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An Ethological Analysis of Human Infant Crying: Answering Tinbergen's Four Questions

Received 5 February 2001; Accepted 12 April 2001

ABSTRACT: *The proximate causes, survival value, ontogeny, and evolutionary history of human infant crying are examined. Experiments and field observations involving infant distress vocalizations and begging calls in avian, mammalian, and nonhuman primate species are considered, as are ethnographic records of infant care and responses to crying in nonindustrialized societies. It is argued that human infant crying evolved as a primarily acoustic, graded signal, that it is a fairly reliable, if imperfect, indicator of need for parental care and that its primary function is to promote parental caregiving. Selection pressures that may have shaped the evolution of crying and its potential for corruption through dishonesty also are discussed.*

Dev Psychobiol 39: 265–285, 2001

Keywords: *infant crying; distress vocalizations; attachment; maternal response; emotional development*

INTRODUCTION

The paradoxical nature of infant crying is immediately apparent to the student of human evolution. Crying is at once highly adaptive in that it motivates care and highly maladaptive in that it also motivates abuse. Crying is commonly thought of as a reaction to pain or unpleasant stimulation, but its appearance often is unprovoked and dissociated from physiological indices of distress. Although crying is relatively rare in adulthood and may be precipitated by events that are beyond the comprehension of an infant (e.g., death of a loved one), adult crying resembles its infant analog in many respects, suggesting both continuities and discontinuities across the life span. While crying is typical of mammalian young, it is in at least one respect unique to humans: Only human infants may cry, sometimes inconsolably as in colic, when in physical contact with a caregiver. Because crying is the primary means of communication for very young infants and continues to be an important part of the emotional repertoire of adults, it has received a good deal of attention from researchers.

In his treatise on the aims and methods of ethology, Niko Tinbergen (1963) highlighted four problems that studies of the biology of behavior must address: causation, survival value, evolution, and ontogeny. Recent reviews of the infant crying literature have tended to focus on only one or two of Tinbergen's questions, typically ontogeny (e.g., Barr, 1990b)

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or evolution (Barr, 1990a; Furlow, 1997; Lummaa, Vuorisalo, Barr, & Lehtonen, 1998). In contrast, the present article considers all four questions simultaneously. Doing so blurs the boundaries somewhat, but helps clarify the interrelations between levels of analysis in ways that can be illuminating. Tinbergen believed, for example, that the developmental timetable of a behavior can itself have survival value. In addition, there has been a lack of integration of infant crying research emanating from different academic disciplines, such as developmental psychology and animal communication, perhaps owing to a lack of common vocabulary or a reluctance to generalize across species. This article draws on research findings and theoretical perspectives from diverse disciplines including cultural anthropology, physiology, clinical neurology, pediatric medicine, and developmental psychology. Finally, the most comprehensive review of the infant crying literature (Murray, 1979) was published over 20 years ago. Although it was an extremely useful reference at the time, there has been sufficient research activity in the field to warrant a more current review. The present article is an updated, multidisciplinary, and integrative review of the infant crying literature using Tinbergen's questions as its organizing framework.

WHAT ARE THE PROXIMATE CAUSES OF CRYING?

Causation refers to the events preceding a behavior which also can be shown to contribute to its occurrence (Tinbergen, 1963). Questions of causation deal with the proximate mechanisms of behavior or how the brain or physiology of an organism produces a particular behavior. In a sense, the cry types discussed both colloquially and in cry research refer to the external causes of crying, such as crying from hunger or for attention. However, crying also occurs with no apparent cause and, once begun, can be self-perpetuating. Its seemingly unprovoked and self-perpetuating nature has led some to attribute internal causes to crying, especially in early infancy. Finally, while the underlying neurophysiological causes of crying are not understood, there is evidence from animal models and brain-injured adults for the involvement of endogenous opioids and serotonin.

External Causes of Crying

There are roughly four types of cries which correspond to events or states known to precipitate crying: the birth cry, pain cry, hunger cry, and attention cry. The birth cry is viewed as morphologically and perceptually different from the crying that soon follows in that it is usually voiceless (Wasz-Hockert, Lind, Vuorenkoski, Partanen, & Valanne, 1968) and may be uniquely human (Wolff, 1987). Other human infant cries are the result of pain or discomfort, including hunger or separation. Infants, for example, will cry following painful stimuli such as vaccination, and reliably 3 to 3½ hr following their last feeding (Stark & Nathanson, 1973). Cold exposure also leads to crying, which in turn generates heat through increases in motor activity (Lester, 1985; Wolff, 1987). The most important proximate cause of infant crying, however, may be being alone (Newman, 1985). Most infants will initiate crying when put down and will stop crying immediately when picked up and held (Bell & Ainsworth, 1972). For this reason, crying has frequently been thought of as attachment behavior caused by physical separation, which thwarts an infant's need to cling to its caregiver (Bowlby, 1958).

The crying of nonhuman young in response to pain, hunger, or separation usually lasts only as long as the cause for crying persists. By contrast, human infants frequently continue to cry even after the cause for crying has been removed (Wolff, 1987). For example, Bard (2000) noted that, like human infants, chimpanzee infants cry when separated from a caregiver, but chimpanzees always stop crying immediately upon being retrieved. Only human infants cry, inconsolably at times, while being held by a caregiver. Once initiated, crying as a behavioral state becomes self-equilibrating in human infants; that is, it maintains itself in relative autonomy of the triggering cause (Wolff, 1987). The apparent independence of crying from external (or exogenous) precipitating causes and its self-perpetuating nature are the reasons early infant crying is often thought of as internal or endogenous in nature (e.g., Brazelton, 1962). By contrast, crying in later infancy (after 2½ months or so) is more reliably linked to specific external events. This shift coincides with a similar one from endogenous smiling to social or responsive smiling and with the disappearance of early postnatal reflexes that are subsequently replaced by voluntary behaviors, perhaps as a result of maturation of forebrain inhibitory mechanisms (Emde, Gaensbauer, & Harmon, 1976).

Internal Causes of Crying

There are numerous internal causes proposed for crying. Sometimes crying is viewed as a means of regulating physiological homeostasis by discharging excess energy and tension (Brazelton, 1962, 1985) or as an unexplained consequence of maturational changes in central nervous system (CNS) organization (Emde et al., 1976). The notion of excess energy being released through crying appeals to adult-centered intuitions about the cathartic effects of crying, but is not easily tested empirically. Maturational explanations that attribute early unexplained fussiness and its disappearance to CNS growth also are unprovable; however, they are bolstered by the numerous studies showing concomitant shifts in EEG patterns and sleep–wakefulness cycles. Perhaps the closest we can come to evaluating the claim that infant crying is internally driven rather than the result of some external or environmental trigger is to compare crying across cultures. The fact that crying reaches its highest level at 6 weeks in diverse caregiving environments (Barr, 1990b) and even among chimpanzee infants (Bard, 2000) lends some support to the idea of a universal, internal cause to early crying, such as CNS growth. Nonetheless, a specific CNS mechanism for the peak and precipitous decline in crying has not been proposed. Finally, the fact that infants reared in non-Western cultures who are rarely allowed to cry do not appear to suffer any health or psychological deficits (e.g., Ainsworth, 1977; Brazelton, 1977; Konner, 1972, 1976) challenges arguments for the necessity of crying as a means of releasing tension or restoring homeostasis in the newborn. To the contrary, compared to their Western peers, non-Western infants are more advanced in certain aspects of neuromuscular and sensorimotor development (Ainsworth, 1963, 1977; Konner, 1976).

