

# Evolutionary-adaptive and nonadaptive causes of infant attack/desertion in mammals: Toward a systematic classification of child maltreatment

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Behaviors comparable to human child maltreatment are observed widely among mammals, in which parental care is mandatory for offspring survival. This article first reviews the recent findings on the neurobiological mechanisms for nurturing (infant caregiving) behaviors in mammals. Then the major causes of attack/desertion toward infants (conspecific young) in nonhuman mammals are classified into five categories. Three of the categories are 'adaptive' in terms of reproductive fitness: (i) attack/desertion toward non-offspring; (ii) attack/desertion toward biological offspring with low reproductive value; and (iii) attack/desertion toward biological offspring under unfavorable environments. The other two are nonadaptive failures of nurturing motivation, induced by: (iv) caregivers' inexperience; or (v) dysfunction in caregivers' brain mechanisms required for nurturing behavior. The proposed framework covering both adaptive and

nonadaptive factors comprehensively classifies the varieties of mammalian infant maltreatment cases and will support the future development of tailored preventive measures for each human case. Also included are remarks that are relevant to interpretation of available animal data to humans: (1) any kind of child abuse/neglect is not justified in modern human societies, even if it is widely observed and regarded as adaptive in nonhuman animals from the viewpoint of evolutionary biology; (2) group-level characteristics cannot be generalized to individuals; and (3) risk factors are neither deterministic nor irreversible.

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News reports of lethal child maltreatment cases often evoke upsetting feelings in listeners and readers and sometimes lead to anger and blame toward the perpetrators, who are mostly parents. Why on earth would some parents abuse their children? Provided that extensive parental care is a prerequisite for infant survival in all mammals, is not the parental motivation hardwired in the mammalian brain as an instinct, often called 'maternal love'? This often-voiced question about human child maltreatment may find some answers in animal studies of parental care. Actually, loss of parental motivation, or even proactive attack to eliminate conspecific young, is quite pervasive in nonhuman mammals.

To better understand the major causes of human child maltreatment from the neurobiological perspective, this article summarizes the basic features of mammalian parental behaviors and recent findings on the neural basis of mammalian parental behavior; in addition, it classifies the major causes of loss of parental motivation in nonhuman mammals.

There are excellent reviews on the neurobiological basis of parental care (e.g., Numan and Insel<sup>1</sup> and Bridges<sup>2</sup>; but see also Numan<sup>3</sup>) but they do not deal, in particular, with the issue in the context of child maltreatment. In addition, there are many wonderful reviews detailing the adaptive causes of child abuse/neglect in humans and animals (e.g., Hrdy,<sup>4, 5</sup> Daly and Wilson,<sup>6</sup> Clutton-Brock,<sup>7</sup> Wilson and Daly,<sup>8</sup> and Maestripieri and Carroll<sup>9</sup>), but these do not include nonadaptive causes derived from psychopathological dysfunctions relevant to child maltreatment, even though clinical medicine has discussed these widely (e.g., Helfer and Kempe<sup>10</sup> and Arnold<sup>11</sup>). Presenting both adaptive and nonadaptive causes in one framework is of value in the context of child

maltreatment, to better illustrate this entire topic and to support future comparative analyses in humans.

Also, it should be pointed out in the beginning that no abuse/neglect of a human child can be justified in modern society, even if its animal counterpart is pervasive and classified as 'adaptive' from the viewpoint of evolutionary biology. Animal evolution and modern society are selected for distinct goals, reproductive fitness (i.e., reproductive success, usually measured as the number of offspring produced by an individual that survive to reproductive age), and human rights, respectively, and thus create an (at least) apparent discrepancy regarding what kinds of behaviors are adaptive in these systems. It has long been debated as a 'nature or culture' or 'biological versus social' divide in sociobiology and anthropology (for review, refer to Segerstrale<sup>12</sup>), and going into the details of this debate is beyond the scope of this manuscript. Instead, here we introduce the statement by Yukimaru Sugiyama, a pioneer in the ethological study on infanticide:

'Ethological studies have been identifying the evolutionary origin of human behaviors in nonhuman animals, and sometimes refer to it as if it were an 'approval' of such behaviors. However, I would like to emphasize here that we should discriminate which to inherit and which to terminate among these animal heritages, to solve problems in human societies on the basis of precise scientific understanding.'<sup>13</sup>

The ultimate goal of these kinds of comparative studies is science-informed prevention and intervention of child maltreatment.

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## Nurturing Behaviors Toward Infants in Mammals

To address the question, ‘Why do some parents abuse or neglect their children?’ an opposite question must be first understood: ‘Why don’t parents neglect or abuse their children in most cases?’ This is because one can understand abnormalities (atypical, rare cases) only after one knows normality (typical, most cases). Therefore, first briefly consider the offspring care that is conserved in mammals.

Mammalian newborns are born immature and depend on maternal milk for nutrition. Nursing (provision of maternal milk) is the hallmark of mammals. In addition to nursing, mammalian post-partum mothers provide extensive care for offspring, such as grooming, helping movement from one location to another (carrying), and protection from environmental hazards.<sup>1, 2, 14–16</sup> Mothers may also perform non-infant-directed maternal behaviors, such as nest-building and aggression against intruders.<sup>17–19</sup> The intensity of maternal care varies largely among species; for example, rabbits have adopted a minimal mothering system, restricted to nest-building during late pregnancy, giving birth in the nest, and 3–5 min of daily contact with the litter for nursing during 30 days of lactation.<sup>20</sup> In contrast, orangutans display continuous maternal care and have the longest nursing period among mammals of 6–8 years.<sup>21</sup> Infants are completely dependent on the mother for transportation and food during the first 2 years and co-sleep in the maternal nest for at least 3 years. Even after the next sibling is born (average interbirth interval = 7.6 years), the young may remain close to the mother, traveling with her, eating with her, and resting in the same tree, until the offspring is about 10 years old. Regardless of such quantitative differences in parental care when comparing primates and lagomorphs, the core components of maternal care depend on a neuroanatomical structure in the basal forebrain that is also found in rodents, as described in the next section.

In about 10% of mammalian species, and 59% of monogamous mammals, fathers directly provide care for their offspring and/or provide food via the mother.<sup>14, 22</sup> Moreover, there are several species among primates (marmosets, tamarins), rodents (beavers, naked mole rats, laboratory mice), and carnivores (red foxes, mongooses) where nonparental individuals, such as older siblings, provide care to young. All of these behaviors are collectively called ‘nurturing (infant caregiving) behaviors’ here because, as described in the next section, these nurturing behaviors depend on the same brain structure, the medial preoptic area (MPOA), regardless of the biological relation of the caregiver to the infant (i.e., mother, father, siblings, or unrelated older conspecifics).<sup>23</sup> Non-parental nurturing behavior (alloparental care) is also observed in humans and, therefore, is of particular interest.

