

Vocal Development: How Marmoset Infants Express Their Feelings

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A new study shows that vocal sequences produced by newborn marmoset monkeys are driven by slow fluctuations in physiological state; the results shed light on the evolution of vocal communication between newborns and parents.

When hearing a scream, a cry, or a laugh, one can often sense the details of the scenario, as if subjective experiences can somehow propagate through vocal sounds and ‘infect’ the listeners with similar feelings [1,2]. How can vocal sounds mirror the internal physiological state of an animal? In this issue of *Current Biology*, Zhang and Ghazanfar [3] report the first detailed investigation of how fluctuations in the state of the autonomic nervous system are ‘transferred’ into vocal sequences in newborn infant marmosets. These vocal sequences could potentially provide mothers with important information about the instantaneous needs of their infants.

How Did Expressive Vocal Communication Evolve?

Imagine a primitive gregarious animal which evolved a muscular constriction inside its tracheal passage. During breathing, a certain level of tightening of the constriction could cause the passage to vibrate and produce a sound, which could broadcast something about the animal’s internal state. Attending to the rate or quality of such vibration could allow these animals to continuously monitor their neighbors and detect if they are, for example, relaxed or excited. Further, if a predator abruptly swallowed one of them, the sudden silence would immediately alarm its neighbors. These cues could evolve into broadband vocal signals, such that the transfer function from physiological state to the acoustic features might carry ever richer information. As illustrated in Figure 1, in addition to broadcasting respiratory events, the vocal apparatus could evolve

the capacity to express respiratory pressure (via modulation of sound amplitude) or muscle tension (via modulation of pitch), and so on. Slow fluctuations in physiological states could then be encoded in vocal sequences.

In vocal learners such as songbirds [4–6] and humans [7], the cerebral forebrain directly controls vocal behavior. The level of cerebral control is thought to increase over development, and consequently, vocalizations become, to a large extent, independent of physiological state. Fine control by the cerebral cortex can give rise to complex and highly stereotyped vocal sequences [5], which carry information more efficiently. For example, with cerebral control, primitive alarm calls that mirror a ‘fight or flight’ autonomic state could be modified, accelerated, or even faked. In sum, one could imagine an early stage in evolution during which vocalization became increasingly more expressive of autonomic state, and a later stage during which vocal patterns were released from low-level physiology to become ‘cerebral’. Empirically, this can be assessed by measuring the degree of coupling between physiological state and vocal behavior, the subject of the Zhang and Ghazanfar paper [3].

Expressive Vocal Sequences in Marmoset Infants

The capacity to communicate physiological state is particularly important in mammalian newborns, who are totally dependent on maternal care, requiring mothers to be agile and attentive to the infant needs. In primates, mothers can be highly attentive to information

about the well being of their infants [8,9]. The Zhang and Ghazanfar [3] paper illuminates how this communication system might work by reporting two discoveries. First, the authors show that slow fluctuations in the autonomic nervous system (at a time scale of several seconds) affect respiratory rate and amplitude, which in turn modifies the acoustic features of calls, resulting in vocal sequences which can potentially encode and communicate even subtle changes in the internal state of the infant. And second, investigating the variability in vocal sequences across infants, they found highest similarity between dizygotic twins, lower between non-twin siblings, and lowest between unrelated marmoset infants.

Zhang and Ghazanfar [3] found that different vocal sequences were, to a large extent, driven by variability in the slow oscillations in autonomic nervous system state. Because the genetic distance between dizygotic twins and non-twin siblings should be similar, vocal sequences produced by the infant seem likely to have mirrored variability in maternal care and colony state. In the case of twins, maternal care and colony state should be similar, whereas in the case of non-twin siblings, the colony state might be different (potentially affecting maternal care), and in the case of non-siblings, yet further variability between mothers can be expected. It seems, therefore, likely that the marmoset infant ‘broadcasts’ its internal state to his mother via vocal sequences. It is possible, however, that other factors, including genetic variability, contribute to variability in vocal sequences.

Implications for Human Speech Development

As mentioned earlier, cerebral control should be expected to decrease the coupling between autonomic state and vocal features. In the primate lineage, humans appear to be an outlier, where cortical control of vocalization is very strong. A critical question is if, and to what extent, the results of Zhang and Ghazanfar [3] can be generalized to explain infant-to-parent communication in humans. We would like to emphasize that little or no empirical information exists to directly connect the new data on marmoset vocalization with vocal behavior and development in human infancy. The influence of autonomic state on vocal sequence similarities described for marmosets in the paper has never been evaluated in human infant vocalization.

In support of a possible connection, Zhang and Ghazanfar [3] cite a paper on human infant cry [10], reporting on quite different procedures and outcomes (not a twin study, not a study monitoring physiological state directly), and in our view this paper is only marginally relevant to the implied marmoset–human connection. Cry vocalizations of human infants would seem to be more comparable to pain or distress screams in other primates than to the vocalizations monitored by Zhang and Ghazanfar [3].

An alternative avenue would be a comparative study of marmoset vocalizations with the human infant ‘protophones’ — the non-cry speech-precursor vocalizations that occur at high frequency from the first days of human life, and reveal capabilities for spontaneous, exploratory vocalization [11,12]. Protophones become more differentiated and speech-like across development presumably as a result of endogenous vocal production as well as complex vocal interactions with caregivers in patterns that have never been reported for non-humans [12,13].

