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The signal functions of early infant crying

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Abstract: In this article I evaluate recent attempts to illuminate the human infant cry from an evolutionary perspective. Infants are born into an uncertain parenting environment, which can range from indulgent care of offspring to infanticide. Infant cries are in large part adaptations that maintain proximity to and elicit care from caregivers. Although there is not strong evidence for acoustically distinct cry types, infant cries may function as a graded signal. During pain-induced autonomic nervous system arousal, for example, neural input to the vocal cords increases cry pitch. Caregivers may use this acoustic information, together with other cues, to guide caregiving behavior. Serious pathology, on the other hand, results in chronically and severely abnormal cry acoustics. Such abnormal crying may be a proximate cause of adaptive infant maltreatment, in circumstances in which parents cut their losses and reduce or withdraw investment from infants with low survival chances. An increase in the amount of crying during the first few months of life is a human universal, and excessive crying, or colic, represents the upper end of this normal increase. Potential signal functions of excessive crying include manipulation of parents to acquire additional resources, honest signaling of need, and honest signaling of vigor. Current evidence does not strongly support any one of these hypotheses, but the evidence is most consistent with the hypothesis that excessive early infant crying is a signal of vigor that evolved to reduce the risk of a reduction or withdrawal of parental care.

Keywords: colic; crying; early infant crying; honest signaling; infanticide; parental care; parent-offspring conflict; separation call; vocalization

> *The baby gazed up at me as ever with wide-open eyes but whether he was hungry or thirsty or felt some other discomfort I couldn't tell. He lay with eyes open and expressionless, like a marine plant in the water of the dusk, simply and placidly existing. He demanded nothing, expressed absolutely no emotion. He didn't even cry.*
> – Father considering his handicapped son in *The Silent Cry,* by Kenzaburo Oe.

1. Introduction

Interpretations of early infant crying are paradoxical. For nearly every claim made about the human infant's cry, the opposite has also been claimed. The infant cry has been characterized as a constellation of acoustically distinct cry types, indicating specific needs such as hunger or sleep, and it has been described as undifferentiated noise. Infant cries can elicit appropriate contact and caregiving behaviors, and they are sometimes the proximate cause of abuse. Infants who cry excessively (i.e., those with colic) have been described as sicker, as healthier, and as in no other way different from their counterparts without colic.

In this target article, I critically examine the various proposed signal functions of early infant crying and develop models of infant crying that attempt to resolve these paradoxes. In mapping out the potential signal functions of the early infant cry, I take advantage of a number of theoretical perspectives, all derived from evolutionary reasoning, including attachment theory, parent-offspring conflict theory, and honest signaling. In characterizing the infant cry and examining its potential signal functions, I bring together diverse literatures, including clinical studies of the infant cry, physiological models of cry production, cry bioacoustics and perception, the child abuse and infanticide literatures, animal studies, and cross-cultural ethnography.

I employ an evolutionary approach to these disparate literatures to form a coherent picture of the signal function of the early infant cry. The application of evolutionary theory to human infant crying has increased in recent years (Barr 1998a; 1999; Furlow 1997; Lummaa et al. 1998; Zeifman 2001). Here I consider the breadth of the proposed signal functions, and critically evaluate their ability to explain the amount, the temporal patterning, and the acoustic proper-

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ties of early infant crying. The scope of this target article is limited to an examination of the signal functions of the infant cry only in the first three months of life (i.e., "early infant crying"). At about 3 months of age, infants undergo a developmental shift in which crying becomes more differentiated, interactive, and intentional (Barr 1990c; Barr & Gunnar 2000; Ostwald & Murry 1985).

The theoretical perspective of the paper is introduced in the following section (sect. 2), in which I argue that human parents pursue a complex reproductive strategy, which can range from selfless care of offspring to infanticide. I consider the implications that such a child-rearing environment has for infant signaling, in particular for the evolution of honest signaling. The examination of the early infant cry proceeds in four additional sections. Section 3 briefly addresses the infant cry as a separation call fostering protection and care by the mother. In section 4 I show how particular acoustic characteristics of cries indicate the level of current distress and overall health, and I develop a model describing how these acoustic properties may influence patterns of infant care and abuse. In the next two sections I address excessive infant crying (i.e., colic). Following Ronald Barr, I argue in section 5 that colic is a normal aspect of infant development, albeit in exaggerated form, and in section 6 I evaluate the signal functions that have been proposed to explain such excessive crying. In the conclusion (sect. 7) I point the way for further research.

Before introducing the relevant evolutionary theory, two important clarifications are in order. First, the evolutionary approach employed here assumes that the behavior expressed by infants and parents has been shaped in part by natural selection, and that individual behavioral responses to their environment may be viewed as potential adaptations that tend to increase survival or reproduction (Barkow et al. 1992; Williams 1966). In taking this view, I do not imply that humans or other animals are making conscious fitness calculations or that they are aware of the fitness effects of their behavior. In order to avoid lengthy and awkward sentences, however, I will employ expressions such as "When the chances for infant survival are low, parents may increase overall reproductive output by terminating parental investment in offspring (i.e., engage in 'adaptive infanticide')," which should be taken as shorthand for

> Natural selection has favored in parents a psychological mechanism that results in the withdrawal of care from their own offspring. This mechanism is activated under conditions in which the infant is unlikely to survive, and selection has favored this flexibility in parental behavior because in past environments the selective withdrawal of care under inauspicious circumstances resulted, on average, in the production of more offspring over a lifetime.

Second, the moral and legal views on abortion and infanticide vary across time, cultures, and individuals. I will advance adaptive explanations for behaviors such as abortion and infanticide in humans, but in doing so I imply neither moral justification nor moral condemnation.

2. Parent-offspring conflict and honest signaling

2.1. The conflict

The most commonly proposed signal function of the infant cry is to alert caregivers to need. This straightforward view of early infant crying presumes that the interests of the offspring and the parent are in agreement. When the infant is hungry, not only does she desire to be fed but the mother also desires to feed her. But the interests of parents and offspring are not always identical. Parent-offspring conflict theory (Trivers 1974) recognizes that the interests of parents and child are indeed largely overlapping, but it emphasizes where the interests of parents and offspring diverge, and this has important implications for the signal function of early infant crying.

The source of parent-offspring conflict is the fact that in sexually reproducing species parents and offspring are not genetically identical, and as a result their genetic interests differ in important ways (Daly 1990; Trivers 1974). The classic example of this conflict is a mother who maximizes her fitness (i.e., number of surviving offspring) by investing her limited resources equally among her offspring, mirroring her equal genetic relatedness to them. From the genetic point of view of each offspring, however, the self is more important than siblings, and each particular offspring seeks to acquire a disproportionate share of parental resources. Genes expressed in the parent, according to the theory, result in behaviors that limit investment in individual offspring, whereas genes expressed in the offspring result in behaviors that seek to increase such investment.

The above hypothetical example does not imply that natural selection will invariably favor parents to partition resources equally in all offspring. Parents may favor younger over older, weaker over stronger, or the converse, depending on circumstances (Daly 1990; Davis & Todd 1999; Hrdy 1999). Additionally, there is a limit to an offspring's evolved selfishness because it also has a genetic interest in its siblings (Daly 1990). Nonetheless, the genetic interests of parents and offspring do not overlap entirely.

Parent and offspring interests diverge most dramatically when parents of a species are prone to withdraw parental investment entirely, or to commit infanticide outright (Daly 1990; Daly & Wilson 1988; Hrdy 1999). When chances for survival of an infant are low, either due to the poor condition of the child or to detrimental circumstances, parents might maximize overall reproductive output by quickly terminating investment in the current offspring. By doing so, they can divert limited resources to other offspring whose expected future fitness is higher than that of the unpromising neonate. For example, parents could divert resources to an existing, older offspring who has already successfully passed through the period of early infant mortality (Daly 1990). Alternatively, parental investment could be diverted to future offspring, when circumstances are likely to be more auspicious. By discriminating among offspring in this way, limited parental resources can be targeted toward those offspring most likely to survive and reproduce themselves, resulting in higher lifetime net reproductive output.

Parental neglect, abandonment, killing, and sometimes consuming of newborn offspring are known to occur in several animal species when the condition of the offspring is poor or the conditions for rearing offspring are unfavorable. Shield bug mothers, for example, place their larger, more viable eggs centrally where they can protect them from predators, and place the smaller, less viable eggs at the periphery where they suffer greater predation (Mappes et al. 1997). Such parental discrimination is also found in several monogamous bird species. For example, white stork parents with large clutches kill their smallest, slowest growing chicks (Tortosa & Redondo 1992), and Hermaan's gull par-

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ents reduce large clutches by selectively killing later-hatched chicks (Urrutia & Drummond 1990). Among mammals, mice kill and consume offspring when litter sizes are too large or when the parental condition is poor (Elwood 1992). Prairie dog mothers in poor physical condition sometimes abandon offspring, make no effort to prevent conspecifics from killing and consuming them, and sometimes participate in the cannibalism themselves (Hoogland 1994; Hrdy 1999).

2.2. Parent-offspring conflict in humans: Infanticide, abuse, neglect, and suboptimal parenting

The quality of parental care in humans is multiply determined by a variety of influences, including characteristics of parents, characteristics of offspring, and the economic, social, and cultural environment (Belsky 1984; 1993; Burgess & Drais 1999). As predicted by parent-offspring conflict theory, human parents often provide suboptimal care, or reduce or withdraw parental investment from offspring, when the prospects for infant survival are low. Such parental investment manipulations may take many forms, such as transferring the costs of child rearing to others by enlisting the support of kin or wet nurses, or fostering out or abandoning offspring (Hrdy 1994). Alternatively, parents may provide suboptimal care or terminate investment in offspring without transfer of costs. Such maltreatment may be viewed along a continuum, ranging from suboptimal parenting, to neglect, abuse, and infanticide. This is not to say that suboptimal parenting, neglect, abuse, and infanticide have identical etiologies (e.g., Chaffin et al. 1996), but the following will show that there is substantial overlap in the risk factors for these phenomena.

