differences in all domains of human caregiving (Mayseless, 2015), it appears that relatively small, domain-specific differences in preferences and motivations for caregiving between sexes are reinforced to fit with traditional gender roles. This results in the striking overabundance of, for example, women being the primary caretaker of babies, and males engaging in high-risk altruism, such as saving the life of a stranger in dangerous situations (Becker and Eagly, 2004; Falk and Hermle, 2018). Overall, women also show stronger motivation for nurturing, but not for protection (Hofer et al., 2017). Also, they are more sensitive to signals of infant cuteness (Hahn and Perrett, 2014), and demonstrate overall higher levels of most aspects of empathy (Baron-Cohen et al., 2015; McDonald and Kanske, 2023). These sex-differences, which are the product of iterative genetic-environmental interactions, are potentially exacerbated under conditions of stress.

5.2. Oxytocin sensitivity and early life influences on caregiving

As described above, oxytocin plays a crucial role in instigating context-dependent caregiving behavior, most notably by reducing cortisol release when exposed to a stressor, and increasing empathic responses (Barchi-Ferreira and Osório, 2021; Heinrichs et al., 2003). The importance of this neuropeptide at the interplay of empathy and stress during caregiving is further underscored by recent animal work which revealed that the effects of oxytocin in the central amygdala are a key mechanism by which social buffering can reduce fear (Hegoburu et al., 2024; Hostinar et al., 2014). Oxytocin can thus facilitate social interaction, and also buffer experienced distress during social interactions. However, individuals differ in their sensitivity of the oxytocin system. There is both variability in the genetic susceptibility to oxytocin, as well as variation in oxytocin release, both centrally and peripherally through the pituitary (Kumsta and Heinrichs, 2013; Landgraf and Neumann, 2004). One source of genetic variation is the diversity in polymorphisms of oxytocin related genes, most studied of which are the oxytocin receptor (OXTR) gene and a gene related to oxytocin release (CD38). For both polymorphism it is however still unclear what the downstream effects of the genetic variation is for their receptor's effectivity, and also the predictive variability for behavioral outcomes is limited (Bakermans-Kranenburg and van IJzendoorn, 2014). A recent meta-analysis also found no overall associations between polymorphism of the OXTR-gene and cognitive or affective empathy (Chander et al., 2022). A factor that potentially has more predictive value, which has recently spurred great interest is epigenetic variability of the oxytocin genes, most notably methylation: the process by which methyl groups attach to the promotor region of genes, limiting their expression (Kraaijenvanger et al., 2019). In one of the first studies that targeted human social behavior, Haas et al. (2016) show that lower levels of methylation of the oxytocin gene are related to a more secure attachment style and better recognition of emotions. Puglia et al. (2018) further demonstrated that lower methylation of the oxytocin receptor gene is related to stronger sensitivity to social information. Based on these findings, we tested whether methylation of the oxytocin related genes predicted subjective and physiological responses to empathy eliciting stimuli of children (Spencer et al., 2022). In line with previous work, we observed stronger responses on both measures, indicative of enhanced empathy, in individuals with lower levels of methylation. Following up on this work, we also showed stronger sensitivity for infant facial features in individuals with lower levels of methylation (Spencer et al., 2024). A recent study by Rilling et al. (2024) further showed that lower methylation was also related to more positive affect towards grandchildren in grandmothers. These findings point out that variation in sensitivity of the oxytocin system relates to caregiving behavior, perhaps mediated by the attenuating role of oxytocin in buffering stress.

The oxytocin system is additionally relevant in the context of caregiving, since this system is sensitive to the influence of caregiving quality in early life. Early adverse experiences seem to reduce the release of and sensitivity to oxytocin, whereas secure attachment relations will have an opposite effect on the oxytocin system (Bos, 2017; Rilling and Young, 2014). Methylation of the oxytocin related genes is malleable under environmental influence, and provides a mechanism for how early life experiences—such as trauma—become physiologically embedded (Cecil et al., 2020; Ellis et al., 2021; Kraaijenvanger et al., 2019). Indeed, a promising finding in a group of mother-infant dyads shows that change in oxytocin receptor methylation was predicted by maternal engagement and child temperament (Krol et al., 2019). Epigenetic variability of oxytocin system genes may thus function as an important physiological parameter that incorporates childhood experiences to influence an individuals' lifelong capacity to deal with stressful situations. For parents and children, it can thereby also provide for a mechanism of the intergenerational transmission of caregiving quality (Bos, 2017). A recent study in prairie voles has convincingly demonstrated for such a mechanism (Meaney, 2001; Perkeybile et al., 2019), which is promising for the work on humans, which is mostly still preliminary.

6. When empathy and caregiving clash under the impact of stress

This review has thus far focused primarily on situations in which (stress-induced) regulation of empathic processes are adaptive in facilitating adequate caregiving behavior. Either during protection, when

immediate defense action is required to safeguard a child, often requiring emotional reactive responses uninterrupted by cognitive deliberation. Or during nurturing and soothing in relatively safe situations, where parents' reflection on the thoughts and motivations of the child ensures caregiving behavior that is tailored to the child's needs and long-term well-being. In the following paragraph we discuss situations in which empathic regulation conflicts with the child's needs, which is therefore is better referred to as *insufficient* regulation or *mis-regulation* of empathy. Two aspects of the stress response are important to consider with respect to the impact on empathy: the *severity* and the *duration* of the response, since activation of the stress-response is not problematic in itself. In contrast, to a certain extent stress is necessary for a caring response. It makes parents get out of bed when their baby cries, or reach out when their toddler shows signs of distress. It's the severity and duration that makes the difference.

6.1. Severe and prolonged stress

In the neuroscience literature, the relation between the stress-load and neurobiological outcomes are often described by an inverted u-shape, where a certain amount of stress is necessary for optimal outcomes, but overstimulation results in detrimental effects on health and psychological functioning (Sapolsky, 2004, 2015). A similar pattern seems to apply to the impact of stress on empathic responding, and thereby likely on caregiving quality. Moderate stress reactivity, also as part of an empathic response to a child in need, can be a potent motivator of caregiving behavior. The few studies that investigated the effect of acute stress on caregiving quality have not revealed negative effects of stress, but neither positive (e.g., Bruinhof et al., 2025; Tronick et al., 2021). The source of stress might however be relevant, i.e., whether it is the child itself eliciting a stress response, or external factors outside the parent-child dyad. A recent study indeed points in this direction, by showing that when the child is the source of stress, mothers have more difficulty in understanding the child's motives (Malcorps et al., 2025). Therefore, dissociating the impact of the sources of stress is an important aim for future studies.

In contrast to the moderate stress induced in experimental paradigms, severe or chronic stress will increase the likelihood of *empathic distress*, defined as a self-oriented, emotional and physiological reaction to witnessing another's suffering. Empathic distress can interfere with providing sensitive support or care, particularly in high-stress contexts such as soothing a distressed child (Batson, 2010). It biases a person towards self-focused responses, that in caring interactions will more likely result in avoidance instead of helping (Eisenberg et al., 1990; Eisenberg and Fabes, 1990). Although empathic distress has a trait component — reflecting both genetic predispositions and enduring patterns shaped by early life stress — it can be elevated under conditions of chronic environmental stress. For instance, Shalev et al. (2023) reported that empathic distress was associated with emotional exhaustion and reduced empathic ability, especially during periods of heightened stress exposure. Similarly, higher empathic distress has been linked to lower sensitivity in both real and simulated parent–infant interactions (Kaźmierczak et al., 2024; Salo et al., 2020) and has been shown to attenuate the positive association between maternal mind-mindedness and child outcomes (Hobby et al., 2023).

Regarding prolonged stress, McEwen's theory of allostatic load may offer a useful conceptual framework for understanding how chronic stress might impair empathic responding and caregiving quality. Allostatic load refers to the cumulative physiological burden resulting from repeated or prolonged activation of stress response systems, including the HPA axis, autonomic nervous system, and immune pathways (McEwen, 1998). While this theory does not directly predict caregiving outcomes, it helps to explain how chronic stress may affect brain regions involved in emotion regulation and social behavior, such as the prefrontal cortex, amygdala, and hippocampus (McEwen, 2017). Empirical work in rodents investigating the relation between stress and caregiving have given detailed insight into how stress related hormones – most importantly corticotrophin releasing factor (CRF), negatively affect maternal caregiving behavior (Sanson et al., 2024). For example, hyperactivation of CRF in subcortical structures such as the Bed Nucleus of the Stria Terminalis (BNST) and the medial preoptic area (MPOA) of the hypothalamus can cause detrimental effects on maternal care, maternal aggression, and maternal anxiety, strongly impacting the quality of care (Klampfl and Bosch, 2019). Interestingly, in lactating rats increases of CRF in the MPOA can also trigger a surge in oxytocin release, which may indicate a negative feedback loop that adaptively couterbalances negative effects of stress on maternal caregiving behavior (Klampfl and Bosch, 2019; Sanson and Bosch, 2022).