Caregiving Effects: Mediating Between External and Internal Causes of Crying

There have long been reports by anthropologists that non-Western infants are quieter and more alert than their Western counterparts (Ainsworth, 1977; Brazelton, 1977; Konner, 1977). An examination of infant caregiving practices in these cultures suggests that an important cause of crying in modern, Western societies like our own may be caregiving practices that discourage physical closeness and frequent feeding, and effectively encourage parents to ignore crying. Infants in industrialized countries are carried only one third of their waking hours in the first 3 months (Lozoff & Brittenham, 1979) compared to 80 to 90% of the time in some nonindustrialized societies (Konner, 1976). Even when Western infants are breast-fed, mothers tend to maintain them on a feeding schedule of every 2 to 4 hr, similar to that of bottle-fed babies (Lozoff & Brittenham, 1979). Finally, when infants are placed in playpens and cribs rather than being carried or co-sleeping, caregivers cannot detect early and subtle discomfort cues like fussing and whimpering and respond to them, and full-blown crying is likely to result. Moreover, because crying is self-perpetuating, once it has begun in earnest it may be more difficult to arrest. Furthermore, unlike their non-Western counterparts, Westernized parents often purposely ignore crying (Bell & Ainsworth, 1972; Bernal, 1972), a practice that has historically been encouraged by some pediatricians (e.g., Spock, 1968) and one that usually escalates crying.

Barr (1990a) has argued that the relatively small amount of physical contact and the infrequent feedings typical of Western child-rearing habits physiologically predispose infants to crying. In a randomized, controlled trial, even small amounts of supplemental holding (less than 2 hr each day when infants *were not* crying) reduced the daily amount of crying in 6-week-olds by 43% in the treatment group relative to controls (Hunziker & Barr, 1986). Likewise, in a correlational study, more frequent, smaller feedings were associated with less fussing and crying in 2-month-old infants of mothers who belonged to La Leche League, a group that advocates frequent nursing, compared to infants of breast-feeding nonmembers (Barr & Elias, 1988). This is not surprising considering the fact that colic, excessive, and inconsolable crying in early infancy often is associated with the production of intestinal gas, which in turn has been related to widely spaced, large feedings in chimpanzee models (Barr, Smith, Konner, White, & McMullan, 1988). In sum, typical infant care in modern, industrialized societies may cause, or contribute to, infant crying.

The Neurobiological Bases of Crying

The neural substrates underlying crying are not well understood because of ethical constraints on experimentation in this domain. As a result, our current understanding is based on inferences drawn from experimentation in animals and brain-injured adults. The emission of infant separation calls in primates is believed to be under the control of the hypothalamic and interrelated limbic system (Panksepp, Siviy, & Normansell, 1985; Torda, 1976), portions of the brain that are concerned with emotional functions (MacLean, 1985). In macaques, removal of parts of the brain homologous to the human speech centers does not interfere with crying, suggesting different areas controlling speech and emotion (Ploog, 1981). The involuntary expression of affect, including facial expression and crying, appears to be controlled by the limbic system in humans, as it is in nonhuman primates, whereas the voluntary expression of emotion may be under cortical control (Myers, 1968). The development of a distinct pathway for controlling voluntary crying may account for the transition from endogenously controlled crying to exogenously controlled crying over the course of the first year of life in human infants (Murray, 1979).

Panksepp and colleagues have proposed a major role for endogenous opioids in the relief of distress vocalizations based on the effectiveness of opioid antagonists in eliciting distress vocalizations in the young of diverse species and opioid agonists in inhibiting them (Panksepp, Meeker, & Bean, 1980). However, even according to these authors, the effects of opioid agonists and blockers are not specific, influencing not only the occurrence of crying itself but also other attachment behaviors which serve to facilitate interaction with the caregiver. The fact that in some other primates, notably the squirrel monkey, electrical stimulation of the rostral cingulate cortex, an area with a high concentration of opiate receptors, consistently elicits vocalization (Ploog, 1981) suggests that endogenous opioids play a role in mediating infant distress reactions.

One common means of calming crying infants, nursing, produces at least some of its calming effects by stimulating the release of endogenous opioids. Small quantities of sweet tastants, including sucrose solution, infant formula, and breast milk, arrest spontaneous crying in human infants (Barr et al., 1994; Barr, Young, Alkawaf, & Wertheim, 1996; Blass, 1997; Zeifman, Delaney, & Blass, 1996) and distress vocalizations in rat pups (Blass & Fitzgerald, 1988). Furthermore, the calm these substances induce is sustained for several minutes. In rat pups, administration of opioid antagonists blocks the quieting properties of the tastants (Shide & Blass, 1989), supporting the idea that the effect is mediated through the release of endogenous opioids. Human infants born to methadone-addicted mothers do *not* quiet in response to taste stimulation as normal infants do (Blass & Ciaramitaro, 1994), suggesting these infants have become habituated to opiate drugs and their natural analogs in utero. Since opioids are powerful and highly addictive conditioning agents, their association with the transition from crying to calming would be one basis for the strong preference an infant shows to his or her primary caregiver. In fact, the opioid system has been hypothesized by several scientists to play a primary role in attachment formation, in part because of the similarity of infant separation reactions to narcotic withdrawal (Panksepp et al., 1985).

Whereas work in mammalian young, including human infants, has emphasized the role of endogenous opioids in calming and distress, work on brain-injured adults suggests that serotonergic transmission may be primarily responsible for emotional incontinence, a condition characterized by uncontrollable outbursts of exaggerated, involuntary facial expressions and pathological laughter or crying. In one study, patients with various CNS diseases causing pathological crying improved with three different selective serotonin reuptake inhibitors (SSRIs) (Nahas, Arlinghaus, Kotrla, Clearman, & George 1998). Similarly, poststroke pathological crying, which may affect as many as 11% of patients 1 year after stroke, is often successfully treated with SSRIs such as fluoxetine (Low & Chong, 1998). There also is evidence from a reported case of uncontrollable crying following a basilar artery embolism that the lesions responsible for uncontrollable crying involve the brainstem serotonergic raphe nuclei and their ascending projections (Larner, 1998). The patient in the case reported became progressively less responsive verbally while she was crying uncontrollably and in a stereotyped fashion, lending further support to the existence of distinct language and emotion circuits in the brain. To the extent that crying is a common symptom of adult depression, and SSRIs a common means of relieving depression, it is perhaps not surprising that serotonin may have a primary role in activating and arresting uncontrollable crying. Of course, whether the neurophysiological mechanisms controlling pathological adult crying are similar to those controlling normal adult or infant crying remains unclear.

Summary

In sum, most human infant crying is caused by hunger, pain or physical discomfort, and by merely being left alone. The degree of "aloneness" (or loneliness) of infants in our culture is exceptionally high compared to infants of other cultures and closely related species. In modern, Western contexts in which infants are out of parents' sight and touch for many hours of the day and night, fussing and low-grade crying may be viewed as a cause of excessive crying. Caregiving practices such as feeding infants on a fixed schedule and having relatively little physical contact may affect infant physiology in ways that predispose infants to crying. Just as additional skin-to-skin contact reliably results in more rapid weight gain and earlier release from the hospital in premature infants (Scafidi et al., 1990) presumably through the suppression of corticosterone and the release of growth hormone

(Schanberg & Field, 1987), low levels of mother–infant contact may effect physiological changes in infant hormone titers and neurotransmitter levels such that excessive crying results. Based on inference from experimentation in nonhuman species and accidental brain injuries in human adults, these physiological effects of caregiving on crying may be mediated through the release of endogenous opioids and serotonin.

WHAT IS THE SURVIVAL VALUE OF INFANT CRYING?

The issue of the survival value of a behavior, its function, addresses the effects rather than the causes of the observed behavior (Tinbergen, 1963) and poses the question of how infant crying enhances fitness. Like other behaviors which have been selected over the course of evolution, there are costs and benefits associated with infant crying, and it is likely that the pattern of behavior observed is some compromise between these competing forces. On the adaptive side, crying is a compelling signal that elicits care and nurturance, usually in the form of holding and offering the breast or bottle. It also conveys useful information to parents about the health and status of their offspring. On the negative end, crying is metabolically costly and may attract predators and annoy caregivers. In modern times, we know excessive crying is a common concern of new parents (St. James-Roberts, Conroy, & Wilsher, 1998), a frequently cited reason for giving up breast-feeding (Bernal, 1972; Forsyth, McCarthy, & Leventhal, 1985), and often the final triggering event in cases of infant abuse and infanticide (Frodi, 1981, 1985).