## Brain Mechanisms for Nurturing Behavior

The neural mechanisms of maternal behavior have been best studied in rodents, especially in laboratory rats and mice. It has been shown that the MPOA (Fig. 1; see also Fig. 2) is the critical hub for nurturing behaviors, demonstrated first in maternal rats<sup>25, 26</sup> and then in male laboratory rats,<sup>27</sup> female hamsters,<sup>28</sup> and both sexes of the biparental California mouse (*Peromyscus californicus*),<sup>29</sup> as well as in rabbits<sup>30</sup> and post-partum sheep.<sup>31</sup> Using laboratory mice, the authors’ research group has identified a small brain region anterior to the hypothalamus, the central part of medial preoptic area (cMPOA; Fig. 1b), and has found that the cMPOA has a central importance for infant caregiving behavior in laboratory mice.<sup>24, 32</sup> After the selective inhibition of cMPOA, fathers, allomaternal virgin females, and even post-partum mothers that have previously shown the highest nurturing motivation stop caregiving and become infanticidal. The cMPOA dysfunction does not affect general health, female mating behaviors, or normal delivery, which indicates that the cMPOA is indispensable specifically for infant caregiving behaviors.

The preoptic area and the adjacent hypothalamus are structurally conserved in mammalian species. Indeed, we have observed that MPOA inhibition also inhibits infant caregiving in the common

marmoset (*Callithrix jacchus*), a new-world primate species.<sup>33</sup> Therefore, these findings obtained in rodents may contribute to understanding the basics of human nurturing behavior and infant-directed aggression in the future.

Functional suppression of the cerebral cortex, especially in the anterior cingulate (ACC) or medial prefrontal (PFC) cortices, may cause varying degrees of nurturing deficits, when the dysfunction is placed in the adult.<sup>34–36</sup> In contrast, dysfunctions of the cerebral cortex placed in infancy tend not to severely disturb nurturing in later life,<sup>37</sup> as is the case for other cortical functions.<sup>38</sup> Moreover, the role of certain regions of the cerebral cortex in nurturing behavior (e.g., the ACC) may be more involved in the cognitive control of nurturing than in motivation, because the subject animals may still contact and carry the offspring, but do so in an erratic manner.<sup>34, 39, 40</sup> Human studies suggest that damage to the frontal cortex, especially the PFC (Fig. 1a), causes social cognition deficits as part of induced executive dysfunction.<sup>41, 42</sup> The frontal cortex is one of the major targets of acquired brain injuries, such as from a stroke, traffic accident, or chronic traumatic encephalopathy (‘punch-drunk’ syndrome seen in boxers and football players), and may increase the risk of mood alterations, apathy, impulsivity, or deficits in social problem-solving. These conditions could secondarily increase the risk of offspring attack/desertion.

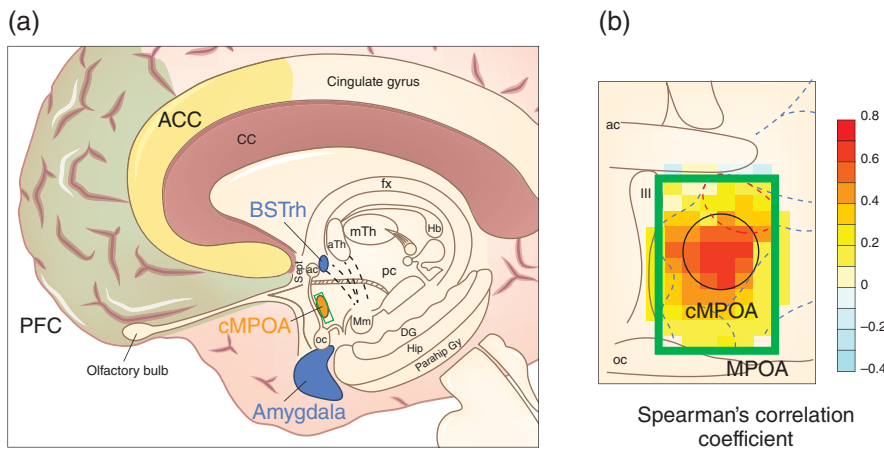
In rats and mice, inhibition of the septum or ventral hippocampus leads to impaired parenting skills, especially spatiotemporal control of retrieval behaviors (see Fig. 2), while retaining parental motivation per se mostly intact.<sup>37, 40, 43, 44</sup>

The amygdala, or amygdaloid complex, is involved in learning about environmental hazards, and in the perception of negative emotions (Figs 1a,2).<sup>45, 46</sup> The amygdala has also been associated with appetitive motivational processes.<sup>47</sup> In rodents, lesions of the central/medial amygdala, or dissection of the stria terminalis (the major output from the amygdaloid complex) do not inhibit and even facilitate nurturing by reducing initial pup avoidance in rats.<sup>40, 48, 49</sup> It should be acknowledged, however, that the amygdalar function may be important for nurturing performance in more naturalistic conditions, such as in stressful and/or complex environmental conditions (see Numan<sup>3</sup> and Kuroda *et al.*<sup>23</sup> for review and Lee and Brown,<sup>50</sup> Numan *et al.*,<sup>51</sup> and Numan<sup>52</sup> for the involvement of the basolateral/basomedial amygdala). In humans as well, bilateral damage of the amygdaloid complex caused by Urbach–Wiethe disease does not grossly inhibit the patient’s role as a mother, although in this situation, reported defective social decision-making related to negative facial expressions may hamper actual social functioning<sup>53</sup> (for other cases of amygdala–hippocampal damage in humans, see also Feinstein<sup>54</sup> and Feinstein *et al.*<sup>55</sup>). Of additional note, hyperactivity of the amygdala primes defensive aggression and is often seen in violent offenders, while hypoactivity of the amygdala is connected to a lack of empathy about the distress of others, leading to proactive aggression.<sup>56</sup>