Although scarce, studies in humans provide partial support for these proposed mechanisms. For example, Levy et al. (2019) found that mothers exposed to chronic trauma showed intact neural responses to empathy-evoking stimuli but reduced empathic behavior, suggesting a disruption in the coherence between brain activity and caregiving behavior. Although the study does not explicitly reference allostatic load, its findings align with the notion that chronic stress may interfere with the behavioral expression of empathy. Similarly, Roepke et al. (2011) reported that Alzheimer caregivers exhibited higher allostatic load and lower caregiving quality, although the mechanisms were not fully delineated.

Taken together, these findings suggest that chronic stress may contribute to empathic distress and reduced caregiving quality, potentially through neurobiological pathways described by the theory of allostatic load. However, more research is needed to establish direct causal links, to translate the work described in rodents to humans, and to clarify the role of individual differences and contextual factors.

6.2. Stress contagion and the carrying capacity of the family system

In many Western societies, caregiving occurs within small nuclear family units, where parents are primary co-regulators of children's emotional states. Because children have limited self-regulatory capacities, they depend on parental support to buffer stress (DePasquale and Gunnar, 2020; Shaver et al., 2016). Empathy, however, also renders stress responses contagious: parents can automatically resonate with a child's emotional and physiological states, as well as with each other's. Research indicates that children's heart rates can track those of their mothers during stress, even without awareness of the stressor (Waters et al., 2014). Similar parent-to-child and child-to-parent stress contagion effects have been observed (Engert et al., 2019), and can be amplified when the parent is already stressed (Tomova et al., 2017; von Dawans et al., 2021; Wolf et al., 2015).

High levels of empathic distress may exacerbate these feedback loops, undermining effective co-regulation, supportive partner relations, and increasing the risk of harsh or inconsistent caregiving (Bos, 2017; Joosen et al., 2013). In the absence of buffering support from extended family or community networks, this dynamic may foster a toxic emotional climate for the child. Also, the continuous demands of caregiving, often conceptualized as parenting stress, can become a significant source of chronic strain. Stress in one domain of life often spills over into others; for example, maternal job stress has been linked to increased irritability and reduced empathy toward children (Repetti and Wood, 1997). Prolonged exposure to such stressors contributes to allostatic load, which can culminate in *parental burnout*: a state characterized by emotional exhaustion, emotional distancing from children, and a sense of ineffectiveness in the parenting role (Mikolajczak and Roskam, 2018; Roskam et al., 2023). This condition shares notable similarities with *compassion fatigue* observed in professional caregiving contexts (Trzeciak et al., 2017). Both parental burnout and compassion fatigue are linked to elevated empathic distress and sustained stress exposure (Mikolajczak et al., 2019), aligning with the predictions of the allostatic load framework.

6.3. Early life stress as a vulnerability factor

Parents with a history of *childhood maltreatment* are especially vulnerable to stress-related caregiving difficulties. Buisman et al. (2018) demonstrated that such parents often exhibit altered autonomic nervous system responses to infant crying, reflecting dysregulated physiological control. Subsequent work showed heightened autonomic reactivity during real-life interactions with their children, and more negative parent-child interactions (Buisman et al., 2019). Moreover, maltreated parents have been found to display reduced accuracy in emotion recognition, which may further undermine empathic responding (Buisman et al., 2024). These physiological and cognitive alterations likely represent the cumulative impact of chronic early stress—an embodied form of allostatic load—that compromises adaptive functioning in the caregiving role.

In summary, adaptive empathic caregiving depends on stress levels remaining within a manageable range. Chronic or severe stress, such as poverty, parental psychopathology, or limited and unstable family relations, particularly when compounded by early adversity, can heighten empathic distress and erode the parent's capacity to co-regulate with the child (Mackenzie et al., 2011). Allostatic load may offer a unifying framework for understanding how repeated stress exposure undermines the physiological and psychological resources necessary for sensitive, empathic and effective caregiving.

7. The reach of empathy and the human motivation to care

Few domains reveal the full spectrum of human nature as clearly as caregiving—where individuals extend care beyond expectation or fail to act when care is urgently needed. Caring is therefore generally seen as a higher moral virtue, which also shows in the role care has in most, if not all, human religions (Mayseless, 2015). Yet, as this review shows, it is not moral virtue that brings forth empathic and caring behavior, but rather evolutionarily shaped neuroendocrine systems that motivate us to protect and nurture the interests of those who need our help: in the first place, our offspring and close others.

It is within the boundaries of these close relationships that empathic processes support the formation of attachment. One of the aims of this review is to foster research at the intersection of attachment theory, research on empathy and stress, and neuroendocrine perspectives on child development and parenting. Recent examples of such integration show the extent to which attachment and empathic processes are intertwined. In children as young as 3–6 years old, attachment security was related with stronger displays of empathic concern, whereas in adults the same construct was related to cognitive empathic abilities (Gallistl et al., 2024; Shoshani, 2024). Of special interest with regard to the current review is a study in couples where one of the partners was subjected to a stressor while the other partner observed (Gallistl et al., 2025). Insecure-avoidant attachment in observing partners was related to increased heart-rate activity in the partner subjected to stress, indicating that the presence of the partner was more a source of stress than of support. A better understanding of the dynamic interactions between stress and empathy during attachment formation can potentially guide the development of interventions better tailored to those that provide and receive care. More knowledge on the biological and contextual factors that bring forth individual variation during this dynamic interaction can help to make these interventions more effective and beneficial (Bos, 2017; Shaver et al., 2016).

Whereas the focus in this review has been on close relationships in the family context, the reach of the described mechanisms are broader. For example, also in the domain of medical and psychological care, the importance of empathy for improvement of patient outcomes received increased attention (Gilbert, 2009; Trzeciak et al., 2017). The mechanisms presented here can encompass informal and formal care relations, based on the perspective that all human caregiving derives from core empathic processes formed in social relations of species that depend on the care of others. This state of fitness interdependence forms the condition for the development of prosocial behavior and altruism which characterizes the human species (Berendzen, 2023; Brown et al., 2012; Swain et al., 2012). Another aspect that characterizes human caregiving, is the flexibility in care relations. As humans we can be altruistic to strangers, and we can care for unrelated others, animals, plants, or even inanimate objects, thanks to our strong anthropomorphic tendencies. Our capability for abstract thinking and planning brings forth the capacity to care for humans that we have never encountered or that not yet exist, such as the concern for the future wellbeing of the next generation. The influential psychologist Erik Erikson coined the term 'generativity' for the motivation to care for the next generation, and defined it as an important goal in adult psychosocial development (Saint Aubin and MacAdams, 2004). Such generative motives can be directed at (grand) children, but can also encompass the motivation to care for a concept as abstract as our future ecosystem, or planet earth. Interestingly, generative motivations are related to self-reported empathic concern, and theorist have suggested an overlap between caregiving motivations, attachment, and generativity (MacAdams, 2000; Versey et al., 2020). More research on how these motivational systems are linked, and how generativity can be fostered, has the potential to contribute to the great challenges we currently face with respect to the future generations. An important question is to what extent empathic motives can drive pro-environmental behavior, as critics have emphasized the shortcomings of empathy with regard to morality and global problems, arguing that empathy counteracts reasoned altruistic decision making, by biasing us toward emotionally salient individuals (e.g. Bloom, 2017). Despite these critics, recent theoretical and empirical work shines a new light on the relation between empathy, prosociality, and altruism, by pointing out that 'empathy and deliberative reasoning aren't necessarily competing forces' (Law et al., 2024). As Mencius described more than two thousand years ago, our care for other derives not from instrumental motives or societal pressure, but from 'the heart'.

