

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 off-

spring 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-

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

^aNumber 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 & Draiss 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; Gonzalez 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	Michésson et al. 2002
Fundamental frequency range (Hz)	200–600	Porter et al. 1988
	250–450	Wolff 1969
	300–600	Furlow 1997
	400–600	Sirvio & Michésson 1976
	450–600	Crowe & Zeskind 1992
	496 ± 95	Michésson et al. 2002
Melody	Falling or rising/falling fundamental frequency	Wolff 1969; Furlow 1997; Michésson 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 pre-selected 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 & Kobylansky 1991; Moller & Swaddle 1997; Thornhill & Gangestad 1999). For example, human pre-term infants and infants with Down’s syndrome exhibit a variety of bilateral morphologic asymmetries, including unequal left versus right hand breadth (Livshits & Kobylansky 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 hypothyroidism ^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 concentration
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				

^aWasz-Hockert et al. 1985. ^bFurlow 1997. ^cNewman 1994. ^dCorwin 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 (Levitky & 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 braking 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 cries 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 esophagitis 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 sucking 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, there-

fore, 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

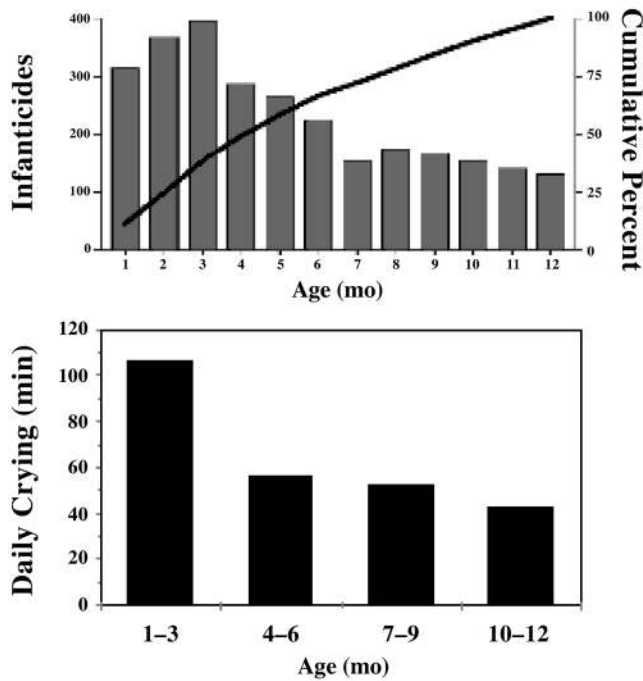


Figure 1. Relationship between number of infanticides and amount of infant crying in the first year of life. Both infanticide and infant crying are highest in the first three months of life, and decrease throughout the year. Infanticide data in the upper panel are from 2776 infanticides in the United 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 hyper-tonia – 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)
^aFrom Corwin et al. 1996; Denes & Pinson 1963; Furlow 1997; Green et al. 2000.

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NOTES

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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.

Open Peer Commentary

What is the evolutionary basis for colic?

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Abstract: An evolutionary model of crying requires consideration of non-human primate data. Chimpanzees do not have colic. Although they have a peak of fussiness at 6 weeks with a decline by 12 weeks whether raised by biological mothers or in a human nursery, their crying is always consolable. Colic may be a by-product of delayed rates of brain development; that is, neoteny.

Excessive early crying, or *colic*, occurs in Western cultures but does not occur in cultures that engage in high amounts of cradling contact (e.g., !Kung, Efe, Nso). In all cultures studied, there is a peak in crying frequency at approximately 6 weeks of life, and a substantial decline in crying frequency by 12 weeks. In chimpanzees it is also true that there is a peak in crying frequency at approximately 6 weeks of life, and a substantial decline in crying frequency by 12 weeks. The duration of crying is what seems to vary as a result of cultural context; excessive crying does not occur in cultures that value and engage in high amounts of cradling contact (Barr et al. 1991; Keller et al., in press). Following this logic, then it seems that the lessening of cradling contact might contribute to excessive crying. When we look at chimpanzees, whose evolutionary history is closest to ours, we see the same biologically based peak of crying, and the same effect of cradling contact (with shorter bouts of crying with 100% cradling contact in mother-raised infants compared with longer bouts of crying/fussing with the 25% cradling contact in a nursery setting). But even in settings with relatively little cradling contact, like in a human-rearing nursery, chimpanzees do not exhibit colic.

Colic in human settings ranged from 2% to 40% (depending on the definition of colic), so we would expect that among the 55 chimpanzees infants studied, somewhere between one and 22 ought to show excessive crying. In fact, not a single infant within the first 3 months of life exhibited inconsolable, excessive crying (Bard 1994a; 2000; 2002). Unusual circumstances, such as inadequate maternal care, resulted in excessive crying in chimpanzees during the first 2 months of life. However, the crying ceased immediately upon resumption of cradling contact, or cessation of overgrooming (Bard 2000). We see, therefore, that chimpanzees are capable of crying for extended periods of time, day after day. However, they do not exhibit inconsolable crying. Even in these extreme circumstances, when crying extends over an hour-long period, when the mother picks up the infant, the infant chimpanzee stops crying.

Chimpanzees are within the same range of helpless behavior as are human infants, with only some small differences distinguishing neonatal neurobehavioral integrity between the species (Bard 1994b; 2004; Bard et al. 1992; 2001). Neurobehavioral integrity during the first 30 days of life is assessed by cluster scores (Lester 1984), reflecting organized functioning in different realms such as motor performance and attention. Statistical comparisons of these cluster scores suggests that there are no clear-cut species differences in neonatal neurobehavioral integrity (Bard 2004). Rather, neurobehavioral integrity in human and chimpanzee neonates is clearly a function of genetic programs interacting with specific social-ecologies. Chimpanzees, however, appear to differ in some as-

pects of behavioral state, most noticeably in arousal, arousability, and in regulation of state, that is, coping with arousal. There was one item, consolability, which was rarely scored for the nursery-reared chimpanzees (2 of 38 subjects), either because they did not reach a crying state, or because they did not remain in a crying state for 15 seconds, that is, they self-calmed. All the human babies (42 of 42) received a score on this item at 2 days of age, but only 35 received a score at day 30, suggesting that maintaining a self-calmed state was a developing ability in human newborns, but an existing ability in 30-day-old chimpanzees. Additionally, chimpanzees at 2 days of age were more responsive to being cuddled by the examiner, compared with three groups of human babies. It seems that these items might reflect important species differences in regulation of behavioral state.

Another example is visual development: In the first month of life, human newborns see best in the range of around 25 cm, whereas chimpanzee newborns see as well at 60 cm as at 25 cm (Bard et al. 1995). The developmental rate of the visual system in chimpanzees is slightly faster than that of humans, but much slower than that of rhesus monkeys (Gibson 1985). Rate of maturation of the visual system, for example, differs in a ratio of 1 to 4 between rhesus and humans (rhesus monkeys' visual acuity at 1 month is equivalent to that of human infants at 4–5 months), and that of chimpanzees is more similar to humans than to rhesus monkeys (Bard et al. 1995). This ratio of 1 to 4 of rhesus monkeys to humans in visual development parallels rates of myelination throughout the brain (brain stem and cortex) (Gibson 1985). Therefore, one can speculate that it is myelination rates that might distinguish the excessive developmental delays found in humans, even compared with chimpanzees. In vision, as in many other systems, humans have the most delayed developmental rate of all primates (e.g., Gould 1977).

An important biobehavioral shift occurs around 2.5 months in humans, when human babies are clearly socially engaged with their caregivers (exhibiting mutual gaze and social smiling), there is a decreased frequency and duration of crying, and infant sleep/wake patterns begin to synchronize with those of adults. These behavioral changes coincide with developing subcortical-cortical connections, with increased cortical control of subcortical activity, and myelination of neural pathways (reviewed in Cole & Cole 2001). Chimpanzees also exhibit these behavioral changes of social engagement with caregivers (Bard 1998; submitted; Bard et al., in press; Myowa 1996), and changes in crying/fussing (Bard 2000) around 2 months of age. Chimpanzees, however, seem to have fewer difficulties in establishing sleep/wake regularities than do human infants (Bard 2004; Balzamo et al. 1972). Recent studies comparing human infants with colic with those without colic only find differences in extended disruption of sleep/wake cycles in babies with colic (White et al. 2000). The comparison of chimpanzee and humans is important, therefore, because they share so many characteristics in infancy and share a long evolutionary history; and yet humans in some cultures get colic, and chimpanzees, regardless of the setting, do not exhibit colic (Bard 2000). The evidence suggests that the existence of colic in the human species may be the result of extraordinarily delayed development, a by-product of neoteny (Gould 1977).

Early infant crying as a behavioral state rather than a signal

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Abstract: I argue that in the first three months, crying is primarily a behavioral state rather than a signal and that its properties include prolonged and unsoothable crying bouts as part of normal development. However, these normal properties trigger Shaken Baby Syndrome, a form of child abuse that does not easily fit an adaptive infanticide analysis.

In his excellent review on signal functions of early crying, Soltis argues that (1) abnormal crying reflecting pathology may be a cause of adaptive infant maltreatment, and (2) the early increase in crying, including colic, is normal and a signal of vigor that evolved to prevent withdrawal of care. I argue that there is a theoretical perspective, two other properties of early crying, and a different consequence not accounted for by these arguments, but that may be complementary.

The theoretical perspective is that “crying” in the first three months is primarily a behavioral state and not a signal, although it functions secondarily as a signal. Following Wolff (1987), the phrase “infant behavioral state” refers to organized behavioral properties of the infant at the level of the intact organism, as when we refer to an infant as *crying*, *awake*, or *asleep*. Behavioral states are the set of discontinuous and distinct modes of behavior, into which infant behavior is organized, that are (1) self-organizing, in the sense that a state is maintained until that pattern of events occurs that results in a shift to another state; (2) relatively stable over time (minutes rather than seconds), and (3) nonlinear, in the sense that a stimulus experienced in one state has a different effect than when experienced in another state (Barr et al. 1999; Wolff 1987). In the Soltis article, “crying” is used in a more restrictive sense, referring to negative vocalizations produced by the organism, or to their function as communicative signals. Reasons to consider crying as primarily a behavioral state are (1) the unique age-related n-shaped pattern of crying amounts (Barr 1990c); (2) analogous age-related shifts in organization of sleep and wakefulness (Wolff 1987); (3) the biobehavioral shift at about four months from “expressive” crying, which is relatively independent of context and presumed to reflect physiological state, to “communicative” crying, which becomes more tied to motor gestures and maternal response, and more intentional (Franco 1984; Gekoski et al. 1983; Gustafson & Green 1991); and (4) the nonlinear, state-dependent responses to stimuli (Graillon et al. 1997; Wolff 1987). Of course, the crying vocalizations may still function as signals, in that caregivers respond to and act on them and derive what meaning they can from them. My argument is that this is a secondary function at this age.

Two properties that occur primarily in the first three months are that crying bouts are prolonged and unsoothable. Recently, many studies have parsed the overall daily amounts of crying into components such as bout (or event) frequencies and durations. These components do not co-vary. For example, increased carrying and holding reduced daily crying and fussing duration by 43% but did not affect bout frequency (Barr 1989; Hunziker & Barr 1986). Further, the early increase and decrease is due primarily (if not exclusively) to bout duration, rather than frequency, changes (Barr 1989; 1990a; 1990b; Barr et al. 1991; 1992). These longer bout durations hold true for all modalities of distress from fussing to “colicky” crying (Barr et al. 2000; St. James-Roberts et al. 1995). In addition, some crying bouts are demonstrably unsoothable to typical care giving responses in the first three months (St. James-Roberts et al. 1995; White et al. 2000).

A consequence of these properties may be a specific form of child abuse; namely, Shaken Baby Syndrome (SBS). Many anecdotal

confessions indicate that perpetrators just wanted to “stop the crying.” SBS differs from most forms of child abuse; when the baby is shaken, there is no negative feedback (such as a mark on the skin or a stinging hand). Indeed, the baby may become quiet, rather than cry more. Parents who would never think of physically hitting their infant may shake them in frustration at the crying. Only when repeated and/or severe enough does the shaking come to clinical attention because of the ensuing brain damage. Although not systematically documented, perpetrator confessions (Brewster et al. 1998) and anecdotes culled from court records and media reports kept by the National Center on Shaken Baby Syndrome implicate crying as the most common stimulus. Furthermore, the age-specific incidence of SBS hospitalizations has the same starting age and shape as the age-specific crying curve (Holliday-Hanson et al. 2001). The peak incidence occurs in the third month rather than the second, probably due in part to repeated shaking in many cases (Alexander et al. 1990; Ewing-Cobbs et al. 1998). The effects are devastating; one-quarter die, and 55–65% of survivors are left with major neurological handicaps and blindness (King et al. 2003). The clinical implications of this are that parents need to be aware of these normal properties of crying to reduce their frustration with the crying. To address this, the National Center on Shaken Baby Syndrome has developed an educational campaign called the “Period of PURPLE Crying.” The letters of the word PURPLE each refer to one of the six properties contributing to care giver frustration (P for peak pattern, U for unexpected timing, R for resistance to soothing, P for the pain-like grimace even when not in pain, L for long crying bouts, and E for evening clustering).

The proposal here is that SBS – and possibly other forms of infant physical abuse – are due to these normal properties of crying; namely, the prolonged and unsoothable bouts that occur in an age-specific and context independent pattern during the early months. Admittedly, it cannot be determined with certainty that SBS cases are limited only to those with normal cry acoustics. Further, SBS does not easily fit an adaptive infanticide analysis since the abuse is not apparent, death occurs in only one-quarter of SBS infants, and the remainder require increased rather than decreased parenting resources. In short, although normal and having possible signal value as vigor, this crying also results in maltreatment, and this maltreatment may not be “adaptive.” If so, the paradox is that the very crying that advertises the infant’s vigor may result in its being killed.

Changing brain activation needs determine early crying: A hypothesis

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Abstract: A proximal mechanism is proposed whereby early crying helps maintain ideal levels of brain activation during the first three postnatal months. The proposal is consonant with both animal and human infant literatures, and new data are presented in its support.

Soltis has provided an evolutionary perspective on the signal function of early crying (i.e., crying during the first three postnatal months). The upper end of the normal crying distribution, anchored by infants with colic, has provoked extensive medical and evolutionary hypotheses, none of which are very compelling, as Soltis suggests, and I concur. The lower end of the distribution, in which the very sick infant’s cry signals weakness and vulnerability – that is, a poor bet for enhancing the parents inclusive fitness – also does not hold out much hope. The weak, grating cry of the very sick infant confirms that which the parent witnesses and

may contribute to the relatively greater incidence of infanticide and neglect suffered by infants at risk for health or born in very unfavorable circumstances. Minimizing losses from sick or weak infants presumably benefits the parents, and as such, infanticide and neglect are traits that can be selected. Yet why should the sick infant signal his weakness to the parents, possibly hastening his demise – particularly among humans in which very few offspring survive, so that indirect kinship benefits are very modest? Other difficulties present themselves. Infanticide is a very rare event. The high frequency of “kangaroo care” of premature infants by both parents and the very high rates of adoption relative to infanticide and neglect, at least in the West, both speak against parental investment as a driving evolutionary force. Ultimate explanations also do not account for the distribution of crying above the low threshold of parental rejection. Nor do they address the *n*-shaped function of crying during the initial three months.

Proximal analyses may prove more profitable. As detailed by Soltis, all agree that crying serves as a discomfort signal that attracts the parents to the isolated infant and through graded intensity attracts attention to the proximal source. I propose an additional function for early crying. Crying, with its attendant endogenous central stimulation is recruited when exogenous stimulation does not meet levels of central activity required for normal brain development.

A number of lines of internal (to crying) and external evidence support this view. First, as Soltis notes, there is substantial cultural variation in crying frequency that is inversely related to daily external stimulation. !Kung San infants who are in contact with their mothers for up to 80% of the day, present the *n*-shaped function; but it is enormously dampened at each point. At the other extreme, colicky infants also present the *n*. Their need for stimulation may be sufficiently severe that it cannot be met through standard parental care. It is interesting in this regard that some parents of colicky infants have found the solution through early hour auto rides or by placing the infant on top of the washing machine during the agitation cycle.

According to a substantial animal literature, dendritic development, especially in hippocampus, reflects stimulation provided by the mother (Gonzalez et al. 2001; Meaney et al. 1989). Moreover, ideal levels of stimulation, attained via the natural pathway of anogenital stimulation, activating central noradrenergic pathways, or pharmacologically via amphetamine injection, maximizes both behavioral preference and neural change (Pedersen et al. 1982; Sullivan et al. 1989). It is of considerable interest that both measures of affect and brain development of infants of depressed mothers are diminished relative to normal (Dawson et al. 1999). Remarkably, children who had suffered a single infant epileptic seizure scored considerably higher in a prospective study on a variety of cognitive evaluations than matched control infants (Chang et al. 2001).

If crying reflects an inadequacy in central arousal, and if central arousal needs are manifest in an *n*-distribution over the first three postnatal months, then a priori predictions can be made about different classes of infant behavior based on the normal crying curve. Our studies (Blass & Camp 2001; 2004) on infant preference for adults based on a single 3.5-minute interaction support this approach. In following a substantial animal and human infant literature on sucrose as a calming and analgesic agent, infants either received sucrose alone or on a pacifier when they were either crying or calm. No single factor accounted for the infant preference at the ages (6, 9, and 12 weeks) that we studied. Preference reflected the levels of activation that the infants were in at a particular age. Week 6 infants, who are at the apex of the crying function, preferred only adults with whom they had interacted when agitated. At weeks 9 and 12, infants preferred adults with whom they interacted when calm. Nine-week-olds preferred adults who had given them a pacifier to suck, thereby increasing level of activation (in principle; Cohen et al. 1998). Calm week 12 infants did not prefer such adults. Rather, they strongly preferred ones who had given them sucrose to taste. Sucrose, through opioid mecha-

nisms, presumably further reduced central activity (Blass & Ciaramitaro 1994). These findings map nicely on to the descending limb of the *n*-shaped function. We are currently testing how well the predictions made by the ascending limb hold.

These are clearly early times for the hypothesis and data presented above. Fundamental physiological, energetic, and neural measures must evaluate the putative changes that I have posited. The proposal that early crying reflects central activation needs has the virtue, however, of generating precise testable hypotheses, based on the *n*-function, in affective domains that are independent of crying. This approach may help identify proximal determinants of positive affect as well as those underlying early crying.

