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

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

NOTE

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## Infant vocalizations: Contrasts between crying and laughter

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

Crying, as noted by Soltis, is a potent, early appearing, species-typical human vocal signal that is uttered in a similar way by members of all cultures and vocal communities. The same can be said for laughing. In the following comparative treatment, I contrast similarities and differences between crying and laughing to better characterize each utterance and illuminate the general issue of innate vocal signaling. Unless otherwise noted, themes concerning crying are taken from the target article by Soltis; those about laughter are from Provine (2000).

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

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

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

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

Crying is an undeniably powerful stimulus that can evoke re-



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

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

## Crying and tears mimic the neonate

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

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

There are, however, several differences between the "begging" behavior of sparrows and humans crying. A sparrow will not show the "begging" behavior again once adult, but humans, by contrast, retain the capacity to cry throughout their lives. And several weeks or months after birth humans add a spectacular feature to their crying repertoire: *tears,* a word remarkably absent in Soltis' article. But Soltis does write (sect. 6.1, para. 2): "During the first three months of life, disagreements over the flow of resources should be lowest. As the period of investment proceeds, however, and the production of a new child becomes increasingly advantageous for the mother, then parent-offspring conflict should increase." If parent-offspring conflict indeed increases about three months after birth, and if the shedding of tears indeed emerges at around the same time, one cannot help but speculate about a causal relation.

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

> In many species of animals, the stimuli emitted by newborns bring about parental care. In fact, the newborns of many species require parental care. Because a newborn has little else to offer than its own appearance and behaviour, it is logical that it is exactly these factors that elicit the parental care.
>
> The crying behaviour of humans is favoured by natural selection because the behaviour resembles or causes resemblance to some of the stimuli emitted by newborns and, therefore, induces helping behaviour.

Some aspects of this resemblance are as follows:

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

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

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

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

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

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

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

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

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



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