There is an additional quality of caregiving: irrespective of whether we nurture our newborn baby, help a relative in need, or make efforts for the future wellbeing of our planet, caregiving has the potential to give meaning to our lives (Mayseless, 2015). While caring may not directly bring happiness, due to the constraints that come along with it and the effort it requires, it does provide for a purpose, which gives a deeper state of 'eudaimonic' happiness. In the context of close human relations, it is this subjective state that perhaps comes most close to the definition of 'love' (Baumeister et al., 2016). It is a quality that facilitates the social and cognitive development of children, brings psychological and health-benefits in adults, and has the potential to protect for intergenerational transmission of maltreatment to occur (Bos et al., 2025; Langevin et al., 2021). As such, caregiving is a central aspect of our lives, since we need to be cared for ourselves throughout our life just as much as we need to care for others. This need is as old as the earliest animals that depended on each other, and has increased in complexity throughout the human lineage.

This review highlighted that caregiving is not merely a moral or cultural construct, but a biologically grounded, stress-sensitive system shaped by evolutionary pressures and individual variation that acts on our fundamental empathic abilities. Recognizing its dual nature—nurturance and protection—and its neuroendocrine regulation offers a deeper understanding of how care emerges, falters, and can be supported across contexts; contributing to the wellbeing of those who care, and are cared for.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Abu-Akel, A., Palgi, S., Klein, E., Decety, J., Shamay-Tsoory, S., 2015. Oxytocin increases empathy to pain when adopting the other- but not the self-perspective. Soc. Neurosci. 10 (1), 7–15. https://doi.org/10.1080/17470919.2014.948637.

Ainsworth, M.D.S., 1978. The bowlby-ainsworth attachment theory. Behav. Brain Sci. 1 (3), 436–438.

Ainsworth, M.D.S., Blehar, M.C., Waters, E., Wall, S.N., 2015. Patterns of Attachment: A Psychological Study of the Strange Situation. Taylor & Francis. ⟨https://books.google.nl/books?id=wK4BCgAAQBAJ⟩.

Avenanti, A., Sirigu, A., Aglioti, S.M., 2010. Racial bias reduces empathic sensorimotor resonance with other-race pain. Curr. Biol. 20 (11), 1018–1022. https://doi.org/10.1016/j.cub.2010.03.071.

Bakermans-Kranenburg, M.J., van IJzendoorn, M.H., 2014. A sociability gene? Meta-analysis of oxytocin receptor genotype effects in humans. Psychiatr. Genet. 24 (2), 45–51. https://doi.org/10.1097/YPG.0b013e3283643684.

Bakermans-Kranenburg, M.J., van IJzendoorn, M.H., 2017b. Protective parenting: neurobiological and behavioral dimensions. Curr. Opin. Psychol. 15, 45–49. https://doi.org/10.1016/j.copsyc.2017.02.001.

Bakermans-Kranenburg, M.J., van IJzendoorn, M.H., 2017a. Oxytocin and human sensitive and protective parenting. Behav. Pharmacol. Neuropept. Oxytocin 421–448.

Barber, B.K., 1996. Parental psychological control: revisiting a neglected construct. Child Dev. 67 (6), 3296–3319. ⟨https://www.ncbi.nlm.nih.gov/pubmed/9071782⟩.

Barchi-Ferreira, A., Osório, F., 2021. Associations between oxytocin and empathy in humans: a systematic literature review. Psychoneuroendocrinology 129, 105268.

Baron-Cohen, S., 2011. Zero Degrees of Empathy: A New Theory of Human Cruelty. Penguin uk.

Baron-Cohen, S., Bowen, D.C., Holt, R.J., Allison, C., Auyeung, B., Lombardo, M.V., Smith, P., Lai, M.-C., 2015. The "reading the mind in the eyes" test: complete absence of typical sex difference in~ 400 men and women with autism. PLOS One 10 (8), e0136521.

Barrett, E.S., Tran, V., Thurston, S., Jasienska, G., Furberg, A.S., Ellison, P.T., Thune, I., 2013. Marriage and motherhood are associated with lower testosterone concentrations in women. Horm. Behav. 63 (1), 72–79. https://doi.org/10.1016/j.yhbeh.2012.10.012.

Bartz, J.A., Zaki, J., Bolger, N., Hollander, E., Ludwig, N.N., Kolevzon, A., Ochsner, K.N., 2010. Oxytocin selectively improves empathic accuracy. Psychol. Sci. 21 (10), 1426–1428. https://doi.org/10.1177/0956797610383439.

Batson, C.D. 2010. Empathy-induced altruistic motivation.

Batson, C.D., 2014. Empathy-induced altruism and morality. In: Maibom, In.H.L. (Ed.), Empathy and Morality. Oxford University Press, pp. 41–58. https://doi.org/10.1093/acprof:oso/9780199969470.003.0002.

Baumeister, R.F., Vohs, K.D., Aaker, J.L., Garbinsky, E.N., 2016. Some key differences between a happy life and a meaningful life. Positive Psychology in Search for Meaning. Routledge, pp. 49–60.

Becker, S.W., Eagly, A.H., 2004. The heroism of women and men. Am. Psychol. 59 (3), 163–178. https://doi.org/10.1037/0003-066X.59.3.163.

Berendzen, K.M., 2023. Understanding social attachment as a window into the neural basis of prosocial behavior. Front. Neurol. 14, 1247480.

Bethlehem, R.A., van Honk, J., Auyeung, B., Baron-Cohen, S., 2013. Oxytocin, brain physiology, and functional connectivity: a review of intranasal oxytocin fMRI studies. Psychoneuroendocrinology 38 (7), 962–974. https://doi.org/10.1016/j.psyneuen.2012.10.011.

Bloom, P., 2017. Empathy and its discontents. Trends Cogn. Sci. 21 (1), 24–31.

Boksem, M.A., Mehta, P.H., Van den Bergh, B., van Son, V., Trautmann, S.T., Roelofs, K., Smidts, A., Sanfey, A.G., 2013. Testosterone inhibits trust but promotes reciprocity. Psychol. Sci. 24 (11), 2306–2314. https://doi.org/10.1177/0956797613495063.

Bornstein, M.H., Tamis-LeMonda, C.S., Hahn, C.-S., Haynes, O.M., 2008. Maternal responsiveness to young children at three ages: longitudinal analysis of a multidimensional, modular, and specific parenting construct. Dev. Psychol. 44 (3), 867.

Bos, P.A., 2017. The endocrinology of human caregiving and its intergenerational transmission. Dev. Psychopathol. 29 (3), 971–999. https://doi.org/10.1017/S0954579416000973.

Bos, P.A., Hechler, C., Beijers, R., Shinohara, K., Esposito, G., de Weerth, C., 2018. Prenatal and postnatal cortisol and testosterone are related to parental caregiving quality in fathers, but not in mothers. Psychoneuroendocrinology 97, 94–103. https://doi.org/10.1016/j.psyneuen.2018.07.013.

Bos, P.A., Hermans, E.J., Montoya, E.R., Ramsey, N.F., van Honk, J., 2010. Testosterone administration modulates neural responses to crying infants in young females. Psychoneuroendocrinology 35 (1), 114–121. https://doi.org/10.1016/j.psyneuen.2009.09.013.

Bos, P.A., Jap-Tjong, N., Spencer, H., Hofman, D., 2016. Social context modulates facial imitation of children's emotional expressions. PLOS One 11 (12), e0167991. https://doi.org/10.1371/journal.pone.0167991.

Bos, P.A., Lesemann, F.H.P., Spencer, H., Stein, D.J., van Honk, J., Montoya, E.R., 2021. Preliminary data on increased reactivity towards children in distress after testosterone administration in women: a matter of protection? Biol. Psychol. 165, 108176. https://doi.org/10.1016/j.biopsycho.2021.108176.

Bos, P.A., Montoya, E.R., Hermans, E.J., Keysers, C., van Honk, J., 2015. Oxytocin reduces neural activity in the pain circuitry when seeing pain in others. NeuroImage 113, 217–224.

Bos, P.A., Montoya, E.R., Terburg, D., van Honk, J., 2014. Cortisol administration increases hippocampal activation to infant crying in males depending on childhood neglect. Hum. Brain Mapp. 35 (10), 5116–5126. https://doi.org/10.1002/hbm.22537.