While crying undoubtedly had costs associated with it throughout its evolutionary history, there may be even greater costs associated with crying in modern times. One explanation for the maladaptive appearance of infant crying in modern society is that the amount of crying that would result in complaint to a physician, curtailment of breast-feeding, or even infant abuse may be unprecedented in our evolutionary history (Barr, 1990a; Devore & Konner, 1974; Konner, 1972; Lozoff & Brittenham, 1979). Modern caregiving practices may deviate from those of the environment of evolutionary adaptedness (EEA) in ways which promote crying of longer duration and greater intensity than earlier levels (Barr, 1990a). Although crying may be designed to compel a parent to act quickly to relieve an infant's distress, it may no longer elicit an empathic response if it exceeds a certain intensity and duration (Murray, 1979). Consequently, although the primary function of crying is to elicit care and nurturance, it may elicit escape (i.e., neglectful) or abusive responses if it cannot be easily terminated through typical caregiving ministrations.

Crying as a Means of Eliciting Care

The view of crying as a signal that evolved to elicit caregiving is supported by the near-universality of interventions which involve close physical proximity and nursing (Bell & Ainsworth, 1972; Bernal, 1972). The fact that deaf parents do not respond appropriately to their infants' crying despite facial cues of distress (Lenneberg, Rebelsky, & Nichols, 1965) also suggests that the sound of an infant's cries is his or her primary means of eliciting care. Although the practice of ignoring crying or delaying response to it is common in Western societies (Bell & Ainsworth, 1972; Bernal, 1972; Hubbard & van IJzendoorn, 1991), this pattern of response contrasts sharply with nonindustrialized societies in which responses to crying are typically immediate (Konner, 1972, 1976).

If crying evolved as a signal to alert mothers and elicit caregiving, we would anticipate the coevolution of reciprocal mechanisms in the target of the signal. Because caregiving was primarily a female endeavor over the course of much of human evolution, we would predict that females—and particularly those of childbearing age—would have evolved mechanisms for perceiving and responding appropriately to infant cries. In fact, crying causes a predictable increase in the temperature of the breasts within 7 min of the onset of crying (Vuorenkoski, Wasz-Hockert, Koivisto, & Lind, 1969) and a milk letdown reflex, which makes the breasts heavy and causes the mother to feel a physical urge to breast feed her infant (Mead & Newton, 1967). In addition to these physiological effects in the lactating mother, mothers have distinct cardiac responses to their own infant's cries which differ from those of fathers. Listening to the same tape-recorded cries of their own infants caused cardiac deceleration followed by rapid acceleration in mothers, a response associated with preparation for action or intervention, whereas it caused only cardiac deceleration in fathers, a response associated with passive attention or orienting rather than active coping. Mothers and fathers were highly accurate in recognizing their own infant's cries, but only mothers were able to identify the cry type accurately (Weisenfeld, Zander-Malatesta, & DeLoach, 1981). When exposed to longer, videotaped segments of unfamiliar crying infants, fathers showed greater physiological reactivity than mothers (Brewster, Nelson, McCanne, Lucas, & Milner, 1998), a pattern that is sometimes thought to set the stage for physical abuse (Frodi & Lamb, 1980). Taken together, these studies suggest that mothers are physiologically primed to respond to infant crying with caregiving. Fathers' responses are less consistent with preparation for caregiving and, in the case of an unfamiliar infant, may even predispose men to respond aggressively toward a crying infant.

Some differences between mothers' and fathers' reactions may be attributable to hormonal changes associated with parturition and lactation or conditioned responses that result from caregiving experience. However, even in samples in which female subjects were not hormonally primed and had no prior caregiving experience, the sexes differ in their ability to interpret cries accurately, with women demonstrating superior perceptual abilities. In one study examining the ability of adults to discriminate between cries, subjects were asked to identify typical cries of four types: birth, hunger, pain, and pleasure (Wasz-Hockert, Partanen, Vuorenkoski, Valanne & Michelsson, 1964). The data indicate that men are considerably less accurate than women at identifying the cry-evoking situation regardless of their level of experience. Fathers and pediatricians, despite substantial caregiving experience, scored lower than women with no caregiving experience. In general, biological factors in the listener associated with potential maternity (i.e., female sex and postpubescence) are associated with more sympathetic and less hostile reactions to cries (Murray, 1985) and superior ability to discriminate their meaning. Given that caregiving by women was almost certainly the norm over the course of human evolutionary history, sex differences in cry perception further attest to the evolution of crying as a signal directed toward the mother. But what exactly is communicated to the mother by her infant's cries?

The Signal Value of Human Infant Cries

There is now substantial evidence that the cry signal is richer in terms of the information it conveys than was once believed. That is, in addition to serving to alert a mother of an infant's need for her attention in a general way, crying communicates information about an infant's state, health, and identity which influences maternal response. For example, in a naturalistic home observation, Wolff (1969) played a tape recording of an infant's hunger cry and, on a separate occasion, played a pain cry to measure the delay before a mother responded. He reported that there was a dramatic difference in the speed of response, with responses to the pain cries being almost immediate. The sudden onset of the pain cry and its dramatic intensity set it apart from ordinary hunger and attention cries. The pattern of differentially responding to cries depending on their intensity is probably one explanation for high rates of ignoring or delaying response to infant crying in home observation studies in North American samples.

A view of crying as a graded signal whose meaning is derived from both intensity cues and contextual factors rather than as a discrete signal which conveys a single message is consistent with the general trend in this direction among mammals more closely related to humans, including primates (Marler, 1976; Wilson, 1975). It also takes into account the functional value of the cry for the parent as opposed to only the infant. Since infant survival enhances parental reproductive fitness, we would anticipate reciprocal mechanisms in the parent that ensure prompt response to crying such as those discussed previously. However, consideration of parent–offspring conflict theory (Trivers, 1974) would suggest certain limits to viewing crying as a strictly "honest" or cooperative signal. Parent and offspring are expected to disagree over the amount of parental resources that should be offered, particularly with increasing infant age. While it may always be in the infant's best interest for the parent to respond to its wails, it may be in the parent's best interests to ignore crying in two cases: when crying is not urgent (i.e., not likely to result in injury or death, thereby decreasing the infant's chances of surviving to reproductive age) and when offspring are unlikely to survive to reproductive age because of injury or illness (which can be gauged by an infant's cries). Indirect evidence suggests that cries functioned as initial indicators of infant viability. Responses to crying following the initial decision to invest in an offspring were likely governed by parents' assessment of whether ignoring crying would result in appreciable negative consequences for their offspring.

In hospitals today, crying is used diagnostically to identify neurologically impaired infants. A normal birth cry is seen as a sign of the newborn's viability, and factors into the infant's Apgar score and similar indices of infant health (Apgar, 1953; Brazelton, 1973). One rare genetic disorder, cri du chat syndrome, earns its name by the abnormally high-pitched cry of infants afflicted with it. Although not a notion that appeals to our romantic perception of the mother–infant relationship, crying may have contributed to parental decisions about whether to invest in caring for a newborn (Furlow, 1997). The cries of premature and abnormal infants, including those with Down syndrome, neonatal asphyxia, brain damage, and hyperbilirubinemia, are markedly distinct in their acoustic features from cries of normal infants. They are of higher or lower pitch than normal cries, have greater variability, and have different temporal patterns (Wasz-Hockert, Michelsson, & Lind, 1985). In perception studies, cries of abnormal infants often receive higher aversiveness ratings than do the cries of normal infants (Frodi, 1985). In real life, nonoptimal health places an infant at increased risk for abuse (Belsky, 1993; Frodi, 1981). Thus, though not its primary function, crying may have steered mothers away from "poor" investments in terms of their own reproductive fitness, freeing them to invest their reproductive energies in offspring more likely to survive and reproduce themselves.