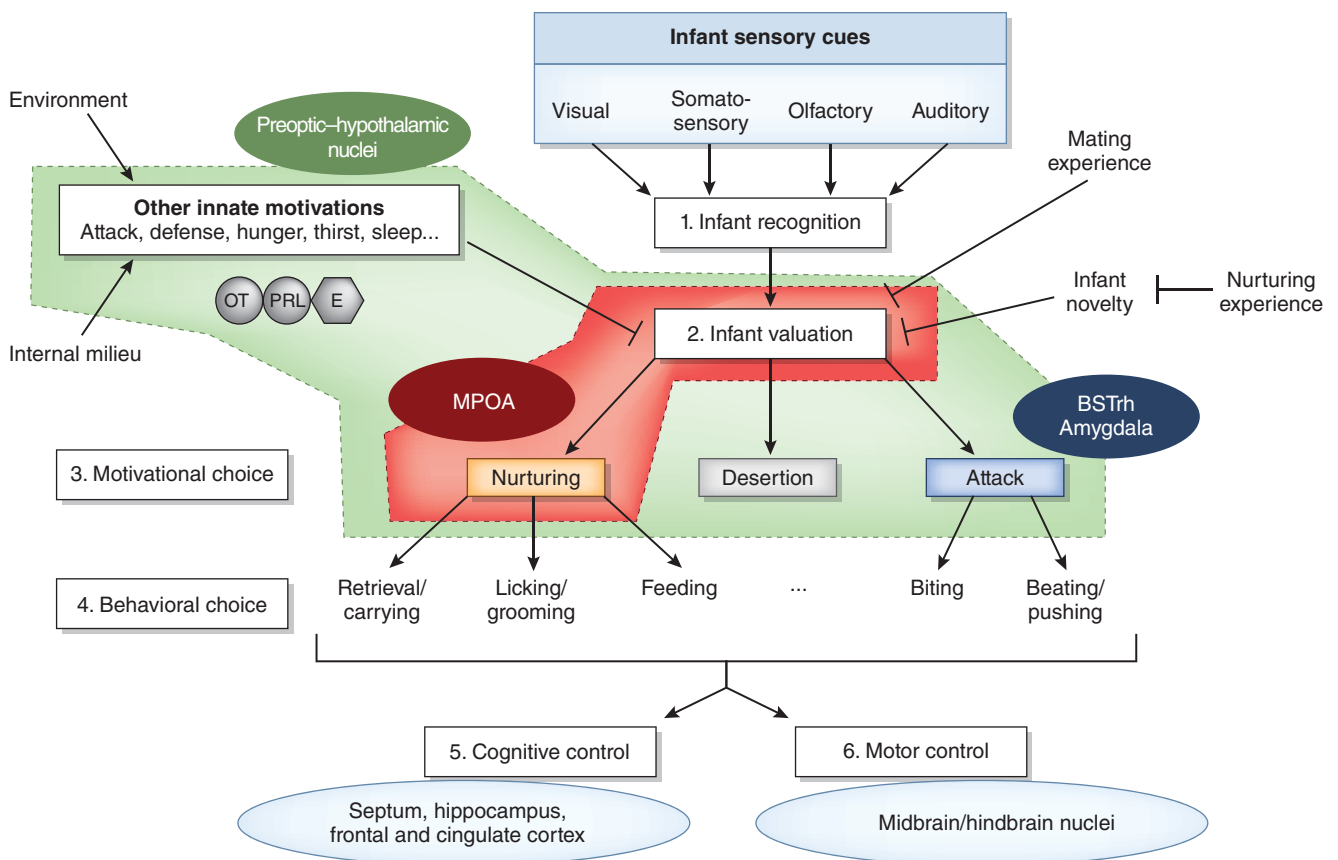
The anterior hypothalamic nucleus and ventromedial hypothalamic nucleus tend to inhibit nurturing behavior, and inhibition of these areas in female rats reduces the latency for initial pup retrieval.<sup>57</sup> These nuclei are known to mediate feeding and defensive behaviors, which are not generally compatible with parenting.

The ventral tegmental area (VTA), nucleus accumbens, and ventral pallidum are also implicated in the execution of maternal behavior, along with other motivated behaviors.<sup>3</sup> The importance of projections from the MPOA to the VTA for nurturing behavior has been repeatedly demonstrated.<sup>58–60</sup> Functional suppression of the ventral pallidum, but not the nucleus accumbens, inhibits nurturing behavior.<sup>50, 61</sup> And dopamine D1 receptor activation in the nucleus accumbens stimulates the onset of maternal pup retrieval, suggesting the dopamine action from the VTA to the nucleus accumbens disinhibits the ventral pallidum for stimulation of nurturing behavior onset.<sup>3, 62</sup>

It was long postulated, and now has been proven, that the preoptic–hypothalamic area contains specific anatomical regions as hubs of distinct instinctive motivations, such as hunger, thirst, sleep,



**Fig.1** The central part of the medial preoptic area (cMPOA) and the other brain regions relevant for nurturing behaviors. (a) Location of the medial preoptic area (MPOA) and other relevant regions in a human brain (parasagittal section). The green rectangle corresponds to the MPOA, shown as a frontal view in (b). ac, anterior commissure; ACC, anterior cingulate cortex; aTh, anterior thalamus; BSTrh, rhomboid part of the bed nuclei of the stria terminalis; cc, corpus callosum; DG, dentate gyrus; fx, fornix; Hb, habenula; Hip, hippocampus; Mm, mammillary body; mTh, medial thalamus; oc, optic chiasm; parahip Gy, parahippocampal gyrus; pc, posterior commissure; PFC, prefrontal cortex; Sept, septum. (b) Location of the cMPOA within the MPOA in a mouse brain (coronal section). The cMPOA is determined by the statistical correlation between the neuronal loss created by neurotoxic lesions and parental behavior deficits.<sup>24</sup> III, third ventricle.



