Can reinforcement learning explain variation in early infant crying?

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

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

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

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

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

Infant colic: Re-evaluating the adaptive hypotheses

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

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

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

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

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

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

Similar to the other adaptive hypotheses, the manipulation hypothesis requires evidence that colic is effective in extracting additional parental investment. We are not sure about the quality of the data on this issue, but anecdotally, it is well known that parents of colicky infants often make extra efforts in holding and feeding them. Colicky infants may also receive additional medical care, as their parents often take them to the doctor. Soltis argues that the timing of colic is inconsistent with the manipulation hypothesis because "if the amount of infant crying reflects the degree of parent-offspring conflict over the length of investment, therefore, then it should start at low levels in early infancy, increase over the duration of investment, and peak at weaning, when conflict is at its greatest" (sect. 6.1, para. 3). In reality, parents and offspring may be in conflict over the amount of investment at any point in time before weaning, conflict can occur about different forms of parental expenditure, and infants can switch from one type of "weapon" to others as they develop (Trivers 1974). Early conflict may be specific to one form of parental expenditure (e.g., rate of breast-feeding) and expressed mostly through crying. Later on, conflict may involve other forms of parental expenditure (e.g., carrying) and additional behavioral and psychological tactics. Therefore, the temporal pattern of early crying is not necessarily incompatible with parent-offspring conflict theory. Soltis also argues that the sixth-week peak and the early evening peaks of colic are difficult to reconcile with the manipulation hypothesis. However, since the same crying peaks are also observed in non-colicky infants, they may simply represent neurobiological processes underlying the expression of early crying without any necessary implications for its adaptive function.

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

Infant crying in context

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

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

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

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