Bos, P.A., Panksepp, J., Bluthe, R.M., van Honk, J., 2012. Acute effects of steroid hormones and neuropeptides on human social-emotional behavior: a review of single administration studies. Front. Neuroendocr. 33 (1), 17–35. https://doi.org/10.1016/j.yfrne.2011.01.002.

Bos, P.A., Riem, M.M., Brummelman, E., 2025. The nature of love revisited: how social bonds shape development. In (Vol. 28, pp. e70005).

Bos, P.A., Terburg, D., van Honk, J., 2010. Testosterone decreases trust in socially naive humans. Proc. Natl. Acad. Sci. USA 107 (22), 9991–9995. https://doi.org/10.1073/pnas.0911700107.

Bosch, O.J., Neumann, I.D., 2012. Both oxytocin and vasopressin are mediators of maternal care and aggression in rodents: from central release to sites of action. Horm. Behav. 61 (3), 293–303.

Bowlby, J., 1983. Attachment, Vol. 1 of Attachment and loss, 2nd ed. Basic Books, New York (In).

Brown, S.L., Brown, R.M., 2006. Selective investment theory: recasting the functional significance of close relationships. Psychol. Inq. 17 (1), 1–29.

Brown, S.L., Brown, R.M., Preston, S.D., 2012. The human caregiving system. Moving beyond self-interest: perspectives from evolutionary biology, neuroscience, and the social sciences, pp. 75-88..

Brown, S.L., Brown, R.M., 2015. Connecting prosocial behavior to improved physical health: contributions from the neurobiology of parenting. Neurosci. Biobehav. Rev. 55, 1–17. https://doi.org/10.1016/j.neubiorev.2015.04.004.

Bruinhof, N., Beijers, R., Lustermans, H., de Weerth, C., 2025. Mother–infant stress contagion? Effects of an acute maternal stressor on maternal caregiving behavior and infant cortisol and crying. J. Child Psychol. Psychiatry.

Buchanan, T.W., Bagley, S.L., Stansfield, R.B., Preston, S.D., 2012. The empathic, physiological resonance of stress. Soc. Neurosci. 7 (2), 191–201. https://doi.org/10.1080/17470919.2011.588723.

Buisman, R.S., Bakermans-Kranenburg, M.J., Pittner, K., Compier-de Block, L.H., van den Berg, L.J., van IJzendoorn, M.H., Tollenaar, M.S., Elzinga, B.M., Lindenberg, J., Alink, L.R., 2019. Parents' experiences of childhood abuse and neglect are differentially associated with behavioral and autonomic responses to their offspring. Dev. Psychobiol. 61 (6), 888–902.

Buisman, R.S., Compier-de Block, L.H., Bakermans-Kranenburg, M.J., Pittner, K., van den Berg, L.J., Tollenaar, M.S., Elzinga, B.M., Voorthuis, A., Linting, M., Alink, L.R., 2024. The role of emotion recognition in the intergenerational transmission of child maltreatment: a multigenerational family study. Child Abus. Negl. 149, 106699.

Buisman, R.S., Pittner, K., Compier-de Block, L.H., van den Berg, L.J., Bakermans-Kranenburg, M.J., Alink, L.R., 2018. The past is present: The role of maltreatment history in perceptual, behavioral and autonomic responses to infant emotional signals. Child Abus. Negl. 77, 23–34.

Carter, C.S., 2022. Sex, love and oxytocin: two metaphors and a molecule. Neurosci. Biobehav. Rev. 143, 104948. https://doi.org/10.1016/j.neubiorev.2022.104948.

Cecil, C.A., Zhang, Y., Nolte, T., 2020. Childhood maltreatment and DNA methylation: a systematic review. Neurosci. Biobehav. Rev. 112, 392–409.

Chander, R.J., Mather, K.A., Cleary, R., Grainger, S.A., Thalamuthu, A., Numbers, K., Kochan, N.A., Armstrong, N.J., Brodaty, H., Henry, J.D., Sachdev, P.S., 2022. The influence of rs53576 polymorphism in the oxytocin receptor (OXTR) gene on empathy in healthy adults by subtype and ethnicity: a systematic review and meta-analysis. Rev. Neurosci. 33 (1), 43–57. https://doi.org/10.1515/revneuro-2021-0038.

Cooke, J.E., Deneault, A.A., Devereux, C., Eirich, R., Fearon, R.M.P., Madigan, S., 2022. Parental sensitivity and child behavioral problems: a meta-analytic review. Child Dev. 93 (5), 1231–1248. https://doi.org/10.1111/cdev.13764.

Crouch, J.L., Skowronski, J.J., Milner, J.S., Harris, B., 2008. Parental responses to infant crying: the influence of child physical abuse risk and hostile priming. Child Abus. Negl. 32 (7), 702–710. https://doi.org/10.1016/j.chiabu.2007.11.002.

von Dawans, B., Strojny, J., Domes, G., 2021. The effects of acute stress and stress hormones on social cognition and behavior: current state of research and future directions. Neurosci. Biobehav Rev. 121, 75–88. https://doi.org/10.1016/j.neubiorev.2020.11.026.

De Dreu, C.K., Kret, M.E., 2016. Oxytocin conditions intergroup relations through upregulated in-group empathy, cooperation, conformity, and defense. Biol. Psychiatry 79 (3), 165–173.

De Wolff, M.S., van IJzendoorn, M.H., 1997. Sensitivity and attachment: a meta-analysis on parental antecedents of infant attachment. Child Dev. 68 (4), 571–591. ⟨https://www.ncbi.nlm.nih.gov/pubmed/9306636⟩.

Decety, J., 2011. The neuroevolution of empathy. Ann. N. Y Acad. Sci. 1231, 35–45. https://doi.org/10.1111/j.1749-6632.2011.06027.x.

Decety, J., Bartal, I.B.-A., Uzefovsky, F., Knafo-Noam, A., 2016. Empathy as a driver of prosocial behaviour: highly conserved neurobehavioural mechanisms across species. Philos. Trans. R. Soc. B 371 (1686), 20150077. ⟨https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4685523/pdf/rstb20150077.pdf⟩.

Decety, J., Svetlova, M., 2012. Putting together phylogenetic and ontogenetic perspectives on empathy. Dev. Cogn. Neurosci. 2 (1), 1–24. https://doi.org/10.1016/j.dcn.2011.05.003.

DePasquale, C.E., Gunnar, M.R., 2020. Parental sensitivity and nurturance. Future Child. 30 (2), 53–70.

Dewall, C.N., Macdonald, G., Webster, G.D., Masten, C.L., Baumeister, R.F., Powell, C., Combs, D., Schurtz, D.R., Stillman, T.F., Tice, D.M., Eisenberger, N.I., 2010. Acetaminophen reduces social pain: behavioral and neural evidence. Psychol. Sci. 21 (7), 931–937. https://doi.org/10.1177/0956797610374741.