Prelinguistic evolution in hominin mothers and babies: For cryin' out loud!

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Abstract: Unlike chimpanzees, human infants engage in persistent adult-directed (AD) crying, and human mothers produce a special form of infant-directed vocalization, known as motherese. These complementary behaviors are hypothesized to have evolved initially in our hominin ancestors in conjunction with the evolution of bipedalism, and to represent prelinguistic substrates that paved the way for the eventual emergence of protolanguage.

Soltis cites cross-cultural evidence to support the hypothesis that selective withdrawal of parental care and infanticide were important variables during infant physiological evolution in our species. It is therefore interesting that mothers among our closest evolutionary cousins, the chimpanzees (in whom fathers are unknown), rarely if ever reject their infants when living in the wild, and some have even been observed (sadly) carrying their babies' corpses for some days after the babies have succumbed to non-maternally caused deaths. However, this observation does not contradict Soltis' suggestion that aversive early infant crying is a common provocation of parental rejection or infanticide in humans, for the simple reason that chimpanzee infants do not cry excessively as human infants do. Nor do chimpanzee mothers engage in the continual streams of vocalizations, known as musical speech, baby talk, or motherese, that universally characterize human mothers. I believe that persistent adult-directed (AD) infant crying and infant-directed (ID) motherese are complementary behaviors that evolved initially in our hominin ancestors in conjunction with the evolution of bipedalism, and that they represent prelinguistic substrates that paved the way for the eventual emergence of protolanguage (Falk 2004).

The target article's analysis of the signal functions of early infant crying is consistent with the “putting the baby down” hypothesis, which focuses largely – but not exclusively – on the signal functions of motherese (Falk 2004). As Soltis documents, human infants frequently cry as honest signals of need, the most common of which appears to be the desire to reestablish physical contact with caregivers (Small 1998; Wolff 1969). Unlike helpless human babies, chimpanzee infants older than approximately two months cling unaided to their mothers' abdomens or backs, so they have little to cry about (although they do whimper and complain on those rare occasions when they fall off [Plooij 1984]). Because of structural constraints that were imposed on the human birth canal by selection for bipedalism in combination with relatively enlarged fetal brain/head sizes, human infants today are born at relatively early stages of development (when their heads are still small enough to negotiate the birth canal) and never develop the ability to cling unaided to their mothers. Therefore, compared to their apelike ancestors, early bipedal hominin mothers literally

had their hands full – of their infants. Prior to the invention of baby slings, hominin mothers would have had to free their hands periodically from infant carrying in order to forage for food. A plausible way to do this would have been to put babies down, preferably nearby where they could be kept under surveillance.

Thus began the evolution of infant crying as an honest signal of need for reestablishing contact with the mother. In a sense, persistent infant cries compensated for the loss of little grasping hands and feet that once clung to mothers' bodies. Also, thus began a concomitant evolution of the special vocalizations of motherese, which functioned initially to sooth, appease, engage, and calm *distal*, complaining (as opposed to *proximal*, content) babies. In a sense, prosodic utterances became disembodied extensions of mothers' cradling arms, since a "squealing baby, in fact, can be stopped dead in its vocal tracks by a sudden stream of baby-talk" (Small 1998, pp. 145–46). For both mothers and babes, then, special vocalizations evolved in the wake of selection for bipedalism in response to reduction of the direct physical contact that was previously achieved by their ancestors' upper and lower extremities. Voices had come into their own!

Today, motherese forms a scaffold upon which language is acquired by maturing infants around the world, and I hypothesize that this was probably true during the emergence of protolanguage in the distant past (Falk 2004). Soltis' work raises the possibility that the signaling functions of early infant crying also played a significant role in the evolution of prelinguistic substrates in early hominins. As he notes, excessive infant crying with certain acoustic properties appears to constitute an honest signal of vigor that elicits nurturing responses in parents (and therefore increases fitness in both parents and offspring). Soltis therefore hypothesizes that colicky infants may, in fact, be relatively vigorous and that they signal this fact to their parents by persistent, intense, and more inconsolable crying that discourages parental withdrawal of support. On the other hand, Soltis suggests that, for unfit infants, it is pitch-related acoustic quality rather than the quantity of crying that triggers abusive responses in caregivers.

Higher overall tones (pitch) comprise an important acoustic feature of motherese, so it is interesting that infant cries of high and variable pitch are often perceived by adults as arousing or aversive (sect. 4.4 of the target article); that such cries can lead to differential allocation of parental resources (or infanticide); and that one study, at least, showed that infants whose mothers perceived their high-pitched cries as negative outperformed other infants on language tests at age 19 months (Lester et al. 1995). These nuggets from Soltis' target article suggest that cries with specific acoustic properties might have been preadaptive for the emergence of protolanguage and, if so, today's cries of colicky infants may specifically signal a sort of prelinguistic vigor. Do colicky babies grow up to have better verbal skills than non-colicky babies? I suspect this question (and the ones Soltis raises about their general fitness) could be addressed relatively easily by designing retrospective or (future) longitudinal studies. Meanwhile, it's clear that, from the moment of their births, human infants object to the insult of being separated from their mothers with persistent cries, while chimpanzee infants remain, for the most part, contentedly and silently attached to their mothers' bodies. The human neonatal pattern of excessive crying continues for several months (the extent varying with the degree of culturally determined physical contact between mother and infant), during which time babies' preference for ID as opposed to AD speech increases (Cooper et al. 1997). Crying then levels off precisely at the time ID speech is used most intensively (with 3- to 5-month old infants) (Stern et al. 1983). Soltis' research has convinced me that motherese and infant crying are two sides of the same coin, that both had long evolutionary histories, and that both may have been important factors during the evolution of prelinguistic substrates in early hominins.

Infant crying in hunter-gatherer cultures

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Abstract: By synthesizing evolutionary, attachment, and acoustic perspectives, Soltis has provided an innovative model of infant cry acoustics and parental responsiveness. We question some of his hypotheses, however, because of the limited extant data on infant crying among hunter-gatherers. We also question Soltis' distinction between manipulative and honest signaling based upon recent contributions from attachment theory.

Soltis innovatively synthesizes complementary aspects of the evolutionary, attachment, and acoustic literatures on infant crying in order to elucidate the adaptive function of infant crying, particularly excessive infant crying. Soltis' laudable model of early infant cry acoustics and parental response tendencies (sect. 4.6), is preceded by two general hypotheses, namely that: (1) infant cries characterized by high pitch, variable pitch, and biphonation are likely to be proximate causes of neglect, abuse, or infanticide; and (2) excessive "normal" crying (colic) honestly signals infant vigor and decreases the risk of neglect, abuse, or infanticide.

Both hypotheses assume that different types of crying affect the risk of neglect, abuse, or infanticide and that these forms of maltreatment were/are common in "premodern" or "traditional" cultures. Unfortunately, the majority of the cultures discussed in section 2.2 and Table 1 involve farmers, pastoralists, or urban industrialists. The case studies cited similarly involve farmers (e.g., Eipo), while research on the abuse or neglect of retarded and chronically ill infants was all conducted in urban-industrial cultures. We know little about abuse, neglect, and infanticide in hunter-gatherer cultures, especially in relation to infant crying. Neglect, abuse, and infanticide certainly exist (see Hill & Hurtado, 1992, for example), but the contexts, especially those surrounding cases in early infancy, are poorly understood. Hunter-gatherer societies may be particularly important for understanding the evolution of infant crying because the foraging way of life characterized most of human history. Hunter-gatherer infancy is characterized by constant holding/touching, frequent breastfeeding (often 4 times an hour), multiple care providers (fathers, siblings, other women, etc. – all very involved, in part, because infants are always held in hunter-gatherer communities), and infrequent crying (Hewlett et al. 2000; Konner, in press). Our own qualitative field observations of Aka and Bofi forager infants indicate that: (1) colic, as defined in the West, is rare or nonexistent; (2) caregivers do not get irritated with unusual or long crying bouts; and (3) young children as well as adults know how to soothe crying infants. Excessive and unusual crying occurs more frequently among the farming neighbors of the Aka and Bofi.

Soltis also assumes that parents alone decide the quantity and quality of care that infants receive (sects. 2 and 6), noting for example, that "parents can partition investment selectively among offspring as they choose" (sect. 2.3, para. 1). Throughout his discussion of signaling, Soltis implies that parents have complete control over the allocation of resources to infants (e.g., nursing, care, etc.) and does not consider care provided by other individuals. This sort of omission is appropriate if we assume that young infants are actually cared for all of the time by parents, as is often the case in the United States, but multiple-person caregiving is common in hunter-gatherer groups. In fact, approximately 40% of the care received by 1- to 4-month-old Aka and Efe forager infants comes from non-parental sources (Hewlett 1989; Tronick et al. 1987), often while parents are also present and caring for their in-

fants simultaneously. For example, Konner (in press) reported that, although !Kung mothers are typically the primary caregivers, mothers alone accounted for only about half of the responses to fretting, whereas the majority (88%) of the frets elicited responses from both mothers and others simultaneously. Because !Kung infants were almost never alone with their mothers, other caregivers made substantial contributions to the quality, degree, and timing of responses to infant frets.

Noting the cooperative care patterns common among contemporary hunter-gatherers, Hrdy (in press) has proposed that humans evolved as cooperative breeders, and Ivey Henry et al. (in press) report that the amount of allocare received by Efe infants is the best predictor of infant survival. Cooperative breeding may reduce the risk of infanticide in hunter-gatherers societies and thus reduce the actual levels of abuse and neglect in “traditional” cultures.

Soltis’ second hypothesis assumes that normal crying universally peaks at six weeks of age, and again the extant data are limited. Data obtained on !Kung hunter-gatherers support the statement, although these data were collected in limited contexts (in-camp only, infant awake, mothers present) and Konner (in press) suggests considerable inter-cultural variability in forager crying patterns. Furthermore, if the sixth week peak is a human universal, then perhaps crying patterns should also be examined among nonhuman primates. If excessive crying at six weeks reduces the risk of infanticide, why doesn’t it occur in higher primates or other animals in which infanticide occurs? Is this pattern uniquely human?

Whereas Soltis cites several studies documenting that specific cry acoustics lead to infant maltreatment in urban industrial cultures, we know of no acoustic studies conducted in forager or other small scale cultures. Our own qualitative observations suggest that this type of crying does not elicit maltreatment in forager cultures, however. Chronically ill infants may not survive, but caregivers continue to be indulgent and responsive rather than abusive or neglectful. Again, caregivers do not show the irritation and stress often described in urban industrial societies.

Finally, Soltis contrasts manipulative and honest signaling, suggesting that manipulative crying involves attempts to obtain care that is not physiologically needed. For example, an infant who is not very hungry may cry manipulatively for nursing, care, or proximity. This argument implies that attention, proximity, and care do not contribute to infant survival, but from an attachment perspective, one could argue that crying for proximity is an honest signal of need for the contact, which promotes attachment and may influence the quantity and quality of care received in the future. Crying for proximity is not necessarily manipulative, therefore, but may contribute to infant survival. Many scholars have noted that children’s attachment behaviors (which include crying and proximity seeking) are responses to caregiving environments, and that these behaviors may enhance survival (Belsky 1997; Chisholm 1996; 1999; Lamb et al. 1984; Main 1990). Insecure attachment patterns (which include elevated levels of crying) may be facultative adaptations, because the patterns help infants with less responsive caregivers to gain more attention and care.

Despite these concerns, Soltis’ model of early infant cry acoustics and parental responsiveness (sect. 4.6) is useful, and is likely to generate valuable field studies. The model is unique because it is multi-leveled and considers the joint and integrated influence of “infant and parental characteristics, household dynamics and economy, and the wider community and culture” (sect. 4.6, para. 4). Such holistic models often generate cross-disciplinary research and scholarship.

We agree with Soltis that early infant crying deserves more attention, and we appreciate his attempt to integrate data from diverse sources. More systematic analyses and data from hunter-gatherer cultures are needed in order to test and develop hypotheses about the evolution and adaptive function of early infant crying.

NOTE

Hillary N. Fouts and Michael E. Lamb are employed by a government agency and as such this commentary is considered a work of the U.S. government and not subject to copyright in the United States.

Is excessive infant crying an honest signal of vigor, one extreme of a continuum, or a strategy to manipulate parents?

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Abstract: An evolutionary account of excessive crying in young infants – *colic* – has been elusive. A study of mothers with new infants suggests that more crying is associated with more negative emotions towards the infant, and perceptions of poorer infant health. These results undermine the hypothesis that excessive crying is an honest signal of vigor.

Following Barr (1998a) and Lummaa et al. (1998), Soltis tentatively favors the argument that excessive infant crying is an honest signal of vigor, with more crying indicating higher infant quality (sect. 6.3). If that were the case, then mothers should have more positive emotions towards colicky infants. Yet many studies indicate otherwise. Although the casual pathways are not clear, there is a robust association between early infant temperament problems, including colic (Beck 1996), and postpartum depression (PPD). PPD, in turn, is robustly associated with reduced maternal care (Beck 1995). Mothers with PPD commonly think about harming their children, display fewer positive emotions and more negative emotions toward them, and are less responsive and sensitive to infant cues (Hagen 1999). Soltis himself notes that “Excessive infant crying is the most common clinical *complaint* of mothers with infants under three months of age” (sect. 5.1, para. 1, emphasis added).

My survey of 129 U.S. mothers with babies aged 3–32 weeks (see Hagen [2002] for details about other aspects of the study) included several maternal self-report items relevant to the excessive crying hypothesis (rated on a 7-point Likert scale):

- How much does your baby cry? (0=Never; 6=Constantly)
- How much in love are you with your baby?
- According to your doctor how healthy is your baby now?
- How much do you worry that your baby might have a problem of any kind?
- What is your “gut feeling” about the health of the baby?
- Has your baby had any health problems since the birth? (Yes/No)

The distributions of the variables were not normal, so non-parametric Spearman rank correlations (r_s) and a Mann-Whitney U test (Z) were computed. Descriptive statistics are reported in Table 1, results in Table 2 (all *p*-values two-tailed):

In each case, more infant crying was associated with lower levels of perceived infant health, more worry about health, and less positive emotions towards the infant, contrary to the vigor signaling hypothesis. The effects were small, and only significant for doctor rating of health and love for the baby. Because crying diminishes after 12–16 weeks, I re-ran the analyses for mothers with infants aged 3–12 weeks. There was little change in effect sizes, although now no results were significant, because of decreased sample size.

This study was not designed to examine infant crying, and no items assessed cry acoustics. It could therefore have been the case that cries with abnormal acoustics were confounded with excessive crying. Under the health signaling hypothesis, if the sample is biased towards infants in good health, that should tend to eliminate infants with abnormal cry acoustics, reducing the confound.

Table 1 (Hagen). *Descriptive statistics*

Variable	N	Min.	Max.	Mean	S.D.
How much does your baby cry?	129	0	5	2.5	1.15
How much in love are you with your baby?	129	0	6	5.7	0.71
Doctor rating of health	128	3	6	5.8	0.56
Worry about health	128	0	6	2.1	1.70
Gut feelings about health	129	3	6	5.4	0.75
Health problems since birth	129	Yes: 43 (33%), No: 86 (66%)			

Table 2 (Hagen). *Association of quantity of infant crying with mother's emotion towards the infant and infant health variables*

	All infants (3–32 weeks old)	Infants 3–12 weeks old (n=82)	Infants with no health problems (n=86)
How much in love are you with your baby?	$r_s = -.20, p = .023$	$r_s = -.15, p = .17$	$r_s = -.19, p = .085$
Doctor rating of health	$r_s = -.20, p = .026$	$r_s = -.10, p = .35$	$r_s = -.18, p = .097$
Worry about health	$r_s = .17, p = .063$	$r_s = .18, p = .12$	$r_s = .14, p = .20$
Gut feelings about health	$r_s = -.11, p = .23$	$r_s = -.094, p = .40$	$r_s = -.11, p = .30$
Health problems since birth	$Z = -1.13, p = .26$	$Z = -1.04, p = .30$	

The same tests were performed for infants with no known health problems since birth. There was no change in sign and little change in effect size, although, again, no results were now significant.

Results of a study not designed to test the vigor hypothesis should be taken with a grain of salt. A careful evaluation of the association between excessive crying, perceptions of infant health, and parental emotions towards the infant that distinguished between crying and other temperament and health problems, that assessed cry acoustics, and that incorporated Soltis' distinction between Wessel's colic and Wessel's plus colic, might indeed reveal more positive perceptions of infant health and more positive parental emotions towards infants who cried excessively but had no other problems. It might also be the case that mothers who experience high rates of infant morbidity and mortality, as ancestral human mothers certainly did, would have a different, and positive, response towards excessive crying (with normal acoustic quality) relative to Western mothers who experience little infant morbidity and mortality (cf. Scheper-Hughes 1992).

I incline towards the view that excessive infant crying is one extreme of a continuum (target article, sect. 5.2), and therefore is not, in and of itself, an adaptation. I will nevertheless throw one more functional idea about parental manipulation into the ring. Soltis correctly notes that models of offspring manipulation of parents must include the possibility that parents evolve to resist manipulation (sect. 2.3). He is a bit too quick, however, to dismiss a manipulative function for excessive crying in young infants based on the argument that parent-offspring conflict (POC) is low for young infants (sect. 6.1). In fact, POC can be high for young infants. POC decreases as the value of the offspring to its parents increases. Because child mortality decreases with age, offspring value increases with age, implying that POC decreases as the infant ages. Rates of infanticide are correspondingly highest in the first three months of life, decreasing thereafter. When resources are plentiful, offspring inclusive fitness may actually increase when parents divert investment to new siblings, reducing weaning conflict. Even the costly and therefore honest signal of vigor hypothesis favored by Soltis assumes parent-offspring conflict (otherwise, the signal could be cheap).

In the environment of evolutionary adaptedness (EEA), excessive crying could have directly and indirectly manipulated parents. Crying might have attracted predators, which would have reduced

not only offspring fitness, but also the fitness of parents and siblings. Crying could also have interfered with parents' conversations and ability to concentrate on other activities. These direct costs would have motivated parents to attend to the offspring. Further, because these costs would also have been imposed on other group members, they would motivate the group to coerce parents to care for their crying offspring.

Solid evolutionary reasoning has been missing from most of the developmental literature since Bowlby's important contributions over 30 years ago. Soltis' efforts here are therefore extremely welcome. Despite my few quibbles, they form an excellent foundation for future work.