Cross-cultural evidence demonstrates that parent-inflicted infanticide in humans occurs overwhelmingly when the child is unlikely to survive (Adinkraw 2000; Bugos 1984; Daly 1990; Daly & Wilson 1984; 1988; Lummaa et al. 1998; Scrimshaw 1984; and see Table 1).[1] The infant's lack of survival prospects can be due to the poor health of the child herself or, more commonly, to unfavorable circumstances external to the child. The most common rationales for infanticide include the birth of a deformed or ill infant, a lack of paternal support, and inauspicious circumstances such as too many children. Other rationales for infanticide include the child being of an unwanted sex and ritualistic killings. Results from studies of industrialized societies are similar to the cross-cultural ethnographic sample (Daly & Wilson 1988; Overpeck et al. 1998; Pitt & Bale 1995; Stroud & Pritchard 2001; Voland & Stephan 2000). For example, in a Canadian sample, younger, unmarried women were most likely to kill their own offspring, and infants less than 1 year old were at highest risk (Daly & Wilson 1988). Similar risk factors have been found in the United States (Overpeck et al. 1998). The poor condition of an infant is a less likely documented motivation for infanticide in industrialized societies, perhaps due to modern medical intervention. But this is not so for abuse and neglect (as discussed below). Additionally, in modern societies, retaliation against a spouse and mental illness of the parent are commonly cited motivations for infanticide. When retaliation or mental illness are contributing factors to infanticide, however, the killing of offspring is more evenly distributed across ages, not selectively targeted toward the young and vulnerable, as in the most likely cases of adaptive infanticide (Dobson & Sales 2000; Stroud & Pritchard 2001). When mental illness contributes to infant maltreatment, this does not necessarily mean that the behavior is not adaptive, however. For example, the risk factors for postpartum depression are much the same as other risk factors for neglect, abuse, and infanticide (e.g., in circumstances inauspicious for successful child rearing), and may be a psychological mechanism activated during such circumstances that leads to the adaptive withdrawal of parental investment (Hagen 1999; 2002).

Cultural contexts constrain the incidence of infanticide. Rates of infanticide by parents are lower in modern societies than in traditional societies, and rates vary substantially among the latter. For example, of nearly 35 million births in the United States from 1983–1991, the infant death rate from infanticide was only 8 in 100,000 (Overpeck et al. 1998). It should be borne in mind, however, that cases of infant death due to abuse and neglect are undercounted (McClain et al. 1993; Overpeck et al. 1998). In traditional societies, infanticide rates range from zero (or near zero) in many traditional African cultures to a high among the Eipo horticulturists of Papua New Guinea, in which 41% (20/49) of live-born infants were killed by parents from 1974 to 1978, in part driven by parental preferences for males (Hrdy 1994). After missionary contact with the Eipo, the infanticide rate was reduced to 10%. These striking differences in infanticide rates across cultural contexts can be explained, in part, by the reversal of the relative costs of abortion and infanticide (Hrdy 1999). In traditional societies, abortion is costly due to the risk to the mother's health, and infanticide is often socially sanctioned. In modern societies, abortions are more often sanctioned and less dangerous whereas infanticide is routinely outlawed. Abortion has replaced infanticide as a means of selectively eliminating offspring. In-

Table 1. *Rationales for infanticide in a cross-cultural sample*

Rationale	Number of mentions[a]
Infant quality	21
Deformed or very ill	21
Paternal support in question	41
Adulterous conception, nontribal sire, sired by mother's first husband	20
Mother unwed	14
No male support	6
Quarrel with husband	1
Inauspicious circumstances	35
Twins	14
Birth too soon or too many children	11
Mother died	6
Economic hardship	3
Wrong season	1
Other (e.g., female infant, rituals, incest)	15

[a]Number of times rationales for infanticide were mentioned across a randomly chosen sample of 35 ethnographies in which the circumstances surrounding infanticide were discussed (adapted from Table 3.1 in Daly & Wilson 1988).

deed, those circumstances that often trigger infanticide – such as poverty, lack of paternal support, and fetal abnormalities – also influence the decision to abort (e.g., Larsson et al. 2002; Lycett & Dunbar 1996; Zlotogora 2002).

Child abuse and neglect occur under circumstances similar to those associated with abortion and infanticide (Belsky 1993). Although child abuse and neglect occur at all child ages, there is a peak in the rate and degree of violence for victims younger than one year of age (Burgess & Drais 1999; Sibert et al. 2002). As in the case of infanticide, common risk factors for abuse and neglect include the poor condition of the infant or child, a lack of spousal or other social support, poverty and unemployment, and large family size (e.g., Albarracin et al. 1997; Becker et al. 1998; Belsky 1993; Chan 1994; Daly & Wilson 1981; 1988; Frodi 1981; Gonzalvo 2002; Kotch et al. 1999; Sidebotham et al. 2002; Vinson et al. 1996). In particular, it has been shown repeatedly that mentally, physically, or behaviorally atypical children are more likely to be neglected and abused. Retarded children, for example, are at exceptionally high risk for abuse, although it has been argued that much of the retardation is a consequence, rather than a cause, of the abusive behavior (Daly & Wilson 1988; Frodi 1981). On the other hand, abuse cannot be the cause of premature birth or congenital abnormalities such as spina bifida, cystic fibrosis, and Down's syndrome. Children with these congenital defects are abused anywhere from 2 to 10 times more often than the population at large, and premature infants are abused twice as often (Daly & Wilson 1981; Frodi 1981). As in the case of infanticide, factors unrelated to child survival are also implicated in abuse and neglect, such as a history of abuse, mental illness, substance abuse, and the cultural values of perpetrators (e.g., Belsky 1993; Chaffin et al. 1996; Ferrari 2002; Klevins et al. 2000; Kotch et al. 1999). Suboptimal parenting (e.g., lower levels of affectionate or nurturant contact), although not considered neglectful or abusive, is also related to similar risk factors such as a sick infant, poverty, a lack of social support, substance abuse, and mental illness (e.g., Black & Krishnakumar 1999; Black et al. 1994; Britton et al. 2001; Crnic et al. 1984; Hashima & Amato 1994; LeCuyer-Maus, 2003; Mann 1992; Newcomb & Loeb 1999).

When the causes of suboptimal parenting, infant neglect, abuse, and infanticide are considered, it is important to note that maltreatment is not likely to be caused by the effects of single variables but rather by the interaction of multiple risk factors at various biological and social levels (Belsky 1993; Wilson-Oyelaran 1989). As such, I am not arguing that infant poor health invariably leads to some form of infant maltreatment in humans, or that this is the most important factor contributing to maltreatment. Nor am I arguing that all cases of infant maltreatment represent the adaptive withdrawal of parental investment as a part of an evolved, fitness-enhancing strategy (i.e., that all behavior is adaptive). The evidence clearly demonstrates, however, that the selective reduction or withdrawal of parental care under unfavorable child-rearing circumstances has been a major aspect of parental behavior throughout human history, and that the poor condition of the infant can be one of many factors contributing to the reduction or withdrawal of parental care. The discriminative allocation of parental resources to offspring over evolutionary time represents a major selective pressure on the physiology and behavior of infants, and may explain some characteristics of the infant's cry.

2.3. Signaling resolutions to parent-offspring conflict

When the goals of parents and infants are divergent in ways described above, how are these conflicts resolved? The simplest case occurs when parents have complete control over the distribution of resources and they can accurately observe the condition of their offspring. In such cases, parents can partition investment selectively among offspring as they choose. However, when parents cannot directly observe the condition of infants, or some component of their condition, then signals from infants to parent may evolve.

The basic problem of communication when interests between parties conflict is honesty. Manipulation was emphasized in early theoretical models of parent-offspring conflict (reviewed by Godfray 1995a; Godfray & Johnstone 2000). In these models, parents monitor the needs of their young but are subject to manipulation because the young exaggerate their needs. These early models assumed that parents and offspring have fixed responses. Parents provide more food to offspring when offspring signal, and offspring signal less when fed. Different models incorporated different types of manipulation, such as exaggerated begging regardless of need, or "blackmailing" parents by reducing one's own fitness until provided with extra food. The typical resolution of these models is intermediate between parent and offspring optima. That is, parents evolve to provide more food to offspring than would yield the parents' highest possible fitness, but each offspring still receives less provisioning than would yield its own highest possible fitness. It is unclear if such manipulative signaling would be sustainable, however, if the models did not assume that parents always yield to offspring begging but, instead, allowed the parental response itself to evolve (Godfray & Johnstone 2000).

Later models have examined the conditions under which honest signaling can evolve (i.e., behavioral or morphological signals that accurately reflect otherwise unobservable characteristics of the signaler). The first type of honest signaling concerns advertising need for resources (Godfray 1991; 1995a; 1995b; Maynard Smith 1991a). Consider a situation in which offspring differ in need but the parent cannot determine that need. Is it possible for a system of honest signaling to evolve, such that only those in need will advertise to parents and that those without need will not? The critical element required for such an honest-signaling system is that there be a fitness cost associated with producing the signal. To see why, imagine two types of offspring, those who signal only when very hungry and those who begin signaling at extremely low levels of hunger. Further imagine that conspicuously advertising need to parents has the side effect of increasing the probability of drawing the attention of predators. If producing the signal imposes such costs, then the offspring who signal when relatively sated may not gain an overall net benefit by signaling. That is, the marginal cost of attracting predators may be greater than the marginal benefit of receiving food. For offspring who only signal when truly hungry, on the other hand, the marginal cost of attracting a predator may be lower than the marginal benefit of receiving food. When infants are not truly needy, they stand to gain little from an additional food item compared to when they are hungry, and natural selection may not favor costly signaling to obtain it. In short, honest signaling of need can evolve when parents cannot reliably detect need directly, producing the signal is costly, and the parental resource is most valuable to the needy.

Animal studies, in particular avian studies, have yielded evidence for communication systems in which offspring honestly signal need to parents. Begging vocalizations by offspring increase with need, parents preferentially feed those who beg, and such begging has been shown to be costly (reviewed in Kilner & Johnstone 1997). Recent scholarship has called these data into question, however, because sibling competition, in which offspring rather than parents control the allocation of parental resources, can result in similar findings (reviewed in Royle et al. 2002). However, there is evidence for honest signaling of need in species that produce one offspring at a time, such that the confounding effects of sibling competition are removed. Wilson's storm-petrels produce single-chick broods, chicks vocalize more when they are in need (low body mass), but only in the presence of their parents, and parents respond by provisioning them with more food (Quillfeldt 2002).