Eisenberg, N., Fabes, R., Miller, P.A., Shell, R., Shea, C., May-Plumlee, T., 1990. Preschoolers' vicarious emotional responding and their situational and dispositional prosocial behavior. MerrillPalmer Q. 507–529.
Eisenberg, N., Fabes, R.A., 1990. Empathy: conceptualization, measurement, and relation to prosocial behavior. Motiv. Emot. 14 (2), 131–149.
Ellis, B.J., Horn, A.J., Carter, C.S., van IJzendoorn, M.H., Bakermans-Kranenburg, M.J., 2021. Developmental programming of oxytocin through variation in early-life stress: Four meta-analyses and a theoretical reinterpretation. Clin. Psychol. Rev. 86, 101985.
Engert, V., Linz, R., Grant, J.A., 2019. Embodied stress: the physiological resonance of psychosocial stress. Psychoneuroendocrinology 105, 138–146. https://doi.org/10.1016/j.psyneuen.2018.12.221.
Falk, A., Hermle, J., 2018. Relationship of gender differences in preferences to economic development and gender equality. Science 362 (6412), eaas9899. https://doi.org/10.1126/science.aas9899.
Fanselow, M.S., 1994. Neural organization of the defensive behavior system responsible for fear. Psychon. Bull. Rev. 1 (4), 429–438. https://doi.org/10.3758/BF03210947.
Farmer, C.G., 2000. Parental care: the key to understanding endothermy and other convergent features in birds and mammals. Am. Nat. 155 (3), 326–334. https://doi.org/10.1086/303323.
Feldman, R., 2015. The adaptive human parental brain: implications for children's social development. Trends Neurosci. 38 (6), 387–399. https://doi.org/10.1016/j.tins.2015.04.004.
Feldman, R., 2017. The neurobiology of human attachments. Trends Cogn. Sci. 21 (2), 80–99. https://doi.org/10.1016/j.tics.2016.11.007.
Fleming, A.S., Corter, C., Stallings, J., Steiner, M., 2002. Testosterone and prolactin are associated with emotional responses to infant cries in new fathers. Horm. Behav. 42 (4), 399–413. https://doi.org/10.1006/hbeh.2002.1840.
Fonagy, P., Target, M., 1997. Attachment and reflective function: their role in self-organization. Dev. Psychopathol. 9 (4), 679–700.
Gallagher, S., Raffone, A., Aglioti, S.M., 2024. The pattern theory of compassion. Trends Cogn. Sci. 28 (6), 504–516. https://doi.org/10.1016/j.tics.2024.04.005.
Gallistl, M., Hamann, J.E., Croy, I., Vrticka, P., Engert, V., 2025. Support or stress? How attachment and relationship dynamics associate with acute psychosocial stress in the presence of the romantic partner. Soc. Sci. Med., 118275
Gallistl, M., Kungl, M., Gabler, S., Kanske, P., Vrticka, P., Engert, V., 2024. Attachment and inter-individual differences in empathy, compassion, and theory of mind abilities. Attach. Hum. Dev. 26 (4), 350–365.
Geangu, E., Benga, O., Stahl, D., Striano, T., 2010. Contagious crying beyond the first days of life. Infant Behav. Dev. 33 (3), 279–288. https://doi.org/10.1016/j.infbeh.2010.03.004.
Gilbert, P., 2009. Introducing compassion-focused therapy. Adv. Psychiatr. Treat. 15 (3), 199–208.
Glasper, E., Kenkel, W., Bick, J., Rilling, J., 2019. More than just mothers: the neurobiological and neuroendocrine underpinnings of allomaternal caregiving. Front. Neuroendocrinol. 53, 100741.
Glocker, M.L., Langleben, D.D., Ruparel, K., Loughead, J.W., Gur, R.C., Sachser, N., 2009. Baby schema in infant faces induces cuteness perception and motivation for caretaking in adults. Ethology 115 (3), 257–263. https://doi.org/10.1111/j.1439-0310.2008.01603.x.
Gonzalez-Liencres, C., Shamay-Tsoory, S.G., Brune, M., 2013. Towards a neuroscience of empathy: ontogeny, phylogeny, brain mechanisms, context and psychopathology. Neurosci. Biobehav. Rev. 37 (8), 1537–1548. https://doi.org/10.1016/j.neubiorev.2013.05.001.
Gordon, I., Pratt, M., Bergunde, K., Zagoory-Sharon, O., Feldman, R., 2017. Testosterone, oxytocin, and the development of human parental care. Horm. Behav. 93, 184–192. https://doi.org/10.1016/j.yhbeh.2017.05.016.
Haas, B.W., Filkowski, M.M., Cochran, R.N., Denison, L., Ishak, A., Nishitani, S., Smith, A.K., 2016. Epigenetic modification of OXT and human sociability. Proc. Natl. Acad. Sci. USA 113 (27), E3816–3823. https://doi.org/10.1073/pnas.1602809113.
Hahn, A.C., Perrett, D.I., 2014. Neural and behavioral responses to attractiveness in adult and infant faces. Neurosci. Biobehav. Rev. 46 Pt 4, 591–603. https://doi.org/10.1016/j.neubiorev.2014.08.015.
Hahn-Holbrook, J., Holbrook, C., Haselton, M.G., 2011a. Parental precaution: neurobiological means and adaptive ends. Neurosci. Biobehav. Rev. 35 (4), 1052–1066. https://doi.org/10.1016/j.neubiorev.2010.09.015.
Hahn-Holbrook, J., Holt-Lunstad, J., Holbrook, C., Coyne, S.M., Lawson, E.T., 2011b. Maternal defense: breast feeding increases aggression by reducing stress. Psychol. Sci. 22 (10), 1288–1295.
Harlow, H., Dodsworth, R., Harlow, M., 1965. Total social isolation in monkeys. Proc. Natl. Acad. Sci. USA 54 (1), 90–97. ⟨http://www.ncbi.nlm.nih.gov/pubmed/4955132⟩.
Heany, S.J., Terburg, D., Stein, D.J., van Honk, J., Bos, P.A., 2020. Neural responses in the pain matrix when observing pain of others are unaffected by testosterone administration in women. Exp. Brain Res. 238, 751–759.
Hegoburu, C., Tang, Y., Niu, R., Ghosh, S., Triana Del Rio, R., de Araujo Salgado, I., Abatis, M., Alexandre Mota Caseiro, D., van den Burg, E.H., Grundschober, C., Stoop, R., 2024. Social buffering in rats reduces fear by oxytocin triggering sustained changes in central amygdala neuronal activity. Nat. Commun. 15 (1), 2081. https://doi.org/10.1038/s41467-024-45626-z.
Heinrichs, M., Baumgartner, T., Kirschbaum, C., Ehlert, U., 2003. Social support and oxytocin interact to suppress cortisol and subjective responses to psychosocial stress. Biol. Psychiatry 54 (12), 1389–1398. https://doi.org/10.1016/s0006-3223(03)00465-7.
