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

Rami Nader, Elizabeth A. Job, Melanie Badali, and Kenneth D. Craig

Department of Psychology, University of British Columbia, Vancouver, BC, V6T 1Z4, Canada. **rnader@interchange.ubc.ca**
eajob@interchange.ubc.ca **badali@interchange.ubc.ca**
kcraig@psych.ubc.ca
http://www.psych.ubc.ca/~kenslab/painlab/ramin.htm

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.

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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 Hadjistavropolous 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

John D. Newman

Laboratory of Comparative Ethology, National Institute of Child Health and Human Development, National Institutes of Health, Department of Health and Human Services, NIH Animal Center 112/205, Poolesville, MD 20837-0529. **jdnewman@helix.nih.gov** **http://gpp.nih.gov/researchers/viewbook/Newman_John.html**

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 &

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