The second type of honest signaling concerns advertising vigorous condition to parents. Consider the situation in which parents are prone to cut their losses and abandon infants of such poor condition that they are unlikely to survive, but the parents cannot observe all aspects of infant condition directly. Under these circumstances, it would behoove high quality offspring (with high chances of survival) to advertise their superior status to parents and avoid infanticide. But what can inhibit low quality infants (with low chances of survival) from producing the same signal? Again, honest signaling can evolve if there are costs to signaling (Grafen 1990a; 1990b; Iwasa et al. 1991; Maynard Smith 1991b; Zahavi 1975; 1977). Specifically, the cost of producing the signal must be higher for low quality infants than it is for high quality infants. If conspicuous signaling is costly, in terms of energetic expense, for example, then high quality infants would be better able to afford the energetic expense required to signal, leaving their low quality rivals signaling less often, or less vigorously. In this case, parents could use vigor of the signal as a reliable cue to nonobservable quality of the infant.[2]

Most of the empirical evidence for honest signaling of quality involves female mate choice (see Andersson 1994). In a variety of species, it has been shown that (1) males possess conspicuous morphological or behavioral signals (e.g., long colorful tails), (2) the signals are costly (e.g., increased predation), (3) the most conspicuous signals are produced by the highest quality males (e.g., those with a genetically based increased resistance to parasites), (4) females preferentially mate with males possessing the most conspicuous signals, and (5) the resulting offspring inherit high quality from the sires. More important for the argument here, there are several animal examples of offspring advertising high quality to parents that results in increased parental investment. In barn swallows, for example, nestling gape color ranges from yellow to red, based on the ingestion of carotenoids. Carotenoids also play a central role in immunostimulation, so that immune-challenged nestlings cannot allocate as much carotenoid to pigmentation. Thus, healthier nestlings can produce brighter, redder gapes, and parents preferentially allocate food to those nestlings with the most brightly colored gapes (Saino et al. 2000). Additionally, American coot chicks possess exaggerated plumage at hatching, parents preferentially feed chicks with the most exaggerated plumage, and neglected chicks with less exaggerated plumage experience lower growth and higher mortality (Lyon et al. 1994).

3. The separation call and mother-infant attachment

The most straightforward signal function of early infant crying is to maintain contact with the caregiver. John Bowlby (1969/1982) proposed a suite of infant attachment behaviors, including infant crying, that serve to establish or maintain proximity to potential caregivers, primarily the mother. While recognizing other important signal functions of crying, such as communicating hunger or discomfort, Bowlby emphasized close physical attachment to the mother herself as an instinctive goal of infants, independent of other needs. Attachment theory is relevant to early infant crying (0–3 months) only insofar as it functions to maintain proximity to the mother. It is only later in development that attachment theory predicts patterns of maternal response that influence the child's developing personality and the formation of a mental model of relationships (Ainsworth 1969; Bell & Ainsworth 1972; Bowlby 1969/1982).[3] Nevertheless, early infant crying is likely an important means by which infants can maintain contact with the mother because active proximity maintenance behaviors, such as following, are not yet possible.

Infant cries possess features and produce effects consistent with this view. Several studies show that human mothers can recognize the cries of their own infants (Formby 1967; Green & Gustafson 1983; Wiesenfeld et al. 1981), and magnetic resonance imaging of mothers showed that the infant cry stimulus results in brain activity in areas hypothesized to be involved in mammalian parenting behavior (Lorberbaum et al. 2002). Moreover, Bell and Ainsworth (1972) showed that infants (0–4 months in age) cry more when out of proximity from their mothers, that crying promotes the reestablishment of contact by the mother, and that such contact is effective at terminating the crying. Similarly, Christensson et al. (1995) showed that newborns reliably cry when separated from mothers and stop crying at reunion. Additionally, cross-cultural evidence shows that indulgent maternal styles are associated with less infant crying compared to maternal styles that do not allow as much physical proximity between infants and caregivers (e.g., Barr et al. 1991; Lee 2000). Infants do not always cease crying when caregiver contact is established, however, as in cases of inconsolable crying (i.e., colic) described later in this target article.

Bowlby speculated that such a signaling system was adaptive during human evolutionary history because maintaining proximity to mothers protected infants from predators. Indeed, the infant cry as a means to maintain proximity with the mother may have a deep evolutionary history. As in human infants, physical separation from the mother evokes separation calls in a variety of mammalian infants, and the acoustic structure of the human infant cry is similar to that of the separation calls of nonhuman primate infants (Hofer 1996; Newman 1985; Newman & Symmes 1982; Panksepp 1998). Moreover, human mothers and infants exhibit a suite of adaptations that are typical of mammalian species that carry their infants, compared to species that tend to cache infants for long periods of time (Blurton-Jones 1972; Zeifman 2001). In caching species, infants are placed in nests or burrows while the mother forages, and feedings are infrequent. In these species, mother's milk is high in fat and protein, infants have independent thermoregulatory mechanisms, and infants do not vocalize when separated. In contrast, in carrying species, including humans, mothers and infants are in more continuous contact and feedings are more frequent. In these species, milk is lower in fat and protein content, independent thermoregulation is poorly developed at birth, and infants do vocalize when separated from mothers.

4. The acoustic characteristics of early infant crying: Current distress and overall health

Here I review the causes and consequences of the acoustic properties of early infant cries. In doing so, I reconcile several opposing themes in the infant cry literature. With regard to infant cry causation, the cry has been viewed variously as a constellation of cry types, as a graded signal that reveals current level of transient distress, and as an invariant signal associated with chronic illness. With regard to consequent parental reactions, the infant cry has been viewed alternatively as a positive stimulus that triggers altruistic action and as an aversive stimulus that triggers abuse. First, I review models of infant cry production, the acoustic properties of the cries of healthy, stressed, and unhealthy infants, and the effects of cries on adult listeners. In sections 4.6 and 4.7, I develop a model of infant cry acoustics and briefly consider the evolutionary history of mother-infant vocal communication systems.

4.1. Infant cry production and acoustics

Three component systems, the respiratory system (lungs and trachea), the vocal cords (larynx), and the vocal tract (pharynx, oral and nasal cavities), produce the infant cry (Denes & Pinson 1963; Golub & Corwin 1985; Green et al. 2000). The source of the cry sound is the vibrating vocal cords of the larynx. Variable air pressure from the lungs and alterations in the tension and length of the vocal cords combine to produce vocal cord frequency. The cry is then filtered as it proceeds through the vocal tract and the lips, resulting in the audible cry.

The nervous system innervates the muscles that control the respiratory system, the vocal cords, and the vocal tract. Most models of infant cry production emphasize the role of the tenth cranial nerve of the parasympathetic nervous system, or the vagus, as the most proximate neural input affecting vocalization acoustics, although other neural inputs are also important (Green et al. 2000). Sympathetic and parasympathetic (vagal) inputs from the autonomic nervous system innervate the laryngeal muscles (Porter et al. 1988). The vagus has an inhibitory effect on the contraction of the laryngeal muscles. A decrease in vagal outflow causes an increase in the fundamental frequency of the infant cry; an increase in vagal outflow decreases the fundamental frequency.

The nucleus ambiguus of the medulla provides the primary vagal input to various organs including the bronchi, esophagus, pharynx, larynx, and heart, thereby regulating and coordinating sucking, breathing, swallowing, vocalizing, and heart rate (Porges 1995; 1997). Acute stresses precipitate a parasympathetic withdrawal of vagal output from the nucleus ambiguus, resulting in a cascade of physiological events including an increase in heart rate and an increase in the pitch of vocalizations (Porges 1995). For example, pain pathways distribute information to the autonomic nervous system via the hypothalamus and medulla (Gauriau & Bernard 2002), resulting in decreased vagal tone and increased cry pitch in infants (Porter et al. 1988). Also, structures of the limbic system, in particular the cingulate gyrus and amygdala, communicate with the nucleus ambiguus via the periaqueductal grey area (Larson et al. 1988; Porges 1995; Vogt & Barbas 1988). Since the amygdala is central to the brain circuitry implicated in negative emotions such as fear and anxiety (LeDoux 1996; Mendoza & Ruy 2001; Panksepp 1998), the branch of the vagus originating in the nucleus ambiguus can mediate the rapid expression of emotional state in the infant cry. In addition to mediating acute stress, vagal tone also responds to chronic stress, which results in persistent vagal tone depression, even while sleeping, and has a chronic effect on cry acoustics (Porges 1995; Porter et al. 1988).

The current study of infant cry bioacoustics is problematic. Acoustic analyses of the infant cry emphasize measures of the fundamental frequency, in part because cry production models emphasize the role of the vagus and its relationship to fundamental frequency. Other cranial nerves that innervate the larynx, pharynx, chest, and neck also may influence cry acoustics, however, and acoustic properties in addition to those most well-studied, as well as noncry sounds such as fussing, may also be important (Green et al. 1995; 2000; Gustafson & Green 1989; Lester 1987). In addition, acoustic measures are not standardized (Green et al. 2000). Early studies analyzed sound spectrograms, yielding measures such as duration of a single cry, minimum and maximum fundamental frequency, and qualitative changes in frequency contour across the cry (e.g., rising or falling frequency). Computer-based methods, on the other hand, quantify acoustic information of digitized cries, yielding somewhat different measures such as cry duration, mean fundamental frequency across a single cry, harmonic frequencies, and the percentage of time cries are phonated, dysphonated, or hyperphonated. Furthermore, computer-based methods differ from one another (Green et al. 1995). Despite the focus on a subset of possible acoustic properties, and the lack of standardization, some consistent findings do emerge with regard to the acoustic properties of cries of healthy, temporarily stressed, and unhealthy infants.

The cries of healthy, nonstressed infants have the following acoustic characteristics (see the Appendix for a glossary of acoustic terms). The average duration of a single cry is about 0.5–1.5 seconds, the fundamental frequency of a cry falls within the 200–600 Hz range, and the melody is either falling or rising/falling, as opposed to rising, falling/rising, or a flat melody (Table 2). Fundamental frequency is generally, but not necessarily, perceived as pitch. Perceived pitch is not related to fundamental frequency, for example, when the fundamental is attenuated, and higher harmonics are accentuated during filtering in the supralaryngeal vocal tract, but for simplicity the two terms will be used interchangeably here. In addition, biphonation, glides, furcations, and noise concentrations are rare or absent in normal cries, but glottal rolls are common (Furlow 1997; Newman 1985; Wasz-Hockert et al. 1985).