Beyond the initial parental decisions about whether to care for a particular newborn infant, infant mortality and survival rates also may determine culturally specific response patterns to crying. LeVine (1977) argued that the "indulgent" caregiving of non-Westernized cultures relative to our own is a reflection of high infant mortality rates in non-Westernized, developing countries. Immediate responses to crying among other indulgent caregiving practices such as frequent feeding counteract the real threat in developing countries of infant disease, malnutrition, and death. Thus, the universal prompt response to crying that has been observed in non-Western cultures may reflect parents' accurate perception of their infants' physical vulnerability. Similarly, the greater willingness of even indulgent parents to ignore crying in older infants reflects the perception of decreased physical vulnerability with increasing age. It is probable that parental decisions about whether to respond to or ignore crying take into account the expected consequences of such actions.

Secondary Functions of Crying in Humans and Related Species

Several other hypotheses regarding the function of crying in other species may be applicable to human infant crying as well. The "allomothering hypothesis" proposed by Todt (1988) argues that the main function of primate crying is to protect the infant from incompetent allomothers and reunite the infant with its own mother. Todt rejects the viewpoint that crying functions primarily to elicit care because of its repellent nature. Moreover, he argues, primate infants are inherently attractive to parents as well as other group members and would therefore be unlikely to find themselves separated from the group. The care infants elicit from nonparental group members, however, may be inept, and crying functions to alert the mother when her infant is in danger because of an allomother's incompetence. Although communal infant care is not a common feature of modern human societies, parents can pick out the cries of their own infant from among cries of similar-age infants (Weisenfeld et al., 1981), and perception of the individuality of cries is robust to degradation across distance (Gustafson, Green, & Cleland, 1994). These data suggest that crying may have functioned to guide nepotistic care during a period in our evolutionary history when group living and communal care were the norm (Gustafson et al., 1994). Similarly, the near-universal emergence of stranger-wariness as a frequent cause of crying in the second half of the first year (Konner, 1972; Ricciuti, 1974) may be taken as evidence that crying functions to reunite the infant with its primary caregiver in preference to a substitute. The allomothering hypothesis is more easily applied to nonhuman primates with relaxed social bonds and considerably more allomothering available to infants than in humans (Todt, 1988). Although the primary function of crying in humans appears to be the elicitation of care, it is likely that crying also serves a secondary function of expressing preferences for one caregiver over another, consistent with Todt's allomothering hypothesis.

Alberts and colleagues (Blumberg & Alberts, 1990; Blumberg, Efimova, & Alberts, 1992) have argued that temperature regulation may be the primary function of ultrasonic vocalization in rat pups, a common model for human infant crying. Although there is some support for the idea that cold temperature causes vocalizations in rat pups, this theory fails to account for distress vocalization caused by the withdrawal of social cues associated with the dam when ambient temperatures are maintained (Hofer, 1996; Shair, Masmela, Brunelli, & Hofer, 1997). Further, because dams give birth to litters rather than singletons or twins and cache their young when they forage rather than carry them, we would expect rat pups to have temperature-regulation mechanisms at birth, including huddling with littermates. In contrast, infants of carrying species (i.e., most primates, including humans) likely regulate their temperature primarily through body contact with mother in the early stages of development. Therefore, cold temperature most likely induces crying in newborns (Wolff, 1987) not because temperature regulation is the primary function of crying, but rather because warmth is one of numerous cues associated with maintaining contact with a caregiver that, when interrupted, can cause crying.

Summary

The fact that females of childbearing age are biologically primed to respond to and interpret infant cries and the near universality of responses that involve holding and feeding together bolster the view of crying as a signal whose function is to elicit care from the primary caregiver. The rich signal value of crying discovered in cry perception studies suggests that crying is a graded rather than a discrete signal, communicating information about the infant's long-term health and viability as well as current needs and state. Parents most likely used information from neonatal crying to determine whether their initial parental investment was warranted and, subsequently, to determine the amount and type of care needed. Crying also may have functioned to identify particular infants to their parents during a period of human evolutionary history when group living and communal infant care were the norm. Like other evolved signals, human infant crying represents a compromise between competing costs and benefits. However, costs may increasingly outweigh benefits with changes in patterns of infant care in recent times. Several authors have suggested that the current maladaptive appearance of crying reflects unique features of infant crying in modern Westernized societies in contrast to the environment in which it originally evolved (Barr, 1990a; Devore & Konner, 1974; Konner, 1972; Lozoff & Brittenham, 1979). Long durations of urgent, high-intensity crying in the presence of a caregiver, characteristic of infantile colic (Wessel, Cobb, Jackson, Harris, & Detwiler, 1954), may tax adults' tolerances thereby eliciting sometimes unsympathetic and even aggressive responses (Murray, 1979).

WHAT IS THE DEVELOPMENTAL COURSE OF CRYING?

The question of ontogeny focuses on changes in the behavior over time and attempts to distinguish internal and outside influences on those changes. It also addresses the question of the survival value of different forms of ontogenetic control (Tinbergen, 1963). Why might it be adaptive for one kind of behavior to be largely controlled by innate factors and another entirely open to the influence of the environment? Despite considerable individual variability in the amount and pattern of crying, there are predictable changes over the course of development that are relatively impervious to outside influence. These changes are linked to other aspects of biological and psychological growth and maturation, such as expansion of the vocal apparatus and growth of memory. In addition to normative developmental changes, there are individual and cultural differences in crying by the end of the first year that strongly suggest crying is shaped by the environment. For example, the environment determines the individual(s) to whom crying and other bids for attention are directed. It also is widely believed that parental responses to crying influence individual differences in the amount of crying, although whether responding to infant crying engenders more or less crying remains a subject of heated debate that has not yet been resolved empirically. Crying remains a powerful tool for eliciting care through adulthood, although the circumstances evoking crying change drastically, and crying becomes a primarily visual signal rather than an acoustic one. Finally, in adulthood, cultural rather than biological variables may largely determine whether individuals inhibit or express crying.

Crying in the First Year

Unlike the amount of crying later in the first year and onward, the basic appearance of the early crying curve is unaffected by differences in caretaking style (Barr, 1990b). The amount of infant crying gradually increases until it peaks at 6 weeks, then decreases until about 4 months when it remains fairly stable until the end of the first year (Bell & Ainsworth, 1972; Brazelton, 1962; Hunziker & Barr, 1986). There is a diurnal pattern to early infant crying which peaks at about 2 months, with the greatest amount of crying being concentrated in the evening hours (Barr, 1990b). Because of the robustness of the early postnatal crying pattern, the pattern of early crying often has been viewed as a reflection of physiological and maturational shifts during the first months of life rather than external triggers (Emde & Gaensbauer, 1981; Emde et al., 1976). The reduction in crying following its peak at 6 weeks corresponds to a decrease in emotional lability and an increase in environmental control of both positive and negative emotions. For example, before 2 months, infants may smile during rapid eye movement (REM) sleep or in response to random social stimuli. After 2 months, infants begin smiling in response to the smiles of others (Emde & Robinson, 1979). Thus, crying in the first 3 months of life is thought to reflect internal state changes in the newborn and is distinguished from crying in subsequent months, which is more responsive to external events including variations in caregiving habits such as amount of holding or frequency of feeding.

A second shift in crying behavior occurs at about 7 to 9 months and corresponds to major cognitive and affective gains at that age (Emde & Gaensbauer, 1981; Zeskind, 1985). Whereas infants initially cry in order to promote proximity to the caregiver, towards the end of the first year they are more likely to cry when the caregiver is nearby (Bell & Ainsworth, 1972). Infants also are more likely to direct crying and other bids for attention toward a particular person, typically the primary caregiver (Bowlby, 1969; Sroufe & Waters, 1976) and to coordinate crying with looking, reaching, and other nonvocal orienting behaviors (Gustafson & Green, 1991). In the second half of the first year, crying is often coupled with signs of the infant's expectations about its results, such as quieting at the approach of a caregiver (Gekowski, Rovee-Collier, & Carulli-Rabinowitz, 1983). Thus, at 7 to 9 months, an infant's crying is often first perceived as "intentional" in that it is now tailored to its audience and the infant appears to be cognizant of its likely result.