Hermans, E.J., Henckens, M.J., Joels, M., Fernandez, G., 2014. Dynamic adaptation of large-scale brain networks in response to acute stressors. Trends Neurosci. 37 (6), 304–314. https://doi.org/10.1016/j.tins.2014.03.006.
Heyes, C.M., Frith, C.D., 2014. The cultural evolution of mind reading. Science 344 (6190), 1243091. https://doi.org/10.1126/science.1243091.
Hobby, L., Bird, A.L., Townsend, M.L., Barnes, J., 2023. Mind-mindedness and preschool children's behavioral difficulties: the moderating role of maternal parenting distress. Dev. Psychopathol. 35 (4), 1584–1596.
Hofer, M.K., Buckels, E.E., White, C.J., Beall, A.T., Schaller, M., 2017. Individual differences in activation of the parental care motivational system: an empirical distinction between protection and nurturance. Soc. Psychol. Personal. Sci. 1948550617728994.
van Honk, J., Schutter, D.J., Bos, P.A., Kruijt, A.W., Lentjes, E.G., Baron-Cohen, S., 2011. Testosterone administration impairs cognitive empathy in women depending on second-to-fourth digit ratio. Proc. Natl. Acad. Sci. USA 108 (8), 3448–3452. https://doi.org/10.1073/pnas.1011891108.
Horrell, N.D., Hickmott, P.W., Saltzman, W., 2019. Neural regulation of paternal behavior in mammals: sensory, neuroendocrine, and experiential influences on the paternal brain. Curr. Top. Behav. Neurosci. 43, 111–160. https://doi.org/10.1007/7854_2018_55.
Hostinar, C.E., Sullivan, R.M., Gunnar, M.R., 2014. Psychobiological mechanisms underlying the social buffering of the hypothalamic-pituitary-adrenocortical axis: a review of animal models and human studies across development. Psychol. Bull. 140 (1), 256–282. https://doi.org/10.1037/a0032671.
Hurlemann, R., Patin, A., Onur, O.A., Cohen, M.X., Baumgartner, T., Metzler, S., Dziobek, I., Gallinat, J., Wagner, M., Maier, W., Kendrick, K.M., 2010. Oxytocin enhances amygdala-dependent, socially reinforced learning and emotional empathy in humans. J. Neurosci. 30 (14), 4999–5007. https://doi.org/10.1523/JNEUROSCI.5538-09.2010.
Inagaki, T.K., 2018. Opioids and social connection. Curr. Dir. Psychol. Sci. 27 (2), 85–90.
Joosen, K.J., Mesman, J., Bakermans-Kranenburg, M.J., van IJzendoorn, M.H., 2013. Maternal overreactive sympathetic nervous system responses to repeated infant crying predicts risk for impulsive harsh discipline of infants. Child Maltreat. 18 (4), 252–263. https://doi.org/10.1177/1077559513494762.
Katznelson, H., 2014. Reflective functioning: a review. Clin. Psychol. Rev. 34 (2), 107–117. https://doi.org/10.1016/j.cpr.2013.12.003.
Kaźmierczak, M., Pawlicka, P., Anikiej-Wiczenbach, P., Łada-Maśko, A., van IJzendoorn, M.H., Bakermans-Kranenburg, M.J., 2024. Couples' empathy and sensitive responsiveness to a crying baby simulator. J. Soc. Pers. Relatsh., 02654075241240078
Keysers, C., 2011. The Empathic Brain: How the Discovery of Mirror Neurons Changes Our Understanding of Human Nature. Lulu.com. ⟨https://books.google.nl/books?id=Ag9cAwAAQBAJ⟩.
Keysers, C., Gazzola, V., 2006. Towards a unifying neural theory of social cognition. Prog. Brain Res. 156, 379–401. https://doi.org/10.1016/S0079-6123(06)56021-2.
Klampfl, S.M., Bosch, O.J., 2019. Mom doesn't care: when increased brain CRF system activity leads to maternal neglect in rodents. Front. Neuroendocrinol. 53, 100735.
Koops, W., 2016. Een beeld van een kind. De ontwikkeling en opvoeding van het kind in historisch perspectief. Boom, *Amsterdam*.
Kraaijenvanger, E.J., He, Y., Spencer, H., Smith, A.K., Bos, P.A., Boks, M.P.M., 2019. Epigenetic variability in the human oxytocin receptor (OXTR) gene: a possible pathway from early life experiences to psychopathologies. Neurosci. Biobehav. Rev. 96, 127–142. https://doi.org/10.1016/j.neubiorev.2018.11.016.
Kraaijenvanger, E.J., Hofman, D., Bos, P.A., 2017. A neuroendocrine account of facial mimicry and its dynamic modulation. Neurosci. Biobehav. Rev. 77, 98–106. https://doi.org/10.1016/j.neubiorev.2017.03.006.
Krol, K.M., Moulder, R.G., Lillard, T.S., Grossmann, T., Connelly, J.J., 2019. Epigenetic dynamics in infancy and the impact of maternal engagement. Sci. Adv. 5 (10), eaay0680. https://doi.org/10.1126/sciadv.aay0680.
Kumsta, R., Heinrichs, M., 2013. Oxytocin, stress and social behavior: neurogenetics of the human oxytocin system. Curr. Opin. Neurobiol. 23 (1), 11–16. https://doi.org/10.1016/j.conb.2012.09.004.
Lamm, C., Bukowski, H., Silani, G., 2016. From shared to distinct self-other representations in empathy: evidence from neurotypical function and socio-cognitive disorders. Philos. Trans. R. Soc. Lond. B Biol. Sci. 371 (1686), 20150083. https://doi.org/10.1098/rstb.2015.0083.
Landgraf, R., Neumann, I.D., 2004. Vasopressin and oxytocin release within the brain: a dynamic concept of multiple and variable modes of neuropeptide communication. Front. Neuroendocrinol. 25 (3-4), 150–176. ⟨http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=15589267⟩.
Langevin, R., Marshall, C., Kingsland, E., 2021. Intergenerational cycles of maltreatment: a scoping review of psychosocial risk and protective factors. Trauma Violence Abus. 22 (4), 672–688.
Law, K.F., Amormino, P., Marsh, A.A., O'Connor, B.B., 2024. Ethical reasoning versus empathic bias: a false dichotomy? Trends Cogn. Sci. 28 (1), 1–4.
Leppanen, J., Ng, K.W., Tchanturia, K., Treasure, J., 2017. Meta-analysis of the effects of intranasal oxytocin on interpretation and expression of emotions. Neurosci. Biobehav. Rev. 78, 125–144. https://doi.org/10.1016/j.neubiorev.2017.04.010.
Levy, J., Yirmiya, K., Goldstein, A., Feldman, R., 2019. The neural basis of empathy and empathic behavior in the context of chronic trauma. Front. Psychiatry 10, 562.
Liu, J.J.W., Ein, N., Peck, K., Huang, V., Pruessner, J.C., Vickers, K., 2017. Sex differences in salivary cortisol reactivity to the Trier social stress test (TSST): a meta-analysis. Psychoneuroendocrinology 82, 26–37. https://doi.org/10.1016/j.psyneuen.2017.04.007.