**Fig.2** Working hypothesis for information flow in the caregiver's brain in response to an infant. 1. *Infant recognition through sensory cues*: The sensory stimuli (olfactory, auditory, visual, and somatosensory) from an infant should be consolidated to produce 'infant recognition'; that is, 'this is a conspecific young animal but not another object or food.' 2. *Infant valuation*: Based on previous experiences and external/internal milieu, the reproductive value of a given infant is estimated. The green area shows the processing that occurs mainly in the preoptic-hypothalamic area, and the red area represents processing involving the medial preoptic area (MPOA). 3. *Motivational choice*: Based on an infant's reproductive value, the motivation to nurture, desert, or attack the infant emerges. The rhomboid part of the bed nuclei of the stria terminalis (BSTrh) and the amygdala are implicated in this attack motivation. 4. *Behavioral choice*: To actuate the chosen motivation, the animal further narrows down which behavior is most effective in the current situation. For nurturing purposes, a maternal mouse generally starts to set the nest in place and then retrieves all the pups into the nest, licks them, and then nurses them. In a special example case, if the pup provided is caged in a mesh box, both infanticidal and nurturing mice begin biting the box vigorously, apparently to remove the pup from the box. 5. *Cognitive control*: To pursue the chosen behavior, the animal needs to plan how to do it. For pup retrieval behavior as an example, spatial cognition to associate the nest location with each pup's location is required. Such cognitive control is inhibited by hippocampal or cingulate cortex lesions. 6. *Motor control*: Motor or postural coordination is required to fine-tune each behavior to the current situation (e.g., size of the infant) E, estrogen; OT, oxytocin; PRL, prolactin.

mating, attack, defense, and nurturing (Fig. 2).<sup>63–65</sup> One animal cannot fulfill these many motivations simultaneously, so these brain hubs in the preoptic-hypothalamic nuclei compete with each other. When

one hub wins against the others, it suppresses other hubs and takes control of the entire body to fulfill its drive for a while. Such competitive connections between different hubs in the preoptic-hypothalamic

area can be postulated as a parsimonious mechanism for the animal's choice of one behavior at a time, designated as 'the great parliament of instincts.'<sup>66</sup> Figure 2 illustrates a working hypothesis describing the information flow from pup exposure to nurturing/desertion/attack, with the relevant brain areas shown as previously discussed. For convenience, this information processing is divided into six steps: (1) infant recognition through sensory cues; (2) infant valuation; (3) motivational choice; (4) behavioral choice; (5) cognitive control; and (6) motor control. Disruption of any of these steps may cause a deficit in nurturing behavior outcome. For more details, refer to the legend for Figure 2 and to the previous review.<sup>23</sup>

### Endocrine and Neurochemical Factors Involved in Nurturing Behavior

Endocrine factors involved in female reproduction are required for the rapid onset of post-partum maternal behavior; classic studies in rats showed that peripartum induction of maternal motivation depends on circulating female reproductive hormones.<sup>67–70</sup> In contrast, nurturing behaviors in male and female non-lactating rats can occur after such rats are continuously exposed to pups for about 7 days; and this pup-stimulated nurturing behavior is not greatly inhibited by hypophysectomy or gonadectomy.<sup>71</sup> These results indicate that there is a basal level of nurturing responsiveness that is independent of hormonal stimulation.

In mice, possibly because of their high basal level of nurturing motivation in nonmaternal females, the role of estrogen appears to be modulatory rather than essential.<sup>72–74</sup> For example, a study by Ribeiro and colleagues demonstrated that siRNA-based *ESR1* knock-down in the MPOA did not increase the pup mortality rate, despite the decrease of nursing duration during the assays; thus, all stimulus pups used for postnatal-day-4–7 pup-retrieval assays were the mothers' own pups (Professor Ana Ribeiro, pers. comm., 2020). It should also be noted that remarkable recent studies demonstrated a critical role of MPOA neurons expressing estrogen receptor alpha on pup retrieval, but did not assess the role of estrogen receptor *per se*.<sup>60, 75</sup>

While a loss-of-function mutation (knockout [KO]) in the prolactin gene resulted in normal maternal behavior, a prolactin receptor gene KO study reported inhibited pup retrieval in mice.<sup>76</sup> Then, a recent study using conditional prolactin receptor KO demonstrated disturbed maternal nursing behavior, but rather normal pup retrieval<sup>77</sup> (see also Kuroda *et al.*<sup>23</sup>).

Similarly, while three conventional oxytocin gene KO lines consistently showed intact maternal behavior,<sup>78–80</sup> an oxytocin receptor gene KO has been reported to delay pup retrieval in mice.<sup>81</sup> Then, a recent study using a conditional oxytocin receptor KO, which depletes oxytocin receptor from the forebrain, reported minimal disturbance of nurturing behavior.<sup>82</sup> The best conclusion at this moment is that oxytocin can facilitate the onset of nurturing behavior, or nurturing behavior under stressful conditions (see Yoshihara *et al.*<sup>83</sup> for more details). There are certainly both hormonal and nonhormonal, experience-dependent mechanisms that induce nurturing motivation, as indicated earlier.<sup>71</sup>

### Genetic Mechanism of Nurturing Behavior

Because earlier articles from the authors of this article have extensively reviewed the genetic contribution to parental behavior,<sup>23, 83</sup> here we briefly mention this issue. Starting from the *FosB* gene first reported in 1996,<sup>84</sup> there are many KO mouse lines exhibiting nurturing behavior defects (for review, see Kuroda *et al.*<sup>23</sup>). Accumulating evidence suggests, however, that most of these mutant mice display nurturing defects secondary to other phenotypes, such as general health decline, insufficient milk production/ejection, or anosmia (mouse parental behavior is highly dependent on olfaction; see Kuroda and Tsuneoka<sup>85</sup>). For example, the initial *FosB* KO mice were reported to be defective specifically in nurturing behavior.<sup>84</sup> The authors of this review successfully reproduced the nurturing behavior

deficits in *FosB* KO mice, including in pup retrieval, nest-building, and placentophagia. Also found, however, were broader abnormalities in the brain, namely, the forebrain-wide upregulation of genes expressed in astroglial cells, which suggest general neuropathological conditions, as well as altered emotional behaviors in *FosB* KO mice.<sup>86, 87</sup> It is now clear that mammalian nurturing behavior cannot be attributed to a single gene, but depends on the neural network, which is centered by the MPOA but regulated from the numerous revisions of the central nervous system.

### Behaviors in Nonhuman Mammals Comparable to Human Child Maltreatment

'Child maltreatment' in humans refers to 'the physical and emotional mistreatment, sexual abuse, neglect and negligent treatment of children, as well as to their commercial or other exploitation.'<sup>88</sup>

In nonhuman mammals, there are behaviors comparable to physical abuse and neglect, in the form of 'physical attack on conspecific young' and 'desertion or withdrawal of parental care,' respectively.<sup>9, 89, 90</sup> This review deals with these two types of maltreatment hereafter. The other two, emotional and sexual abuse, are not dealt with in this article.