Sleep-wake processes play a key role in early infant crying

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Abstract: The crying curve across early infancy may reflect the developing interaction between circadian and homeostatic processes of sleep-wake regulation. Excessive crying may be interpreted as a misalignment of the two processes. On the basis of the proposed mechanism, excessive crying may be an honest signal of need, namely, to elicit parental resources to modulate the behavioral state.

Soltis presents an interesting approach to understand the purpose of early infant crying by using evolutionary reasoning. When searching for the crying function, however, we need a clear idea of what the phenomenon essentially is. Examining the physiological properties of crying is a promising way to understand its meaning. For example, Soltis uses acoustic characteristics of crying as a phenomenological description to propose an evolutionary model for the crying signal.

In this commentary, I propose an alternative explanation for excessive infant crying. I agree with Soltis that developmental processes of sleep-wake behavior may underlie the temporal pattern of crying across the first months of life. But the fundamental

question relates to the contributing mechanisms. My perspective suggests that we may better understand infant crying by examining ontogenetic changes of sleep-wake regulation.

Crying is commonly considered to be a behavioral state of high arousal (Prechtl & Beintema 1964; Thoman 1990; Wolff 1987). Mechanisms modulating and controlling behavioral states like sleep and wakefulness evolve over the first months of life (Prechtl 1984). Appropriate models providing a conceptual framework to examine how such regulatory mechanisms may develop have rarely been provided. This gap is rather surprising, since models describing putative sleep-wake processes in adults have been used for many years (Akerstedt & Folkard 1995; Borbély 1982; Borbély & Achermann 2000; Daan et al. 1984).

The clock-like circadian process and the sleep-wake dependent homeostatic process play pivotal roles in the control of vigilance states in the adult (Borbély & Achermann 2000). The circadian process determines diurnal levels of alertness and sleep tendency independent of prior waking and sleep (Dijk & Czeisler 1995; Folkard et al. 1985). Alertness reaches its maximal levels in the early evening and its trough in the early morning, corresponding to the course of the core body temperature (Folkard et al. 1985). The homeostatic process mediates the rise of sleep pressure during waking and its dissipation during sleep (Borbély 1982; Daan et al. 1984). The longer the waking period lasts, the higher sleep pressure becomes. In the adult, the rise of homeostatic sleep drive during waking is opposed by the increasing circadian alertness in the course of the day, allowing adults to maintain constant levels of vigilance throughout the waking period (Achermann & Borbély 1994; Daan et al. 1984; Edgar et al. 1993). Conversely, during sleep, the rising circadian sleep tendency counteracts the declining homeostatic sleep pressure, ensuring maintenance of sleep (Dijk & Czeisler 1994). The alignment of the two processes is thus a prerequisite for the biphasic sleep-wake cycle across the adult 24-hour day.

The circadian rhythm of core body temperature appears at four weeks and increases in strength over the first few months of life reflecting the infant's developing circadian process (Glotzbach et al. 1994). The increasing circadian drive may generate a rise in alertness across the day providing the basis for predicting the late afternoon and evening clustering of infant crying. The diurnal rhythm of crying becomes progressively more distinct, reflecting the increasing strength of the circadian drive.

The developmental course of the homeostatic process during early life remains minimally elucidated. Animal experiments have demonstrated that homeostatic sleep mechanisms are present already in the first postnatal weeks (Alföldi et al. 1990; Frank et al. 1998). Studies in human infants have reported that sleep electroencephalographic markers reflecting sleep homeostasis appear as early as in the first 2 months of life (Jenni et al. 2004; Salzarulo & Fagioli 1992). I hypothesize that already in young infants sleep tendency increases in the course of the day despite intermittent decreases of sleep pressure as a result of daytime naps. Daytime waking episodes are longer than daytime sleep episodes and therefore may increase global homeostatic sleep pressure across the day.

I propose that the developing ability of the infant to increase sleep pressure during the day may counteract the circadian alertness in the early evening to maintain a balanced vigilance state. In other terms, hyperalertness and excessive crying may occur, when circadian alertness is not opposed by homeostatic sleep pressure.

The typical crying curve across the first months may reflect the developing interaction between the circadian and homeostatic process, while the evening clustering of crying may be driven mainly by the circadian drive. This hypothesis favors the notion of independent processes for the diurnal peak and the age-related 6-week peak of crying. Other cry characteristics, such as the high interindividual variability (Barr 1990c), could also be explained with individual differences in the initial occurrence of homeostatic and circadian processes and their alignment. The day-to-day variation may be driven by the homeostatic process depending on waking and sleeping behavior across individual days. In the described per-

spective, excessive crying may be interpreted as a misalignment or lack of coordination between the two processes, in particular at the end of the day. In contrast to Soltis' view, I believe that such a perspective supports the idea that excessive crying is primarily an honest signal of need, namely, to elicit additional parental resources and attention to modulate the behavioral state.

Soltis argues that infant care practices affect early infant crying despite the global validity of the crying curve. In fact, comparative ethnographic analysis opens the possibility to study diverse caretaking and sleep practices and their influence on behavioral state regulation and crying. In many traditional cultures, infants are carried continuously, are able to sleep under any circumstances and cry less (Worthman & Melby 2002). In these societies, polyphasic sleep-wake cycles are predominant and long periods of wakefulness for gathering and socialization processes occur at night. From an evolutionary perspective, the adaptive pressure to become entrained to the biphasic 24-hour sleep wake rhythm may be higher in Western cultures, where most activities are scheduled in the daytime hours. Thus, intrinsic biological processes may exert less influence on behavioral state regulation in the traditional societies, where infant regulatory demands are fulfilled by extrinsic mechanisms of the caretaking environment.

Ontogenetic and phylogenetic changes of sleep-wake processes play a key role in understanding crying behavior. Future studies in which sleep and wakefulness during early infancy are manipulated will shed more light on the development of circadian and sleep homeostatic processes, and eventually on excessive infant crying and its function.

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Imagine imaging neural activity in crying infants and in their caring parents

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Abstract: Soltis' paper contains little data on the underlying neural substrate of the discussed signal function of early infant crying – probably because there is amazingly little known about it. We here discuss the interest of functional neuroimaging as an objective measurement of brain activity in (1) early infants during crying and (2) parents hearing their offspring cry.

Soltis proposes a model for the signal effect of cry acoustics on parental response, based on human and animal evolutionary history. We enjoyed reading this comprehensive review summarizing vast literatures ranging from bioacoustics and ethnography to animal and infanticide data. We largely agree with the author's claims and doubts. In this commentary, we add to the discussion the role of functional neuroimaging in elucidating some of the remaining questions and in testing the proposed model. We will discuss the interest and possibilities of measuring brain activity in (1) the crying infant and (2) the parent hearing the cries.

Soltis addresses the issue of the communicative content of crying in terms of *honest* signaling of need or vigor, or *manipulative* signaling. We regret the use of the term *manipulation* in that it might have a negative connotation. It implicitly assumes that the cries are dishonest and that the infant somehow "voluntarily" undertakes a shrewd or devious action for its own advantage. It is still a matter of debate at what age human infants show signs of engaging in activities for which conscious awareness is thought to be

necessary (e.g., communication). However, babies in the three first months of life (the target age in Soltis' paper) are generally not considered to have the minimal form of higher-order thought regarded necessary for access and phenomenal consciousness (e.g., Perner & Dienes 2003). Manipulative crying would then be a conditioned, merely "unconscious" reflex. The hypothesized *manipulative* signaling of early excessive crying (by which infants would attempt to gain a disproportionate share of parental resources) should *not* be regarded as *dishonest* abuse of the infant's limited communicative arsenal. In our view, functional neuroimaging (i.e., positron emission tomography – PET, functional magnetic resonance imaging – fMRI, electroencephalography – EEG, and magnetoencephalography – MEG) might help to clarify the "meaning" of infant cries and to solve the question whether, and to what extent, the cries are *reflex* or *voluntary* (for review see Prochazka et al. 2000).

Can these techniques be used in early infants? Obviously, for reasons of radioprotection, PET has limited value in healthy infants. fMRI currently offers the best spatial and temporal resolution but remains challenging in non-collaborating subjects. So far, most fMRI studies in young children necessitated sedation, making the study of conscious cognition or action inappropriate. A recent fMRI study, however, reported changes in blood oxygen level dependent (BOLD) signals in the superior temporal cortex during auditory stimulation in non-sedated neonates (Anderson et al. 2001). Similarly, MEG has also recently proved capable of measuring neonatal brain activity (i.e., spectral power in 2–7 Hz range; Anastasiadis et al. 2001). The real interest would be to measure brain activity in *crying* infants. Factorial designs would compare "manipulative," "colic," and "honest" (pain or hunger) cries. Parametric designs would correlate neural activity with graded acoustic characteristics of the cries (e.g., fundamental frequencies). For the time being, this is still a dream. However, technological advances (solving movement susceptibility) might make it a reality. Similarly, despite several technical problems, in utero measurement of auditory fetal brain activation has been recently performed by both fMRI (Moore et al. 2001) and MEG (Zappasodi et al. 2001). In the meantime, EEG seems more affordable and has the major advantage to be able to measure variations in infant brain function in naturalistic situations. Using EEG, it has been shown that right frontal activation asymmetry in 1-month-old infants is related to more frequent sad and pre-cry faces (Jones et al. 1997b). A preliminary longitudinal study showed that 3-month-old infants with this right frontal EEG asymmetry still showed this pattern at 3 years old and were found less empathetic during simulated maternal distress (Jones et al. 1997a). Infants who cried in response to maternal separation had greater right frontal asymmetry during the preceding baseline period compared with infants who did not cry (Davidson & Fox 1989). Right frontal EEG asymmetry is thought to reflect negative affect. In newborns, it correlates with elevated cortisol levels and "depressive symptoms" of the Brazelton Neonatal Behavior Assessment Scale (Brazelton 1973) and a greater number of state changes during sleep/wake behavior observations (Field et al. 2002). Recent EEG data obtained in neonates show that disagreeable (e.g., a noxious heel-stroke; Fernandez et al. 2003) or agreeable stimulation (e.g., smelling lavender or rosemary; Sanders et al. 2002) respectively induces a right or left frontal activation (i.e., spectral power asymmetry in the 3–6 Hz range). Interestingly, this right frontal asymmetry (indicator of negative affect) was not observed in infants who had received a sucrose solution (not water) prior to the noxious heelstroke (Fernandez et al. 2003). These studies show that EEG spectral power analyses are a promising tool for the study of the signal function of crying. In our opinion, ongoing methodological improvements for EEG (e.g., Freeman et al. 2003) and event related potentials (ERPs; e.g., Quiñan Quiroga & Garcia 2003) data analysis and interpretation will further increase its usefulness in deciphering the hypothesized "protolanguage" of crying.

Second, functional neuroimaging offers the possibility to test

Soltis' proposed model which predicts that "acoustically normal" pain or hunger cries would engage a neural network known to be involved in "positive emotions" (eliciting positive parental caregiving), whereas "acoustically abnormal" cries would activate "negative emotion" – related brain areas (resulting in reduction or withdrawal of care or even abuse). This could be done by examining the effect of infant cries on brain activity in parents, using parametric or factorial designs (e.g., correlation with behavioral/physiologic indices or personality and temperament measures). Preliminary studies have already shown the feasibility of this approach. Using ERPs, it was shown that hearing an infant's cry resulted in faster habituation and longer response latencies of the auditory cortical potentials, as compared to hearing a neutral word (Purhonen et al. 2001b). Interestingly, when mothers heard their own newborns' cries, responses were larger in amplitude than those observed in non-mothers. The authors interpreted their data as reflecting a general increase in arousal, enabling the mother to be continuously alert to the infant's signals and signs of distress (Purhonen et al. 2001a). As briefly mentioned in the target article, fMRI has shown that in breastfeeding first-time mothers, hearing infant cries (compared with hearing noise) activates a large neural network thought to be involved in maternal behavior (Lorberbaum et al. 1999; 2002). Unfortunately, the authors did not compare these results to a non-mother control group. We have recently studied "canonical" brain activation related to passive listening to newborn cries (Elinx et al. 2002).

Figure 1 illustrates that despite the observed variability of induced feelings, each and every non-parenting control subject activated amygdala and posterior cingulate cortex, areas known to play a key role in emotion (LeDoux 2000; Maddock 1999). Others have also observed robust amygdala activation elicited by listening to crying (but also to laughing), even when the crying was un-

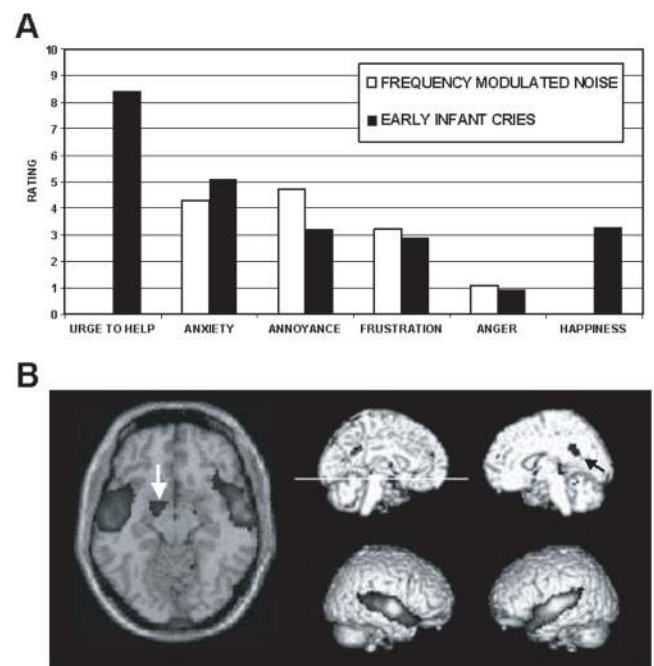


Figure 1 (Laureys & Goldman). (A) Mean ratings of feelings induced by passive listening to cries of a newborn baby and to matched frequency modulated noise, obtained in 15 volunteers. Scores go from 0 (absent) to 10 (highest possible) on a verbal analogue scale. (B) Regional increases in cerebral blood flow (gray areas) when hearing cries compared to noise, measured by H_2O^{15} -PET and shown on a spatially normalized MRI. Each of the 15 subjects (8 of them males, age ranging from 18 to 63 years, none parenting a baby) activated the amygdala (white arrow) and posterior cingulate cortex (black arrow).

attended (Sander et al. 2003, Sander & Scheich 2001). Future testing of Soltis' proposed model by means of functional imaging will benefit from our increasing understanding of the neural correlate of positive versus negative emotions (for recent review see Wager et al. 2003).

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From an undifferentiated cry towards a modulated signal

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Abstract: The colic cry as a signal of undifferentiated vigour, and not a disease, is good news. This hypothesis also has neurobiological perspectives. Feeding increases the pain threshold of the infant and has an effect on its brain functions. These may contribute, by neurobiological mechanisms, to the gradual decline in the tendency for excessive crying during the first months of life.

Although the cry is a typically human signal with its characteristic physiological signs, vocal signals with a similar meaning are also used by other species. The *undifferentiated* character of excessive early infant crying, which probably lacks a counterpart in other species, is more difficult to understand than other types of cry signal. The cry as a signal functions primarily as a nonverbal form of communication and is bound to have effects on the receiver that remain outside cognitive consciousness, despite its affective recognition.

Knowledge of the character of the early cry signal is therefore important, and studies summarising research findings in this field are welcome. For mothers who wrestle with how to manage an excessively crying baby, it is surely a relief to learn that such crying, often labelled as colic, is, in fact, an infant signal that resides within the normal communication range. Soltis' summary of the studies analysing the acoustic structure of cry signals demonstrates that the colic cry does not differ significantly from other healthy infant cries. The common type of colic cry, without organic alterations, follows a diurnal rhythm and occurs mainly in the afternoon and early evening hours. In contrast to the view of many anxious mothers, colic crying thus shows regularity, seen also in the peaking of crying at the age of 6 weeks and gradual waning after 12 weeks.

These data put excessive early infant crying within the developmental frame of the first three months of infant life. Crying as a signal is predominantly used by the infant in adapting to the post-natal conditions of life, which demand initiative and vigour of the infant in attaining vital care. This contrasts with intra-uterine conditions, where care was provided by automatic biological means and required no special effort by the infant. Crying can therefore be considered as a signal that evinces a bridging process in the slow transition from intra-uterine life to extra-uterine reality.

Data from several sources, many of them presented in the target article, suggest that the age of approximately three months represents a turning point after which, normal developmental conditions provided, the relationship between the infant and the caretaking environment begins to take on a more regulated, interactive, and communicative pattern, indicating that a new level of psychophysiological organisation has been reached (Spitz 1959; Stern 1985). As Soltis mentions, the emergence of self-regulated interaction of the infant with the environment is paralleled by sev-

eral physiological measures that show functional changes approximately at this time-point. The cry becomes more of a signal that can be used for increasingly specific purposes.

Soltis discusses the nature of the early infant cry from several important viewpoints. The conclusion that the cry functions as a graded signal that slowly acquires an interactive meaning from an early undifferentiated cry in the beginning of life, is convincing. Although probably alien to common sense, the interpretation of early excessive crying as a signal of vigour is logical, though not yet proven.

The consequence of excessive early infant crying – that is, does it elicit caring or abandoning responses by the caretaker? – is obviously an important issue. The outcome is determined by several factors, as Soltis demonstrates. It depends on the intensity and quality of the cry signal, on the characteristics of the receiver and on her psycho-physiological and psychosocial conditions. It is also determined by wider societal and cultural factors. As long as the cry signal remains unsettled, the infant is inconsolable, and the cry cannot be managed in a predictable way, the caretaker remains in a conflicted position. It is more difficult to identify with the crying infant when the signal is undifferentiated than with a cry that can be understood. How much poorly organised crying the caretaker can tolerate then becomes crucial. The message that even excessive crying can express infant vigour is therefore important. It helps mothers to identify positively with their infants already in the undifferentiated neonatal stage. This conclusion needs to be spread to the potential consumers of this information.

The cry of a neonate is often associated with hunger. Besides supplying nutrition, feeding of the newborn seems to have an effect on its brain activity, as the mean amplitude of the electroencephalogram of the newborn is higher in the posterior cortical areas during feeding than immediately after (Lehtonen et al. 1998). Adequately meeting the vital needs of the infant thus has plausible neurobiological effects and may leave traces on the brain (Polen & Hofer 1999).

