

# A paradox in the evolution of primate vocal learning

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**The importance of auditory feedback in the development of spoken language in humans is striking. Paradoxically, although auditory-feedback-dependent vocal plasticity has been shown in a variety of taxonomic groups, there is little evidence that our nearest relatives – non-human primates – require auditory feedback for the development of species-typical vocal signals. Because of the apparent lack of developmental plasticity in the vocal production system, neuroscientists have largely ignored the neural mechanisms of non-human primate vocal production and perception. Recently, the absence of evidence for vocal plasticity from developmental studies has been contrasted with evidence for vocal plasticity in adults. We argue that this new evidence makes non-human primate vocal behavior an attractive model system for neurobiological analysis.**

A wide variety of observations and experiments show that the acoustic structure of non-human primate signals undergoes little modification during vocal development [1–3]. In sharp contrast, studies of adults have shown evidence for modification of acoustic features of vocal signals in a variety of contexts [4–6].

In this article, we aim to review the evidence on vocal learning in non-human primate infancy and adulthood, to motivate research at the neural level and to set the stage for a more thorough understanding of the evolution of this capacity in humans. We begin with a brief discussion of vocal learning in animals. We then review the literature on non-human primate vocal learning in development, and follow this with a discussion focused on adult data. We argue that non-human primates should provide the next frontier of exploration on the neurobiology of vocal plasticity: (i) because of the inherent interest in finding a model system that is taxonomically close to humans, and (ii) because the paradoxical comparative and developmental data raise interesting questions concerning underlying mechanisms, both peripherally and in the CNS.

The term ‘vocal learning’ has been used to describe a suite of disparate vocal behaviors. We have adopted the following distinctions [7,8]: (i) vocal comprehension learning occurs when the appropriate response to a vocalization is learned; (ii) vocal production learning arises when specific spectrotemporal features of a vocalization depend on specific auditory experiences; (iii) vocal usage learning arises when the social or ecological context in which the

call is used is learned. For example, when an infant learns that the word ‘apple’ refers to a round, red, edible fruit, vocal comprehension learning has occurred; when they learn how to say the word ‘apple’, vocal production learning has occurred; and when they learn that saying the word ‘apple’ will result in being given an apple, vocal usage learning has occurred. There is plentiful evidence for both usage and comprehension learning in non-human primates [8]. The case for vocal production learning, however, is much less clear.

Currently, the most successful model system for vocal production learning is the songbird, with many significant parallels to humans. For example, both groups require auditory experience with species-typical vocalizations during an early sensitive period in order to develop normal adult vocal behavior, and both exhibit greater vocal plasticity during development than in adulthood (although some songbirds retain vocal plasticity throughout life) [9]. Unlike human language acquisition, however, vocal production learning in songbirds is largely restricted to song – a vocalization that in most species is produced only by males. Increasingly convincing evidence suggests that vocal production learning does occur in non-human primate adults, in both sexes and in a wide variety of call types. This similarity to human language learning, combined with the closer taxonomic status of non-human primates to humans and the similarity of the basic perceptual and production apparatus [10], makes the study of non-human primate vocal production learning crucial to understanding the evolution of human language. We focus on the evidence for and against vocal production learning in non-human primate infants and adults.

## Vocal development

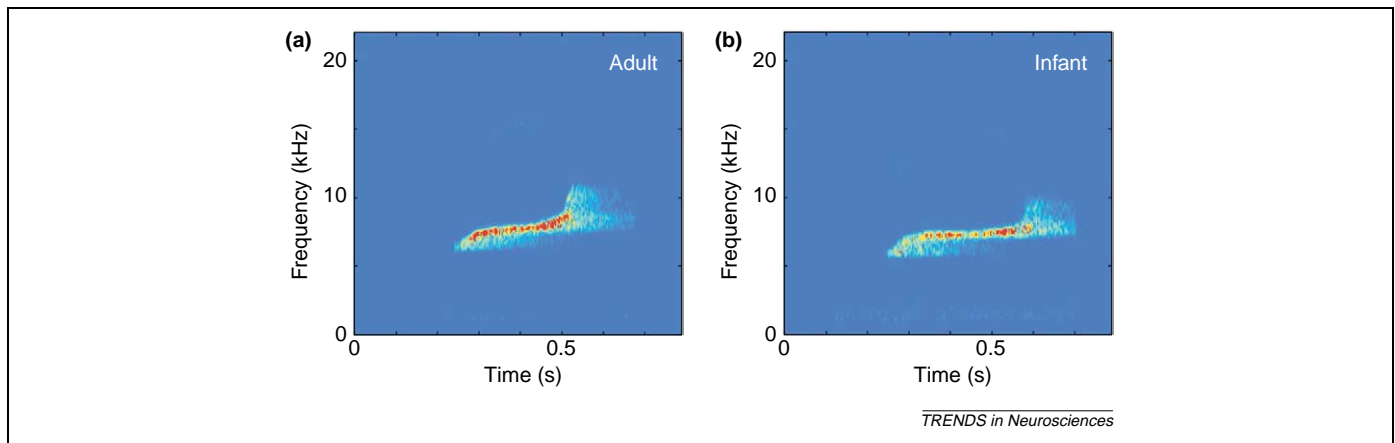
Primate vocal development has been studied in a variety of ways – by observing normal vocal development and by restricting auditory experience with species-typical vocalizations by deafening, isolation or cross-fostering.