### Distinction Between Attack and Desertion in Nonhuman Mammals

The differences between physical abuse (attack) and neglect (desertion) are of significant importance (e.g., see Hrdy<sup>5</sup> and Humphreys and Zeanah<sup>91</sup>). Maestripieri and colleagues pointed out that physical abuse and neglect may occur simultaneously in humans but seldom occur simultaneously in their seminatural colony of macaque monkeys.<sup>92</sup> In other mammalian species, however, there are reported cases where these two types of maltreatment occur concomitantly or one after another, such as in post-partum rabbits in both laboratory and field studies, *Peromyscus californicus*,<sup>93</sup> and in laboratory mice.<sup>85</sup> In these species, mothers often consume the pups' bodies as a food source (cannibalism) when they stop nursing them and/or when the pups get weakened, complicating a distinction between desertion and attack. It is also noted that MPOA lesions cause simple nonretrieval in rats, while in mice, they cause active pup biting,<sup>24, 32</sup> suggesting that the choice between pup desertion and attack can vary among species, especially with nonadaptive causes. Therefore, whenever possible, this review specifies which type of maltreatment is dominant in a certain context, and when both may occur, this is designated as attack/desertion.

### 'Adaptive' Versus 'Nonadaptive' Causes of Infant Maltreatment

Parental investment, including parental care, is one of the most important parameters of reproductive success of animals and has been studied extensively in evolutionary biology.<sup>94, 95</sup> In particular, the 'parent-offspring conflict' theory<sup>96, 97</sup> predicts premature termination of parental care whenever the costs of parental care outweigh its benefits and has been very successful in explaining 'adaptive' causes of infant maltreatment. 'Adaptive' means that such maltreatment is beneficial for the reproductive fitness of the parents and, therefore, belongs to the normal or typical behavioral repertoire of this species. If the individuals of a certain species are placed under the same conditions, at least a significant proportion of them perform the same way.

It should be briefly mentioned again that even if the same types of infant attack/desertion are widely observed and regarded as adaptive in nonhuman animals, no child abuse/neglect can be justified in modern human society, in which children's rights must be protected (Table 1, Remark 1).

In contrast to 'adaptive' maltreatment, 'nonadaptive' infant maltreatment does not increase the reproductive success of the performer. Nonadaptive maltreatment can be derived from the dysfunction of the caregiver's neural system, as all animal behaviors are, proximately, manifestation of activities of one's nervous system. Although

evolutionary selection pressure acts on the genome to shape the animal's behavior to maximize its reproductive fitness, animal parents never calculate the cost–benefit ratio of their parental care. Rather, each animal parent behaves simply according to the ‘feeling’ or motivation it has toward the offspring at each moment, which is mediated by its evolutionarily selected neural system. This gap between the ultimate causes and proximate mechanisms<sup>98, 99</sup> is manifested in ‘misplaced parental care’ toward infants of other species, which is a nonadaptive byproduct of the neural system for parental care.<sup>100, 101</sup> The same gap is also apparent in the nonadaptive maltreatment cases in which the neural system for parenting failed to function properly. Such cases derived from brain dysfunction have been of significant interest in clinical psychology and psychiatry<sup>10, 102</sup> and are worth including in the systematic classification of infant maltreatment.

**Classification of Infant Maltreatment in Mammals**

Based on the general discussion in the preceding section, here we classify the major causes of attack/desertion in nonhuman mammals as summarized in Table 1.

By referring to previous literature reports, ‘adaptive’ causes of infant maltreatment are subdivided into three types: (i) attack/desertion of non-offspring; (ii) attack/desertion of biological offspring with low reproductive value; and (iii) attack/desertion of biological offspring under unfavorable rearing environments.<sup>7, 8</sup> In actual cases, however, there is significant individual variability in the influence of these causes on the details of nurturing behavior as performed (Table 1, Remark 2) because the development and functioning of relevant neural circuits vary among individuals.

‘Nonadaptive’ causes of maltreatment are subdivided into (iv) inexperience and (v) direct brain dysfunctions.

It should be noted that the multiple factors belonging to (i)–(v) are neither deterministic, irreversible, nor independent from each other (Table 1, Remark 3). Rather, factors classified in (i)–(v) interact with each other sometimes additively and sometimes compensatively to the net risk and resilience of infant maltreatment. The brain circuits are shaped under genetic and brain organic influences by earlier experiences and function in a given social environment. Such biological

and social factors mutually interact every moment to dynamically remodel each other. Both biological and social factors contribute to shape one's present behavior, which in turn influences the surrounding people and changes one's future social environment. Thus, a bio-social approach that takes all of these factors into account is required to fully understand the context of one's behavior in a given society.<sup>103–105</sup>

**‘Adaptive’ Attack/Desertion of Infants**

**Attack/desertion of non-offspring**

First, consider instances where males attack non-offspring conspecific young. This type of male infanticide is widely seen in mammals that form polygynous societies, where one or a few alpha males monopolize multiple females for a certain period before losing dominance to other males, such as among langurs, baboons, lions, and mountain gorillas.<sup>89, 90, 106</sup> When an outsider male that does not have a recent mating experience encounters an infant, it should not be that male's own offspring, a condition termed ‘low parenthood confidence’ (in species with internal fertilization, parenthood confidence is lower for males than for females, and is called ‘uncertainty of paternity’).<sup>7</sup> For such a male, eliminating the non-offspring infant will terminate lactation in the mother, thus increasing the male's opportunity to mate with the female.

The majority of virgin male laboratory mice perform this type of infanticide toward unfamiliar pups, unlike spontaneously nurturing virgin female mice. After mating, however, the same male gradually stops performing infanticide and becomes paternal by the time of delivery of its own offspring.<sup>107, 108</sup> Interestingly, at least for laboratory mice, these paternal male mice provide care even toward non-offspring; this is because males cannot detect their own offspring with certainty from the given social context or from the pups' sensory cues (uncertainty of paternity). Therefore, males simply rely on the timing after mating to refrain from infanticide, and if these fathers do not have another mating experience they resume infanticidal behavior after 50–60 days. At least in *CF-1* mice, the timing of the behavioral change is measured by the number of days after ejaculation via a circadian clock in the male's brain, as an artificially shortened or elongated light–dark cycle alters the timing of males' behavioral changes (i.e., their behavioral changes occur according to the number of days experienced, rather than by the actual time length).<sup>109</sup> This phenomenon has been known for many years, but the neural mechanisms for this behavioral transition have not been addressed. Our research group has reported that pheromone signaling is responsible for the infanticidal response of male mice<sup>108</sup> and that the rhomboid part of the bed nuclei of the stria terminalis (BSTrh; Fig. 1), a small fore-brain region belonging to the extended amygdala, is specifically activated by infanticidal motivation and facilitates infanticidal action.<sup>32</sup> The cMPOA sends inhibitory inputs to the BSTrh and the mating-induced modulation of this circuit underlies the behavioral transition from infanticide to paternal care.<sup>32, 110</sup>