Changes in crying which reflect biological maturation also result in changes in the functional significance of crying (Lester, 1985). At 5 or 6 months, responses to strangers become cautious, and by 9 to 12 months, fear of strangers and of separation from the usual caregiver often prompts crying (Ricciuti, 1974). The ability to react to an impending separation rather than merely respond to its effects depends on cognitive growth which has only recently occurred, namely the ability to anticipate a future event (Kagan, 1982). The newly developed fears of strangers, unfamiliar surroundings, or abandonment are adaptive in that they coincide with the emergence of independent locomotion and with the increased potential that locomotion brings for encountering new persons or surroundings or for accidentally becoming separated. Crying provides a tether, allowing exploration while ensuring safety by alerting the caregiver to unexpected circumstances that may bring danger. Since crawling provides the infant some measure of control over his or her proximity to the caregiver, proximity seeking as a cause or function of crying recedes in importance (Zeifman, 2001). Thus, crying changes not only in terms of its pattern and amount over the course of the first year but also in terms of its proximate causes and functional significance. Crying continues, however, to be a marker of attachment to particular individuals whose mere presence may alleviate crying and whose departure may induce vigorous crying.

Maternal Responses to Crying and Subsequent Crying

Investigations of the impact of the environment on the development of infant crying have focused on maternal response and its impact on subsequent emotional and psychological development. Contrary to learning theory, popular opinion, and pediatric advice at the time, Bell and Ainsworth's (1972) pioneering longitudinal study found that promptness of maternal response is associated with a decline in the frequency and duration of crying over the course of the first year and more rapid development of noncrying means of communication. In comparing crying in the four quarters of the first year of life, Ainsworth and colleagues found that, by the end of the first year, individual differences in crying reflect the history of maternal responsiveness rather than constitutional differences in infant irritability. Bell and Ainsworth's findings, however, have been criticized on methodological grounds (Gewirtz & Boyd, 1977; Lamb, Thompson, Gardner, & Charnov, 1985), and efforts at replication have not been successful (Hubbard & van-IJzendoorn, 1991). Several studies have confirmed that infant crying is not stable or meaningfully related to maternal response before 3 months and that it becomes increasingly linked to maternal response throughout the first year (Acebo & Thoman, 1995; St. James-Roberts et al., 1998; St. James-Roberts & Plewis, 1996). However, it is not clear whether mothers who ignore their babies cause their babies to cry more or, alternatively, whether mothers of babies who cry more eventually ignore their babies' crying.

One of the methodological issues making it nearly impossible to interpret the results of Bell and Ainsworth's (1972) study is the lack of independence of maternal response and infant crying measures. Maternal unresponsiveness to crying would almost certainly be correlated with increased crying if infant crying is generally terminated by maternal response and the two are measured simultaneously, as they were in the original Ainsworth study, instead of in different contexts (Gewirtz & Boyd, 1977). Another methodological problem plaguing the original study and attempts to replicate it is the emphasis on promptness of response without much regard for the quality or type of maternal intervention. Hubbard and IJzendoorn (1991) attribute their failure to replicate Bell and Ainsworth to a lack of distinction in their own study between severe- and mild-distress vocalization. If only severe-distress vocalizations (e.g., pain or hunger cries) are conceptualized as requiring prompt response, the Hubbard and van-IJzendoorn study may have grossly overestimated rates of ignoring crying and, in doing so, underestimated the actual impact of letting severe crying go unheard. To date, no longitudinal study of maternal response to infant crying has taken into account the concept of “differential responsiveness” to cries depending on their intensity (Hubbard & van-IJzendoorn, 1991). A study in which infant crying propensity and qualitative maternal responses are measured both in the home and in other contexts would be a valuable addition to the clinical crying literature.

In later formulations, Ainsworth articulated a more nuanced description of the effects of early maternal responsiveness, taking into account consistency of response in addition to promptness (Ainsworth, Blehar, Waters, & Wall, 1978). According to attachment theory, individual differences in attachment behavior, including crying, can be classified into three characteristic patterns rooted in an infant's experience of the attachment figure's emotional availability. Ainsworth and colleagues observed infants' reactions to stressful situations such as the approach of an unfamiliar adult and a brief separation from the mother. Infants whose mothers had responded promptly and reliably to crying in the home were less likely to cry excessively or cling to their mothers because, according to Ainsworth, they felt emotional security. However, mothers who reliably ignored crying also had infants who cried less than average, presumably because they had become accustomed to being ignored. These infants often appeared calm during separations, but showed other signs of distress such as elevated heart rates (Spangler & Grossmann, 1993).[Q15] Although crying had been extinguished, these infants were no less emotionally anxious than other infants. Finally, the highest levels of crying and other overt behavioral signs of insecurity such as clinging were shown by infants whose mothers sometimes responded appropriately to crying and at other times ignored it. It might be inferred that because crying was sometimes an effective means of procuring aid, infants in this group persisted in trying to gain the attention of their caregivers. If the effects of maternal response on infant emotional expression depend on consistency as well as promptness of response, previous studies in which promptness alone was considered may have failed to uncover the real effects of maternal response on subsequent crying.

Crying in Later Infancy and Childhood

After the peak of stranger anxiety at around 24 months and concurrent with the rapid development of spoken language, crying appears to drop off rather precipitously. In the second year, crying often makes its appearance in the context of “temper tantrums” or situations in which children experience frustration, for example, because they do not wish to comply with parental wishes (Gesell & Ilg, 1943). The addition of frustration to the list of causes for crying coincides with the appearance of planful, deliberate action and the opportunity it presents for goals to be thwarted. Other situations that frequently elicit crying in laboratory investigations include caregiving episodes such as diaper change, physical injuries such as a fall, and separation from parents (Kopp, 1992). Crying does not disappear during childhood, rather it is encompassed within and elaborated by other recently developed communication skills including, most notably, language.

Individual differences in the frequency of crying episodes among preschoolers of similar chronological age provide further insight into the relationship between crying and other forms of communication. In several studies, progress in language development is inversely related to crying; that is, children with more advanced language skills than their age-mates are less likely to resort to crying than children with less developed language skills. For example, when incidences of crying during a laboratory study of 18-month-olds were examined, children who cried were far more likely than those who did not cry to be limited to one-word sentences and to have not yet achieved two-word sentences (Kopp, 1992). This finding is consistent with the observations of Bell and Ainsworth (1972), who reported that infants who cried less at the end of the first year were more likely to develop noncrying modes of communication such as facial expressions, bodily gestures, and noncry vocalizations than those who cried more. Taken together, these data strongly suggest that crying is utilized when alternative means of communication do not yet exist or fail to achieve desired goals (Reynolds, 1928). They also support the notion of crying as a means of communication rather than popular notions of crying as a means of releasing pent-up energy or tension.

Crying Beyond Childhood

Crying remains a compelling signal of physical or emotional injury in later childhood and adulthood, and a means of soliciting aid and assistance from others when in need. However, there are several notable changes in crying over the course of later development, including a reduction in the frequency of episodes, greater complexity of eliciting circumstances, increased selectivity of target or audience, and inhibition of crying in public places. There also is a shift in the salience of the various components of crying, with crying being primarily an acoustic signal in infancy and a visual one in later childhood and adulthood. In fact, according to Darwin, very young infants do not even shed tears when they cry (Darwin, 1872; although see Apt & Cullen, 1964 for an opposing view). Although there is a characteristic facial expression associated with infant pain (Craig, 1998), deaf parents do not respond appropriately to their crying infants (Lenneberg et al., 1965). Likewise, in an experiment conducted by Moss and Robson, a majority of mothers of 3-month-olds failed to respond when told by experimenters that their infants were crying in another room, although they had responded to audible cries when observed in the home (Harper, 1971). In contrast, adult crying may or may not be accompanied by vocalizations, but its distinguishing feature is the appearance of tears (Vingerhoets, Cornelius, Van Heck, & Becht, 2000). Furthermore, only humans produce tears when they cry, in contrast to all other primates (Bard, 2000). The significance of tears and other visual components of crying in adults is noteworthy because, on the whole, the behavioral components that make up crying as an organized behavior remain constant.