This effect on the electroencephalogram seems to wane, however, before the age of three months (Lehtonen et al. 2002). At three to four months, the brain of the infant begins to produce rhythmic theta activity regulated by a subcortical pacemaker that allows the synchronous activity of large cortical neuronal populations and facilitates the modulation of cortical activity (Niedermayer 1993). From this age, infant feeding begins to reinforce the theta rhythm (Lehtonen et al. 2002). Similar responses have also been observed in other infant-caretaker interactions, including those that provoke crying (Futagi et al. 1998). As sucking and oral sucrose increase the pain threshold of the infant (Blass & Watt 1999; Carbajal et al. 2003), repetitive feeding may contribute to the decline in undifferentiated crying by strengthening the infant's pain threshold. Mastery of distress in developing infants is thus dependent on the neurobiological effects of caretaking, which we still, however, poorly understand.

Furthermore, there is evidence that during the post-delivery period, mothers are neurophysiologically sensitised towards infant signals (Purhonen et al. 2001a), and that female subjects' neurophysiological processing of infant crying is different compared with neutral auditory signals (Purhonen et al. 2001b). Postnatal adaptation thus also seems to pertain to the mother's neurobiological functions, with possible implications for how the cry signal is tolerated.

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Can reinforcement learning explain variation in early infant crying?

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Abstract: We welcome Soltis' use of evolutionary signaling theory, but question his interpretations of colic as a signal of vigor and his explanation of abnormal high-pitched crying as a signal of poor infant quality. Instead, we suggest that these phenomena may be suboptimal by-products of a generally adaptive learning process by which infants adjust their crying levels in relation to parental responsiveness.

In applying evolutionary signaling theory to infant crying, it might be interesting to note the increasing recognition among biologists (e.g., Godfray & Johnstone 2000; Royle et al. 2002) that current theory is far too simplistic to account for the complex dynamics of parent-offspring interactions. A major problem in translating current models to reality is that the net benefit from begging or crying depends not only on the value of the resource to the offspring, but also on the probability that begging or crying will succeed in gaining this resource. Therefore, when we expect offspring to optimize their costly signaling efforts in relation to expected benefits (as required by honest signaling theory), we also expect them to somehow "know" how effective their begging and crying will be in eliciting parental response. Because signaling effectiveness can vary with environmental conditions, parental state, and competitive dynamics, it must be assessed from external cues. Reinforcement learning has been suggested as a mechanism by which offspring can adjust their begging or crying to the most effective levels (e.g., Kacelink et al. 1995; Lotem 1998; Stamps et al. 1985), and recent experiments with bird nestlings show that offspring of similar quality and physiological needs can learn to beg at remarkably different levels (Kedar et al. 2000; Rodríguez-Gironés et al. 2002). An important implication of these findings is that variation in offspring begging or crying may reflect differences in learning dynamics and personal history, rather than differences in need or quality.

With this background in mind, let us now consider Soltis' suggestion that excessive crying, or colic, is a signal of vigor. While this is certainly a possibility, we doubt whether in modern societies, where food is readily available, differences in the net profitability of crying can still be large enough to produce the observed differences between colicky and non-colicky babies. In this respect, we agree with Wells (2003) that the current fitness cost of colic is probably low, and that excessive crying is no longer an indicator of high quality: the vast majority of infants today can probably afford to be colicky. The question, however, is what causes the considerable variation in the amount and intensity of crying among healthy babies? Based on what we have learned from birds, we suggest that much of the observed variation in infant crying may reflect differences in learning dynamics and history rather than infant quality or need. Like bird nestlings, human infants must also predict the net benefit of their costly signaling, and they might also be doing so by reinforcement learning. The tricky point with learning, however, is that under the same combination of costs and benefits, learning may still produce quite different behaviors as a result of differences in the dynamic sequence of the learning process. Therefore, in a population of healthy infants and wealthy parents, where actual variation in the costs and benefits of crying is low, a considerable amount of variation in crying may be a result of these differences in learning dynamics. We agree with Soltis' view that colic can be seen as merely the extreme of a natural range of variation, but we suggest that reinforcement learning may be the key to understanding this range of variation.

Colic may develop when a series of intense crying bouts (perhaps caused by a transient period of distress or illness) has been rewarded by the parents and has led to an escalation in crying. This

escalation may not be easy to reverse, because the typical response of a sleepless parent would still reinforce elevated cries more than benign ones. At this stage, the general indulgence or toughness of the parents is not so important, as the key change needed is to turn around the differential reinforcement regime of intense versus benign crying. Normally, this turn-around may become possible only after physiological and developmental processes result in some reduction in infant demand, usually towards the third month of life. Only then may babies be content for longer periods of time, and parents may then be able to reinforce low-intensity crying, before it rockets up in intensity, frequently enough to change infant behavior. Changing the reinforcement regime of colicky babies during the natural peak in colic predisposition may not be easy. However, there is evidence for some success in applying behavioral treatments for colic (Wells 2003; Wolke 1993).

Let us also consider the idea that abnormal high-pitched crying (over 1000 Hz) is a signal of poor quality. The evolution of such crying is actually quite puzzling because it appears to be maladaptive: Healthy babies never exceed the 730 Hz limit when in transient pain or immediate distress, and abnormally high-pitched cries appear less effective, and may even elicit neglect or abuse. One way to explain high-pitched crying is to accept Soltis' view that chronically sick infants may unavoidably produce high-pitched calls as a by-product of their pathologies, and that in choosing between not crying at all and crying with abnormally high pitch, the latter is still more adaptive. Yet, here too, reinforcement learning may play a role. Let us assume that it is generally adaptive for babies to modulate the fundamental frequency of their cries based on past experience. What would be the effect of such a learning strategy on chronically ill babies? We suggest that as long as their parents continue to care for them, chronic stress and failure to be comforted by feeding would cause infants mainly to use, and therefore to be reinforced by, high-pitched crying. As with colic, we expect rapid escalation, because, up to the point of total neglect, parents are still more likely to respond to cries of higher frequencies than to cries of lower frequencies. The ill baby, on the other hand, may still do best by using learning to adjust his crying frequencies to the most effective levels. Under this view, abnormally high-pitched crying did not evolve as a signal of poor quality, but rather, it is an abnormal by-product of using an adaptive learning rule under pathological circumstances.

Infant colic: Re-evaluating the adaptive hypotheses

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Abstract: Colic may allow infants to obtain additional investment from their parents. The lack of clear fitness costs of colic and of differences in condition between colicky and non-colicky infants is inconsistent with the hypotheses that colic is an honest signal of need or vigor. These and other characteristics of colic, however, are consistent with the hypothesis that colic is a manipulative signal.

The core symptom of colic is "excessive, inconsolable crying that begins and ends without warning" (target article, sect. 5.1, para. 1). The target article suggests that colic represents the upper end of the crying distribution in early infancy and that it may be an honest signal of vigor that evolved to reduce the risk of infanticide. In this commentary, we re-evaluate the adaptive signaling hypotheses of colic and conclude that the evidence is more consistent with the manipulation hypothesis than with the honest signal of vigor hypothesis.

The quality of the parental response to colic is crucial to the un-

derstanding of its function. Soltis argues that there is no evidence that colic alone, in the absence of other clinical symptoms, may increase the risk of infant abandonment, abuse, or infanticide. In this commentary, we assume that his reading of the literature on this issue is correct and that parental responses to colic tend to be positive rather than negative. Accordingly, we selectively focus on adaptive hypotheses that assume that colic allows infants to extract additional investment from their parents. However, any evidence linking colic to increased risk of infant abandonment, abuse, or infanticide would change our interpretation of this phenomenon considerably.

The honest signal hypotheses assume that colic is costly to infants. Evidence that crying has metabolic costs and that such costs are higher for low quality (low weight and preterm) infants than for high quality (normal weight, full-term) infants (Rao et al. 1997) is important, but clear fitness costs of colic have not yet been demonstrated. Assuming that colic does indeed have fitness costs, there are two possibilities. One possibility is that colic is an honest signal of need. Another possibility is that colic is a handicap (Zahavi & Zahavi 1997) used by higher-quality infants to advertise their vigor. The data, however, indicate that colic is not associated with transitory need and that colicky infants are neither inferior nor superior to other infants in terms of their overall physical and health condition. Therefore, the data support neither version of the honest signal hypothesis. The honest signal of vigor hypothesis discussed in the target article argues that the specific function of colic is to minimize the risk of parental infanticide. There is no evidence, however, linking colic to infanticide. Colic does occur in the age period in which infants are most vulnerable to infanticide, but, as Soltis notes, both colic and risk of infanticide could be independently correlated with a host of other events occurring in the first three months of life. In summary, the lack of clear evidence for fitness costs of colic and for differences in condition between colicky and non-colicky infants is inconsistent with the honest signal hypotheses. The signal of vigor hypothesis suffers from the additional weakness that there is no evidence that colic may reduce the risk of infanticide.

The hypothesis that colic is a manipulative signal assumes that the increase in crying associated with colic does not result in significant fitness costs to infants. Manipulation is suggested by the observation that colic is aversive to caregivers. Whether this property results mostly from the amount of crying, its pitch, or its inconsolability, the fact remains that parents describe colic crying as “excessive” and undesirable. Whenever an aversive signal is used to obtain additional investment from another individual, this suggests conflict of interest and manipulation. The manipulation hypothesis is also consistent with the failure to detect health problems in colicky infants. In this view, colicky infants are normal infants who succeed in obtaining additional investment from their parents in the first three months of life, which are often crucial for infant survival. One possibility is that colic is heritable and under frequency-dependent selection. In this view, colic is effective only because it is relatively rare; if parents gave birth only to colicky infants, they would become skeptical about the babies’ signaling and unlikely to provide additional investment. Another possibility is that colic is a conditional strategy activated by prenatal or perinatal environmental cues.

Similar to the other adaptive hypotheses, the manipulation hypothesis requires evidence that colic is effective in extracting additional parental investment. We are not sure about the quality of the data on this issue, but anecdotally, it is well known that parents of colicky infants often make extra efforts in holding and feeding them. Colicky infants may also receive additional medical care, as their parents often take them to the doctor. Soltis argues that the timing of colic is inconsistent with the manipulation hypothesis because “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” (sect. 6.1, para. 3). In reality, parents and offspring may be in conflict over the amount of investment at any point in

time before weaning, conflict can occur about different forms of parental expenditure, and infants can switch from one type of “weapon” to others as they develop (Trivers 1974). Early conflict may be specific to one form of parental expenditure (e.g., rate of breast-feeding) and expressed mostly through crying. Later on, conflict may involve other forms of parental expenditure (e.g., carrying) and additional behavioral and psychological tactics. Therefore, the temporal pattern of early crying is not necessarily incompatible with parent-offspring conflict theory. Soltis also argues that the sixth-week peak and the early evening peaks of colic are difficult to reconcile with the manipulation hypothesis. However, since the same crying peaks are also observed in non-colicky infants, they may simply represent neurobiological processes underlying the expression of early crying without any necessary implications for its adaptive function.

In conclusion, although we agree with Soltis that there is no strong support for any of the adaptive hypotheses of colic, we maintain that, if anything, the characteristics of colic are more consistent with the manipulation hypothesis than with the honest signal of vigor hypothesis. More efforts need to be made to develop contrasting predictions from these adaptive hypotheses and to test them with empirical data. The possibility that colic may be the result of an interaction between early neurobiological development and dramatic changes in infant carrying and feeding practices in very recent human evolutionary history, needs to be given further consideration as well.

Infant crying in context

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Abstract: Our focus has been on the role of early cry as a commanding source of information about infant pain and distress that requires interpretation by an adult caregiver. Its inherent ambiguity may offer an adaptive advantage, as resolution requires adult presence and scrutiny of other behavioral, physical, and contextual factors.

Young infants have fewer means of signaling distress than do older infants, for whom crying slowly develops into speech acts. Infants also do not have alternative behavioral means allowing escape or control of sources of pain; hence, communication of internal states to potential caregivers is imperative. In this sense, the early infant cry can be viewed as an encoded signal, which then needs to be decoded and interpreted by a caregiver to determine how to respond to the infant. Soltis’ paper compels one to reflect on the communicative value of cry in relation to the behavior, situation, and developmental contexts of the infant, and the circumstances governing the lives of parents.

As Soltis observes, the evidence indicates that cry emerged as a general distress call, representing a continuum of infant distress rather than signaling qualitatively different internal states such as pain or hunger (Fuller 1991). Crying in a young infant is often an ambiguous stimulus, with caregivers usually unable to discern the source of the distress, unless other information is available (e.g., evidence of injury, ill health, time since feeding). The inferential task is more challenging when no precipitating event is evident and the usual battery of palliating efforts (feeding, rocking, pacifiers, etc.) proves ineffective. We have characterized crying as a “distant early warning signal” (Craig et al. 2000), as it has a low threshold for instigation and is highly salient in commanding both caregiver attention and presence to seek clarifying information concerning the source of distress.

While cry serves as an important cue frequently used in making judgments of pain in infants, once attention has been attracted, its importance diminishes because it is not definitive. In studies of nurses judging infant pain, cues such as context, facial activity, and body movement, as well as vocalizations, were identified as "frequently useful" in making pain ratings (Fuller & Conner 1996; Pigeon et al. 1989; Shapiro 1993). In a survey of nurses, restlessness and facial activity were more frequently identified as indicators of pain in infants than cry (Howard & Thurber 1998). In a study of parents judging pain in infants receiving immunization injections, infant vocalizations were secondary to facial activity in importance as cues (Smith et al. 2002). These studies examined self-reports of cues, whereas others have explored the strength of the relationship between cues and assessed pain levels. In a study of parents viewing videotapes of infants receiving heel lances, facial activity accounted for 43% of the variance in ratings of pain sensation and 49% of the variance in ratings of pain affect, while fundamental frequency accounted for only an additional 2% of the variance (Craig et al. 1988). In another study by Hadjistavropoulos et al. (1994), cry characteristics accounted for 38% of the variance in observer pain ratings, while facial activity accounted for 49% of the variance in ratings. When facial activity and cry characteristics were considered together, they accounted for 54% of the variance in pain ratings, leading to the conclusion that cry was mostly redundant to facial activity. Once attention has been attracted, therefore, caregivers rely more on directly observable cues, because they provide more specific information.

This is not to argue that the signal value of infant cry is unimportant, but rather, that it needs to be viewed in relation to infant behavior, environment, and social context. Soltis suggests that chronically abnormal acoustic characteristics of infant cry may be a precipitating factor for neglect, abuse, and infanticide in humans, and he outlines an excellent series of studies that would incorporate features of contextual factors and caregiver characteristics and reactions in order to understand mechanisms for caregiver judgments and actions. Appreciating infant well-being and survival necessitates an understanding of not only cry and infant characteristics, but also the caregiver and the relationship to the child. For example, caregivers having greater experience with infants are more accurate in differentiating between different types of cries (Craig et al. 1988; Owens 1984), and therefore are more likely to be able to identify sources of infant distress. In addition, characteristics of the caregiver, such as cognitive biases, sensitivity, knowledge of and relationship to the infant, can influence this process (Craig et al. 1996).

Caregivers unable to determine the source of an infant's distress could respond with either frustration or denial. A caregiver faced with an infant crying for unknown reasons may respond with abuse out of a sense of complete exasperation and frustration with being unable to soothe or quiet the child. Conversely, a caregiver may suspend sensitivity to an infant's crying if faced with the unacceptable reality that an infant is suffering and nothing can be done to relieve that distress (McGrath & McAlpine 1993); this could potentially result in neglect. As Soltis correctly points out, these extreme responses to abnormal infant crying likely originate in adult dispositions prior to parenthood.

Finally, although Soltis limits his discussion to early infant cries, before the age of three months, the target article invites speculation about the processes whereby maturation and experience enhance the signal functions of crying. Little is known about how crying becomes a speech act and how language concerning pain and distress emerges and comes to control caregiver behavior across infancy. Neurodevelopmental maturation of infants and social learning factors likely lead to changes in cry acoustics, and this can influence the signal functions of cry. Recent calls for an exploration of developmental changes in infant pain cry (Green et al. 2000) suggest the importance of considering developmental factors in the communicative aspects of cry.

It is now important to follow up with research to provide empirical basis for this area of study, taking into account behavioral,

social, environmental, and developmental context. We are grateful to Soltis for provoking debate into the field of communication of infant distress.

Infant crying and colic: What lies beneath

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Abstract: The neural structures implicated in crying are reviewed, based on studies in animals. Brain regions involved include the anterior cingulate gyrus (a cortical structure), amygdala, thalamic tegmentum, periaqueductal gray of the midbrain, and the nucleus ambiguus of the caudal brainstem. It is hypothesized that the crying associated with colic may be a manifestation of differing developmental stages in the brain circuits involved.

Soltis has provided a useful overview of infant crying, a topic not heretofore covered in a *BBS* target article. His main thesis is that crying, including the excessive crying associated with colic, is an adaptation by which an infant signals its need and vigor to caregivers. The acoustic details of crying, basic elements of which are regulated by vagal mechanisms, matter in terms of their signal value and play a role in the quality of parental care. From an evolutionary perspective, crying in human infants perpetuates the ancient function of signaling distress or discomfort and increasing proximity to, and caregiving behavior from, parents and other caregivers.

This commentary will address several points that deserve further elaboration, drawing from comparative studies and neuroscience.

Neural circuits mediating crying and their maturation have been identified in animal studies. In some nonhuman primates, infant cry sounds continue to be produced into adulthood, and serve to reunite separated individuals from their mate or social group. These so-called *isolation calls*, or *separation cries* are acoustically similar to the "cry sounds" produced by infants of these species during periods of maternal separation (such as accidental falling off from the mother while being carried, or, when older and more independent, when frightened or hungry) (cf. Newman 1985). Because the functions and acoustic details of the cry sounds of most nonhuman primates (and many other mammals) are so similar across species (including humans), I have suggested that the mammalian infant cry and the mechanisms regulating its production have had a conservative evolutionary history. Our understanding of these regulatory mechanisms is still rather primitive, but some details are beginning to emerge. While it is true that brain stem motor neurons of the vagus nerve innervating the larynx undoubtedly have an important role in regulating basic acoustic features of infant cries, they do not operate in the absence of higher-order brain stem and cerebral control.