4.2. The infant cry as a graded signal of distress

Infant crying is clearly a means by which infants can communicate needs (e.g., hunger, pain, or discomfort) to caregivers, who may be alerted to appropriately satisfy those

Table 2. *Normal infant cry characteristics*

Acoustic parameter	Values	Source
Duration (sec)	0.4–0.9	Newman 1985
	1.4 ± 0.6	Michelsson et al. 2002
Fundamental frequency range (Hz)	200–600	Porter et al. 1988
	250–450	Wolff 1969
	300–600	Furlow 1997
	400–600	Sirvio & Michelsson 1976
	450–600	Crowe & Zeskind 1992
	496 ± 95	Michelsson et al. 2002
Melody	Falling or rising/falling fundamental frequency	Wolff 1969; Furlow 1997; Michelsson et al. 2002

needs (e.g., by feeding, protecting, or soothing). It is a matter of some controversy, however, as to whether there are acoustically distinct cry types (e.g., hunger cries or pain cries) to which caregivers can respond specifically without additional contextual cues (reviewed by Gustafson et al. 2000).

Work in the 1960s by the so-called Scandinavian cry group is often cited in support of the cry types hypothesis (see Gustafson et al. 2000; Wasz-Hockert et al. 1985). Researchers recorded birth cries, pain cries (during vaccination), hunger cries (4 hours after feeding), and pleasure cries (after feeding). Listener subjects identified the four cry types better than chance (55% correct versus 25% expected). Gustafson et al. (2000) criticized this work, however, because the best exemplars of each cry type were preselected by researchers, and listeners were given the four a priori categories in advance, both of which conditions increased the likelihood of accurate assignment. Additionally, the results were collapsed across all four cry types, so that the positive effect could have been due to only the most easily distinguishable cries, such as the contented coos and babbles that constitute the "pleasure cry." In a replication of earlier work, however, exemplars for each cry type were chosen at random, and results for the four cry types were presented separately (Wasz-Hockert et al. 1968). Additionally, the replication showed that the four cry types differed statistically along several acoustic dimensions, such as fundamental frequency and melody, although the differences were quantitative rather than qualitative. The accuracies in identifying birth, pain, hunger, and pleasure cries were 48%, 63%, 68%, and 85%, respectively (grand mean = 66%).

Other studies also show that subjects can distinguish between cry types. Wiesenfeld et al. (1981) showed that mothers could identify pain cries (rubber band snap) versus anger cries (taking away pacifier or physical restraint) of their own infants better than chance when given three categories from which to choose (pain, anger, or other; 66% correct versus 33% expected). Gustafson et al. (2000) also showed that mothers could identify pain versus hunger cries better than chance when given six cry categories from which to choose (44% correct vs. 17% expected).

When subjects are given open-choice tests, however, the evidence for cry types is not as strong. In an early study by Sherman (1927), cries were elicited from babies by late feeding (hunger cry) and by dropping, restraining, or pricking with a pin (pain cries). Non-mother subjects behind a screen were asked to judge the "emotional characteristics" of the cries, but there was no agreement among listeners, leading to the conclusion that infant cries were merely "undifferentiated noise" (Gustafson et al. 2000). More recently, Muller et al. (1974) played cries elicited by hunger (pulling the nipple away), pain (rubber band snap), and startling (clap of wooden blocks close to the ears). Again, without a priori categories, subjects could not differentiate the cry types, even of their own children. Participants tended to attribute all cries to hunger.

An alternative to the cry types model is the view of the infant cry as a graded signal (Gustafson et al. 2000; Murray 1979). According to this view, vocalizations vary quantitatively on some acoustic dimension, such as duration or frequency, and that graded change along the dimension reflects motivational or emotional state.

There is evidence that the acoustic characteristics of the infant cry function as a graded signal of physical pain (Craig et al. 2000). For example, Porter et al. (1986) showed that during the steps of circumcision, which become increasingly invasive and presumably more painful, individual infant cries became shorter and more frequent, the maximum fundamental frequency increased and became more variable, and harmonics became less distinct. The preoperative maximum fundamental frequency of infant cries was well within the normal range (441 Hz), rose moderately during restraint and preparation (517–640 Hz), and reached the highest levels during the most invasive procedures (707–730 Hz). Postoperatively, the fundamental frequency of infant cries returned to baseline (469 Hz). Similarly, Johnston and Strada (1986) examined infant cries for 1 minute after a painful immunization. The first one or two cries were relatively long and high pitched (mean 627 Hz), followed by a period of apnea. For the remainder of the first 30 seconds, cries were lower pitched (540 Hz) with some dysphonation. During the last 30 seconds, cries pitch was further reduced (478 Hz), and was rhythmic with a rising/falling tone (i.e., normal crying was reestablished). Other studies have also shown that cries elicited by pain have higher fundamental frequencies, as well as other defining acoustic characteristics, such as increased amplitudes and tenseness (Craig et al. 2000; Fuller 1991; Fuller & Horii 1988).

Current evidence supports the notion that the infant cry acts as a graded signal of current distress, at least with regard to pain, although the existence of cry types should not be ruled out. There may be a few basic types of cry (e.g., cries associated with sudden intense distress such as pain, and those associated with low intensity but growing discomfort such as hunger), and there may be graded variation within each type (Gustafson et al. 2000).

4.3. Chronically abnormal cry acoustics are linked to severe illness

In section 4.1 I showed that transient changes in infant cry acoustics reflect acute changes in current levels of distress. Infant cries whose acoustic properties persistently and severely deviate from the norm, however, are associated with chronic poor health (Corwin et al. 1996; Furlow 1997; Green et al. 2000; Newman 1994; Wasz-Hockert et al. 1985). Table 3 summarizes these data. The abnormal infant cry is associated with chromosomal, endocrine, metabolic, and neurological disturbances, as well as malnourishment, toxicity, and low birth weight. Infants with acoustically abnormal cries are also at long-term risk. Infants whose cries had the highest fundamental frequencies, for example, performed poorly on cognitive tests at ages 18 months and 5 years, and asphyxiated infants whose cries were most abnormal in terms of high fundamental frequency, variable fundamental frequency, short duration, and the presence of rising or falling/rising melodies, were the most likely to develop neurological sequelae, including epileptic convulsions, mental retardation, and death (Green et al. 2000; Wasz-Hockert et al. 1985).

In these studies the most common cry characteristic indicating serious pathology is an unusually high fundamental frequency (i.e., very high-pitched crying), often up to three times the normal frequency (compare Tables 2 and 3). Biphonation (the simultaneous production of two fundamental frequencies) is also commonly associated with pathology. One mechanism producing biphonated cries is the independent vibration of the left and right vocal folds at unrelated frequencies (Fitch et al. 2002). Biphonation may be an example of "fluctuating asymmetry" in the voice (Fitch et al. 2002; Mende et al. 1990). Fluctuating asymmetry refers to small departures from bilateral morphologic symmetry, and greater asymmetry is considered an indicator of developmental instability or poor phenotypic quality (e.g., Livshits & Kobyliansky 1991; Moller & Swaddle 1997; Thornhill & Gangestad 1999). For example, human preterm infants and infants with Down's syndrome exhibit a variety of bilateral morphologic asymmetries, including unequal left versus right hand breadth (Livshits & Kobyliansky 1991). Other acoustic qualities of the cry associated with poor health are rapid alterations in fundamental frequency (e.g., vibrato and glides), and rising, falling/rising or flat cry melodies (Table 3). Low fundamental frequency is also associated with a few serious disorders (e.g., Down's syndrome), suggesting that excessively high or low pitch is indicative of poor health.

4.4. Infant cry acoustics affect adult perceptions and physiology

Infant cry acoustics convey acute and chronic distress in infants, but how do these signals relate to parental responses? The most common measure of reactions to infant cries employed questionnaires to obtain adult reactions to tape recordings of infant cries that vary in acoustic structure. Commonly, infant cries of high and variable pitch (usually, but not always, from unhealthy infants, or elicited by a painful stimulus) are variably characterized as aversive, urgent, arousing, grating, piercing, distressing, saddening, or sick, compared to cries that are lower and less variable in pitch (Boukydis 1985; Brennan & Kirkland 1982; Craig et al. 2000; Crowe & Zeskind 1992; Frodi 1985; Lester et al. 1992; Porter et al. 1986; Wiesenfeld et al. 1981; Wood & Gustafson 2001; Zeskind & Marshall 1988; Zeskind & Shingler 1991). Studies that manipulated pitch (or other properties) of cries, independently of other acoustic characteristics, have confirmed these results (Dessureau et al. 1998; Protopapas & Eimas 1997; Zeskind et al. 1992).

A few studies also asked subjects to anticipate their behavioral responses to infant cries. Some studies indicated that high and variable pitched crying would lead to ignoring the infant, abusing the infant, or other nonoptimal responses (Frodi 1985; Frodi & Senchak 1990; Zeskind & Shingler 1991). In other studies, however, the cries of high-risk infants and acoustically abnormal cries elicited more positive responses, such as shorter anticipated latency to respond and more "tender and caring" responses (Gustafson et al. 2000; Wood & Gustafson 2001; Zeskind 1980). Also, Lester et al. (1995) showed that infants whose mothers rated their high-pitched cries as negative scored higher on language and cognitive tests at age 19 months, compared to infants of mothers who did not rate high-pitched cries as negative. This result suggests that accurate perception of high-pitched crying may lead to positive responses in mothers.

High- or variable pitched cries produce autonomic arousal, as measured by, for example, heart rate or skin conductance (Boukydis 1985; Crowe & Zeskind 1992; Frodi 1985; Frodi & Lamb 1980; Wiesenfeld et al. 1981; Zeskind 1987). Additionally, some studies have shown that abusers, or those determined to be likely to abuse, exhibit higher autonomic responses to high-pitched cries (Crowe & Zeskind 1992; Frodi 1985; Frodi & Lamb 1980; Zeskind 1987). Donovan and Leavitt (1985) showed that viewers exhibit higher autonomic responses to crying infants compared to smiling infants. It is not clear what specific behaviors such autonomic arousal is likely to motivate. Frodi (1985) argued that increased autonomic response motivates abuse, whereas Donovan and Leavitt (1985) argued that it motivates help. Zeskind (1987) argued that heart acceleration and deceleration reflect aversiveness and special attention, respectively.

These studies of adult perceptual and physiological responses to infant cries do tell us that the infant cry is emotionally salient and arousing to adult listeners, especially the high-pitched cry. They do not tell us, however, that such crying elicits any uniform positive or negative response from actual parents. The child abuse and infanticide literature, on the other hand, can yield information on the risk factors associated with abuse and killing of offspring.