It is possible to speculate on the adaptive significance of this shift from a primarily acoustic signal to a primarily visual one and its timing. Like other acoustic signals, infant crying is metabolically costly (Brignol, Rao, Blass, Marino, & Glass, 1993; Thureen, Phillips, Baron, DeMarie, & Hay, 1998) and, in the environment in which humans evolved, may have involved substantial predation risk. Selection of a less costly alternative may therefore be behind the transformation of crying to a predominantly visual signal in adulthood. To be effective in garnering aid from any distance, an immobile infant would have had no choice but to utilize an acoustic signal to alert a caregiver. Independent locomotion, however, introduces an alternative strategy for delivering a message: delivering oneself in person and presenting a primarily visual signal to the target. Given the obvious disadvantages of a primarily acoustic signal, a greater dependence on the facially expressive aspect of crying and diminished reliance on vocalization might be adaptive as the ability to locomote emerges.

This explanation presumes that crying, even when silent, is communicative. But why then do older children and adults frequently inhibit crying in public or seek privacy before a crying episode? One explanation may be the growing awareness with maturity that there are costs to crying besides the consumption of limited energy and being located by a predator when vulnerable. While motivation to arrest the aversive sound of crying underlies its effectiveness for eliciting care from loved ones, the same motivation may precipitate avoidance and even abuse from those less altruistically inclined (Murray, 1979, 1985). In fact, preschoolers who show an awareness of cultural display rules and are able to regulate their negative emotions during social interaction are better liked by both their peers and their teachers (Eisenberg et al., 1993). Consequently, most children learn to direct crying toward individuals who are highly motivated to provide care for them and inhibit crying in the presence of those who may be disinclined to tolerate it. Adults often perceive crying as a form of emotional blackmail in relationships (Frijda, 1986) and are embarrassed when co-workers cry (Plas & Hoover-Dempsey, 1988). Appreciation of the demands crying places on others and the negative reactions crying can engender may therefore be among the reasons adults most often cry in the privacy of their own homes (Becht & Vingerhoets, 1997) and only in front of loved ones.

Summary

Infant crying follows a relatively fixed developmental trajectory in the first 3 months of life and becomes subject to environmental influences by the end of the first year. Changes in crying reflect the growing cognitive capacities of the infant: As the infant develops the mental capacity to imagine consequences (i.e., mental representation), the threat of maternal separation induces crying, if crying previously successfully reunited the infant with his or her caregiver. Similarly, as planful, deliberate action emerges with development of the prefrontal cortex, the thwarting of goals is often the precipitating factor in temper tantrums that include crying. Although crying remains a powerful means of eliciting care from loved ones, the circumstances that elicit crying change somewhat, and crying becomes a relatively rare occurrence in adulthood. Adults may still cry when they feel powerless and alone, but they often seek privacy before crying episodes, and their crying often consists of facial expressions of sadness and pain accompanied by tears (i.e., "weeping") rather than the loud, audible wails of infants and young children. These changes likely reflect the capacity of the adult to satisfy his or her own needs compared to an infant, the growth of the capacity to inhibit negative emotion, and the cognizance that crying and other displays of weakness may engender avoidance or abuse rather than care if directed toward the wrong individual.

WHAT IS THE EVOLUTIONARY HISTORY OF CRYING?

One goal of evolutionary inquiry is to elucidate the selection pressures which have shaped a particular trait, characteristic, or behavior (Tinbergen, 1963). In the absence of a fossil record of behavior, this goal is typically achieved through the comparison of closely related species and of populations within a species in an attempt to understand the influence of selection on behavior evolution. By examining infant signals in other species, we gain insight into the selection pressures that may have shaped human infant crying, including ecological variables and strategic conflicts with adult "receivers," namely parental caregivers. Speculation about the course of human evolution requires consideration of the environment of evolutionary adaptiveness (the EEA) rather than our current environment since modern industrial society and the selection pressures it imposes represents a minute proportion of human evolutionary history (Lozoff & Brittenham, 1979). Toward that end, infant crying in Western societies must be compared to that of contemporary hunter-gatherer societies, whose current environment approximates that of most of human history. Through these and other indirect means, inferences can be made about the selection pressures that have shaped the evolution of infant crying.

The Evolution of Infant Vocal Communication

Why would an acoustic signal, with all of its inherent costs, evolve as the primary means of maternal–offspring communication instead of either a chemical or visual signal? The answer to that question may give insight into what the signal evolved to accomplish and the circumstances surrounding its evolution. Chemical communication has the advantage of being bioenergetically cheap to produce but, since pheromones cannot be detected as they move farther from their source, they are only useful in short ranges (Gerhardt, 1983). Visual signals are conspicuous at long range, but they are only effective when there is sufficient light, and they are easily detected by predators (Gerhardt, 1983). Acoustic signals, on the other hand, are effective both day and night and in environments in which vision is limited (Gerhardt, 1983). In fact, investigators believe that the first transitional reptilelike mammals were nocturnal and lived in the dark, densely populated forest floor where vocal communication would have been a useful adjunct to olfaction and vision for maintaining maternal–offspring contact (MacLean, 1985). Additionally, in contrast to most visual signals, acoustic signals can be turned on and off so that they are only conspicuous and metabolically costly while actually being used. Crying, as we know it, likely evolved as an occasional means of communication rather than a constant one, with tactile and olfactory communication predominating at close mother–infant range.

Function–Structure Relations in Auditory Signals

Despite the fact that infant vocal communication probably evolved because of its ability to span some distance and its usefulness to parents for locating young in the dark, infant vocalizations share acoustic features of warning and alarm signals that may make them difficult for predators to utilize for homing in on prey. Like other emergency and alarm signals, infant crying is tonal, has a gradual onset, and is high pitched, making phase comparisons and localization difficult (Marler, 1955). High frequency sounds such as infant crying do not travel as far as low frequency ones, so that crying would most likely reach conspecifics located in the immediate vicinity of a distressed infant before reaching more distant, roaming predators. Thus, the acoustic properties infant cries share with other alarm calls somewhat diminish the potential that they would be used by predators to locate infants and prey upon them and their parents.

Within acoustic communication, ecological variables influence whether a signal is primarily discrete or graded. Discrete signals function in an on–off manner with no gradations in intensity and meaning, whereas graded signals are variable and increase in intensity with the signaler's level of motivation (Murray, 1979). Among nonhuman primates, discrete signals are more common among tree-dwelling primates and graded signals among terrestrial ones (Wordon & Galambos, 1972). Long-distance sound signals that function without elaboration from other sense modalities or contextual information are best served by relatively invariant discrete signals (Marler, 1967, 1976). Territoriality, for example, is associated with loud, far-reaching, and discrete signals. In contrast, signals functioning over a shorter distance will tend to be graded because they will be less hindered by noise in the environment and they can be enhanced by visual cues to transmit more subtle meanings. Thus, discrete signals will have distinct, symbolic meanings whereas the meaning of graded signals depends on their intensity and contextual information.

Evidence as to whether crying evolved as a discrete or graded signal can be gleaned from examining the perceptual abilities of receivers. Discrete signals should be matched by perceptual mechanisms and responses in the receiver that are categorical (Marler, 1976). Listeners are adept at distinguishing between the cries of healthy and sick newborns, but are less adept at distinguishing between cry types. Studies have demonstrated that adults can discriminate between cries emitted under widely discrepant circumstances (e.g., birth and pain cries; Wasz-Hockert, Partanen, Vuorenkoski, Michelsson, & Valanne, 1964), but not more closely related ones (i.e., hunger vs. pain cries; Gustafson & Harris, 1990; Muller, Hollien, & Murray, 1974; Sherman, 1927). On the other hand, listeners are capable of making fine distinctions between cries of varying intensity level (Gustafson, Wood, & Green, 2000). For example, Porter, Miller, & Marshall (1986) recorded cries at various points during an unanesthetized circumcision as the procedure became progressively more intrusive and, presumably, more painful for the infant. Listeners correctly identified the cries associated with the most intrusive points in the procedure as most urgent. Likewise, Wolff (1969, 1987) reported that when he, as a participant observer in the home, played a previously recorded pain cry while an infant was napping, mothers responded frantically whereas they took their time to respond to played-back hunger cries. In sum, adult listeners easily distinguish between crying of varying intensity level, but are unable to discriminate between different cries elicited under different circumstances, such as hunger versus pain cries.