Early studies in lightly anesthetized cats showed that stimulating the cut surface of the midbrain produced meows and other vocalizations (Kelly et al. 1946). More recently, Buchwald et al. (1988) stimulated the hypothalamus in freely moving cats and produced meows similar to the cat's natural isolation calls. Disruption of normal vocal patterns by selective lesions is a good indicator of the importance of a brain region in a given behavior. Lesions of the thalamic tegmentum in adult squirrel monkeys produced disruptions of the normal acoustic patterning of isolation peeps (the species-specific isolation call) without altering the tendency to make these calls in the appropriate context (Newman & MacLean 1982). Bilateral lesions in and adjacent to the midbrain periaqueductal gray resulted in selective mutism, in that lesioned animals failed thereafter to make isolation peeps, but continued to make other vocalizations, such as shrieks when caught (Newman &

MacLean 1982). One cortical area in particular, the anterior cingulate gyrus, has been implicated in cry production in several studies. In a species of CF-FM bat (a species that produces long whistle-like notes when searching for prey), stimulating the midline limbic cortex (comparable to the cingulate gyrus of primates) produced CF whistles, calls that are structurally similar to infant isolation calls (Cooler & O'Neill 1988). In macaques, Robinson (1967) found that stimulating the midline cortex below the genu of the corpus callosum resulted in "coo" calls (this species' isolation call, but also used in other social contexts). Jürgens and Ploog (1970) elicited tonal vocalizations, including the isolation peep, by stimulating in the corresponding region of the squirrel monkey brain. Sutton et al. (1981) found that ablating the peri-genual anterior cingulate gyrus in macaques eliminated production of coos in macaques trained to make coos under operant conditions. MacLean and Newman (1988) likewise found that lesions of the peri-genual region of the anterior cingulate cortex in adult squirrel monkeys eliminated production of the isolation peep in a more natural setting not involving operant conditioning. Few studies have examined the brain substrates mediating isolation call production in infants, but Newman and Bachevalier (1997) reported that bilateral ablation of the amygdala in macaque neonates resulted in production of fewer isolation coos, and coos with less inflected frequency peaks when tested between 6 months and 1 year of age. Interestingly, bilateral ablations of area TE in the inferior temporal cortex, considered to be a higher visual processing region, led to animals that were more vocal and, at least in males, made more noisy calls when separated in the 6-month to one-year age period.

Is the excessive crying associated with colic a manifestation of developmental delay or dysregulation? As the brief review above indicates, several brain regions extending the entire length of the neural axis (cortex to brain stem motor neurons) can influence crying in terms of the tendency to cry and the acoustic details of the cry sounds. Given the complex interactions likely to occur between these structures, it seems possible, should the maturation of neural circuits not proceed at the same rate for all of the relevant structures, that variability in infant crying behavior might ensue. Circuits underlying responsiveness and tendency to cry that mature at a different rate than circuits underlying cry acoustics could lead either to bouts of poorly regulated crying or cry sounds that tend toward outliers in their acoustic details. Evidence for both of these is presented in Soltis' target article. To test this hypothesis, it would be necessary to evaluate the developmental status of specific brain circuits associated with crying in subjects for which detailed information on their crying behavior was also available. Given the lack of feasible methods for studying the maturation of specific brain circuits in human infants, continued findings from animal studies will be important for future investigations aimed at testing this hypothesis.

NOTE

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Infant vocalizations: Contrasts between crying and laughter

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Abstract: Crying and laughter are innate, preverbal, species-typical vocalizations that have similarities and differences which are mutually illuminating.

Crying, as noted by Soltis, is a potent, early appearing, species-typical human vocal signal that is uttered in a similar way by mem-

bers of all cultures and vocal communities. The same can be said for laughing. In the following comparative treatment, I contrast similarities and differences between crying and laughing to better characterize each utterance and illuminate the general issue of innate vocal signaling. Unless otherwise noted, themes concerning crying are taken from the target article by Soltis; those about laughter are from Provine (2000).

Crying and laughing both develop very early in life; crying is already present at birth, while laughing emerges about four months later. Crying is often performed by solitary infants, in contrast to laughter, which is seldom produced outside of social settings. These differing degrees of sociality are consistent with their purpose; crying is the solicitation of attention by a caregiver, who may not be present, while laughter is a play vocalization engaging an already present person. Laughter is an important form of pre-speech communication that contributes to bonding between infant and mother. The infant responds to maternal touching and tickling with laughter and smiling, acts reinforcing further maternal touching until it becomes excessive, when the infant begins to fuss and cry. Infant laughter and associated smiling are powerful, reinforcing stimuli that encourage the mother to maintain the behavior that evoked it. In contrast, infant crying is a highly aversive stimulus to the mother, who works to terminate it. Although crying and laughing differ greatly in function and social context, they nicely complement each other and contribute to infant survival and development.

Regarding the issue of "honesty of signaling" in crying, Soltis should consider the constraints against dishonesty. Species-typical vocalizations such as crying and laughing are under minimal conscious control and are poor candidates for behavioral shaping. The best demonstration of the lack of conscious control over crying and laughing is to attempt to cry or laugh on command. About half of the people I have asked to laugh comment that they cannot do so on command, and those who attempt to laugh produce obviously false simulations. Although similar data are not available for crying, I expect the same result. Recognition of the difficulty in voluntarily producing such expressive acts as crying and laughing was a motive for the development of the technique of method acting – actors try to produce a convincing emotional expression by imagining themselves in a situation that evokes that emotion. The limited voluntary control that we have over crying and laughing indicates that we should be reluctant to explain these acts in terms of rational choice. We do not "decide" to cry or laugh.

Although there are neurological constraints on the "honesty" of crying and laughing, atypical expressions of these utterances are leading examples of abnormal and inappropriate affect, significant symptoms of psychopathology and neuropathology. Frequent comorbidity of crying and laughter suggests related brain mechanisms for the two acts. Consider, for example, the emotional lability sometimes observed in amyotrophic lateral sclerosis (ALS) and other instances of so-called pseudobulbar palsy. The patient may bawl uncontrollably in response to minor sadness or laugh uncontrollably in response to the joy of seeing an old friend. (Some patients may laugh until they cry, but the converse is not observed.) Epileptic seizures may drive either laughter or crying by producing the emotionless expressive act or secondarily by producing the associated emotional state.

Although not mentioned by Soltis, preliminary evidence suggests that infant crying is contagious (Simner 1971). The crying of one infant triggers crying in its neighbors. Contagion provides an amplifier effect, spreading a vocal signal from individual to individual in a behavioral chain reaction. The contagiousness of laughter is better known, and is the basis for the notorious laugh tracks on television situation comedies. However, you can still get laughs if you throw away the joke and just keep the laugh track – laughter is sufficient to trigger laughs and smiles in an audience. The age of onset of contagious laughter is unknown. Contagious signaling is an effective but neglected means of synchronizing the biological state and behavior of individuals in groups.

Crying is an undeniably powerful stimulus that can evoke re-

sponses as varied as caregiving and, in rare cases, infanticide. Laughter is an equally potent stimulus, although its power is often underestimated in our feel-good, be-happy culture, with its false assumption that laughter is a response to humor. (Only 10–15% of adult, pre-laugh conversation is remotely joke-like.) The ancients lived in a less politically correct time and witnessed first-hand that laughter is, at best, a two-edged sword. Plato, for example, thought that laughter could undermine authority and threaten the state. While laughing *with* others can be a joyous communal experience, contemporary news reports remind us that laughing *at* others (jeering or ridicule) can lead to violence ranging from ethnic cleansing to homicide.

The contrasts between crying and laughing are so plentiful and informative on so many levels that students of one of these signals can benefit from considering the other. This comparative analysis prevents researchers from settling into the sometimes artificial conventions that occur when these vocalizations are studied by themselves.

Crying and tears mimic the neonate

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Abstract: This commentator has no argument with the explanations given by Soltis. Yet a different approach to the phenomenon of crying might be fruitful. Neonates elicit care. It is hypothesized that non-neonates evolved to mimic, when in need, the appearance of the neonate by crying and by shedding tears, thus inducing helping behavior by the spectator.

I presume that answers quite similar to the ones Soltis gives for the crying behavior of human infants would satisfactorily explain aspects of the behavior of infants belonging to other species; for example, sparrows, whose young noisily and conspicuously “beg” for food.

There are, however, several differences between the “begging” behavior of sparrows and humans crying. A sparrow will not show the “begging” behavior again once adult, but humans, by contrast, retain the capacity to cry throughout their lives. And several weeks or months after birth humans add a spectacular feature to their crying repertoire: *tears*, a word remarkably absent in Soltis’ article. But Soltis does write (sect. 6.1, para. 2): “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.” If parent-offspring conflict indeed increases about three months after birth, and if the shedding of tears indeed emerges at around the same time, one cannot help but speculate about a causal relation.

At this point I cannot resist the temptation to inform the readers about a general explanation of crying and tears that I conceived of some twenty years ago. Here are two citations out of the *Human Ethology Newsletter* (now renamed the *Human Ethology Bulletin*).

In many species of animals, the stimuli emitted by newborns bring about parental care. In fact, the newborns of many species require parental care. Because a newborn has little else to offer than its own appearance and behaviour, it is logical that it is exactly these factors that elicit the parental care.

The crying behaviour of humans is favoured by natural selection because the behaviour resembles or causes resemblance to some of the stimuli emitted by newborns and, therefore, induces helping behaviour.

Some aspects of this resemblance are as follows:

1. The wetting of the face with tears – compared to the face of the newborn, which is wet with amniotic fluid.

2. The jerking, almost spasmodic respiration of a crying person – compared to the first respiratory efforts of a newborn.
3. The screaming of a crying person – compared to the first screams of a newborn.
4. The closed eyes, the wrinkled skin around the eyes, the spotted coloration of the facial skin, and the open mouth – all are very much alike in a newborn and in a nonneonate who cries. (Roes 1989)

What I argued is that humans who cry mimic the appearance of neonates. A neonate by definition sends out honest signals of being in need. I speculate that natural selection favoured individuals in need who mimicked the neonate, because individuals able to mimic these signals would get more help.

Presumably, the ability to cry spread through the species, as well as the ability to recognise this signal. The sight of a crying individual is instantly and universally recognised by the human spectator.

The fact that babies don’t shed tears until several weeks or months after birth can now also be explained: The mimicry is perfected with tears only when this perfection is needed, that is, when parent-offspring conflict increases.

I still like this general idea of crying and tears as a mimic of neonates. Can it be disproved?

The development of parent-infant attachment through dynamic and interactive signaling loops of care and cry

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Abstract: In addition to the infant cry being a signal for attention, it may also be a critical component of the early formation of attachments with caregivers. We consider the complex development of that attachment, which involves reciprocal interactive signaling and a host of evolutionarily conserved caregiver factors.

From an infant’s point of view, a cry may be considered a signal of vigor and need for attention, food, and protection – each critical to the infant’s survival. But the cry may also have a critical role in the formation of attachments with caregivers. Infant-caregiver attachment requires a system of reciprocal communication, with feedback from caregivers being critical to the interpretation of the infant’s cry. Caregiver-infant attachment is a complex process requiring both the signaling of the infant through cry and other behaviors, as well as “feedback” from caregiver behaviors. Both participants in this dyad may be seen as “receiving” and “transmitting” over certain ranges under the influence of a range of factors. Many features of the infant side of caregiver-infant signaling are emphasized in the review by Soltis, but further consideration of the parental side is warranted. Caregiver “input-output” cry-response behaviors may range from neglect and abuse, to appropriate care, to the potential for over-care according to various interacting factors, including the caregivers’ perceptual hardware, psychology, and preparation for caregiving, and immediate social environment.

A considerable literature has recently emerged regarding the neurobiological and genetic substrate that apparently regulates the initiation of parenting across mammalian species. In humans, the initiation of parental caregiving includes a set of highly conserved set of behaviors and mental states that are crucial for reproductive success and may reflect both an individual’s genetic endowment and the early experience of being cared for as a child. In humans, the initiation of maternal behavior is associated with intense parental preoccupations (Leckman & Mayes 1999; Leckman et al 1999; Leckman et al. 2004). The content of these pre-

occupations includes intrusive worries concerning the parents' adequacy as parents and the infant's safety and well-being. Even before the child is born, parents preoccupy themselves with creating a safe and secure environment for the infant. Major cleaning and renovation projects are commonplace as the human form of nest building unfolds. Uppermost among parental concerns are safety and unimpeded access. Safety issues include the cleanliness of the infant's immediate environment. After birth this same sense of heightened responsibility will compel parents to check on the baby frequently, even at times when they know the baby is fine. Cleaning, grooming, and dressing behaviors also carry a special valence inasmuch as they permit the closeness between parent and infant and provide for frequent inspection of the infant's body and appearance.

The central role of maternal care in early life is also well demonstrated in rodent studies, in which maternal behavior involves a complex set of activities, including nest repair, sniffing and exploration of pups, mouthing, pup retrieval, licking, grooming, and various forms of nursing (Pryce et al. 2001), behaviors that bear some phenomenological similarity to the intense cleaning, checking, nesting, and proximity maintenance seen in humans. Classic lesion studies done in rodent model systems have implicated the medial preoptic area (MPOA) of the hypothalamus, the ventral part of the bed nucleus of the stria terminalis (BNSTv), and the lateral septum (LS) as regions pivotal for regulation of pup-directed maternal behavior (Kalinichev et al. 2000a; 2000b; Numan 1994; Numan & Numan 1997; Numan & Sheehan 1997; Sheehan et al. 2000). Estrogen, prolactin, and oxytocin can act on the MPOA to promote maternal behavior (Bridges et al. 1990; Numan et al. 1977; Pedersen et al. 1994). Oxytocin appears to play an especially important role in facilitating the onset, rather than the maintenance, of maternal attachment to pups (Insel 1997). Ascending dopaminergic systems associated with reward pathways (Koob & Le Moal 1997) also appear to play a crucial role in facilitating maternal behavior. And there may be a critical interaction between dopaminergic neurons and oxytocin pathways. For example, pup retrieval and assuming a nursing posture over pups were blocked in parturient dams by infusions of an oxytocin antagonist into either the ventral tegmental area (VTA) or MPOA (Pedersen et al. 1994). The initiation of maternal behavior thus involves specific neural circuitry; and with pregnancy, structural and molecular changes occur in specific limbic, hypothalamic, and midbrain regions. Furthermore, at least nine genes have been identified as necessary for the expression of one or more aspects of maternal behavior (Leckman & Herman 2002).

Given the intricate cascade of neurobiological and genetic events that appear to set the stage for early parental behaviors, it is reasonable to presume that parents are also primed to respond to their infants' cries as signals of need and potential danger and also, that there may be considerable individual variability in the parental response based in part on individual differences in the neurochemical and genetic systems regulating early parental behaviors. While these individual differences have been largely unexplored in humans, it is worth considering how parents "receive" and "process" crying as a part of the initiation of parental behavior, and then how parental response shapes the infants' continued signaling. Recent neuroimaging studies have begun to examine human parental response to infant cries (Lorberbaum et al. 2002; Swain et al. 2003). In these studies, more activity has been measured in medial prefrontal, orbitofrontal and cingulate cortices, thalamus, midbrain, hypothalamus, and striatum in response to infant cry versus control noise conditions. This underlines the importance of these structures in normal human parental cry response and lays the groundwork for considering the neural substrate of caregiver behavior that is affected by mental illness. Parental psychopathology could either increase the latency to the provision of care as in the case of mood disturbances (e.g., depression or anxiety) or make it noncontingent, as in substance abuse or parental psychosis. These disturbances in affect regulation may also influence how a parent receives and processes the

infant's cry – and in turn affects the feedback loop between parent and infant. Finally, a parent's own cry-response behavior is also shaped by his or her own early life experiences, family, and culture. Indeed, infant cry and caregiver feedback may be part of each infant's early development of meaning, and set protective and vulnerability factors for its own future mental health.

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Shouldn't mother know best?

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Abstract: We find the idea that infant crying arises from thermoregulation more consistent with a coregulatory account of its evolutionary history than it is with the informational account advocated in the target article.

One of the striking features of biological explanations of behavior is how often they resort to implicit mentalism. Many interesting instances of implicit mentalism are found in the deception/honest signaling/manipulation literature cited by Soltis. This literature makes no sense in the absence of the mentalistic doctrine of privileged access – the idea that the signaler is in possession of information about its own mind which the signal-receiver needs but cannot know unless the signaler provides it. This mentalist notion has led biologists to ask quasipsychological questions, such as, "When will nature select for organisms that provide accurate information about their own mental states?"

For privileged access models to work as potential explainers of mother-infant interaction, the signaling baby has to have some *self-knowledge* that its caregivers need and don't already have. The notion of self-knowledge is notoriously perplexed. Even if one gets by such tricky questions as "Who is the knower of the self apart from the self that is known?" and "Does the self that is known know what the knower of the self knows about it?", one is still left with the empirical question of how this supposed self-knowledge is gathered and why it should be of inherently better quality than information that can be gathered about the organism by others.

Thompson and collaborators (Thompson 1997; Thompson & Valsiner 2002) have criticized the mentalist model of communication because of its aheuristic commoditization of animal interaction. In their account, the intentional notion of information, "information about" should play no part in theories about animal interaction. We have been exploring an alternative perspective on the evolution of animal interaction, the assessment/management (A/M) perspective (Owings & Morton 1997). Instead of focusing on the transfer of a commodity, *information*, between signaler and signalee, the A/M perspective focuses on the regulatory interaction between them (Bowlby 1969/1982; Powers 1937; 1973).

The A/M perspective makes possible an account of infant crying that does not rely on mentalism and privileged access. The assertion of privileged knowledge on the part of the infant seems particularly questionable in discussions of human infants interacting with their mothers. Perhaps, if humans had evolved in an age of two-job families and nurseries with interrooms, one might make an argument for such a privilege, but human maternal-infant interaction did not evolve under these circumstances. In the environment in which humans evolved, the infant was on the mother's body – or at least somebody's body – 24 hours a day. Under these circumstances, everything that passed into and out of the baby's

body, came from or was delivered to the body of the mother. To be sure, the baby's nervous system has many highly developed functions, but the mother's is vastly more complex and autonomous. How could the baby possibly have known something the mother did not know a hundred times more precisely? Moreover, if an infant's crying depended on the ability of the infant to give caregivers information they lack, we would expect infants to cry more as they become more knowledgeable about the relation between the world and self. In fact, they cry less.