4.5. Cry acoustics and infant maltreatment

The cross-cultural ethnographic evidence presented earlier demonstrates that the poor quality of an offspring is a common risk factor for neglect, abuse, and infanticide in humans (see sect. 2.2 and Table 1). Although the relationship between abnormal characteristics of the offspring and maltreatment is clear, it is not clear directly from these literatures that high-pitched or otherwise abnormal crying is a precipitating factor. Several considerations do suggest that

Table 3. *Pathological conditions of infants and associated acoustic characteristics of infant cries*

Condition	Fundamental frequency (Hz)	Biphonation	Melody	Glide	Other
Asphyxiation – peripheral[a]	High pitch mean max: 1000	>20%	Rising, or falling/rising >30%	>10%	
Asphyxiation – central[a]	High pitch Mean max: 1460	>20%	Rising, or falling/rising >30%	>10%	
Bacterial meningitis[a,b,c]	High pitch Mean max: 750–1000	49%	Rising, or falling/rising 24%	11%	
Cardio-pulmonary disorder[b]	High pitch	Present			
Chromosome 13 & 18 trisomy[b]	Low pitch		Flat		
Chromosome 4 & 5 abnormalities[b]	High pitch				
Congenital hypo-thyroidism[a]	Low pitch Mean min: 270 Mean max: 470				
Cri-du-chat syndrome[a,c]	High pitch, Mean: 600–1000		Flat (36%) Rising (23%)		
Cocaine exposure in utero[b]	High pitch				
Colic[b]	High pitch				
Diabetic mother[a,b]	High pitch Mean max: 1480				
Down's syndrome[a,b]	Low pitch Mean min: 270 Mean max: 510		Flat (63%)		Long duration mean: 4.5 sec
Krabbe's disease (malformation)[a]	High pitch Mean min: 590 Mean max: 1120		Rising/falling (27%)		
Herpes simplex viral encephalitis[a,b]	High pitch	Present		Present	Noise con--centration
Hydrocephalus[a,b,c]	High pitch Mean min: 430 Mean max: 750–970	14%	Flat	8%	
Hyperbilirubinemia[a]	High pitch Mean min: 960 Mean max: 2120	49%			Furcation
Hypoglycemia[a,b]	High pitch mean max: 1600	67%		18%	Vibrato
Lead exposure[b]	High pitch				
Low birth weight[b]	High pitch				
Metabolic disorders[b]	High pitch				
Neurological symptoms[b]	High pitch				
Obstetric/delivery complications[b]	High pitch				Short duration
Premature birth[a]	High pitch Mean min: 570 Mean max: 1360				
SIDS[d]	High pitch				

[a]Wasz-Hockert et al. 1985. [b]Furlow 1997. [c]Newman 1994. [d]Corwin et al. 1996.

it may be a factor, however. First, infants with defects that are associated with abuse are the same infants who present abnormal cry acoustics such as high-pitched crying. Second, parents have described crying as the most proximate cause triggering abuse and infanticide (e.g., Frodi 1981). In one study, crying was the proximate cause of fatal abuse in 58% (14/24) of cases (Brewster et al. 1998). In another, 70% (16/23) of mothers whose infants' cries were excessive, high-pitched, and "shrieking" had fantasies of abusing, abandoning, or killing their crying infants (Levitzky & Cooper 2000). Third, experimental evidence demonstrates that high-pitched crying sometimes, but not always, elicits strong negative emotions in adult listeners (see the sources cited above), and these negative emotions are stronger in abusers than in nonabusers (Crowe & Zeskind 1992; Frodi 1985). With regard to the last point, it is possible that the aversion threshold toward acoustically abnormal cries differs across adults and that it originates in adult dispositions prior to parenthood. For example, pregnant women who later rated their infants as "difficult" showed higher autonomic arousal to recordings of a healthy infant cry, and expressed stricter child-rearing attitudes, compared to pregnant women who later rated their infants as "easy" (Frodi et al. 1989).

4.6. A model of early infant cry acoustics and parental response

Here I propose a model of the signal effects of infant cry acoustics that will require further evidence to confirm (discussed in sect. 7, Conclusions and Prospects). For illustrative purposes, I focus on the fundamental frequency because it has been particularly well-studied, but the same logic can be applied to other acoustic properties. In healthy infants, the acoustic properties of the early infant cry function as a graded signal to adult listeners. The fundamental frequency of the cry conveys salient information regarding degree of distress. The physiological connection between distress and high-pitched crying is mediated by the vagus, in particular the branch of the vagus linking the nucleus ambiguus to the larynx. During acute stress (e.g., pain or fear), the sympathetic nervous system is activated and the parasympathetic nervous system is attenuated. As part of the parasympathetic withdrawal, vagal tone is lowered, fostering a multitude of physiological reactions including an increase in heart rate and a rise in the pitch of vocalizations (Porges 1995; 1997; Porter et al. 1988). According to this view, the cry acts generally to alert caregivers of nonspecific need (e.g., Ostwald & Murry 1985), but the acoustic properties (including, but not limited to, fundamental frequency) vary as a direct reflection of autonomic nervous system activity and emotional state, providing caregivers with information concerning the intensity of infant need or distress. Such acoustic information may influence the latency and urgency of response in caretakers. The actualization of specific responses is likely influenced by a combination of information in addition to the cry sound, such as infant facial expressions and gestures (Craig et al. 2000; Green et al. 1995; Gustafson & Green 1991; Johnston & Strada 1986), as well as by the context (e.g., time since feeding; Bernal 1972).

When infants are chronically ill or stressed, then crying is chronically abnormal, characterized by extremely high pitch, variable pitch, and the presence of biphonation (Table 3). Although the same mechanisms that mediate transient changes in cry pitch during acute stress may also operate when infants are chronically ill, the acoustic abnormalities associated with severe pathology differ from transient acoustic changes associated with acute stress in two important ways. First, the acoustic abnormalities are chronic. Low birth weight children, for example, persistently exhibit mean vagal tones 2.2 times lower than the norm, even while sleeping (Porges 1995), and diminished vagal input to the larynx produces higher fundamental frequencies (Green et al. 2000; Porges 1995; Porter et al. 1988). Second, acoustic deviations associated with severe pathology are greater in degree than acoustic deviations associated with transient distress. Specifically, the fundamental frequency of normal cries is 200–600 Hz, whereas the fundamental frequencies observed in transient pain cries, for example, are only slightly outside this range (up to 730 Hz). The fundamental frequencies of cries associated with severe pathology, on the other hand, are usually greater than 1000 Hz (Table 3). Finally, biphonated cries, a possible instance of fluctuating asymmetry resulting from developmental instability, are rare or absent in normal infants but are common in infants with pathology.

In contrast to infant cries within the normal range described above, including those associated with transient distress, the more chronically and severely abnormal infant cries are, the more likely they are to be a proximate cause of adaptive neglect, abuse, or infanticide. In premodern environments, severely ill infants would have had very low chances of survival, and theory predicts that selective withdrawal of investment can be adaptive in such circumstances. Moreover, evidence demonstrates that severe illness in infants can precipitate maltreatment, and because severe illness is precisely what chronically abnormal crying reveals, the infant crying can be the proximate cause of abuse. The persistently abnormal cry (along with other infant characteristics such as listlessness or small size) may activate psychological mechanisms in caregivers that include converting the infant cry from a motivator of sympathetic altruism (e.g., Hoffman 1975; Murray 1985) to a motivator of abuse or infanticide (e.g., Frodi 1985; Frodi & Lamb 1980; Mann 1992). This view of dynamic psychological dispositions in parents is supported by the fact that high-pitched crying is often viewed as aversive, and, more important, that abusive parents react more strongly and negatively to high-pitched cries than do nonabusive parents (e.g., Crowe & Zeskind 1992; Frodi 1985). Indeed, one study has shown high-pitched crying to be associated with fantasies of infant maltreatment (Levitzky & Cooper 2000).

The proposed effects of infant cry acoustics can be integrated into the multilevel model of parenting determinants described earlier. According to the multilevel model, factors such as infant and parental characteristics, household dynamics and economy, and the wider community and culture jointly influence patterns of parental care and abuse. The most important point is that maltreatment is multiply determined by many factors, and single variables are unlikely to be necessary or sufficient determinants of maltreatment (Belsky 1993). The persistent and severely abnormal cry may be one of many factors influencing parenting choices. For example, a lack of spousal and other social support could create a condition in which a new parent withdraws care from a burdensome infant, in particular if cultural and parental values do not rule out infanticide or abandonment. Under these circumstances, the poor condition of the child, gleaned in part by the persistently abnormal acoustic quality of crying, may tip the scales in some parents from acceptance to rejection. This is not to say that persistent and severely abnormal crying will invariably result in infant abandonment or maltreatment. Under the same circumstances, but with strong spousal and social support, for example, even very sick infants may not be maltreated. Additional scenarios could be produced in which healthy infants may or may not be maltreated, depending on circumstances. The model does predict the following, however. All things being equal, normal acoustic variation in the infant cry, including that associated with autonomic arousal due to transient distress, is that most likely to elicit positive caregiving. On the other hand, the more acoustically abnormal cries are, both in terms of their persistence and distance from the normal range, the more likely that crying will result in the reduction or withdrawal of parental care, including suboptimal care, neglect, abuse, abandonment, and infanticide.

4.7. The evolution of the early infant cry and mother-infant communication

The comparative anatomy of living animals suggests that the larynx evolved vocalization capabilities very late relative to the integrated and evolutionarily conserved autonomic nervous system that innervates it. The autonomic nervous system is developed in all vertebrates and is evolutionarily conserved, particularly in tetrapods (Butler & Hodos 1996). In primitive vertebrates (air-breathing fish), however, the larynx functions as a protective valve involved in feeding and swallowing (Butler & Hodos 1996; Hofer 2002). As air breathing increased in importance, the vertebrate larynx strengthened to accommodate additional functions such as optimizing airflow and protecting the lungs from foreign matter. Only later in vertebrate evolution was the larynx further modified for additional functions including vocalizing (Armstrong & Netterville 1995; Hofer 2002; Kirchner 1993; Laitman & Reidenberg 1997). This evolutionary history demonstrates that the vagal regulation of conserved laryngeal functions such as swallowing and breathing was already in place when the derived laryngeal function of vocalizing evolved. As part of the overall autonomic stress response, therefore, vagal input to the larynx regulating conserved functions would have concurrently affected vocalization acoustics as well. The vagus also regulates the stress response in other organs such as the bronchi, esophagus, pharynx, and heart. Acoustically distinct early infant crying during acute and chronic stress is likely a necessary by-product of integrated autonomic nervous system mobilization, and parents may have evolved to react to this acoustic information.