Luberti, F.R., Carre, J.M., 2024. Testosterone's role in modulating human behaviors relevant to mating and parenting. Front. Neuroendocr. 72, 101112. https://doi.org/10.1016/j.yfrne.2023.101112.
MacAdams, D.P., 2000. Attachment, intimacy, and generativity. Psychol. Inq. 11 (2), 117–120.
Mackenzie, M.J., Kotch, J.B., Lee, L.C., 2011. Toward a cumulative ecological risk model for the etiology of child maltreatment. Child Youth Serv. Rev. 33 (9), 1638–1647. https://doi.org/10.1016/j.childyouth.2011.04.018.
MacLean, P.D., 1985. Brain evolution relating to family, play, and the separation call. Arch. Gen. Psychiatry 42 (4), 405–417. https://doi.org/10.1001/archpsyc.1985.01790270095011.
Maibom, H.L., 2022. The Space Between: How Empathy Really Works. Oxford University Press.
Majdandžić, M., de Vente, W., Bögels, S.M., 2016. Challenging parenting behavior from infancy to toddlerhood: etiology, measurement, and differences between fathers and mothers. Infancy 21 (4), 423–452.
Malcorps, S., Vliegen, N., Rutherford, H.J., Luyten, P., 2025. Mentalizing under maternal stress (MUMS): using a baby simulator to investigate the impact of child-focused distress on maternal mentalizing and arousal. Dev. Psychopathol.
Mayseless, O., 2015. The Caring Motivation: An Integrated Theory. Oxford University Press.
McDonald, B., Kanske, P., 2023. Gender differences in empathy, compassion, and prosocial donations, but not theory of mind in a naturalistic social task. Sci. Rep. 13 (1), 20748. https://doi.org/10.1038/s41598-023-47747-9.
McEwen, B.S., 1998. Stress, adaptation, and disease. Allostasis and allostatic load. Ann. N. Y Acad. Sci. 840 (1), 33–44. https://doi.org/10.1111/j.1749-6632.1998.tb09546.x.
McEwen, B.S., 2017. Neurobiological and systemic effects of chronic stress. Chronic Stress 1, 2470547017692328.
McMahon, C.A., Bernier, A., 2017. Twenty years of research on parental mind-mindedness: empirical findings, theoretical and methodological challenges, and new directions. Dev. Rev. 46, 54–80.
Meaney, M., 2001. Maternal care, gene expression, and the transmission of individual differences in stress reactivity across generations. Annu. Rev. Neurosci. 24, 1161–1253.
Mehta, P.H., Prasad, S., 2015. The dual-hormone hypothesis: a brief review and future research agenda. Curr. Opin. Behav. Sci. 3, 163–168.
Meier, I.M., van Honk, J., Bos, P.A., Terburg, D., 2021. A mu-opioid feedback model of human social behavior. Neurosci. Biobehav. Rev. 121, 250–258. https://doi.org/10.1016/j.neubiorev.2020.12.013.
Meijer, W.M., van, I.M.H., Bakermans-Kranenburg, M.J., 2019. Challenging the challenge hypothesis on testosterone in fathers: limited meta-analytic support. Psychoneuroendocrinology 110, 104435. https://doi.org/10.1016/j.psyneuen.2019.104435.
Meins, E., Fernyhough, C., Wainwright, R., Clark-Carter, D., Das Gupta, M., Fradley, E., Tuckey, M., 2003. Pathways to understanding mind: construct validity and predictive validity of maternal mind-mindedness. Child Dev. 74 (4), 1194–1211. https://doi.org/10.1111/1467-8624.00601.
Mikolajczak, M., Gross, J.J., Roskam, I., 2019. Parental burnout: what is it, and why does it matter? Clin. Psychol. Sci. 7 (6), 1319–1329.
Mikolajczak, M., Roskam, I., 2018. A theoretical and clinical framework for parental burnout: the balance between risks and resources (BR2). Front. Psychol. 9, 886.
Mischkowski, D., Crocker, J., Way, B.M., 2016. From painkiller to empathy killer: acetaminophen (paracetamol) reduces empathy for pain. Soc. Cogn. Affect Neurosci. 11 (9), 1345–1353. https://doi.org/10.1093/scan/nsw057.
Montag, C., Gallinat, J., Heinz, A., 2008. Theodor Lipps and the concept of empathy: 1851-1914. Am. J. Psychiatry 165 (10), 1261. https://doi.org/10.1176/appi.ajp.2008.07081283.
Morris, A.S., Criss, M.M., Silk, J.S., Houltberg, B.J., 2017. The impact of parenting on emotion regulation during childhood and adolescence. Child Dev. Perspect. 11 (4), 233–238.
Nelson, E.E., Panksepp, J., 1998. Brain substrates of infant-mother attachment: contributions of opioids, oxytocin, and norepinephrine. Neurosci. Biobehav. Rev. 22 (3), 437–452. https://doi.org/10.1016/s0149-7634(97)00052-3.
Nitschke, J.P., Bartz, J.A., 2020. Lower digit ratio and higher endogenous testosterone are associated with lower empathic accuracy. Horm. Behav. 119, 104648. https://doi.org/10.1016/j.yhbeh.2019.104648.
Nitschke, J.P., Bartz, J.A., 2022. The association between acute stress & empathy: a systematic literature review. Neurosci. Biobehav. Rev., 105003
Nitschke, J.P., Forbes, P.A., Lamm, C., 2022. Does stress make us more—or less—prosocial? A systematic review and meta-analysis of the effects of acute stress on prosocial behaviours using economic games. Neurosci. Biobehav. Rev. 142, 104905.
Nitschke, J.P., Pruessner, J.C., Bartz, J.A., 2022. Stress and stress-induced glucocorticoids facilitate empathic accuracy in men but have no effects for women. Psychol. Sci. 33 (10), 1783–1794.
Nitschke, J.P., Sunahara, C.S., Carr, E.W., Winkielman, P., Pruessner, J.C., Bartz, J.A., 2020. Stressed connections: cortisol levels following acute psychosocial stress disrupt affiliative mimicry in humans. Proc. Biol. Sci. 287 (1927), 20192941. https://doi.org/10.1098/rspb.2019.2941.
Numan, M., 2006. Hypothalamic neural circuits regulating maternal responsiveness toward infants. Behav. Cogn. Neurosci. Rev. 5 (4), 163–190. https://doi.org/10.1177/1534582306288790.
Panksepp, J., 1998. Affective Neuroscience: The Foundations of Human and Animal Emotions. Oxford University Press.
Panksepp, J., Panksepp, J.B., 2013. Toward a cross-species understanding of empathy. Trends Neurosci. 36 (8), 489–496. https://doi.org/10.1016/j.tins.2013.04.009.
Panksepp, J., Siviy, S.M., Nomansell, L.A., 1985. In: Reite, M., Fields, T. (Eds.), Brain Opioids and Social Emotions. Academic Press, pp. 3–49.
Perkeybile, A.M., Carter, C.S., Wroblewski, K.L., Puglia, M.H., Kenkel, W.M., Lillard, T.S., Karaoli, T., Gregory, S.G., Mohammadi, N., Epstein, L., 2019. Early nurture epigenetically tunes the oxytocin receptor. Psychoneuroendocrinology 99, 128–136.
Pleck, J.H., 2012. Integrating father involvement in parenting research. Parenting 12 (2-3), 243–253.
Preston, S.D., 2013. The origins of altruism in offspring care. Psychol. Bull. 139 (6), 1305–1341. https://doi.org/10.1037/a0031755.
Preston, S.D., de Waal, F.B., 2002. Empathy: Its ultimate and proximate bases. discussion 20-71 Behav. Brain Sci. 25 (1), 1–20. https://doi.org/10.1017/s0140525x02000018.
Prochazkova, E., Kret, M.E., 2017. Connecting minds and sharing emotions through mimicry: a neurocognitive model of emotional contagion. Neurosci. Biobehav. Rev. 80, 99–114.
Procyshyn, T.L., Dupertuys, J., Bartz, J.A., 2024. Neuroimaging and behavioral evidence of sex-specific effects of oxytocin on human sociality. Trends Cogn. Sci. 28 (10), 948–961. https://doi.org/10.1016/j.tics.2024.06.010.
Puglia, M.H., Connelly, J.J., Morris, J.P., 2018. Epigenetic regulation of the oxytocin receptor is associated with neural response during selective social attention. Transl. Psychiatry 8 (1), 116. https://doi.org/10.1038/s41398-018-0159-x.
Repetti, R.L., Wood, J., 1997. Effects of daily stress at work on mothers' interactions with preschoolers. J. Fam. Psychol. 11 (1), 90.
Rijnders, R.J.P., Terburg, D., Bos, P.A., Kempes, M.M., van Honk, J., 2021. Unzipping empathy in psychopathy: empathy and facial affect processing in psychopaths. Neurosci. Biobehav. Rev. 131, 1116–1126. https://doi.org/10.1016/j.neubiorev.2021.10.020.
Rilling, J.K., 2013. The neural and hormonal bases of human parental care. Neuropsychologia 51 (4), 731–747. https://doi.org/10.1016/j.neuropsychologia.2012.12.017.
Rilling, J.K., Lee, M., Zhou, C., Gonzalez, A., Lindo, J., 2024. Grandmotherhood is associated with reduced OXTR DNA methylation. Psychoneuroendocrinology 168, 107122.
Rilling, J.K., Young, L.J., 2014. The biology of mammalian parenting and its effect on offspring social development. Science 345 (6198), 771–776. https://doi.org/10.1126/science.1252723.
Roellke, E., Raiss, M., King, S., Lytel-Sternberg, J., Zeifman, D.M., 2019. Infant crying levels elicit divergent testosterone response in men. Parenting 19 (1-2), 39–55.
Roepke, S.K., Mausbach, B.T., Patterson, T.L., Von Känel, R., Ancoli-Israel, S., Harmell, A. L., Dimsdale, J.E., Aschbacher, K., Mills, P.J., Ziegler, M.G., 2011. Effects of Alzheimer caregiving on allostatic load. J. Health Psychol. 16 (1), 58–69.
Roskam, I., Aguiar, J., Akgun, E., Arena, A.F., Arikan, G., Aunola, K., Besson, E., Beyers, W., Boujut, E., Brianda, M.E., 2023. Three reasons why parental burnout is more prevalent in individualistic countries: a mediation study in 36 countries. Soc. Psychiatry Psychiatr. Epidemiol. 1–14.
Royle, N.J., Smiseth, P.T., Kölliker, M., 2012. The Evolution of Parental Care. Oxford University Press.
Saint Aubin, E. d, MacAdams, D.P., 2004. The Generative Society: Caring for Future Generations. American Psychological Association.
Salo, V.C., Schunck, S.J., Humphreys, K.L., 2020. Depressive symptoms in parents are associated with reduced empathy toward their young children. PLOS One 15 (3), e0230636.
Sanson, A., Bosch, O.J., 2022. Dysfunctions of brain oxytocin signaling: implications for poor mothering. Neuropharmacology 211, 109049.
Sanson, A., Demarchi, L., Bosch, O.J., 2024. Neuroendocrine basis of impaired mothering in rodents. Neuroendocrinology of Behavior and Emotions: Environmental and Social Factors Affecting Behavior. Springer, pp. 83–108.
Sapolsky, R.M., 2004. Why Zebras Don't Get Ulcers, 3rd ed.). Owl Books.
Sapolsky, R.M., 2015. Stress and the brain: individual variability and the inverted-U. Nat. Neurosci. 18 (10), 1344–1346. https://doi.org/10.1038/nn.4109.
Schaller, M., 2018. The parental care motivational system and why it matters (for everyone). Curr. Dir. Psychol. Sci. 27 (5), 295–301.
Schüler, J., Zimanyi, Z., Radtke, V., Stoffel, M., Ditzen, B., 2025. The role of" Social" in the TSST: Social support and social motives partly moderate psychobiological stress responses in addition to biological sex. Psychoneuroendocrinology 177, 107440.
Seibt, B., Muhlberger, A., Likowski, K.U., Weyers, P., 2015. Facial mimicry in its social setting. Front. Psychol. 6, 1122. https://doi.org/10.3389/fpsyg.2015.01122.
Shalev, I., Eran, A., Uzefovsky, F., 2023. Fluctuations and individual differences in empathy interact with stress to predict mental health, parenting, and relationship outcomes. Front. Psychol. 14, 1237278. https://doi.org/10.3389/fpsyg.2023.1237278.
Shamay-Tsoory, S.G., Abu-Akel, A., Palgi, S., Sulieman, R., Fischer-Shofty, M., Levkovitz, Y., Decety, J., 2013. Giving peace a chance: oxytocin increases empathy to pain in the context of the Israeli-Palestinian conflict. Psychoneuroendocrinology 38 (12), 3139–3144. https://doi.org/10.1016/j.psyneuen.2013.09.015.
Shaver, P., Mikulincer, M., Gross, J., Stern, J., Cassidy, J., 2016. A lifespan perspective on attachment and care for others: Empathy, altruism, and prosocial behavior. In (pp. 878-916)..
Shoshani, A., 2024. The roots of compassion in early childhood: relationships between theory of mind and attachment representations with empathic concern and prosocial behavior. J. Exp. Child Psychol. 242, 105880.
Singer, T., 2006. The neuronal basis and ontogeny of empathy and mind reading: review of literature and implications for future research. Neurosci. Biobehav. Rev. 30 (6), 855–863. https://doi.org/10.1016/j.neubiorev.2006.06.011.