An advantage of the A/M perspective is that it is ultimately physiological, not psychological, in its imagery. It focuses on organisms as regulatory systems, responding to cue variables that stand in for variables of interest to their survival and reproduction. It thus provides an account of the evolution of signals based on a system of regulatory interactions between parties, not on the exchange of mythic commodities between them.

Soltis' theory that laryngeal braking is the origin of infant crying is compatible with the idea that "communication" arises from assessment/management cycles. Laryngeal braking may be a regulatory maneuver that augments gas exchange in the lungs by elevating intralung pressure, and so may feed the increased metabolic rate needed to heat a cooling animal. (For an alternative maneuver, see Blumberg & Sokoloff 2001.) From an assessment/management point of view, laryngeal braking or some similar regulatory compensation for cooling seems a reasonable first step in a historical account of the evolution of mother-infant "communication." It is characterized as part of a regulation in which an assessment of cues to the consequences of cooling causes the infant's physiology to use the respiratory apparatus to compensate for those changes.

But – the A/M account would continue – the sounds made in the course of laryngeal braking provide opportunities for assessment by the mother. Features of laryngeal braking thus themselves become cues that the baby is in need of thermoregulatory assistance. That such a cue is available makes it possible for the mother to manage the baby's thermoregulation by bringing the baby more closely to her body.

Now the fact that the mother is assessing the laryngeal braking itself provides management opportunities for the baby. By enhancing those features of laryngeal braking that the mother is assessing, the baby is able to manage the speed and quality of the mother's response. This in turn selects the mother for assessing these emphasized features more exclusively.

The final step comes when the baby increases the range of circumstances in which these emphasized features are deployed. This liberates the cry features from the context of hypothermia and makes it possible for them to be correlated with other features of the baby's circumstances that are crucial to the mother's fitness.

We think a thermoregulatory account provides a much more satisfactory management/assessment explanation for the origins of infant crying than the respiratory drama hypothesis that Thompson and his collaborators have offered. In that account, babies' cries arise because mothers are assessing the respiration of their infants and infant cries broadcast their respiratory patterns. Not only have we been unable to confirm the most interesting implications of this theory (e.g., Falcon et al., under review), but, on reflection, we believe the theory has a flaw which the Soltis laryngeal braking hypothesis lacks. The respiratory distress hypothesis invokes the problematic breathing apparatus of human infants, which is a compromise between avoidance of choking and the demands of speech, which begins to develop around 4 months. Not only does this theory imply that crying would be greatly diminished or absent in the early months, but, more important, it implies that crying should be a uniquely human activity. While it is true that humans cry more than other mammals, human infant crying does not seem all that discontinuous with the crying of other primates, particularly when one takes into account the fact that first-world human infants are being cared for in an environment very different from that for which they were designed (Owings & Zeifman, in press). That being the case, an assessment/management account based on the more phylogenetically general hypothesis that moth-

ers are tracking infant thermoregulation seems to be more plausible. By emphasizing the role of low vagal tone in the mediation of cry pitch variation as well as other responses to stressors, Soltis also offers an explanation for how a mother's attention to thermoregulation could lead by short steps to cries becoming cues to other forms of infant regulatory challenges.

Thermoregulation seems particularly plausible as the anlage for infant crying. What a mother should be assessing is neither the fitness of her offspring nor its present level of distress (in exclusion), but a relation between them, the value to her own fitness of delivering an additional packet of parental effort to the present offspring. This relation is a complex function of current fitness, short-term distress, and the resources mother has available for self-maintenance and caregiving. Cues to greater infant need or fitness should not always lead to greater deployment of care. For example, if the mother has limited resources, then cues to greater need might actually result in termination of care, since the level of resource demanded would be greater than the level the mother is capable of providing. Even if the mother has adequate resources, cues to greater fitness will elicit less care if the infant is so fit that additional care will not result in a proportionate increase in the mother's fitness. Thermoregulation seems a particularly suitable mediator of these relationships: The fact of thermoregulation is a cue to current distress and the ability to thermoregulate is a cue to long-term fitness, since this ability requires energy resources that can be mobilized through muscular activity. By crying vigorously, the infant therefore not only provides cues to the damage to mother's long-term fitness, of not providing immediate assistance, it also provides cues to the long-term value of aiding this infant as opposed to other present or future ones.

Developmental changes of infant cries – the evolution of complex vocalizations

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Abstract: The signal functions of infant crying cannot be understood properly without due attention to their ontogenetic development. Based on our own research on the development of infant cries, we argue that the controversies in cry literature will not be solved by static models, but that progress will be made only when considering ontogenetic changes in interpreting cry data.

There is a remarkable increase of research within the field of pre-speech development. This has been stimulated mainly by new findings of language-relevant perceptive abilities during early infancy (Friederici & Wessels 1993; Jusczyk 1997; Jusczyk et al. 1993). Although there is a general agreement on the importance of earliest pre-speech phases for later speech and language development, we are still confronted with a great bias toward studies focusing on babbling and later sound productions. Soltis' article is highly relevant as its reevaluation of the state of the art serves to promote the somewhat underrepresented cry research. However, Soltis' attempt "to illuminate the human infant cry from an evolutionary perspective" (target article, Abstract) lacks a crucial aspect, namely, the consideration of ontogenetic changes of cry features.

There are a number of reports dealing with developmental processes in infants' crying, but most of them investigate simply aspects of quantity (e.g., the amount of crying during the first weeks or months). In our studies (e.g., Lind & Wermke 1997; Mende et al. 1990; Wermke 2002; Wermke et al. 1987; 1996), we focused on structural changes of infant cries. We could show that

the developmental changes of structural properties (e.g., fundamental frequency modulation and related variables) in spontaneous (“mitigated”) cries follow a unidirectional program: One of the first building blocks of cry melody development is a simple rising-falling cry melody (melody = time function of the fundamental frequency). A first differentiation of spontaneous cries happens by a combination of these rising-falling melody patterns to pattern sequences created by a simple repetition or concatenation. The simplest form of complexification is a double-arc cry melody. Beyond duplications we also observed multiple repetitions within one cry to form ever more complex patterns (cries consisting of multiple-arc melodies).

Further refinement of laryngeal coordination and the mastering of tuning between the melody and resonance frequencies (Wermke et al. 2002b) during the first weeks of life provide several elementary abilities, which are at the disposal of other pre-speech vocalizations. A “training” process of this type is an important prerequisite for speech and language acquisition, especially for the acquisition of prosodic primitives.

A recent study investigating the melodies of 780 harmonic cries in 30 (14 male) healthy monozygotic twins¹ strongly supports the above mentioned developmental principles. The melodies were grouped into single-arc melodies and multiple-arc melodies and the frequency of occurrence displayed over the age of the infants (Fig. 1).

The most obvious tendency shown in Figure 1 is the nearly steady increase in the frequency of occurrence of complex (multiple-arc) melodies. This reveals a relatively continuous, unidirectional development from the early prevailing simple cry structures (single-arc-melody) to complex melodies. It is easy to understand that such developmental changes will influence the “classical” cry parameter. It could also be shown in this twin study that the synchronicity and the concordance in the melody development for monozygotic twins is much higher than that for unrelated pairs of subjects of the same sex and age from the same sample (Wermke 2002). The monozygosity, and hence the higher synchronicity of development, resulted in a much clearer manifestation of the universality of development than would have been the case in an average population. The melody changes sketched here are a strong argument for the relevance of the developmental aspects of human infants’ cries important for evaluating recent attempts to illuminate the human infant cry from an evolutionary perspective. The described melody development probably reflects a specific signal function of human infants’ cries that is at least as important from an evolutionary perspective as the functions summarized by Soltis.

The disparate and highly inconsistent values for cry parameters provided in the literature are not mainly a result of the different

methods applied, as Soltis argues, but are, in our view, at least partially attributable to the fact that the majority of cry researchers did not adequately consider developmental changes of cry features. Hence, a reevaluation of the data in the cry literature under consideration of the now well-described developmental changes (including *reorganization phases*) might be helpful in resolving the paradoxes thematized by Soltis. Such a developmental perspective may have the potential to reveal the hidden consistency of the available cry data. This would clearly go beyond the signaling vigor hypothesis proposed. Note that we are not claiming that the model proposed by Soltis is inadequate, only that some of the data on which his interpretations are based are inadequate or insufficient for drawing the respective conclusions. The fact that the signal functions of the human infant cry have been shaped by a long evolutionary adaptation process also means that these signal functions are strongly related to the acoustic cry features. Yet exactly these sections in the target article are quite unsatisfying (sects. 4.1. and 4.3). Although referring to the lack of standardization in cry analysis and to some methodological controversies, Soltis implicates that we know the “normal infant cry characteristics” and moreover that we might be able to differentiate between “normal” and “abnormal” cry variables in individual infants. This is simply not valid. There has been invaluable work in this field over the last 40 years, but as long as cry researchers do not “correct” their cry scores with specific respect to the rapidly ongoing developmental processes during the first weeks of life, a cry-diagnosis will fail and we will not solve the controversies in the cry literature. It is not only the field of cry-diagnosis which suffers from the fuzziness of cry scores, but there is also an impact on the fields of research related to developmental biology, pre-speech development, child abuse, and infanticide.

In our longitudinal studies, we strongly correlated all cry parameters to the age and the maturational state of the infant (e.g. Mende et al. 1990; Wermke 2002; Wermke et al. 1987; 1996; 2002a; 2002b; Lind & Wermke 2003) and obtained quite stable prognostic results as well as data consistency when retrospectively reanalyzing cry data under consideration of the developmental outcome of the children (first results: Wermke & Friederici 2004). We found that the relative percentage of multiple-arc melodies produced in cries during the first 14 weeks is a significant predictor of spontaneous word production performance at 18 months.

We fully agree with Soltis’ prospect conclusion, that much remains to be learned about the signal functions of early infant crying. However, we strongly recommend an inclusion of structural developmental data before further testing any hypothesis.

NOTE

1. Spontaneous cries of the twins were recorded several times during their stay at the hospital. Recordings were repeated in six-week intervals (+/- 2 weeks) in the home environment. In total, 1,100 cry signals of infants between birth and the 16th week of life were investigated and cries containing large regions of subharmonics or noise were excluded from the melody analysis (N=386). The remaining 714 cry melodies could be assigned to melody types (single- vs. multiple-arc-melodies). Spectral analysis and melody computations were made using a CSL-Speech Lab 4300/MDVP (Kay Elemetrics).

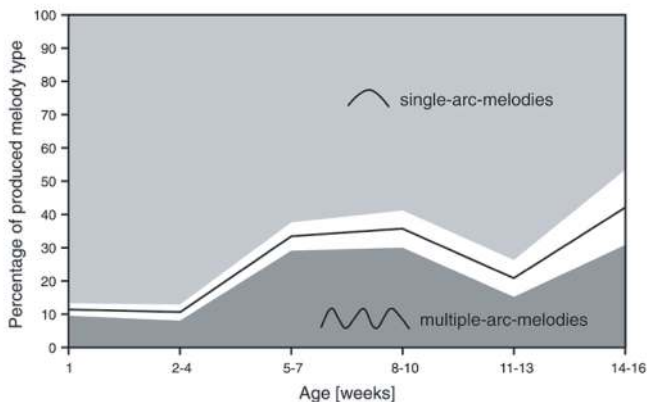


Figure 1 (Wermke & Friederici). Developmental changes of the relative frequency of occurrence of single-arc-melodies (upper part) versus multiple-arc-melodies (lower part) from all infants over the first 16 weeks of life (total amount of arc-like melodies: N=781; standard errors marked by the white line).

On the utility of an evolutionary approach to infant crying

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Abstract: Soltis’ analysis of signal functions of young infants’ cries stimulates testable questions regarding abuse, neglect, and infanticide. Nevertheless, his evolutionary perspective oversimplifies the cry event, and does little to promote developmental analysis of crying during infancy. Studies of the cry in its behavioral and developmental context are needed if we are to understand the proximate causes of optimal and suboptimal care.

Soltis' attempt to explain all communicative crying within the first three months of life from an evolutionary perspective is both interesting and problematic. The fact that this perspective can address data from several disciplines makes it an attractive tool for synthesizing a diverse and sometimes contradictory literature. Even so, the perspective carries the potential to oversimplify infant crying, and to lead research efforts away from understanding the cry's role in both domain-specific (social and communication) development and the overall development of the child. In this commentary, I argue that: (1) Soltis' focus on the cry sound obscures the richness of the cry event; (2) an evolutionary perspective does little to stimulate developmental analyses of crying; (3) consideration of the complexity of the cry event, and its development, are necessary for understanding parent-infant interaction, both optimal and suboptimal.

Soltis describes the cry's function in general terms, considering only its evolution as a vocal signal of infant health or "vigor." Furthermore, the context in which the cry occurs is characterized rather simply: either the context favors infant survival, or it does not. While this approach has generated questions about the proximate causes of abuse, neglect, and infanticide (target article, sect. 7, "Conclusions and prospects"), it oversimplifies the cry event, which includes temporal changes in acoustics, as well as visual cues about the infant's level of distress and, indeed, about whether he or she is crying at all.

Crying from healthy young infants has a complex acoustic structure that changes during a long cry bout (Green et al. 1998). Moreover, acoustic changes over time relate to adults' ratings of infant distress (Wood 2002), and the cry's "aversiveness" (Zeskind et al. 1985), in ways predicted by the graded signal view of crying. Soltis argues that when crying is persistent and acoustics are outside the normal range (i.e., when a child is unhealthy), caregivers could opt to provide suboptimal care. What would happen if a healthy child were regularly left to cry for long periods (e.g., in a busy household)? Would the acoustics of the child's long cry bouts become "abnormal" and so aversive that adults would provide suboptimal care? Analysis of parent-child interactions during long cry bouts would provide this information, whereas an evolutionary perspective that focuses on the cries of unhealthy infants may shed little light on such matters.

Crying occurs in concert with facial expressions and other behaviors, and Soltis' concentration on the sound itself obscures this observation. Two studies are relevant here. Green et al. (1995) presented nonparent adults with cries and noncry vocalizations from 3-month-old infants in both an audio-alone condition (just the sound), and an audio plus video condition (which showed the infant producing the sound). The adults were significantly better at correctly identifying cries from 3-month-olds when the sounds were paired with the video than when they were played alone. This was not true for noncry sounds. When the videotapes were edited so that cry faces were paired with noncry sounds, and vice versa, adults labeled noncry sounds that were paired with cry faces as cries. The visual information (facial expressions) thus took precedence over the auditory information (the sounds themselves). In another study, nonparents were able to use only the facial expressions of crying 3-month-olds to distinguish very distressed infants from those who were less distressed (Irwin 1999). These studies show that young infants' cries occur within the context of other behaviors, and that these behaviors may have as much or more influence on cry perception as the sound alone. It is therefore useful for researchers to consider the cry as a "multiply specified signal" (Irwin 1999), which includes the infant's sounds and facial expressions. Moreover, the existence of such cry complexity at 3 months of age suggests that developmental changes occurred earlier, a point Soltis' perspective does not address.

Little is known about the development of crying in healthy children, especially with regard to qualitative changes during infancy (Hopkins 2000). Where changes are documented, their underlying mechanisms are not well understood. An evolutionary perspective such as Soltis' does little to stimulate needed inquiry into

infant cry development. Indeed, Soltis' discussion is limited to crying in the first 3 months because "At about 3 months of age, infants undergo a developmental shift in which crying becomes more differentiated, interactive, and intentional" (sect. 1, para. 3). If we assume that crying during the first 3 months serves only to maintain proximity to the caregiver, and to signal the infant's health, then we neglect an essential question: What qualitative changes occur in the cries of young infants, both healthy and unhealthy, and how do the changes affect adult-child interactions? There is evidence that crying undergoes changes during the first 3 months (beyond those associated with the "cry curve") that may reflect the beginnings of "differentiation" or reorganization of existing communicative behaviors.

In a longitudinal study, Hopkins and van Wulfften Palthe (1987) showed that fussing (a vocalization whose definition often overlaps with definitions of crying; Hopkins 2000) and cooing appeared at 6 weeks of age. Between 2 and 3 months, fussing and cooing became a new vocalization, "interrupted fussing," characterized by alternations between the two kinds of vocalizations. Thus, the components of crying were reorganized before the infants were 3 months of age. Interestingly, Hopkins (2000) noted that the alternations between fussing and cooing were accompanied by changes in facial expressions (cry faces during fussing, smiles during cooing). This observation indicates that crying in healthy children is a complex communicative event, even before the third month of life. Studies that consider the entire event (not only the sound) can provide insight into the changes in young infants' crying, and the mechanisms for the changes.

Soltis provides a provocative analysis of the possible signal functions of early infant crying. While his evolutionary perspective generates questions, it overlooks the complexity and development of the cry event. An understanding of optimal and suboptimal parent-infant interaction depends on consideration of the cry in its behavioral and developmental context. An evolutionary perspective does not promote such consideration.

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Colic and the early crying curve: A developmental account

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Abstract: The hypothesis that excessive early infant crying evolved to reduce the risk of withdrawal of parental care is disputed on the grounds that excessive infant crying is irritating and imposes fitness losses rather than gains. Alternative explanations for the early crying curve that take into account development on the part of the infant and the emerging infant-caregiver bond are proposed.

Soltis should be commended for a comprehensive review and novel synthesis of the early infant crying literature. His review highlights the fact that we cannot yet adequately explain the early crying curve or the prevalence of colic. The author's claim that the weight of the evidence favors the "signaling vigor" hypothesis over other explanations, however, seems to overlook inconsistencies with the data and plausible alternative explanations.

The main premise of the signaling vigor hypothesis, that infants cry to advertise their health and stave off neglect or infanticide, ignores the highly irritating quality of crying. The negative reaction of adults to even normal infants' cries is reflected in, among other things, the adjectives used in rating scales to describe cries (e.g., grating, annoying, sickly). As a result of these negative reactions, colic has at least short-term negative consequences for infants that, had they occurred over the course of human evolution, would

almost certainly have imposed fitness losses rather than gains. For example, colic is a frequent complaint brought to pediatricians and a common reason for giving up breast-feeding. When parents are confronted with a colicky infant, they usually seek medical help because of the perception that the infant is ill. Why would a signal of vigor so often be mistaken as a sign of illness? Although the noxiousness of infant crying is part of what makes it effective for mobilizing a parent's response, it is hard to imagine a scenario in which an infant's *continued* crying even after a parent picks it up would be helpful in thwarting abuse, abandonment, or infanticide.