The following simple evolutionary sequence gives an idea of how natural selection may have elaborated laryngeal functions and the behavior of mothers to form communication systems. Hofer (2002) separated rat pups from their mothers and showed that consequent ultrasound separation vocalizations involved "laryngeal braking" (increased air pressure when the larynx closes on escaping air), and that this phenomenon regulated recovery from hypothermia. Crying in human infants also retains a thermoregulatory function by generating heat (Lester 1985). Hofer argued that laryngeal breaking first evolved in mammalian infants because it facilitated recovery from hypothermia when maternally separated, and that the behavioral complex involving separation calls and retrieval came into being when mothers later evolved to respond to those ultrasound emissions by retrieving their separated infants. To this it could be added that early mammalian infant vocalizing also varied acoustically as a function of autonomic nervous system arousal, and that mothers later evolved to respond differentially to infant cries according to these varying acoustic characteristics.

As Furlow (1997) has argued, if parents evolved the ability to determine the level of infant distress based on the acoustic properties of cries, then these properties can be considered to be honest signals of need. Crying is metabolically costly (Rao et al. 1997), the autonomic arousal producing acoustic changes (e.g., in fundamental frequency) imposes additional costs (Nelson 2000), and there is evidence that the fundamental frequency of cries accurately reflects the degree of physical pain.[4] Because such cry acoustics are likely unalterable manifestations of autonomic nervous system activity, however, they may not necessarily result in increased care from parents. As I argued earlier, cries resulting from transient distress are more likely to increase care, but under some circumstances chronically and severely abnormal cries resulting from serious pathology may inhibit care.

5. Excessive crying and colic

5.1. The colic syndrome

Excessive infant crying is the most common clinical complaint of mothers with infants under three months of age (Forsyth et al. 1985). The core symptom of colic is excessive, inconsolable crying that begins and ends without warning (Gormally & Barr 1997; Lehtonen et al. 2000). Colic is most commonly defined according to Wessel's operational "rule of 3's," in which an infant cries for more than three hours a day, for more than three days a week, for more than three weeks (Wessel et al. 1954). Definitions of colic based on the amount of crying, namely, Wessel's rule of 3's and its variations (Sijmen et al. 2001), are collectively known as "Wessel's colic."

There are also definitions of colic that are qualitatively different, however, which include symptoms in addition to the amount of crying (e.g., Lester 1997). Such additional symptoms include (1) high-pitched crying, (2) hypertonia (e.g., clenched fists, flexed legs, grimacing, distended abdomen), and (3) flatulence, regurgitation, vomiting, or diarrhea. I will refer to excessive crying meeting Wessel's criteria but with any of these additional symptoms as "Wessel's plus colic" (following Gormally & Barr 1997). Colic is also characterized by two temporal crying patterns (Barr 1990c; Gormally & Barr 1997; Lehtonen et al. 2000). Developmentally, crying increases from two weeks after birth, peaks in the middle of the second month, and resolves by the fourth month. Diurnally, crying bouts cluster in the late afternoon and early evening hours, and this clustering pattern is most marked during the sixth week peak in overall crying (Barr 1990c). Prevalence rates vary widely (ranging from 2–40%), depending on the definition used and whether or not the infants are from a referred clinical population or a community sample (Barr 1999; Canivet et al. 2002; Sijmen et al. 2001; Sondergaard et al. 2000).

In what follows I argue that what is labeled as colic represents the extreme cases of an otherwise normal and universal increase in crying during the first few months of life. I go on to discuss factors that may contribute to variation in the amount of infant crying, such as maternal style and infant temperament. I evaluate the potential signal functions of excessive crying in section 6.

5.2. Colic is part of the normal infant crying curve

An n-shaped curve of increased crying during the first three months of life is a typical feature of human development, and those with colic comprise the extreme end of this distribution. Brazelton (1962) first detected the infant crying curve in data gleaned from the diaries of 80 mothers. Since then, various methodologies have shown that the crying pattern of infants is characterized by an overall increase in crying until about age 6 weeks, followed by a gradual decrease in crying until 3 or 4 months, after which it remains relatively stable (Barr 1990c; Lehtonen et al. 2000). In addition, crying undergoes a diurnal rhythm, with clustering in the late afternoon and early evening hours, and this diurnal clustering is most marked during the sixth week peak in overall crying (Barr 1990c). These same developmental and diurnal patterns are found in both "normal" infants and infants with colic (Lehtonen et al. 2000; St. James-Roberts & Halil 1991; St James-Roberts et al. 1994).

The crying curve manifests itself across different cultural contexts. The !Kung (South African hunter-gatherer society) exhibit a crying curve similar to a Dutch sample (Barr et al. 1991). Both Manili and London infants experience a sixth week crying peak, and the diurnal cluster of early evening crying (St. James-Roberts et al. 1994). Similar amounts of crying, the same evening cry clustering, and similar incidences of persistent crying characterize Denmark, United Kingdom, and North American infants (Alvarez & St James-Roberts 1996). Taken together, the data indicate that the crying curve in infants is a common property of neonates in a wide variety of cultural contexts, although it should be remembered that within populations there is always extensive individual variation. Excessive criers labeled as having colic are simply those individuals who show the most extreme form of an otherwise normal and universal crying curve.

5.3. An organic etiology of colic is rare

In a minority of cases colic has known organic etiology, but in these cases infants exhibit symptoms in addition to excessive crying. Gormally and Barr (1997) and Lehtonen et al. (2000) estimated that 5% to 10% of colic cases are due to organic disorder. The most common of such etiologies are cow's milk protein intolerance, and (rarely) other ailments such as fructose intolerance and infantile migraine. There is weak evidence for other organic causes such as reflux esophagitus and lactose intolerance. Most important, colicky infants with organic etiology are those who have symptoms in addition to excessive crying (i.e., Wessel's plus colic), such as high-pitched crying, arched back, regurgitation, vomiting, and diarrhea (Barr 1999; Gormally & Barr 1997; Lehtonen et al. 2000). Part of the reason behind the perception that colic is associated with disease is that those studies showing such an association are based on highly selective samples of excessive criers with additional symptoms of organic disease (Gormally & Barr 1997).

Some recent studies have continued to show that colic is associated with poor health, such as low fetal birth weight and maternal smoking (Sondergaard et al. 2000; 2001). In these cases, too, however, infants identified as colicky possess symptoms in addition to excessive crying, such as flexed legs, distended abdomen, and excessive flatus. Kanabar et al. (2001) showed that lactase-treated feed reduced crying by more than 45% in colicky infants, indicating the specific organic etiology of lactose intolerance, but the definition of colic included spasm, lower limb flexure, and diarrhea. In short, when colic simply refers to excessive crying (i.e., Wessel's colic), then it is not attributable to or associated with organic pathology, but when it refers to that subset of cases in which there are additional symptoms (i.e., Wessel's plus colic), then it is more likely attributable to organic causes.

5.4. Colic cries are not acoustically abnormal

If most cases of colic are not due to illness, then cries of infants with colic should not be the high-pitched cries associated with illness (Table 3). However, Lester et al. (1992) and Lester (1997) showed that infants with colic have higher and more variable pitched cries than do controls. High-pitched crying itself was part of the definition of colic in both studies, however, so it is not surprising that those subjects did present acoustic abnormalities, including, of course, higher pitched cries. Moreover, infants in both samples had symptoms in addition to excessive and high-pitched crying, such as premature birth or hypertonia. These infant subjects were drawn from that small subset of colicky infants with physical ailments (Wessel's plus colic). Even so, the mean fundamental frequency of their cries was well within the normal range (492 Hz for "colic" infants and 414 for controls; see Table 2).

Zeskind and Barr (1997) showed that cries of colic infants (without additional symptoms) do have higher mean fundamental frequencies than those of controls, but the cries are within the normal range (mean 591 Hz for colic, and 498 for controls). St. James-Roberts (1999) found no significant difference between the mean fundamental frequency of Wessel's colic cries (491 Hz) and controls (458 Hz). Finally, infants with Wessel's colic and controls do not show differences in autonomic nervous system balance (which affects cry pitch) during the time of colic or after its resolution (Kirjavainen et al. 2001). For the most part, infants with colic produce higher pitched cries than their non-colicky counterparts only when they have Wessels' plus colic, and there is no evidence that infants with colic (by any definition) have fundamental frequencies outside the normal range.

5.5. Maternal style affects early infant crying

Despite the cross-cultural validity of the early infant crying curve, cultural and individual variation in maternal style can attenuate the crying curve. In particular, increased responsiveness to fussing or crying infants lessens the overall amount of infant crying. For example, the number of crying *bouts* is the same for both !Kung and western infants, but the total *duration* of !Kung infant crying is half that of the western infants (Barr et al. 1991). Unlike most western mothers, !Kung mothers carry their babies continuously (>80% in the daytime), engage in continuous feeding (4 times/hr), and are highly responsive to infant fretting (92% response within 15 sec), usually with breast-feeding (Barr et al. 1991; Konner & Worthman 1980). This contrasts with the normative western caregiving style in which infants are not in constant contact with mothers and crying infants are often deliberately ignored up to 40% of the time (Barr 1999). Generally, traditional societies are characterized by the indulgent maternal style (Barr 1999; Zeifman 2001).

Within western societies, variation in maternal style also has been shown to affect the amount of early infant crying. Crying decreases when mothers increase infant carrying (Hunziker & Barr 1986), eliminating the 6-week peak in crying, but not the diurnal clustering. St. James-Roberts et al. (1995) replicated this methodology, however, and found that increased infant carrying did not decrease crying amount. In another study comparing La Leche League (an avid pro-breast-feeding group) mothers to "standard" breastfeeding mothers, frequent nursing reduced the number of crying episodes at 2 months of age (Barr & Elias 1988).

5.6. Infants with colic do not have difficult temperaments

When the excessive crying diagnostic of colic resolves, no long-term differences persist between infants with colic and those without it, although the parents of infants with colic may *perceive* that they do (Barr & Gunnar 2000; Gormally & Barr 1997; Lehtonen et al. 2000). In some studies claiming that a difficult temperament and colic are associated with one another, measures of temperament were recorded before colic resolved, and the excessive crying and fussing diagnostic of colic also contributed to the difficult temperament designation (e.g., Carey 1972). Using this methodology, infants with colic have difficult temperaments by definition (Barr & Gunnar 2000).