A multivariate analysis of the acoustic characteristics of cry types confirms that cries do not differ according to what caused them; instead, cries appear to differ in intensity based on the degree of discomfort experienced by the infant (Wasz-Hockert et al., 1968). Cry types only can be identified to the extent that they are related to differing levels of intensity of infant distress. Hunger cries left unattended eventually assume the acoustic characteristics of pain cries (Wolff, 1987), further supporting the inference that crying is graded along a continuum of intensity rather than a series of discrete signals for each cry-evoking situation. Like other graded signals that derive their meaning from both acoustic and nonacoustic cues, parents use contextual information (e.g., time last fed) to determine the cause of crying in the natural environment (Murray, 1979). The data indicate that infant crying is a graded rather than a discrete signal, which provides little information about the cause but a great deal of information about the severity of infant distress.

Is Infant Crying Honest or Manipulative?

Consistent with the view of crying as a graded signal, many Western parents ignore crying below a certain threshold level of intensity. One reason for the common Western practice of ignoring low-intensity crying is the widespread belief that infant crying, at least at times, is manipulative. The classical ethological view, which emphasized cooperation and the exchange of honest information in signal evolution, has been supplanted by an alternative view emphasizing the struggle between individuals with discrepant genetic interests (Dawkins & Krebs, 1978). According to this alternative view, natural selection favors actors who successfully manipulate the behavior of other individuals whether or not this is to the advantage of the manipulated individuals. At the same time, natural selection will work on reactors to make them resist manipulation if it is to their disadvantage, resulting in an evolutionary arms race between actors and reactors like that between predator and prey (Dawkins & Krebs, 1978). Thus, even signals between cooperating individuals with shared genetic interests and goals, like those between parents and offspring, may be vulnerable to deceit.

Given the fact that parents and offspring do not share identical genetic interests, parents benefit by allocating resources according to the need of their offspring whereas individual offspring benefit by misleading parents about their need and acquiring more resources than parents are selected to give (Trivers, 1974). Selection would favor infants who most effectively persuade their parents to invest in them and parents who are able to resist false or exaggerated demands. These competing selection pressures, however, would make wide-scale deception an evolutionarily unstable strategy because if a "lying" mutant arose and was propagated, the signal itself would fall into disuse when it no longer provided the receiver with useful information. The occasional use of deceit, however, cannot be ruled out (Johnstone, 1997). Therefore, the question of whether offspring distress signals are reliable indicators of infant condition remains relevant.

In general, if there is a physical link between a signal and some underlying aspect of the signaler's physical condition, then lying may be physically impossible (Johnstone, 1997). The link between neonatal condition and cry acoustics is well established (Furlow, 1997), suggesting that dishonesty is unlikely in early infancy due to physical limitations. Premature infants produce weak "cry attempts" and have trouble producing the full-blown cry of a healthy, full-term infant (Boukydis, 1985). In the first months of life, before locomotion becomes prominent, situations that generate crying produce proportionate physiological changes in heart rate and cortisol (Gunnar, 1999), also suggesting a tight linkage between physical condition and crying. As infants get older, however, crying and other distress-related behaviors often are dissociated from physiological indices of distress (e.g., Gunnar, Brodersen, Krueger, & Rigatuso, 1996). By the end of the first year, when infants are known to escalate or inhibit crying depending on their audience, the physical link between the infant's condition and behavior appears to have unraveled or at least to have loosened. And when an animal's choice of display is not or is no longer constrained by physical condition, we might expect selection to favor exaggeration.

Zahavi's (1975, 1977) handicap principle may explain why animals do not typically adopt exaggerated signals even when they are physically capable of doing so. The handicap principle asserts that only superior individuals can endure the fitness costs of elaborate displays. If an animal can endure the predation risk that comes with a conspicuous sexual display, for instance, it must be fit. In the case of begging or crying, signalers differ in the benefits they stand to gain by eliciting a response (i.e., need) rather than in their abilities to bear the cost of a display (i.e., quality; Godfray, 1991; Maynard Smith, 1991). According to this line of reasoning, only in truly hungry individuals would the benefits of being fed outweigh the costs of crying (Godfray, 1991). Experimental evidence supports the handicap principle: When hunger levels of magpie nestlings were experimentally manipulated through artificial feedings, the smallest and hungriest birds begged loudest (Redondo & Castro, 1992). The handicap principle would explain why infant crying from hunger becomes more intense with passing time, despite the increasing metabolic cost of producing the sound. Formal models also have provided support for the principle that signals can accurately reflect the quality or need of the signaler, provided they are costly (Maynard Smith, 1994).

While the handicap principle would predict reliable information most of the time, it does not preclude the possibility of occasional deceit, provided a signal remained, on average, honest (Johnstone, 1997; Johnstone & Grafen, 1993). In particular, if certain signalers find it cheaper than others to produce a certain signal for a given level of need than do other individuals, they will be able to produce a signal that exaggerates their need and thereby elicit more favorable responses than they would if their signal were a reliable and strictly honest indication of their need. So long as such individuals are rare enough and the disadvantage to receivers slight enough, such individuals and their occasional "cheating" would not disrupt the evolutionary equilibrium of the signaling system (Johnstone & Grafen, 1993). In keeping with this notion, older infants may find it easier to cheat than newborns since they can more easily bear the costs of crying and they are less dependent on and, consequently, stand to gain less from parental care. Provided tantrums are occasional, older infants may succeed in attaining more parental resources than they otherwise would have by exaggerating their distress. In fact, one recent hypothesis concerning excessive human infant crying posits that it may be a form of manipulation designed to stave off sibling competition by promoting and prolonging lactation and thereby increasing the interval between births (Lummaa, Vuorisalo, Barr, & Lehtonen, 1998). However, so long as crying remains a costly signal to produce (and we have every reason to believe it does), it usually will be a reliable indicator of infant need and only occasionally, most likely in older infants and children, be prone to exaggeration.

Crying in Other Mammals: Caching and Carrying Species

Other clues about the evolution and function of human crying come from examining crying in the broader context of caregiving behavior in other mammalian and primate species. Among terrestrial mammals, species can be divided into those with continuous contact between mother and infant (i.e., carrying species) and those with only intermittent contact (Blurton-Jones, 1972; Lozoff & Brittenham, 1979). In continuous contact or carrying species, the young are carried by, hibernate with, or follow the mother. In caching species, by contrast, the young are cached in secluded places or left in nests or burrows while the mother forages for food. Both caching and carrying are associated with distinct physiological and behavioral adaptations (Ben Shaul, 1962; Blurton-Jones, 1972), including patterns of crying. For example, in caching species, infants are adapted for widely spaced feedings; as a result, mothers' milk is higher in fat and protein content, infants suck faster, and feeding sessions are of shorter duration than in continuous feeders. Infants of caching species have mechanisms for independent thermoregulation and require maternal stimulation for elimination, so as not to advertise their position to predators with the odor of their urine or feces (Blurton-Jones, 1972). For similar reasons, crying in caching species would be expected to subside soon after the mother departs from the nest. The composition of human breast milk is identical in fat and protein content to that of continuous feeding apes; human infants suck slowly, and feeding sessions are comparatively long (Ben Shaul, 1962; Blurton-Jones, 1972). Additionally, human infants have poorly developed mechanisms for thermoregulation at birth and cry loudly and for long periods of time when separated from their mothers. Therefore, carrying and continuous feeding of young are not only characteristic of all nonhuman primates but there is overwhelming evidence that it was once characteristic of humans as well.