While there is strong evidence that colic is not associated with long-term illness, there is no compelling evidence that colic is associated with increased vigor. It is misleading to argue from exceptional cases – cases in which impaired infants emit weak cries or do not cry at all – that excessive crying under normal conditions indicates better health. The strongest evidence for an association between vigor and crying is the report (de Vries 1984) that Masai infants with more difficult temperaments were more likely to survive a drought than their complacent counterparts. It is probable, however, that the infants who didn't cry much when the initial temperament measures were taken were already succumbing to the effects of poor living conditions and scarce resources. The study, in fact, was conducted at the height of a 10-year drought. The most dehydrated infants in the sample would have had difficulty emitting a costly signal, but this does not inform the signal function of crying under normal conditions. Sickly infants probably don't smile or urinate as much as healthy infants, but we cannot infer from these correlations that the function of smiling or urinating is to signal vigor. Under normal conditions, there are likely to be negative consequences for infants on either extreme of the crying continuum – those who don't cry enough to have their needs met, and those who cry excessively or inconsolably.

Soltis points to the similarity in the temporal pattern of early crying and probability of infanticide as further evidence supporting the view of crying as a vigor signal designed to dissuade parents from withdrawing care, but acknowledges that alternative explanations are possible. Developmental changes in the infant, and in the parent-infant relationship, may better explain the dramatic decline in infanticide rates at three months. At around three months, infants shift from expressing emotions primarily in response to changes in internal states to expressing emotions in response to external stimuli, including parents. For example, a newborn's smile, which is likely to occur during REM sleep, is replaced with a truly social smile in response to parents' prodding. Sustained eye contact makes its appearance, too, replacing the jerky eye movements of the newborn period, and infants stay awake for longer periods of time. Many parents report that their infants begin to seem human to them as a result of these changes in social responsiveness, and that they, in turn, are overcome with feelings of parental love (Stern 1977). The drop in infanticide risk after three months of age most likely reflects the emotional bond that has formed between the parent and infant, as well as the reality that it's more difficult to neglect or harm an infant who looks you in the eye, smiles, reaches toward you, and even giggles with delight when you enter the room, than one who is less developed.

If the decline in crying at three months is not a function of diminished infanticide risk, then what accounts for the near-universal pattern of early crying? The parent's experience of taking care of her infant, and the infant's experience of being cared for, may contribute to the decline in infant crying. The *n*-shaped early crying curve (Barr 1990c) may reflect a process whereby the infant and caregiver learn each other's habits and become increasingly coordinated. With the experience of being cared for in a predictable fashion, infants come to anticipate caregivers' actions in the first few months of life, and may be expected to cry less as a result. Because the transition from crying to calm is a highly motivated context for learning about the caregiver, caregiver characteristics – such as voice or scent – may also become powerful cues for arresting crying. For example, a newborn infant is likely to cry

until experiencing the physical changes associated with having his or her needs met, such as the warmth of the mother's body or the taste of milk on the tongue. In contrast, an older infant may stop crying when a parent merely enters the room. Caregivers may contribute to reductions in crying as well, by becoming adept at anticipating and meeting the needs of their infants.

What then, in addition to promoting proximity, is the function of early crying? Infants typically become attached to the individual who has most reliably responded to their cries. Crying-soothing sequences are rewarding for parents as well in that the punishing sound of crying is arrested and the unpleasant autonomic arousal it triggers is attenuated. One function of early infant crying may be to bring the infant and parent together repeatedly in this emotionally charged situation, fostering an emotional bond.

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Author's Response

The developmental mechanisms and the signal functions of early infant crying

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Abstract: The majority of the commentaries focused on excessive crying and colic and included two major themes: the consideration of proximate physiological mechanisms, and challenges to my interpretation of the signal functions of early infant crying amount. I initially concluded that none of the competing signaling hypotheses enjoyed strong support, but I nevertheless favored the signaling vigor hypothesis above the signaling need and manipulation hypotheses. Consideration of the neurobiological causation of the *n*-shaped crying curve and further evidence and argumentation concerning the potential signal functions, however, do not allow for the elevation of any one of these hypotheses above the others, and it remains the case that none are strongly supported. Taken together, however, the target article and commentary do provide a solid foundation for further research. In the target article, I also proposed a model of how infant cry acoustics can influence patterns of care and abuse. Commentary has enriched this model by including the consideration of developmental changes in cry acoustics across early infancy, and by further integrating the cry signal with other modalities of communication and with later development. I trust that the foregoing will show that the joint pursuit of the proximate mechanisms and the potential signal functions of early infant cry amount and cry acoustics should prove fruitful. Before embarking on my reevaluation, however, I begin this response by addressing the issue of consciousness in evolutionary accounts of signaling.

R1. Signaling and consciousness

Three of the commentaries suggest that the signaling theory put forth in the target article implies, or requires, that 0- to 3-month-old infants consciously and voluntarily signal to caregivers, for example, to manipulate them or honestly signal to them, and for this reason conclude that such the-

oretical considerations are unrealistic (**Provine, Laureys & Goldman, Thompson, Sokol, & Owings [Thompson et al.]**). Although I agree that the theoretical literature I reviewed is peppered with terminology that *implies* optimally self-aware and knowledgeable infants capable of exerting conscious control over the signals they emit, in fact, the theory does not *require* conscious awareness in infants or caretakers. The lack of an elucidation of the proximate mechanisms that promote behavior in theoretical models is responsible for the implication of consciousness. I tried to make this clear in the final paragraph of the Introduction (target article, sect. 1), in which I warned readers about the terminological shorthand that I would employ, explained that voluntary action motivated by fitness considerations is not a requirement of the theoretical models, and provided an illustration involving adaptive parental infanticide. Additionally, I complemented these theoretical considerations by providing proximate explanations of mother–infant communication systems in sections 4.6 and 4.7. I refer readers again to those sections, and warn that shorthand expressions will also be employed in this response. I provide an additional example. If the physiological threshold for hunger were lower in some infants than others, and those infants with the lower thresholds cried more and received more food from mothers, for example, I may (or may not) call that “manipulative signaling,” but in no case would I be implying consciousness – rather, merely physiologically determined vocal responses to hunger level that differed among infants and the subsequent effects on caregiver behavior.

Thompson et al. were most critical, claiming that the theoretical underpinnings of the target article *require* consciousness and arguing against focusing on information transfer in animal communication. They emphasize the “assessment/management” perspective put forth by Owings and Morton (1997; 1998). The assessment/management perspective properly emphasizes that vocal output of animals may not be designed for transferring information, but that receivers are nevertheless capable of assessing such signals and acting upon them. I believe that this distinction between information transfer and assessment/management is a false one. Indeed, information transfer is part of the assessment/management perspective. To see why, consider the following argument from Owings and Morton (1998): These authors argue correctly that larger animals produce lower-frequency vocalizations than smaller animals, not because larger and smaller animals consciously and voluntarily decide to do so, but in part because of the constraints that body size imposes on the acoustic quality of vocalizations. They note that in California wrens, territorial males use a low-frequency growl vocalization during the first stage of a conflict with an intruder: “Stage 1 continues with the production of a *growl* [by A] coincident with the attack when A is nearly upon B. This low-frequency, harsh vocalization is a universal indicator of large size that, due to this symbolism, intimidates” (Owings & Morton 1998, p. 239). But this description is not devoid of information transfer. If assessor B was intimidated by A’s low-frequency growl because it is a universal indicator of large size, then the response of the assessor would be due to the information about body size that was inherent in the vocalization.

The irony of the commentary by **Thompson et al.** is that, in spite of its overall negative tone, most of their examples of the “correct” assessment/management approach come directly from my target article. This is because my tar-

get article is consistent with both the assessment/management approach and the information transfer approach. As Thompson et al. note approvingly in their commentary, I formulated a model of infant cry acoustics and an evolutionary scenario that does not require any consciousness (sects. 4.6 and 4.7). I proposed that early mammalian infant physiological adaptations that served a thermoregulatory function when separated from mothers resulted in ultrasonic emissions (“laryngeal braking”). Note that this argument involves no conscious control by infants over vocalizations, and that the initial adaptation was not designed for information transfer. I went on to argue (and again Thompson et al. summarize me approvingly in their commentary) that mammalian mothers may have later evolved to respond to these ultrasound emissions to locate separated infants, and may have evolved to respond with varying urgency based on the specific acoustic properties such as the fundamental frequency. That is, natural selection shaped caretakers to take advantage of information about location and possible degree of distress from the vocal emissions of infants. Avoiding the word “information,” but still claiming that mothers are able to assess cues of infant characteristics that are inherent in infant vocalizations, does not change the fact that vocalizations can exert their effects on receivers because of their informational content. A shorthand way of describing the full account of the evolved mother–infant communication system elucidated in section 4.7 may be “Infants use vocalizations to signal location and mothers use this information about location to retrieve their infants,” which may imply consciousness, but the full account provides an evolutionary explication that does not require it. Incidentally, a careful reading of the commentary by Thompson et al. reveals that much of their wording also implies consciousness. For further discussion of the problem of intentionality in animal communication, and the false dichotomy between the information transfer approach and other approaches such as the assessment/management approach, see Seyfarth and Cheney (2003).

I am in full agreement with **Thompson et al.**’s elaboration of my step-by-step scenario describing the evolution of mother–infant communication systems, and with the assessment/management approach in general. The theory that I reviewed in section 2.3 admittedly ignores these physiological mechanisms, which the assessment/management perspective properly emphasizes (in fact, the theory ignores all proximate mechanisms), but it is not inconsistent with them. Thus, the only outstanding disagreement is the result of the mistaken view that the theoretical section of the target article not only implies, but also requires, consciousness in infants.

R2. Colic and the n-shaped crying curve

Many of the commentators focused on excessive crying and colic, augmenting my analysis by elaborating proximal determinants, adding developmental perspectives, and challenging my conclusion that the evidence best supports the “signaling vigor to avoid maltreatment” hypothesis. Here I would like to summarize these welcome contributions to this enigmatic phenomenon and reevaluate my conclusions based on them. I start by summarizing the developmental and physiological determinants of the n-shaped crying curve, after which I discuss the various alternative signaling

functions of colic, and discuss several areas of important future investigation.

R2.1. Ontogeny and phylogeny

Four commentaries (**Bard, Jenni, Lehtonen, Newman**) offer developmental and physiological perspectives on the causation of the n-shaped crying curve that were largely lacking in the original target article, in which I emphasized mainly the most proximate (vagal) input to the vocal cords. In contrast, Newman reviewed a series of animal studies demonstrating that brain regions along the entire neural axis, from the cortex to the brainstem, can influence the tendency to cry and cry acoustics. He proposed that differing maturational rates of the neural circuitry in different areas involved in speech may result in excessive crying and colic in early infancy. In a similar vein, Bard argued that colic may be a by-product of delayed rates of development in humans (neoteny) as compared to our closest extant relative, the chimpanzee. As in humans, chimpanzees exhibit an n-shaped crying curve that can be attenuated by an indulgent maternal style, but unlike humans, chimpanzee infant crying is consolable, and infant self-calming during crying bouts is more pronounced. The biobehavioral shift at 3 months of age in human infants (see commentary by **Barr**) that includes a cessation of excessive crying also coincides with an increase in cortical–subcortical neural connections, an increase in cortical control of subcortical activity, and myelination of neural pathways. Bard concludes that inconsolable crying and colic may be a manifestation of this delayed maturation of the brain prior to the biobehavioral shift. Lehtonen cites studies showing that repeated feedings may increase the threshold for pain in infants, indicating that caregiving interactions may contribute to the downward half of the n-shaped crying curve by exerting neurobiological effects on infants.

Finally, **Jenni** argues that the n-shaped crying curve reflects the misaligned interaction of circadian and homeostatic processes in the developing infant. In adults, alertness is lowest in the early morning and highest in the early evening, following the temperature circadian rhythm. The homeostatic process mediates increased sleep pressure across the wake cycle, but it is opposed by the circadian rhythm that increases alertness until early evening, allowing for the maintenance of wakefulness. Opposite processes maintain sleep. In infants, the circadian temperature rhythm appears at 4 weeks and further develops across the first few months of life. Although it is unclear when homeostatic processes develop in human infants, Jenni hypothesizes that hyper-alertness and excessive crying may occur because the developing homeostatic sleep pressure does not sufficiently oppose circadian alertness pressure. The strength of this hypothesis is that it accounts for both the n-shaped crying curve across early development and, importantly, the early evening cry clustering.

All four of these analyses point to potential proximal causes of the universal crying curve, and their strength lies in the developmental and/or evolutionary perspectives that they employ, and as such they are excellent guides for future research into the physiological underpinnings of the early infant crying curve. Although firm conclusions regarding specific details cannot be drawn, it seems safe to conclude that the n-shaped crying curve is a manifestation of the developing nervous system of the human infant.

How does this understanding shape our thinking about the potential signal functions of early infant cry amount? **Bard** argues that because the n-shaped crying curve can be explained as a by-product of delayed maturation in infants, for example, that no signaling function is necessary. This is true (regardless of which specific physiological determinants of the crying curve turn out to be most relevant), but it does not preclude signaling functions. As **Barr** noted in his commentary, elucidating the universal developmental processes that account for the n-shaped crying curve (and the crying state itself) is not incompatible with the potential for the cry to act as a signal to conspecifics. Proximate mechanisms do not rule out adaptive explanations. If variation in cry amount among infants reflected important infant characteristics, for example, then caretakers may have evolved facultative responses to these different crying amounts. The four major perspectives from which behavior can be analyzed are proximate mechanisms, adaptive explanations, evolutionary history, and development. Although some commentators seem to suggest that differing perspectives of examining behavior are in opposition to one another (**Blass, Wood**), they should be viewed as complementary (**Zeifman** 2001).

R2.2. Manipulative signaling revisited

In the target article, I evaluated three potential signaling hypotheses – manipulation, honest signaling of need, and honest signaling of vigor – and concluded that, whereas the evidence was not strong for any of these hypotheses, the evidence was most consistent with the signaling vigor hypothesis. Several commentators disagreed with this evaluation and proposed alternatives.

Hagen and **Maestripieri & Durante** each argued that I dismissed the manipulation hypothesis too quickly (sect. 6.1). In arguing against it, I claimed that parent–offspring conflict should be most pronounced at weaning, in which case manipulative crying should increase across infancy, but that the opposite is the case. Both of these commentators correctly note, however, that parent–offspring conflict can be strong at times in addition to weaning, including in early infancy. In fact, Hagen points out that parent–offspring conflict may be exceptionally high in the first three months of life, because infants who have not successfully passed through the early period of high infant mortality are of less value to their parents (in fitness currency), which will increase parent–offspring conflict. He bolsters this argument by noting that the incidence of parent-inflicted infanticide is highest in the first three months of life (see Fig. 1 of the target article). **Zeifman** augments this reasoning with a proximate psychological mechanism, noting that the reduced risk of infanticide across the first year of life may be mediated by the parent's increasing emotional attachment to the infant, coincident with the 3-month biobehavioral shift when infants become more interactive with their environment and their caregivers.

In arguing against the manipulative view of crying, I also claimed that parent–offspring conflict over feeding or comfort could not be expected to follow temporal patterns of excessive crying, in particular the sixth-week peak and the early evening clustering. Here too, however, **Maestripieri & Durante** argue persuasively that manipulative signaling cannot be dismissed due to this patterning, because the general temporal patterns may be related to developmen-

tal processes, but that variation in the amount of crying among individuals may reflect deferring degrees of manipulation (see section R2.1 in this response). I agree that the developmental and diurnal patterns of excessive crying may well result from universal neurobiological development, but that variation in the overall cry amount across infants may still signal infant characteristics.

Maestriperi & Durante go on to highlight evidence that is inconsistent with or ambiguous with regard to the signaling vigor hypothesis, such as the lack of a clear connection between colic and exceptional vigor, the unclear causal arrow explaining the positive correlation between infant cry amount and infanticide probability across the first year of life (Fig. 1; sect. 6.3), and the lack of evidence that increased crying reduces maltreatment or infanticide. **Maestriperi & Durante** argue that while colic may be aversive to caretakers, it may nevertheless increase care and, as such, is best viewed as a manipulative signal. They add that crying amount may be influenced by parenting styles or environmental circumstances, such as the dramatic changes in caregiving practices over recent evolutionary time, from a more to a less indulgent caregiving style. **Hagen** argued that colic also may have been a manipulative signal in hunter-gatherer environments. In such environments, crying may have attracted predators, forcing parents to give immediate aid, and because of close group-living, other group members may have pressured parents to care for their excessive criers. I will revisit the merits of the manipulation hypothesis in a later section, but first summarize commentators who argue in favor of the “honest signaling of need hypothesis,” which I also rejected in the target article.

R2.3 Honest signaling of need revisited

The thrust of my argument against this hypothesis was twofold (sect. 6.2). First, I claimed that, in general, excessive crying was not associated with transient distress or permanent poor health, and second, I argued that transient needs were unlikely to follow the developmental and diurnal patterning of the crying curve. **Blass, Jenni, Swain, Mayes, & Leckman (Swain et al.)**, and **Fouts, Lamb, & Hewlett (Fouts et al.)** provide alternative arguments that excessive crying could be an honest signal of need. Earlier in this response I summarized Jenni’s view that the n-shaped crying curve reflects the misalignment of circadian and homeostatic processes in early infancy. To this he added that such crying can be viewed as an honest signal of need to have the behavioral state modulated (i.e., to be soothed during the hyper-alert state). According to this argument, individual variation in cry amount could be explained by different maturational rates of the two systems in infants, and differences in caregiving style may also contribute to the variation. Jenni notes that infants may be better adapted to caregiving styles of traditional societies, with more flexible infant sleep/wake cycles and ample activity and contact at night during the evening cry clustering. To the extent that differences in cry amount are a reflection of the degree of misalignment of the circadian and homeostatic processes, it may be viewed as an honest signal of need, which can nevertheless be ratcheted up or down depending on differences in caregiving styles across cultural contexts. **Blass** complements Jenni’s argument by noting that during the sixth-week peak in the n-shaped crying curve, infants pre-

fer adults who have interacted with them when they were agitated (i.e., they prefer consolers), but that at later ages, infants prefer adults who interacted with them when they were calm. **Blass** also points out that crying helps maintain ideal levels of brain activation during the first three months of life, and provides evidence from animal studies that mother’s interactions with infants can promote dendritic development. Finally, **Swain et al.** and **Fouts et al.** emphasize the benefits of caregiver contact, such as promoting the attachment process, independent of other needs such as hunger or pain (also see section 3 in target article). Taken together, all four of these commentaries highlight infant needs in addition to those on which I focused in the target article (such as provisioning of food) and have to my mind successfully resurrected the plausibility of cry amount as an honest signal of need.