One way to avoid this circularity is to examine older children with and without histories of colic to see if difficult temperaments persist after the excessive crying has resolved. In general, such studies show that parents may perceive their formerly colicky offspring as "difficult," but actual behavioral or physical differences are not apparent (Barr & Gunnar 2000; Lehtonen et al. 2000). For example, in four colic follow-up studies summarized by Barr (1998b), mothers of excessive criers often perceived their infants as difficult, and were themselves distressed even after the colic resolved. In the majority of cases, however, there was a reduction in infant crying, little maternal distress, and normal attachment relationships. Additionally, St. James-Roberts et al. (1998) found that infant negative behaviors at age 6 weeks do not predict behavior at age 15 months, and Canivet et al. (2000) showed no long-term differences between ex-colics and controls in behavior, growth, weight, height, or days in the hospital. In both studies, however, parents rated their formerly colicky children as more emotional or difficult.

5.7. Infant responsivity affects early infant crying

Infant characteristics are also likely to contribute to variation in the amount of early infant crying. I have argued in this target article that colic is not a manifestation of infant temperament. Barr and Gunnar (2000) have offered a related explanation (also see Blum et al. 2002), the *transient responsivity hypothesis,* according to which infants differ in their responsivity to similar stimuli, and these differences are manifested as variable amounts of crying. The key difference between the temperament hypothesis and the transient responsivity hypothesis is that according to the former, individual differences among infants are permanent features of the individual's constitution, and according to the latter the differences among infants are transient.

Supportive evidence for the transient responsivity hypothesis is that the pattern of early infant crying itself (i.e., the crying curve) is transient, as described above. Crying undergoes a developmental change at around age 3 months, at which time the crying becomes less frequent but more context-dependent, intentional, and communicative (Barr 1990c; Barr & Gunnar 2000; Ostwald & Murry 1985). Furthermore, sleep patterns, attention to visual stimuli, and cortisol response to immunizations also undergo a similar developmental curve. Finally, measures of temperament and emotional regulation in early infancy are not predictive of later stages of development, but measures taken after age 3 months are (Barr & Gunnar 2000).

The increased responsivity of infants with colic may be due, in part, to an opioid-dependent mechanism regulating crying behavior (Barr & Gunnar 2000; Panksepp et al. 1988). Sucrose is an opioid-dependent calming agent in both crying infants and maternally separated nonhuman primates. The initial suckling stimulus and the sucrose itself exert independent calming effects, with the sucrose effect lasting longer and mediated by opioids. The crying of infants with colic is regulated just as much as controls in the first minute after sucrose exposure, but infants with colic return to crying sooner than controls during the late opioid-dependent phase. This suggests that the variation in amounts of infant crying may be due in part to variation in the opioid-mediated regulation of crying, and that those infants characterized as having colic may be those least regulated.

6. The signal functions of excessive infant crying

6.1. Excessive crying as a manipulative signal

Lummaa et al. (1998) and Barr (1999) argued that early excessive crying in infants may, in addition to serving other functions, be a manipulative signal by which infants attempt to gain a disproportionate share of parental resources. Specifically, excessive crying prolongs the period of investment for an individual offspring by increasing breast-feeding, maintaining a longer state of lactational amenorrhea, and thereby postponing the next pregnancy. Indeed, in traditional societies, interbirth intervals are often long (up to 4 years), in large part as a result of continuous breast-feeding and resultant lactational amenorrhea, and crying is often a proximate cause of breast-feeding (Barr 1999; Barr et al. 1991; Blurton-Jones 1986; Konner & Worthman 1980; Zeifman 2001).

Further consideration of parent-offspring conflict, however, contradicts this manipulative view of the signal function of early infant excessive crying. The conflict between parents and offspring should increase and become most pronounced at the end of the period of parental investment. During the first three months of life, disagreements over the flow of resources should be lowest. As the period of investment proceeds, however, and the production of a new child becomes increasingly advantageous for the mother, then parent-offspring conflict should increase. In fact, it has been argued that in hunter-gatherer societies interbirth intervals that are too short are *disadvantageous* for the mothers' lifetime reproductive output because of the cost of carrying infants and food at the same time (Blurton-Jones 1986; 1987; Winterhalder & Smith 2000). Additionally, close birth spacing is one of the principal rationales for infanticide in the cross-cultural survey (Table 1).

If the amount of infant crying reflects the degree of parent-offspring conflict over the length of investment, therefore, then it should start at low levels in early infancy, increase over the duration of investment, and peak at weaning, when conflict is at its greatest. The crying curve of early infancy, however, shows the opposite temporal pattern. Crying peaks in the second month and is greatest in the first three months of life compared to later infancy and toddlerhood. This is not to say that crying and other behaviors are not used in later development as a means of prolonging investment. I am merely arguing that this is an unlikely explanation for increased crying in early infancy.

Manipulative crying need not be narrowly construed as only functioning to prolong investment and postpone the next birth, but could function to increase attention and care throughout early infancy. It might be argued that individual variation in the amount of crying could be explained by differences in parental styles, with indulgent parental styles resulting in less manipulative crying and less indulgent styles resulting in more manipulative crying. The temporal pattern of early excessive crying is difficult to reconcile with this notion, however. Manipulative crying that exaggerates need for attention or breast-feeding, for example, cannot be expected to exhibit the sixth week peak or the early evening peaks that are observed.

6.2. Excessive crying as an honest signal of need

Another possible signal function is that excessive early infant crying is an honest signal of need, according to which individual variation in crying amount honestly reflects different resource requirements. One requirement of this hypothesis is that there be costs associated with crying. Rao et al. (1997) documented that infant crying is energetically costly, with a 13.2% increase in metabolic rate compared to resting. Another prediction is that excessive crying should be associated with either transient distress or permanent poor health. There is no clinical evidence, however, that excessive crying is associated with immediate, transitory needs, such as distress or hunger. In fact, transitory stresses cannot be expected to follow the distinct temporal patterns of early infant excessive crying, such as the sixth week peak or the diurnal pattern of early evening clustering. Neither does excessive crying reflect overall poor health. Only in a minority of cases, when additional symptoms are involved (i.e., Wessel's plus colic), is excessive crying associated with illness. In short, there is no support that excessive crying observed in early infancy is associated with an increased need for parental resources.

6.3. Excessive crying as an honest signal of vigor

Barr (1998a) and Lummaa et al. (1998) argued that excessive crying or colic may be an honest signal of vigor to avoid infanticide. This argument does not require that infant variation in quality be the only factor influencing cry amount. For example, I argued that maternal style explains some of the variation in the amount of infant crying. An indulgent maternal style may explain the higher *average* amount of early infant crying in the !Kung compared to western societies. Within each population, however, there is still extreme individual variation in the overall amount of early infant crying, and these within-population differences may be explained by variation in infant quality.

Current evidence is more consistent with this view than with the two hypotheses discussed above. First, such signals are adaptations to those specific environments in which parents withdraw investment or kill infants when the prospects for infant survival are low. Abundant cross-cultural evidence indicates that such selective withdrawal of parental investment is a normative aspect of our species' behavioral repertoire. Second, in order for such signals to be honest, the cost of crying has to be higher for low quality infants than for high quality infants. Two studies demonstrate this key prediction. Rao et al. (1997) showed that infant crying is energetically costly, and, more important, they demonstrated that metabolic expenditure is higher for low quality (low weight and preterm) infants than for high quality (normal weight, full-term) infants. Similarly, in a mock physical examination White et al. (2000) found that infants with colic cried longer, more intensely, and more inconsolably than infants without colic. Despite increased crying, however, infants with colic did not show any differences in heart rate, vagal tone, or cortisol secretion during the examination. Furthermore, daily salivary cortisol levels of excessive criers were also indistinguishable from controls, despite the fact that they cried for more hours per day. These results suggest that colicky infants experience no more physiological stress as a result of excessive crying compared to infants who cry less.

Third, if excessive crying is a signal of high quality then infants with colic should have higher survival or better developmental outcomes compared to other infants. Supportive evidence of this is not strong, however. The fact that crying is less costly for infants with colic compared to controls does suggest that the infants with colic may be of higher *current* quality than infants who cry less, but there is no clinical evidence showing that infants with colic are in better health or have better outcomes than infants who cry less. Of course, infants who are severely ill may cry very little or not at all, so that the lower bound crying amount (i.e., little or none), compared to all other cry amounts, is related to infant survival in the way predicted by the signaling vigor hypothesis. But it is unclear if the remainder of the variation in cry amount is also related to health or survival. It is possible that modern medical environments mask most health differences among infants who cry in different amounts. The differences in survivability between excessive criers and those who cry less may only become apparent in more variable environments, when conditions are sometimes exceptionally poor. Supportive evidence for this view comes from a study of the Massai, traditional African subsistence herders (deVries 1984). Masai infants identified before a drought as having difficult and fussy temperaments were more likely to survive the drought (5/6 = 83%) compared to those infants with easy temperaments (2/7 = 29%). It should be noted that the infants were past 4 months of age, however, when the normal infant crying curve has normally resolved.