The Zhang and Ghazanfar [3] study should motivate students of infant vocal development to investigate the influence of autonomic state on vocal sequence patterning. Any attempt at straightforward demonstration will be complicated by the fact that human infants show massive

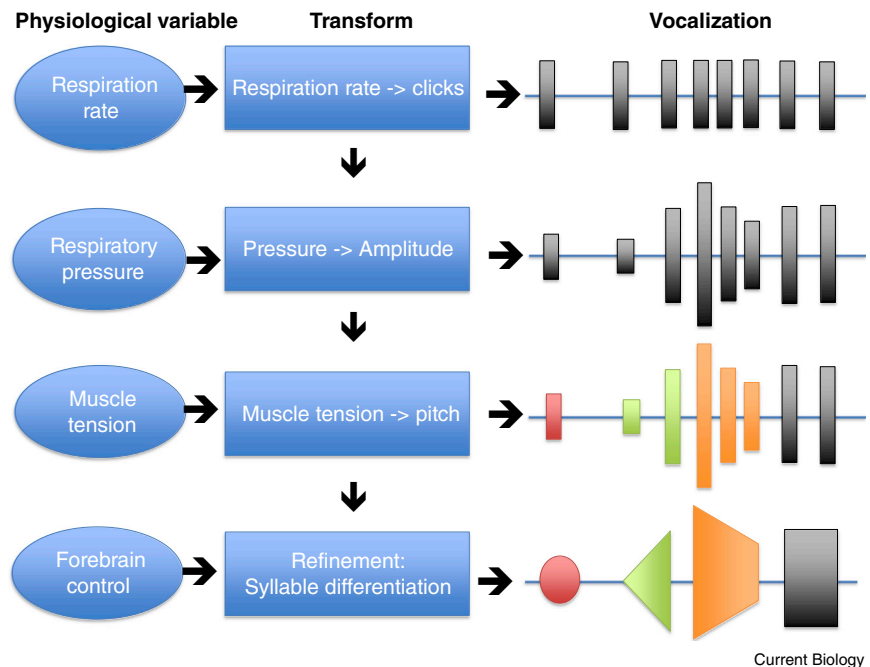


Figure 1. A hypothetical scenario for the evolution of vocal communication.

In a primitive animal, slow fluctuations in respiratory rate are mirrored in the rate of vocalization. As the channel evolves, additional physiological variables start affecting acoustic features until, eventually, fine forebrain control drives differentiation of syllable type, producing vocal sequences, which may carry rich information about behavioral state.

flexibility in how they express emotions with the protophones [14]. All the major protophone types (squeals, vocants, growls) occur on varying occasions with a full range of reliably discernible facial affect (from positive to neutral to negative) by at least three months of age [15], and presumably these expressions occur in varying autonomic states. Determining whether protophones show flexibility earlier in infant development, or alternatively that they are driven mostly by fluctuations in autonomic state, is critical for evaluating the extent to which the results of Zhang and Ghazanfar can be generalized to provide insights about newborn-to-parent communication in humans.

A comparison of human protophones and marmoset infant vocalizations will likely provide fascinating insights into the roles of autonomic state across development. Such comparative studies could aim at quantifying the flexibility of emotional expression across human and non-human primates. In non-human primates, flexibility of emotional expression for individual vocal categories has not yet been convincingly

demonstrated. As for studies of vocal development in human infants, one might say that Zhang and Ghazanfar [3] have thrown down the gauntlet to researchers in human infancy to begin to evaluate empirically the possible role of autonomic state in human infant vocalizations, both cries and several subcategories of protophones. And similarly, existing results from human infant vocal development challenge researchers in primatology to offer further evaluations of vocal development in non-humans. Vocal development in non-human primates should be compared more directly with the progression of flexible vocal expression and vocal interactivity that leads to speech in humans. In these ways we may be able to build on this intriguing new paper [3] toward more fully illuminating the foundations of human vocal expression in the primate lineage.

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Animal Evolution: Are Phyla Real?

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A recent study compares developmental gene expression among very distantly related animal species and interprets the results as providing biological justification for phyla. Several problems in the design and interpretation of the study call this conclusion into question.

The seeds of modern efforts to understand biodiversity were sewn by the botanist Carl Linnaeus [1]. He had the critical insight that the diversity of life is hierarchically nested in groups that are each characterized by particular suites of traits. Animals with hair (mammals), for example, are a nested subset of animals with four limbs (tetrapods). Tetrapods are a nested subset of animals with vertebrae (vertebrates). This remarkable insight is even more astonishing when one recognizes that it preceded, and in many ways enabled, the understanding that this diversity was produced through evolution by common descent [2]. Evolution explains the process that gives rise to this nested pattern — the traits that characterize more inclusive groups (e.g., the four limbs of tetrapods) evolved prior to the traits that

characterize more restricted groups (e.g., the hair of mammals).

Linnaeus sought to bring additional structure to his nested taxonomy. His work preceded the concept of phylogenies — evolutionary trees that describe the relationships between organisms — which now provide a mechanism-based framework for describing the nested structure of diversity. He therefore invented ranks — uniform levels of nesting that he applied across groups of organisms — to organize his understanding of diversity. The original ranks designated by Linnaeus were kingdom, class, order, genus and species [1], and others, including the phylum [3], have been added since. As phylogenies improve, some have called for the abandonment of ranks [4] to avoid implying that different clades given the same rank,

for instance the phyla Echinodermata and Mollusca, are somehow equivalent. Advocates for the continued use of ranks have argued that they are still useful organizational aids that help convey which clades are within others, but have emphasized that ranks do not reflect distinct biological patterns or processes and have called for others to stop trying to imbue them with biological significance [5]. Even so, it is still common in the literature, as exemplified by a new paper from Levin *et al.* [6], to treat ranks as a biological pattern to be explained rather than as a human-created organizational aid.

All living animals are now placed in about 35 animal phyla. For much of their history, the animal phyla have been the maximally inclusive groups of animals that were thought to be monophyletic (i.e., include all the descendants of their