‘Adaptive’ infanticide toward non-offspring as a reproductive strategy is not performed only by males. There are many reports where females perform infanticide toward non-offspring young; for example, during late pregnancy, wild mouse females perform infanticide more than males,<sup>111</sup> possibly to eliminate competitors of their own offspring in terms of natural resources. Similarly, non-offspring infanticide is performed by competitor females among marmosets and meerkats, that is, species in which infant care is shared among non-breeding family members (termed ‘cooperative breeding’; note that this technical term by the conservative definition does not simply mean the existence of help from nonparents but requires an association with reproductive skew, which is the bias of reproductive success among same-sex individuals along with their social rank).<sup>112, 113</sup> A recent work suggests that potential direct rewards of gaining reproductive resources (such as alloparenting) for their direct offspring have a stronger influence on the expression of female aggression than

**Table 1.** Classification of infant attack/desertion in mammals

<p><b>‘Adaptive’ attack/desertion of infants</b></p> <p>(i) Attack/desertion of non-offspring</p> <p>(ii) Attack/desertion of biological offspring with low reproductive value</p> <p>(iii) Attack/desertion of biological offspring under unfavorable rearing environments</p> <p><b>‘Nonadaptive’ attack/desertion of infants</b></p> <p>(iv) Caused by inexperience</p> <p>(iv-1) Lack of experience of being nurtured and socialized appropriately in early life</p> <p>(iv-2) Lack of experience observing others' parenting and interacting with infants</p> <p>(iv-3) Lack of on-site experience as a parent</p> <p>(v) Caused by disturbance of caregivers' brain mechanisms required for adequate nurturing behaviors</p>
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\*Remark 1: No kind of child abuse/neglect is justified in modern human society, even if it is widely observed and regarded as adaptive in nonhuman animals.

\*Remark 2: Group-level characteristics cannot be generalized to individuals.

\*Remark 3: Risk factors are neither deterministic, irreversible, nor mutually exclusive.

the indirect costs of attacking young that have distant kinship with the offending females.<sup>114</sup>

In both cases, although infanticide of non-offspring appears unethical, it is performed to increase the offender's reproductive fitness and is therefore regarded as an 'adaptive' reproductive strategy in nonhuman mammals.

Notably, an apparently similar phenomenon is reported in humans, namely, the 'Cinderella effect,' where an adult tends to abuse or neglect non-offspring children more frequently than biological offspring.<sup>115, 116</sup> Across multiple countries and cultures, the risk of abuse is about six times higher, and the risk of lethal child abuse is 50 to 100 times higher, toward nonbiological children than toward biological children. In addition, even when stepparents are not explicitly aggressive, disregarding the needs or investing less (such as lower expenses for education and health care in humans) toward the unrelated children compared to their offspring is commonly observed in both humans and nonhuman animals.<sup>117</sup> These findings manifest a conceptual commonality with other animals, in the sense that there is at least some preference for one's own children over those of others. It must be quickly added, however, that this type of attack on non-offspring cannot be regarded as being within the normal or most frequent repertoire of human behaviors. Most foster parents, stepparents, and *de facto* parents (who take care of the child but are not legally registered parents) nurture their non-offspring children very well; thus, group-level data cannot be generalized to individual behavior (Table 1, Remark 2).<sup>118</sup> It should also be emphasized that even if these phenomena are apparently similar to animal cases, this does not mean that the underlying brain mechanisms are the same.

#### 'Adaptive' attack/desertion of biological offspring with low reproductive value

If the reproductive value and investment cost are equivalent for each offspring, distributing parental care equally to all members of their offspring maximizes parental reproductive success.<sup>119</sup> However, these variables often differ among each offspring, litter, and sex. For example, when resources are temporarily limited, parents might be expected to adjust their expenditure on parental care in relation to the variation in its benefits to their offspring and in its costs to themselves.<sup>120</sup> Parental expenditure toward the current offspring is assumed to increase the offspring's reproductive value but to lower the parent's subsequent reproductive success. In contrast, the conservation of resources for future reproduction will lower the reproductive value of current offspring but will increase the parent's subsequent reproductive success.<sup>7</sup> Where the reproductive value of the offspring falls to low levels, parents might increase their fitness by premature termination of parental care for some or all of their offspring, provided that this enhances either the fitness of survivors or their own capacity for future expenditures.

Major determinants of the reproductive value of each offspring include, first, the offspring's *age*. Because the likelihood of offspring eventually breeding increases with the offspring's age, parental valuation of their young may be expected to increase conspicuously over days. Therefore, when resources are limited, parents might lose their nurturing motivation earlier for their younger and smaller offspring and try to save the older and larger ones, if all other conditions are equal. In humans, cross-cultural studies showed that hard-pressed parents who cannot raise children born too close together generally sacrifice the younger child.<sup>121</sup>

Any congenital or acquired *damage/dysfunction* of offspring may also influence parental motivation. During parturition, many mammalian mothers consume the placenta, umbilical cord, and amniotic membrane attached to newborns and often eat unresponsive newborns (or those displaying signs of weakness) at the same time.<sup>122, 123</sup> In mice, weak or injured pups may be eaten or expelled from the nest by the mother.<sup>23, 124</sup> In humans, it is well known that poor health status is an important risk factor for child abuse/neglect.<sup>121</sup> However, especially once the offspring have survived the neonatal period, many

mammalian parents employ conservative decision rules not to abandon a temporarily unresponsive offspring and sometimes continue to carry dead offspring for an extensive period of time, as observed in chimpanzees, monkeys, dolphins, and dogs.<sup>125–127</sup>

Equal investment in both *sexes* of offspring is an evolutionarily stable strategy.<sup>119</sup> However, in polygynous species, males exhibit a higher variance in fitness than females; thus, from a mother's perspective, extra investment in a son may yield greater returns if the mother is in good condition during a period of parental investment (but if the mother is in poor condition, investing in daughters will increase fitness).<sup>128</sup> In humans, female-selective infanticide occurs in many societies, whereas unequivocal accounts of male-selective infanticide are difficult to find.<sup>8</sup>

In the case of species producing multiple siblings at a time, reduction of the *litter size* may sometimes reduce parental motivation.<sup>129</sup> The parents often abandon a healthy small litter entirely to facilitate the next gestation period. The proximate cause of this phenomenon may be insufficient nipple and ventral somatosensory stimulation.<sup>129</sup>

Alternatively, in species normally producing one offspring at a time, which include macaque monkeys and humans, excess neonates are often eliminated from *twins* or triplets to reduce the parental burden and possible loss of both young.<sup>7, 130</sup> Parental overburdening can also be caused by a baby born too soon after the last one.<sup>8</sup> The elimination bias can reflect the size/well-being of each neonate (the older or larger offspring is generally favored), and the desertion of an unwanted one is generally performed early to minimize unnecessary investment.