R2.4. Honest signaling of need versus manipulation

The aforementioned commentators have successfully defended both the *manipulation* and the *honest signaling of need* hypotheses. The distinction between these two views hinges on the costs of crying (see section 2.3 for a fuller treatment). Briefly, if crying is costly, then the signals are more likely to be honest because it may not pay the non-needy or the less needy to produce a costly signal, but it may well pay a truly needy individual to do so. Crying is not only energetically costly, but is more costly for low-quality than high-quality infants (sect. 6.3, para. 2), and for this reason I favor the honest signal of need over the purely manipulative view of excessive infant crying. In addition, the mathematical models of manipulative infant signaling that I reviewed (sect. 2.3) did not allow the parental response to evolve; but in cases where manipulative signaling is common in the population, it may be unlikely that parental responses would evolve to continue to respond to such ubiquitous but “meaningless” signaling. Having said that, even in systems where signals are generally honest indicators of need, cheating (i.e., manipulation) can still be a rare strategy. Indeed, as **Maestriperi & Durante** note, excessive crying may be a frequency-dependent strategy that is successful only at low frequencies, and I agree with this reasoning. I now turn to the influence of caregiving practices on cry amount.

R2.5. Caregiving style revisited

Various commentators emphasize that variation in caregiving practices can influence cry amount (**Barr, Fouts et al., Lotem & Winkler**, and **Maestriperi & Durante**; also see section 5.5 in the target article). **Lotem & Winkler** argue that colic is not a signal of vigor, as I argued, but is a suboptimal by-product of a generally adaptive learning process by which infants adjust their crying levels in relation to parental responsiveness and other environmental circumstances. The differences in rates of crying might not be based on individual differences in need or quality but on reinforcement regimes, in which, for example, parents who reward crying with increased care or attention may reinforce and thereby increase crying. They also suggest that such rewarding of excessive crying for a relatively short period may nevertheless exert long-lasting increases in crying that are difficult to reverse until infant physiological demand is reduced, perhaps at the 3 month biobehavioral

shift. This is an interesting idea that stands in stark contrast to the more widely held notion that increased attention reduces crying amount. If indulgence of crying infants increased crying, one may expect an increase in the number of cry bouts or increases in cry bout length in indulgent cultural contexts, as exemplified, for example, by the !Kung hunter-gatherers, but this is not the case. As Barr notes in his commentary (also see section 5.2 in the target article), the number of cry bouts is similar across varying cultural contexts and across early infancy. It is the prolongation of cry bouts that accounts for the n-shaped crying curve across development and the differences across cultural contexts. For example, increased carrying and responsiveness among the !Kung is associated with a decrease in cry bout duration but not bout frequency, supporting the notion that parental response in fact decreases cry amount. I agree with the general contention of Lotem & Winkler that variation in crying amount may be influenced by the interaction of different parental styles (reinforcement regimes) and differences in infant learning responses to such parental practices, but I believe the evidence to date is most consistent with the notion that increased indulgence results in shorter crying bouts and less overall crying.

Fouts et al. amplify this view, arguing that increases in crying associated with insecure attachment patterns may be viewed as a facultative adaptation to less indulgent caregiving environments. They propose that colic and abuse are rare in hunter-gatherers, and that increases in excessive crying and abuse are associated with dramatic changes in childcare practices, such as the transition from communal caregiving practices characteristic of hunter-gatherers to the largely biparental caregiving practices of modern societies. They make the point that most of the cases of infanticide and infant maltreatment that I cite (Table 1 of the target article), while cross-cultural in nature, are short on hunter-gatherer societies, the social context most relevant to the environment in which most of human evolutionary history unfolded (the so-called environment of evolutionary adaptedness; see Note 1 in the target article). Fouts et al. admit that infant maltreatment exists among hunter-gatherers (citing Hill & Hurtado 1992) but argue that their own work shows that among the Aka and Bofi hunter-gatherers, in which communal caregiving is the norm, colic is low or nonexistent, caregivers do not become irritated but remain indulgent with chronically ill infants, and, because of such communal care, the circumstances under which parent-inflicted infanticide might occur are much less likely. I do agree that the indulgent communal style of caregiving that is characteristic of traditional societies reduces cry bout duration, and concur that it is likely to reduce the risk of infanticide, but I think that it would be premature to conclude that the incidence of suboptimal care, maltreatment, infanticide, or abandonment of offspring in hunter-gatherer societies is too low to be of evolutionary importance.

R2.6. Re-evaluation of the signal functions of excessive crying

The foregoing contributions concerning the potential proximate determinants and the potential signaling functions of the n-shaped crying curve can be combined to formulate the following model. The n-shaped crying curve across the first three months of life, and the early evening peaks in cry-

ing, are likely universal manifestations of neurobiological development. Nevertheless, there is extensive individual variation in the overall amount of crying. Three general areas may help to explain this variation. First, infants may differ in the degree and timing of neurobiological maturation and integration, with those experiencing less integration exhibiting more crying. To the extent that this results in more care and that caregiver contact or soothing positively modulates the behavioral state, it may be viewed as honest signaling of need. Second, infants may differ in needs (or manipulatively signaling those needs) that are unrelated to neurobiological maturational rates, such as hunger, and these differences could exaggerate or attenuate the n-shaped crying curve in different individuals. This variation may be explained by honest signaling of need or jointly by honest signaling of need and manipulation. As I argued earlier in this response, I think it is unlikely that manipulative signaling alone can explain the majority of signaling, but may parasitize common honest signaling of need when it is rare. Third, differences in caregiving styles, in particular the dramatic differences between communal care of offspring exhibited by hunter-gatherers compared to bi- or uni-parental households in modern, industrialized societies, may also contribute to cry amount, with more indulgent caregiving styles associated with less crying. To the extent that excessive crying in less-indulgent contexts results in more care, it also may be considered an honest signal of need or manipulation, and again I favor the signaling of need hypothesis with manipulation as a possible rare strategy.

In making room for the plausibility of the honest signaling of need and manipulation hypotheses, I do not imply that I have abandoned the notion that excessive crying may be an honest signal of vigor to avoid infanticide, as I emphasized in the target article (sect. 6.3). Rather, I have revised my evaluation such that I now hesitate to elevate any one of these three hypotheses above the others (except that manipulative crying could not, by itself, explain the majority of the variation), and I thank the commentators for their thoughtful contributions that have convinced me of alternative plausible signaling scenarios. I believe, however, that all are in agreement that we do not know which signal functions, if any, are inherent in crying amount. In fact, as **Maestriperi & Durante** note, many of the arguments hinge on the notion that excessive crying increases care, as I argued in the target article, but that if this is not the case, then radical re-evaluation of the signal functions of excessive crying will be needed. This brings me to the next section.

R2.7. Does excessive crying increase or decrease care?

The answer to this question is fundamental to an understanding of the signal functions of excessive crying, and all three signal functions proposed in the target article presuppose that excessive crying results in some benefit for infants. Several commentators, however, argued that such excessive crying may decrease care. **Hagen** argued that colic cannot be a signal of vigor (and by extension, neither a signal of need nor a manipulative signal) because it produces negative reactions in parents. He provides questionnaire data on parents suggesting that more crying was negatively associated with "love for the baby" and with the doctors' ratings of infant health. Likewise, **Zeifman** also emphasized

that cries in general are aversive and as such may impose fitness costs on infants. There are two problems with these arguments about the fitness costs of excessive crying. First, they are based on parental perceptions of infant crying and as such do not directly answer the question of what behavioral responses are elicited. Even when crying produces frustration, if it results in increased care (including taking infants to the doctor), then it will benefit the infant. As **Maestriperi & Durante** note, such aversive signals that nevertheless produce positive results are a hallmark of manipulation. In fact, **Zeifman** argues that such “aversive” crying benefits the infant by bringing the mother into contact with her, fostering the building of an emotional bond between the mother and infant throughout early development. The second problem, as **Hagen** notes, is that in these formulations no distinction is made between cries of different acoustic characteristics. I provided ample evidence that the acoustic quality of cries (e.g., cry pitch) has a strong influence on parental perceptions (sects. 4.4 and 4.6).

Perhaps the strongest evidence that excessive crying results in negative outcomes is offered by **Hagen**, who notes that infant temperament problems, including excessive crying, are associated with postpartum depression (PPD), and that PPD is associated with decreased care (Beck 1996). In this meta-analysis too, however, **Hagen** notes that no distinction was made between cry acoustics and cry amount, and there was no explanation of how they may have independently affected parental response. Additionally, in these studies infant temperament designations were based on the perceptions of mothers with PPD, who may have been biased with regard to the temperaments of their children for uncorrelated reasons.

Barr examines shaken baby syndrome (SBS) as a gravely negative parental response to early infant crying. Although **Barr** recognizes that maternal styles can attenuate the crying curve, he notes that much excessive crying associated with the crying curve is inconsolable. He argues that otherwise nonabusive parents may be susceptible to SBS because of the frustration caused by crying that does not cease in spite of parental efforts to feed or otherwise comfort an infant. He notes that crying is the most often stated precipitating stimulus triggering SBS, and that the incidence of SBS has a similar start time and the same shape as the n-shaped crying curve. **Barr** also notes, however, that it is not known how cry acoustics may contribute to SBS, in the way I argued in the target article (sect. 4.6). In addition, it is not specified whether or not the infants were excessive criers (i.e., were on the high end of the crying curve). In conclusion, despite the addition of new data and reasoning by commentators, the extent to which excessive crying and specific cry acoustics interact with other circumstances to influence parental responses remains unclear.

R2.8. Future research

I was particularly intrigued by the commentaries that explored developmental mechanisms that promote the universal n-shaped crying curve. Although these causal explanations do not require any signaling functions, they do not preclude them, and proximate mechanisms can shed light on adaptive hypothesizing. I believe it would be enriching for both avenues of investigation to proceed apace. The research reviewed in the target article and in the commentaries that is most relevant to the evolutionary signaling hy-

potheses examined here, was nevertheless not designed with these hypotheses in mind. To shed empirical light on the hypothesized signaling functions of early infant crying, studies will have to be designed specifically to test these hypotheses (also see section 7 in the target article). How do cry acoustics and cry amounts independently affect parental responses? How do these two dimensions of crying interact with other variables, such as environmental circumstances and caregiving styles, to produce caregiving responses? In addition, more studies of hunter-gatherers will be particularly valuable. As has been noted extensively in the target article and in the commentaries, modern environments are very different from those in which most of human evolutionary history unfolded, and in this regard the upcoming book on child development in hunter-gatherers highlighted by **Fouts et al.** will be a welcome contribution (**Hewlett & Lamb**, in press). Generally, all studies should be embedded in the multilevel model that takes into account factors of infants, caretakers, and the social and cultural environment in producing the infant-caregiver relationship. According to this model, for example, cry characteristics such as amount and acoustic quality will not uniformly elicit specific responses in parents, but will interact with parental dispositions and variable environmental circumstances to produce parental responses (sect. 4.6, para. 4).

Laureys & Goldman examine the possibilities of using neuroimaging techniques to help us understand the meanings of infant crying and the effects of cries on caregivers, and I believe that this avenue of research shows much promise. Cries that vary on some acoustic dimension or in their amount and inconsolability, for example, could be correlated with brain activity related to motivational or emotional state. For example, electroencephalography (EEG) has shown that right frontal activation asymmetry is associated with negative affect (e.g., sad and pre-cry faces) in infants. Observation of cry causation, bioacoustic analysis of cry sounds, and such neuroimaging of crying infants may prove a powerful combination of tools for helping to decipher the signal functions of the infant cry. Similarly, such imaging techniques can be employed to better understand parental reactions to infant cries with variable characteristics, such as my proposed model of differential reactions to acoustically normal versus pathological cries (sect. 4.6 in the target article). In addition, **Swain et al.** describe the neuroendocrinology of mothering behavior, and variation in this dimension may also be correlated with parental responsiveness. **Laureys & Goldman** provide data on the verbal responses and the brain activity of 15 nonparental males presented with infant cries. The top three verbal responses were “urge to help,” “anxiety,” and “annoyance”; and all males showed activation in the amygdala and posterior cingulate cortex, areas associated with emotional arousal. It should be noted that actual behavioral responses are important in addition to brain activity. Nevertheless, neuroimaging techniques on both infants and caregivers in crying contexts will allow us to better understand the potential signal functions of the cry based both on the acoustic quality and the quantity of crying.

R3. The acoustic properties of infant cries

A major part of the target article was my proposed model of infant cry acoustics and their contribution to patterns of care and abuse (sect. 4.6 in the target article), but it re-

ceived less attention from commentators than the sections on colic. I hope that it will not be passed over in future thinking about the early infant cry because of its potentially important influence on caregiver behavior. Critical evaluations by three commentators elaborate my model in fruitful ways (also see **Swain et al.** earlier). **Zeifman and Wermke & Friederici** emphasize that the acoustic properties of early infant crying will be difficult to study if changes in cry characteristics across early infancy are ignored. In the target article, changes in cry amount were considered across early infancy (i.e., the n-shaped crying curve), but cry acoustics were implicitly treated as uniform across the first three months of life. **Wermke & Friederici** provide important evidence that infant cry acoustics also develop across the 0- to 3-month time frame that I considered, and by way of example, they note an increase in melody complexity across early infancy. To the extent that cry characteristics change over early infancy, what is “normal” for a newborn may not be normal for a 1-month-old infant, which in turn may not be normal for a 2-month-old, and so on. This is a very welcome addition to my model, which was static in this regard, but the same logic of my model still applies (sect. 4.6 in the target article). Cry acoustics that are outside the normal range (for a particular age) may nevertheless influence the urgency of response, and exceptionally abnormal cries (for a particular infant age) may reveal underlying pathology. In addition, the trajectory of acoustic change over time may also be reflective of competent development.

Lotem & Winkler argue that caregiver reinforcement regimes may result in adjustment of acoustic quality in infants across early development. If mothers rewarded infants when certain acoustic qualities of cries were present, then this might have precipitated an increase of cries exhibiting those particular qualities. This reasoning is a welcome enrichment to the model that I proposed, but it depends on the facultative responses of infants that modulate the acoustic qualities of their cries. **Lotem & Winkler** argue, for example, that the severely abnormal crying of infants with pathology (Table 4) may also have a learning component, such that this severely abnormal crying also may increase if caregivers react positively to it, in which case they view it as a by-product of an adaptation expressed under pathological conditions. Although I believe the evidence to date suggests that abnormal cry acoustics associated with severe pathology are unavoidable physiological consequences of the underlying pathology (sect. 4.7 in the target article), and as such are unlikely to be modified through learning, the general idea of examining reinforcement mechanisms that may shape infant cry acoustics should be pursued.

R4. Other signals

It is unlikely that the infant cry signal is the only signaling modality by which infant behavior potentially modifies the behavior of caregivers. **Wood** notes that in addition to crying, infant signaling modalities include other vocalizations such as fussing and facial expressions. To this I would add other visual cues such as body movements, as well as olfactory and tactile communication. Similarly, **Nader, Job, Badali, & Craig (Nader et al.)** view the cry as a “distant early warning system,” which they view as ambiguous but that acts as a siren to alert care-givers of need, after which care-givers rely mainly on other cues, such as facial expres-

sion, to determine specific need. In support of this, **Nader et al.** cite studies showing that among nurses visual cues were better at indicating level of pain in infants than were crying cues. The observation of both commentators are consistent with the model that I proposed in the target article (sect. 4.6, para. 1). I also characterized the cry signal as a siren alerting caregivers of general need, and as one signal modality among many, such as facial expression and context, that can provide cues to caregivers of specific need. The only point of contention I have is the description by **Nader et al.** of the cry sound as ambiguous with regard to specific meaning. While it is true that there is not strong evidence for acoustically distinct cry types (although even this cannot be ruled out altogether), there is good evidence that the cry may act as a graded signal that reflects degree of pain (sect. 4.2 in the target article). The fact that other signaling modalities may also be important does not diminish the salience of the infant cry.

Provine compares cry vocalizations to laughter and smiling, contrasting the cry as an aversive stimulus, which elicits caregiving behaviors that may diminish the crying, with smiling and laughter a rewarding stimulus, which reinforces caregiving behavior. Thus, crying and laughter (as well as other communicative modalities, including visual, olfactory, and tactile modalities) may together contribute to the infant-caregiver relationship. **Roes** adds that tears, which arise several weeks to several months after birth, may be another visual representation of internal state to which caregivers may attend. **Roes** goes on to discuss the signal functions of tearful crying in human adults, which may be successful at eliciting attention, and perhaps help and care, because of the way in which this behavioral complex mimics the neonate. Taken together, these commentators correctly point out that the cry signal should be understood as just one of many sensory modalities by which the infant-caregiver relationship is mediated.

Falk integrates early infant crying with later vocal communication between mothers and infants that may have formed the basis for the emergence of protolanguage during human evolution. With the evolution of bipedalism and large brains, he argues, human infants were born at early stages of development and never develop the ability to cling to their mothers (also see commentary by **Bard**). Because of this, conflict between carrying and other activities in mothers resulted in infants being set down more, and increased the need for vocalizations as signals for reestablishing contact with the mother. In addition, **Falk** notes that persistent adult-directed crying and specialized infant-directed vocalizations (i.e., “baby talk” or “motherese”) are unique to humans. In early infancy, caregiver contact is necessary for soothing, but as infants grow older, caretaker vocalizations alone may be sufficient for soothing. Indeed, such motherese is used most intensively when infants are 3 to 5 months of age, just after the biobehavioral shift in infants, and at this time vocal communication alone between caregivers and infants may begin to stand in for actual contact and may constitute the substrate from which human protolanguage evolved.

R5. Conclusion

In the target article, I closed by expressing hope that my review of the infant cry signal would stimulate further scientific inquiry into this aspect of the infant-caregiver rela-

tionship. If these commentaries are a sign of the improvements in our understanding that my contribution triggers, then I believe I have been successful. It is my hope that the continued search for a better understanding of the early infant cry will not only increase knowledge for its own sake, but also contribute to the welfare of families.

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Letters “a” and “r” appearing before authors’ initials refer to target article and response respectively.

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