Slaughter, V., 2015. Theory of mind in infants and young children: a review. Aust. Psychol. 50 (3), 169–172.
Spencer, H., Lesemann, F.H.P., Buisman, R.S., Kraaijenvanger, E.J., Branje, S., Boks, M. P., Bos, P.A., 2024. Facing infant cuteness: how nurturing care motivation and oxytocin system gene methylation are associated with responses to baby schema features. Horm. Behav. 164, 105595.
Spencer, H., Lesemann, F.H.P., Kraaijenvanger, E.J., Overbeek, G., Montoya, E.R., Branje, S., Boks, M.P., Bos, P.A., 2022. Oxytocin system gene methylation is associated with empathic responses towards children. Psychoneuroendocrinology 137, 105629.
Storey, A.E., Walsh, C.J., Quinton, R.L., Wynne-Edwards, K.E., 2000. Hormonal correlates of paternal responsiveness in new and expectant fathers. Evol. Hum. Behav. 21 (2), 79–95. https://doi.org/10.1016/s1090-5138(99)00042-2.
Sunahara, C.S., Wilson, S.J., Rosenfield, D., Alvi, T., Szeto, A., Mendez, A.J., Tabak, B.A., 2022. Oxytocin reactivity to a lab-based stressor predicts support seeking after stress in daily life: implications for the Tend-and-Befriend theory. Psychoneuroendocrinology 145, 105897. https://doi.org/10.1016/j.psyneuen.2022.105897.
Swain, J.E., Konrath, S., Brown, S.L., Finegood, E.D., Akce, L.B., Dayton, C.J., Ho, S.S., 2012. Parenting and beyond: common neurocircuits underlying parental and altruistic caregiving. Parenting 12 (2-3), 115–123.
Taylor, S.E., 2006. Tend and befriend: biobehavioral bases of affiliation under stress. Curr. Dir. Psychol. Sci. 15 (6), 273–277.
Taylor, S.E., Klein, L.C., Lewis, B.P., Gruenewald, T.L., Gurung, R.A., Updegraff, J.A., 2000. Biobehavioral responses to stress in females: tend-and-befriend, not fight-or-flight. Psychol. Rev. 107 (3), 411–429. https://doi.org/10.1037/0033-295x.107.3.411.
Ter Horst, G.J., Wichmann, R., Gerrits, M., Westenbroek, C., Lin, Y., 2009. Sex differences in stress responses: focus on ovarian hormones. Physiol. Behav. 97 (2), 239–249. https://doi.org/10.1016/j.physbeh.2009.02.036.
Tolstoy, L., 2016. Anna karenina. Penguin Books.
Tomova, L., von Dawans, B., Heinrichs, M., Silani, G., Lamm, C., 2014. Is stress affecting our ability to tune into others? Evidence for gender differences in the effects of stress on self-other distinction. Psychoneuroendocrinology 43, 95–104.
Tomova, L., Majdandžić, J., Hummer, A., Windischberger, C., Heinrichs, M., Lamm, C., 2017. Increased neural responses to empathy for pain might explain how acute stress increases prosociality. Soc. Cogn. Affect. Neurosci. 12 (3), 401–408.
Tronick, E., Mueller, I., DiCorcia, J., Hunter, R., Snidman, N., 2021. A caretaker acute stress paradigm: Effects on behavior and physiology of caretaker and infant. Dev. Psychobiol. 63 (2), 237–246.
Trzeciak, S., Roberts, B.W., Mazzarelli, A.J., 2017. Compassionomics: hypothesis and experimental approach. Med. Hypotheses 107, 92–97. https://doi.org/10.1016/j.mehy.2017.08.015.
Varricchio, D.J., Moore, J.R., Erickson, G.M., Norell, M.A., Jackson, F.D., Borkowski, J.J., 2008. Avian paternal care had dinosaur origin. science 322 (5909), 1826–1828.
Versey, H.S., Kakar, S.A., John-Vanderpool, S.D., Sanni, M.O., Willems, P.S., 2020. Correlates of affective empathy, perspective taking, and generativity among a sample of adults. J. Community Psychol. 48 (8), 2474–2490.
Vieira, J., Olsson, A., 2023. The convergence between defence and care in mammals..
de Waal, F.B., 2008. Putting the altruism back into altruism: the evolution of empathy. Annu Rev. Psychol. 59, 279–300. https://doi.org/10.1146/annurev.psych.59.103006.093625.
de Waal, F.B.M., 2010. The Age of Empathy: Nature's Lessons for a Kinder Society. Crown Publishing Group. ⟨http://books.google.nl/books?id=bc1Kye_c5X8C⟩.
de Waal, F.B.M., Preston, S.D., 2017. Mammalian empathy: behavioural manifestations and neural basis. Nat. Rev. Neurosci. 18 (8), 498–509. https://doi.org/10.1038/nrn.2017.72.
Wager, T.D., Davidson, M.L., Hughes, B.L., Lindquist, M.A., Ochsner, K.N., 2008. Prefrontal-subcortical pathways mediating successful emotion regulation. Neuron 59 (6), 1037–1050. https://doi.org/10.1016/j.neuron.2008.09.006.
Wang, H., Zhen, Z., Zhu, R., Yu, B., Qin, S., Liu, C., 2022. Help or punishment: acute stress moderates basal testosterone's association with prosocial behavior. Stress 25 (1), 179–188. https://doi.org/10.1080/10253890.2022.2054696.
Waters, S.F., West, T.V., Mendes, W.B., 2014. Stress contagion: physiological covariation between mothers and infants. Psychol. Sci. 25 (4), 934–942.
Weisz, E., Cikara, M., 2021. Strategic regulation of empathy. Trends Cogn. Sci. 25 (3), 213–227. https://doi.org/10.1016/j.tics.2020.12.002.
Wingenfeld, K., Kuehl, L.K., Janke, K., Hinkelmann, K., Dziobek, I., Fleischer, J., Otte, C., Roepke, S., 2014. Enhanced emotional empathy after mineralocorticoid receptor stimulation in women with borderline personality disorder and healthy women. Neuropsychopharmacology 39 (8), 1799–1804. https://doi.org/10.1038/npp.2014.36.
Witteman, J., Van, I.M.H., Rilling, J.K., Bos, P.A., Schiller, N.O., Bakermans-Kranenburg, M.J., 2019. Towards a neural model of infant cry perception. Neurosci. Biobehav. Rev. 99, 23–32. https://doi.org/10.1016/j.neubiorev.2019.01.026.
Wolf, O.T., Schulte, J.M., Drimalla, H., Hamacher-Dang, T.C., Knoch, D., Dziobek, I., 2015. Enhanced emotional empathy after psychosocial stress in young healthy men. Stress 18 (6), 631–637. https://doi.org/10.3109/10253890.2015.1078787.
Zimmer-Gembeck, M.J., Rudolph, J., Kerin, J., Bohadana-Brown, G., 2021. Parent emotional regulation: a meta-analytic review of its association with parenting and child adjustment. Int. J. Behav. Dev. 46 (1), 63–82. https://doi.org/10.1177/01650254211051086.