#### 'Adaptive' attack/desertion of biological offspring under unfavorable rearing environments

In adverse circumstances, such as low food availability, unusual climate, high predatory pressure, or overcrowding in a given space, parents may respond by deserting or even eating some or all of their offspring.<sup>7, 131, 132</sup> Cannibalism of pups is reported to be adaptive in order to help mothers meet their own nutritional or other physiological demands in mice<sup>133</sup> and is also suspected in many other species.<sup>89</sup> In human ethnographic literature, the largest number of filicide cases fell under Category (iii), such as famine, poverty, and unwed/widow cases, which all limit nurturing resources.<sup>8</sup> General health problems of parents, such as a physical or mental disease state, may inhibit proper caregiving just like environmental hardships, and could also be included in Category (iii).

Instances of mothers deserting their offspring that have been attacked by biologically unrelated males, as discussed in relation to Category (i), may fall into Category (iii) as having an unfavorable social environment. Hanuman langur mothers are normally very maternal and sometimes carry a dead infant until it becomes mummified. The same mothers, however, do not seriously defend their infants from infanticidal male immigrants, may become insensitive to offspring distress signs caused by the assault, and sometimes abandon their infants before death.<sup>13, 101</sup> Moreover, when the infant has disappeared or died, the mothers start soliciting the infanticidal males for copulation. Mouse and lion mothers show maternal aggression toward intruder males but often fail to defend their young. They also start mating with infanticidal males soon after infant elimination.<sup>19, 134</sup>

These changes in maternal mindset surprised and puzzled the pioneering field researchers<sup>13</sup> but can be explained from a perspective of female reproductive fitness as follows<sup>135</sup>: In these species, males are larger and have more weaponry than females. It is too dangerous and difficult for mothers to keep protecting their young from stalking infanticidal males. If mothers are still young, they have future reproductive opportunities. Therefore, they do not take the risk and they choose the second-best option, which is giving up the current offspring and mating with the infanticidal male immediately for the next reproduction. Interestingly, Hrdy noted that one

older Hanuman langur female that had already ceased to menstruate repeatedly charged the infanticidal males.<sup>135</sup> Because Hanuman langurs are matrilineal, any infants in this older female's group may have had kinship with her. She would not have reproduced again, therefore such a self-sacrificing attack to retrieve her relative would not have cost much in terms of reproductive fitness, even if her charge against an infanticidal male had been unsuccessful in the end.

Similarly, in human child abuse cases, maternal psychological changes toward biological children have been observed after the mother had started a new relationship and cohabited with a different man. A famous example of this type of child abuse led to the *Kelsey Smith-Briggs Child Protection Reform Act* in 2006<sup>136</sup>. In this case, the mother and her child had lived uneventfully when she was a single mother, with abundant evidence of her attentiveness to the child. The mother-child relationship had changed after her new partner had come to live with her: When the stepfather began to physically abuse the child, the mother did not effectively defend the child and sometimes even joined him, although the partner also displayed violence toward the mother herself. Similar cases have been reported worldwide, puzzling child-protection officers in terms of the reason for discontinuing maternal affection. One study even attributed the increased risk of physical child abuse in stepfather households to the mother, rather than to her partner (i.e., the stepfather of the abused children).<sup>137</sup> While the precise mechanisms causing this phenomenon should be identified in the future, in current child-protection practices, it should be kept in mind that maternal attentiveness in one social condition does not guarantee the same attentiveness in another social setting.

### 'Nonadaptive' Attack/Desertion of Infants

#### Nonadaptive attack/desertion of infants caused by inexperience

Although 'parental motivation' is innate in mammals, this does not mean that all individuals can provide parental care without any learning experiences. This is true even for simpler instinctive behavior, such as drinking and feeding. Although thirst and hunger are the most primitive innate motivations, infants need substantial practice to be able to eat or drink from a cup without spilling the food or water from their mouths. Parenting is much more complex and requires various experiences to improve. There are at least three kinds of experiences that are shown to increase parental performance: (iv-1) experience of being nurtured and socialized appropriately in early life; (iv-2) experience observing others' parenting and interacting with infants; and (iv-3) on-site experience as a parent.

Before going into each subcategory, it should be noted that the insufficient social experiences caused by a lack of 'average expectable environment' of that animal species<sup>138, 139</sup> actually influence behavioral development via the individual's brain mechanisms; that is, the influence of the past environment is engraved in the brain through learning and memory to act on one's present behaviors. In this sense, Category (iv) 'inexperience' is also a malfunctioning of brain systems in a broad sense and may not appear to be sharply contraposed to Category (v) 'brain dysfunctions.' However, maladaptive behaviors caused by inexperience may often be corrected by providing the experience in a supportive social environment (see, for example, Novak and Harlow<sup>140</sup>). Alternatively, in a case where the nonadaptive behaviors are caused by a tumor in the frontal cortex,<sup>141</sup> removal of the tumor should be the first option for intervention and can be the most effective way to regain the adaptive behavior. Therefore, from a clinical perspective, it is useful to dissociate these two categories. Moreover, brain circuits interact with social stimuli every moment to remodel each other dynamically. Both biological and social factors contribute to shaping one's social behavior and thus should be taken into account to fully understand the context of one's behavior in a given society (i.e., the 'biosocial basis of behavior'<sup>103, 105</sup>).

#### Experience of being nurtured and socialized appropriately in early life

Empirical evidence indicates that experiencing a poor nurturing environment in early life may affect parental capabilities later in life.<sup>142, 143</sup> Especially in primates, the early social environment forms the basis of not only nurturing behavior but also other social behaviors, as well as mental development in general, such as anxiety, stress resilience, and behavioral coping style.<sup>144–148</sup> These various effects should collectively affect parental ability in adulthood.

In rodents, on the other hand, the effect of completely socially isolated rearing conditions starting from postnatal day 1 or 4<sup>149, 150</sup> was shown to be milder and did not significantly eliminate social behaviors, including parenting, although quantitative deficits were often observed. Therefore, it is probable that primates are much more dependent on the early social environment to shape adult social behavior, while rodents perform social behaviors more innately. It is important to keep these species differences in mind.