Finally, the temporal pattern of excessive early infant crying mirrors the expected and observed temporal pattern of the probability of infanticide in humans. Theory predicts that psychological mechanisms influencing the continuation of parental investment in offspring should be activated soon after birth, so that losses can be cut early if the prospects for infant survival are poor. Indeed, the observed incidence of infanticide by parents is highest in the first three months of life, then decreases over the rest of the first year (Daly & Wilson 1988; Overpeck et al. 1998). Figure 1 shows that the amount of infant crying over the first year

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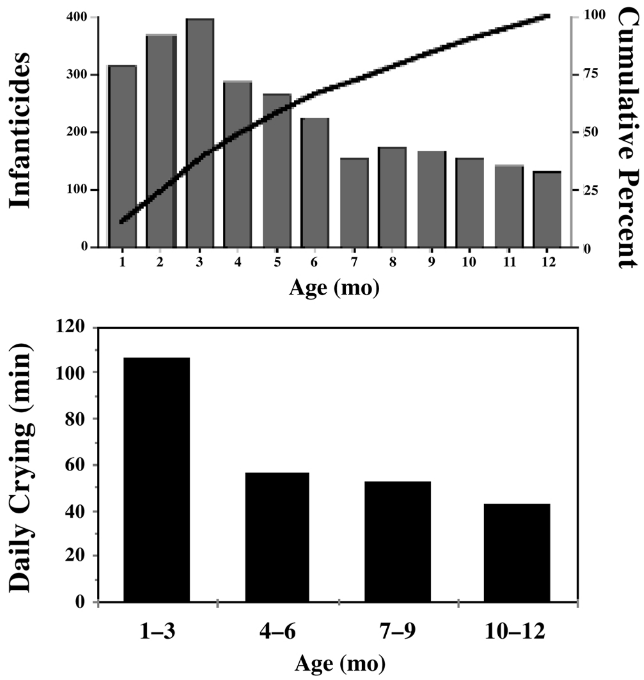

Figure 1. Relationship between number of infanticides and amount of infant crying in the first year of life. Both infanticide and infant crying are highest in the first three months of life, and decrease throughout the year. Infanticide data in the upper panel are from 2776 infanticides in the United States (from Figure 1 of Overpeck et al. 1998). Crying data in the lower panel are for 590 infants in Denmark (redrawn from data in Figure 1 of Alvarez & St. James-Roberts 1996). Upper panel copied with permission. Copyright 1998 Massachusetts Medical Society. All rights reserved.

mirrors this temporal pattern of infanticide risk (Alvarez & St. James-Roberts 1996; Barr 1990c).

This pattern is consistent with the interpretation that excessive crying has evolved to signal vigor to avoid the withdrawal of parental care, but it is also consistent with other interpretations. First, the causal relationship could be reversed, such that excessive infant crying is itself a proximate cause of infanticide. Two studies are relevant here. Brewster et al. (1998) examined 32 cases of infanticide among U.S. Air Force personnel and found that crying was the proximate trigger of the fatal abuse in 58% of cases (14/24 for which data were available), and that colic was indicated in the medical records of 35% (7/20) of cases. However, no definition of colic was available, there was no control group for comparison, the average age of death was about 5 months (past the usual resolution of colic), and only 10% (2/20) of parents reported colic to their physicians. The authors concluded that colic was overestimated by physicians due to crying at visits that resulted from nonfatal physical injuries prior to the infanticides (12/22 = 55% of cases). In another study, mothers of infants identified as having colic had fantasies of abuse and infanticide (Levitzky & Cooper 2000). Those infants had Wessel's plus colic, however, which included high-pitched crying, shrieking, and hypertonia – symptoms in addition to the excessive crying identified with colic. Earlier, I suggested that the acoustic quality, not the quantity of crying, was the trigger for abuse fantasy (sect. 4.5). At present there is no strong evidence showing how excessive (or acoustically abnormal) crying influences the immediate abusive responses of caregivers.

Second, infanticide and excessive crying may not be causally related to one another but each may be independently related to early development. As I have argued, infanticide may be most likely at younger ages because it benefits parents to cut losses early if the infant has diminished survival chances. At the same time, increases in crying during early infancy may be part of developmental processes unrelated to infanticide probability, such as sleep-wake cycles specific to the first three months of life (Lester 1985; Zeifman 2001). Unlike the previous two hypotheses, however, the pattern conforms to expectations from the signaling vigor hypothesis. In conclusion, although the evidence in support of the signaling vigor hypothesis is not strong, it is more consistent with this hypothesis than with the signaling need or manipulative signaling hypotheses.

7. Conclusions and prospects

The human infant cry literature is fraught with controversy. Here I evaluated evolutionary approaches that may illuminate the signal functions of the early infant cry. Overwhelming cross-cultural evidence suggests that the reduction or withdrawal of optimal care when child-rearing circumstances are unfavorable is a prominent feature of human evolutionary history. Such an environment of uncertain parental care constitutes a strong selective pressure on the human infant, including its cry signal, which can influence the behavior of potential caregivers.

Of course, the most obvious signal function of the early infant cry is to maintain proximity and elicit care from caregivers, and I do not dispute that essential role for infant crying. Although there is not strong evidence for acoustically distinct cry types that reflect specific needs, there is evidence that the acoustic properties of infant cries function as a graded signal, at least with regard to level of pain. To further investigate the communicative content of infant crying, it will be necessary to identify the set of acoustic parameters that contain the most salient information. The universe of potentially important cry acoustics is large, and the choice of the most important acoustic measures should continue to be developed based on physiological models of cry production, keeping in mind that the voice acoustics may be affected by activity along the entire vocal production pathway, including respiration, vocal fold behavior, and vocal tract shape. In addition, acoustic measurement needs to be standardized. With such acoustic properties and measurements in hand, statistical techniques (e.g., discriminant analysis) can be used to determine the extent to which cries resulting from different causes can be categorized into acoustically distinct types, or to further show how graded acoustic variation reflects degree of distress. Naturalistic observations and perceptual experiments on parents (preferably using the cries of their own infants) can determine if and how parents attend to these acoustic properties of cries.

I proposed a model describing how the acoustic characteristics of infant cries may influence patterns of parental care and abuse. Some of the most important evidence regarding this proposal is precisely that which is unavailable, namely, the immediate and cumulative parental responses to infant cries depending on the acoustic qualities of cries. In the case of negative responses such as neglect, abuse, and infanticide, this is not surprising because the most proximate precursors to such maltreatment cannot be directly observed and such parents are not enthusiastic participants in research. Future work on maltreatment, in particular when infant health is compromised, should include information on the acoustic properties of infant cries, questionnaires or interviews of parents, and studies of cry perception to determine the relationship of cry quality to maltreatment potential, maltreatment fantasy, and actual maltreatment. With regard to variation in parenting that does not involve maltreatment, naturalistic home audiovisual recordings could yield information on acoustic analysis of cries and parental responses. Additionally, experiments on the perception of infant cries that vary in quality should be continued to determine the physiological and anticipated behavioral responses of parents, in particular to cries of their own offspring. Finally, the perception of crying as particularly aversive in abusers could result from the cumulative effects of acoustically abnormal crying, unfavorable child-rearing circumstances, or prior dispositions in abusive parents. Longitudinal studies of parents will be necessary to understand how parental characteristics, child-rearing circumstances, and the acoustic qualities of cries influence adverse parental responses to cries.

There was no strong support for any of the proposed signal functions of excessive early infant crying, although the data were most consistent with the signaling vigor hypothesis. To further test these ideas, the immediate and cumulative effect of crying amount on parental behaviors needs to be investigated, in much the same way as I proposed to investigate parental responses to cry acoustics. Additionally, further light may be shed on the relationship between excessive infant crying and infant health by investigating infants in traditional societies where environments may be more variable than in industrialized societies.

Much remains to be learned about how infant crying contributes to the infant-caregiver relationship. I hope this evaluation of the evolutionary approach to understanding the early infant cry will stimulate further scientific inquiry into this fundamental aspect of the human experience.

APPENDIX: GLOSSARY OF ACOUSTIC TERMS[a]

Term	Definition
Cry	Vocalization during a single expiration
Duration	Total time of vocalization during single expiration
Fundamental frequency (F_0)	Lowest frequency component of the cry, generally perceived as pitch, measured in hertz
Maximum F_0	Highest hertz value of a cry
Minimum F_0	Lowest hertz value of a cry
Mean F_0	Average hertz value across a cry
Harmonics	Component frequencies of the cry higher than the fundamental frequency
Rising melody	F_0 rises across cry
Falling melody	F_0 falls across cry
Flat melody	F_0 does not change across cry
Biphonation	Simultaneously produced fundamental frequencies (also: bifurcation)
Dysphonation	Aperiodic vibration of vocal cords; turbulence generated at vocal cords
Hyperphonation	High F_0 (1000–2000 Hz)
Furcation	F_0 of strong cry splits into more than 1 weak cry, each with its own pitch
Glide	Rapid rise or fall in F_0 (600 Hz/0.1 s)
Vibrato	Rapid falling and rising F_0
Glottal roll	Low pitched sound at end of cry
Noise concentration	High energy peaks in cry (2000–2500 Hz)

[a]From Corwin et al. 1996; Denes & Pinson 1963; Furlow 1997; Green et al. 2000.

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NOTES

1. Throughout the paper I emphasize cross-cultural ethnography. The way of life in traditional societies, in particular in hunter-gatherer societies, is the best extant representation of the environment in which most of human evolutionary history unfolded, the so-called environment of evolutionary adaptedness, or EEA (Barkow et al. 1992; Bowlby 1969/1982). This is not to say that traditional societies of modern times are perfect representations of all earlier human societies. The concept of the EEA has been criticized for painting a too-homogeneous picture of the 2 million years that it spans and for not recognizing the possibility of more recent evolutionary change in humans (Irons 1998). Nevertheless, a cross-cultural approach offers the most inclusive view of the human condition, including that of our evolutionary past, and I follow that approach here.

2. In the condition-dependent handicap described in the text, low quality infants simply cannot produce the signal, or cannot produce it as conspicuously, as high quality infants. In the related strategic choice handicap, low and high quality infants can produce any level of the signal, but the marginal cost at the same level of signal is higher for low quality infants than it is for high quality infants. For a low quality infant, then, the marginal cost of producing a certain level of signal may be higher than the marginal benefit of reducing the probability of infanticide, and so no increase in the signal level would be favored. For a higher quality infant, on the other hand, the marginal cost of producing the same level of signal may be less than the marginal benefit of reducing the probability of infanticide, and an increase in signaling would be favored (see Grafen 1990a). In both scenarios, parents can use the signal to evaluate infant quality. Additionally, there can still be some cheating in "honest"-signaling systems, as emphasized in the manipulation models described in the text, but signaling is reliable if most signals are honest (Johnstone 1997; Johnstone & Grafen 1993).

3. According to this view, children develop secure attachments when mothers are available, responsive, and accepting, and they develop (possibly different forms of) insecure attachment when mothers are not, although child temperament may also contribute to the attachment process. These different forms of attachment may themselves be adaptive responses to specific rearing environments (Chisholm 1996; Hrdy 1999; Lamb et al. 1985; Zeifman 2001).

4. Infant crying that mimics need in the absence of autonomic arousal could be a manipulative signal to gain extra parental care or attention. The role of acute and chronic stress in determining early infant cry acoustics dominates the empirical literature, however, so it is unclear what amount of variation in infant cry acoustics, if any, remains unexplained by such autonomic arousal.