Among nonhuman primates, mother–infant dynamics are characterized by the expected pattern of almost constant carrying and continuous feeding. Infant crying because of hunger is rare because infant and mother are always together and the nipple is constantly available for nursing (Newman, 1985). In laboratory studies, only one situation reliably evokes crying in nonhuman primate infants—the physical separation of an infant from its mother. In the wild, an infant who is accidentally dropped or falls off its mother lets off a stream of sounds that provide the mother with the auditory cues necessary for retrieval. Crying is only heard from infants left behind, injured, or otherwise in need of assistance. In theses situations, the crying of nonhuman primate infants is described as closely resembling or indistinguishable from that of human infants (Fossey, 1972; van Lawick-Goodall, 1968). The similarity of patterns of crying across a wide range of primate species (Newman & Symmes, 1982) suggests that the mechanisms controlling infant crying have had a conservative evolutionary history and that they probably share a common function (Newman, 1985). The excessive amounts of human infant crying in comparison to other primates may be the result of infant caregiving habits in modern times that are markedly different than those to which human infants were adapted over the course of primate evolution.

Crying in Nonindustrialized Human Societies

Of course, generalization about the evolutionary history of crying and infant care from other species to humans must be qualified because of species differences. To gain an understanding of the characteristic human pattern of infant care and responses to crying, it is therefore helpful to examine human societies whose day-to-day circumstances most closely resemble those under which humans evolved. Because the mode of subsistence for 99% of the human species' 2- to 3-million-year history was hunting and gathering, data from the few surviving aboriginal foraging groups may provide the best available indication of the kind of care to which the human infant was originally adapted (DeVore & Konner, 1974). An examination of infant care among such groups reveals infant care patterns more consistent with our evolutionary history as a continuous contact, carrying species. Among the !Kung of Botswana, for example, infants are carried in a sling which offers constant contact and continuous feeding. Because infants are in constant contact, caregivers can detect subtle discomfort cues like fussing and whimpering and respond to them before full-blown crying occurs, and crying is met with universal and immediate maternal response (Konner 1972, 1976). Among this nonindustrialized population, in other words, crying and responses to it closely resemble those of nonhuman primates. Numerous studies have shown that the !Kung approach to infant care and crying is typical of other nonindustrialized, hunter-gatherer societies (e.g., Ainsworth, 1977; Brazelton, Robey, & Collier, 1969).

Compared to non-Western samples, infants reared in modern, Westernized cultures are rarely held and often are left to cry for long periods of time. Researchers report deliberate nonresponse to almost half of crying episodes in the first 3 months in U.S. samples (Bell & Ainsworth, 1972), and between 1 and 2 and 3/4 hr per day of crying for the newborn to 2-month-old infant is considered normal (Brazelton, 1962; Rebelsky & Black, 1972). Colic, excessive crying with no known organic basis, is a common affliction of infants, affecting 20 to 40% of infants in Western societies (Hewson, Oberklaid, & Menahem, 1987; Stahlberg, 1984). Given the metabolic costs involved in crying and the predation risk over the course of human evolution, this amount of crying is remarkable. A survey of infant care among nonhuman primate species and contemporary hunter-gatherer societies suggests that the amount and pattern of infant crying typical of modern Western societies like our own might be, evolutionarily speaking, a fairly recent phenomenon and the result of modern caregiving practices that limit physical contact between infants and caregivers, inhibit prompt responses to fussing, and exacerbate crying.

Summary

Infant vocal communication most likely evolved as a supplemental means of maintaining mother–infant contact under conditions where olfaction and vision alone were inadequate. Like other graded signals, crying is enhanced by contextual cues that convey information about the degree of infant distress. There is little evidence for discrete, symbolic meanings in cries, and cry types can only be distinguished to the extent that they correspond to varying levels of infant distress. The common practice in Western cultures of ignoring crying below a certain threshold of intensity because it is believed that crying is often "dishonest" is not supported by experimental evidence or formal models of animal communication. To the contrary, the fact that crying is costly to produce and, at least in early infancy, tightly linked to physical condition strongly suggests that it is typically an accurate reflection of infant distress and need for parental intervention. Finally, a survey of crying in nonhuman primate species and non-Western human societies provides evidence that rates of infant crying are far lower than in Western societies.

CONCLUSION

Western caregiving practices, such as relatively infrequent feeding and comparatively limited holding, may affect infant physiology in ways that promote crying. Although the survival value of infant crying is almost certainly that it tends to elicit caregiving, long bouts of high intensity, urgent crying may provoke caregiver avoidance or, worse, caregiver aggression. The reality that crying is an inherently aversive stimulus may account for the evolved tendency to selectively direct it toward the one or two individuals who are genetically motivated to respond positively. In addition to alerting a caregiver of the infant's need for care, crying conveys information about the infant's state and condition that guides decisions about what care to provide. Although it is commonly believed that babies sometimes "fake" crying, the potential costs are so great that crying is probably more often an accurate reflection of real need, particularly in early infancy. The fact that infant distress vocalizations while in contact with an adult caregiver are absent in other species and quite rare in nonindustrialized human societies suggests that its manifestation in Western, postindustrial cultures may represent a departure from the norm and a distortion of an evolved, otherwise adaptive, tendency. In turn, the unusually high rate of crying typical of Western cultures may have negative consequences for infant–parent bonding in general and, on rare occasions, even precipitate abuse.

The preceding ethological analysis of human infant crying has potentially important research as well as clinical implications. From a research perspective, we have yet to fully uncover the physiological mechanisms underlying crying. A more precise understanding of the physiological basis of crying may spawn new treatments for attachment and mood disorders. In addition, more work is needed documenting developmental changes in crying, including the effect of caregiver response on subsequent crying and on emotional expression. Changes in the acoustic features of crying over the course of early development should correspond meaningfully to the acquisition of developmental milestones such as walking and to environmental factors such as number of siblings. An appreciation of crying across species and cultures also would dictate a change in the way researchers conceptualize optimal parenting and sensitivity. Indeed, if human infants evolved mechanisms for acquiring maternal care similar to those of other continuous contact young, maternal (and parental) sensitivity may be better indexed by practices such as holding and frequent feeding that prevent crying than by traditional measures currently used in research such as responsiveness to crying. Practically speaking, if crying is a fairly reliable indicator of infant need and one that parents have evolved mechanisms for responding to, advising parents to ignore crying may be inappropriate and even harmful. Although pediatric advice has become more liberal and child-centered on the matter of responding to crying rather than ignoring it, there is still no shortage of manuals laying out behaviorist regimens for extinguishing crying and getting babies to sleep through the night (e.g., Ferber, 1985; Spock & Parker, 1998). While these methods may be successful, the repercussions for infants' emotional development and the development of the parent–child relationship have not been explored. Future research should examine these and other questions.

Tinbergen (1963) proposed four questions to guide the analysis of the biological bases of behavior: What are its causes, function(s), developmental course, and evolutionary history? In the present article, these questions were addressed from a multidisciplinary and broad phylogenetic perspective. Considering all four of Tinbergen's questions at once highlights the interrelations and "fuzzy" boundaries between them and also accentuates the manner in which each individual question informs the others. The present review incorporated findings from animal communication, cultural anthropology, signal design theory, and the neurobiology of emotion that rarely find their way into developmental psychologists' discussions of human infant crying. In my view, crossing traditional boundaries between disciplines and species has generated and will continue to generate new insights. I hope the present overview of empirical and theoretical work will culminate in a richer and more precise understanding of human infant crying.

NOTES

This article was initially conceived as a doctoral qualifying exam in the Department of Human

Development at Cornell University. I am indebted to Steve Robertson for initially suggesting the organizing framework of this article. I also thank Anne Scott Beller, Leslie Berkelhammer, Jeff Cynx, Cindy Hazan, Bob McAulay, Carolyn Palmer, Rick Thompson, and three anonymous reviewers for their feedback and comments on earlier versions.

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