#### Experience observing others' parenting and interacting with infants

Young primates often have opportunities to observe older females rearing their infants. When possible, young females may try to interact with these infants and gain experience with infant care before their own parturition.<sup>101</sup> These alloparenting practices are shown to increase parental capability at least in certain primate species, such as common marmosets.<sup>151, 152</sup>

#### On-site experience as a parent

Empirical evidence indicates that in many species, young parents show lower breeding outcomes than do older parents. Several field studies suggest that not only breeding skills but also feeding skills increase with age in many iteroparous (i.e., giving birth multiple times) species, and the total costs of rearing offspring may often be smaller for experienced parents than for inexperienced parents.<sup>7</sup>

For example, in a report of Japanese macaques, the rate of neonatal desertion was 40% for the first birth but was almost zero for the second birth in the same females.<sup>153</sup> A high rate of offspring desertion in primiparous young females was also noted in lions and mice.<sup>23</sup> Primiparous mothers may not only lack nurturing experience but also suffer from high physical stress caused by first-time parturition. An extreme example is spotted hyenas<sup>154</sup>: Because they have an unusually thin and elongated birth canal, primiparous parturition is very difficult, thus, 60% of neonates and more than one-tenth of mothers die during labor. However, the second births are less troublesome.

It is relevant that there are numerous human studies showing that 'teenage mothers' are one of the major risk factors for maternal infanticide.<sup>155</sup> Of course, this phenomenon cannot be attributed solely to maternal age, but the maternal economic status and marital status should also be considered as covariates. Daly and colleagues argued that the rate of infanticide by biological mothers declines steeply with maternal age, even when the sample is restricted to unwed mothers. This phenomenon could also be compatible with the declining reproductive value in older mothers.<sup>6</sup>

#### Nonadaptive attack/desertion of biological offspring caused by disturbance of caregivers' brain mechanisms required for adequate nurturing behaviors

Even when the early social environment and the current rearing environment are both appropriate, parents may fail to provide adequate nurturing toward biological offspring due to direct brain malfunction. Such malfunction is an inevitable cause of offspring attack/desertion, as all normal behaviors depend on specific brain circuits.

For example, experimental bilateral dysfunction of the cMPOA (Fig. 1) specifically eliminates parenting and leads to infanticide even among multiparous mouse mothers.<sup>24, 32</sup> However, such specific damage in the bilateral cMPOA, without affecting the surrounding preoptic-hypothalamic area, should be rare in

natural settings. The cMPOA is in the preoptic–hypothalamic complex, which contains multiple brain centers for sleep, feeding, osmoregulation, body temperature maintenance, and autonomic regulation. Bilateral cMPOA dysfunction caused either by congenital malformation, trauma, or cerebrovascular disorder may also be life-threatening at the same time, so that will not create an actual case of infant maltreatment. On the other hand, unilateral cMPOA damage may be endured and could partially affect nurturing motivation.<sup>24</sup> It is possible that such incomplete cMPOA dysfunction combined with environmental stress leads to heightened risk of offspring attack/ desertion.

The possible contribution of other brain areas, such as the amygdala, PFC, and several preoptic–hypothalamic nuclei responsible for instinctive motivational drives incompatible with nurturing behaviors, was addressed in an earlier section, ‘Brain mechanisms for nurturing behavior,’ and in Figure 2. In one remarkable example,<sup>141</sup> a large tumor in the right orbitofrontal cortex was found in a man with acquired pedophilic symptoms. He made sexual advances toward his stepdaughter and was legally removed from the home. After conviction for child molestation, he experienced headaches and balance problems, leading to a visit to an emergency department of a university hospital, where a brain scan revealed the tumor. After surgical removal of the tumor (hemangiopericytoma), his pedophilic symptoms ceased. About 10 months later, he developed a persistent headache and began to collect pornography again. Another brain scan showed tumor regrowth. His behavioral symptoms resolved following tumor re-resection. This case clearly illustrates the importance of the prefrontal cortex in controlling social behaviors.

In addition, a wide range of parental psychiatric conditions from mental retardation, mood disorders, post-partum depression, and substance abuse<sup>11, 156, 157</sup> may lead to decreased parental functioning, though the effects are not strictly confined to particular brain areas. It should also be noted that major psychiatric disorders can explain rather a small fraction of cases.<sup>158</sup>

## Concluding Remarks

This article proposes a comprehensive classification of causes/contexts of mammalian infant maltreatment that is intended to be useful in understanding the risk factors for physical abuse and neglect of children. The human–animal similarities do not necessarily prove the same mechanisms. However, having a potential animal model will greatly contribute to understanding human cases, as the relevant brain areas have been and will be further elucidated using animal models.

Identifying risk factors for child maltreatment should never induce stigmatization of people with those factors. For example, the ‘intergenerational transmission of child abuse’<sup>159</sup> has been widely believed since its first publication, as if the abused children were destined to abuse their children. However, many later research studies showed milder or even scarce effects of the history of abuse and that the majority of abused children will not repeat child abuse to the next generation.<sup>160, 161</sup> The same caution is also valid for the Category (v) neurobiological factors; any neurological damage or psychiatric disorder alone cannot inevitably lead to child maltreatment. The human brain shows enormous plasticity to compensate for dysfunction in one area with the surrounding intact areas, therefore, many symptoms of brain damage can be recovered from. The aim of risk assessment is to better understand the specific needs of each parent and family, and to provide tailor-made measures clinically and societally.

Finally, it should be acknowledged that, to save children, parents need to be supported by their society, because each parent, as a mammalian individual, may not be able to meet their children’s needs due to inexorable adversities.

‘Just as children are absolutely dependent on their parents for sustenance, so in all but the most primitive communities, are parents, especially their mothers, dependent on a greater society for

economic provision. If a community values its children it must cherish their parents.’<sup>147</sup>

Early parenting interventions should be the best way to prevent child maltreatment, mental and physical health problems caused by child maltreatment, and can also be an economically efficient investment for our society, reducing the social cost caused by these problems in offspring.<sup>162</sup> Deeper scientific understanding of the underlying mechanisms of child maltreatment will contribute to creating better measures to help parents and child caregivers in the future.

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The authors declare no conflict of interest.

## Author contributions

K.O.K, together with Y.S. and K.S. constructed this framework and wrote the manuscript.

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