## Normal vocal development

Some non-human primates produce vocalizations that are adult-like in structure as early as the first day of life [1]. Although such vocalizations might be produced in inappropriate contexts [11], the fact that their acoustic structure appears to be adult-like in the absence of significant auditory experience, suggests that there is little vocal production learning (Figure 1).

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**Figure 1.** Adult (a) and infant (b) squirrel monkey (*Saimiri sciureus*) isolation peeps. The isolation peep of an infant can be very similar to that of an adult. Early studies found that the isolation peep is one of the many non-human primate vocalizations that undergo little, if any, spectrotemporal modification during development [1].

Not all calls, however, are adult-like from birth. Changes in the acoustic structure of vocal signals during development have been found in a variety of species: pigtail macaques (*Macaca nemestrina*) [12], vervets (*Cercopithecus aethiops*) [2,13], pygmy marmosets (*Cebuella pygmaea*) [14] and squirrel monkeys (*Saimiri sciureus*) [15]. In a recent study on squirrel monkeys, Hammerschmidt and colleagues [16] showed acoustic changes in all 12 call types examined, including those shown by Winter and colleagues [17] to be adult-like from day one.

The presence of ontogenetic changes in acoustic structure is a prerequisite for vocal production learning, but not evidence for it. Modifications in call morphology might also result from maturational processes (e.g. as the vocal tract of the growing infant grows longer, it produces lower frequency sounds) rather than from vocal production learning [8]. To address definitively the importance of auditory input on the development of normal vocalizations, it is necessary to prevent experience with species-typical vocal signals. If vocal production learning is responsible for the observed changes in acoustic structure, the absence of a normal adult acoustic 'template' [18] will result in infant vocalizations that are abnormal in spectrotemporal structure, whereas if maturational processes are at work, manipulation of auditory feedback will have no effect.

### Social isolation

It is clear that social isolation can have strong effects on non-human primate vocal signals. Newman and Symmes [19] have shown that the vocalizations of isolate-reared rhesus macaques exhibit a variety of individually distinctive spectrotemporal abnormalities relative to controls.

Other early isolation experiments failed to find changes in vocal behavior [17,20,21]. These results have since been confirmed in more recent studies by Hammerschmidt and colleagues on vocal development in rhesus macaques and squirrel monkeys [16,22]. However, one early study [21] did note that 'nonspecific' vocalizations occurred more frequently in isolate-reared chimpanzees (*Pan troglodytes*) than in wild-born controls, and that these nonspecific vocalizations often accompanied stereotypical

movements. These stereotypical movements are symptomatic of the major problem in social isolation experiments: social isolation has negative effects on social behavior in general. It is possible, therefore, that vocal abnormalities observed in infants raised in isolation are the result of social isolation in general, rather than poverty of the acoustic environment in particular. One way around the problem of general social deprivation is to prevent exposure to species-typical vocalizations without interfering with normal social experience. This has been accomplished by deafening infants soon after birth.

### Deafening

Winter and colleagues [17] deafened one isolate-reared squirrel monkey infant. Analyses revealed no difference between the frequency and duration of isolation peeps and cackle calls of this infant and normal controls. Although Talmage-Riggs *et al.* [23] are widely cited as showing that deafening has no effect on vocal development [24,25], this study was in fact performed on adult animals, and therefore addresses the importance of auditory feedback for the maintenance, rather than the development, of vocal behavior. Roupe and colleagues [26] have recently deafened common marmoset (*Callithrix jacchus*) infants immediately after birth and tracked their vocal behavior to adulthood. They report that some infant-typical call types persisted into adulthood in the deafened animals, and that some adult call types displayed spectrotemporal abnormalities, suggesting, contrary to previous reports, the presence of auditory-feedback-mediated vocal production learning during development.

### Cross-fostering

A less invasive method for depriving an infant of species-typical acoustic input is cross-fostering, in which an infant of one species is raised by a mother of a different species. If auditory experience is crucial in shaping vocal production, then the cross-fostered infant should produce vocal signals that are more similar to its foster mother than its biological mother. Masataka and Fujita [27] have reported that cross-fostered rhesus macaque (*Macaca mulatta*) and Japanese macaque (*M. fuscata*) infants acquired an acoustic feature of the food coo of their foster mother,

suggesting that some vocal production learning might occur in these species. However, this study is problematic for two reasons. First, the findings have not been replicated by a more thorough cross-fostering study of the same two species [3]. Second, Owren and colleagues showed that the food calls of rhesus and Japanese macaques do not differ significantly in their acoustic morphologies. Therefore, an analysis of food calls in cross-fostered infant macaques cannot address the role of auditory experience in the production of species-typical vocal signals.

The general picture of non-human primate vocal development that emerges is one in which there is little vocal production learning. However, many of the studies have small sample sizes (in terms of individuals and vocalizations), sample only part of the repertoire (often only a single call type) or analyze only a small and simple set of spectrotemporal features. All of these features could reduce the probability of observing vocal plasticity.

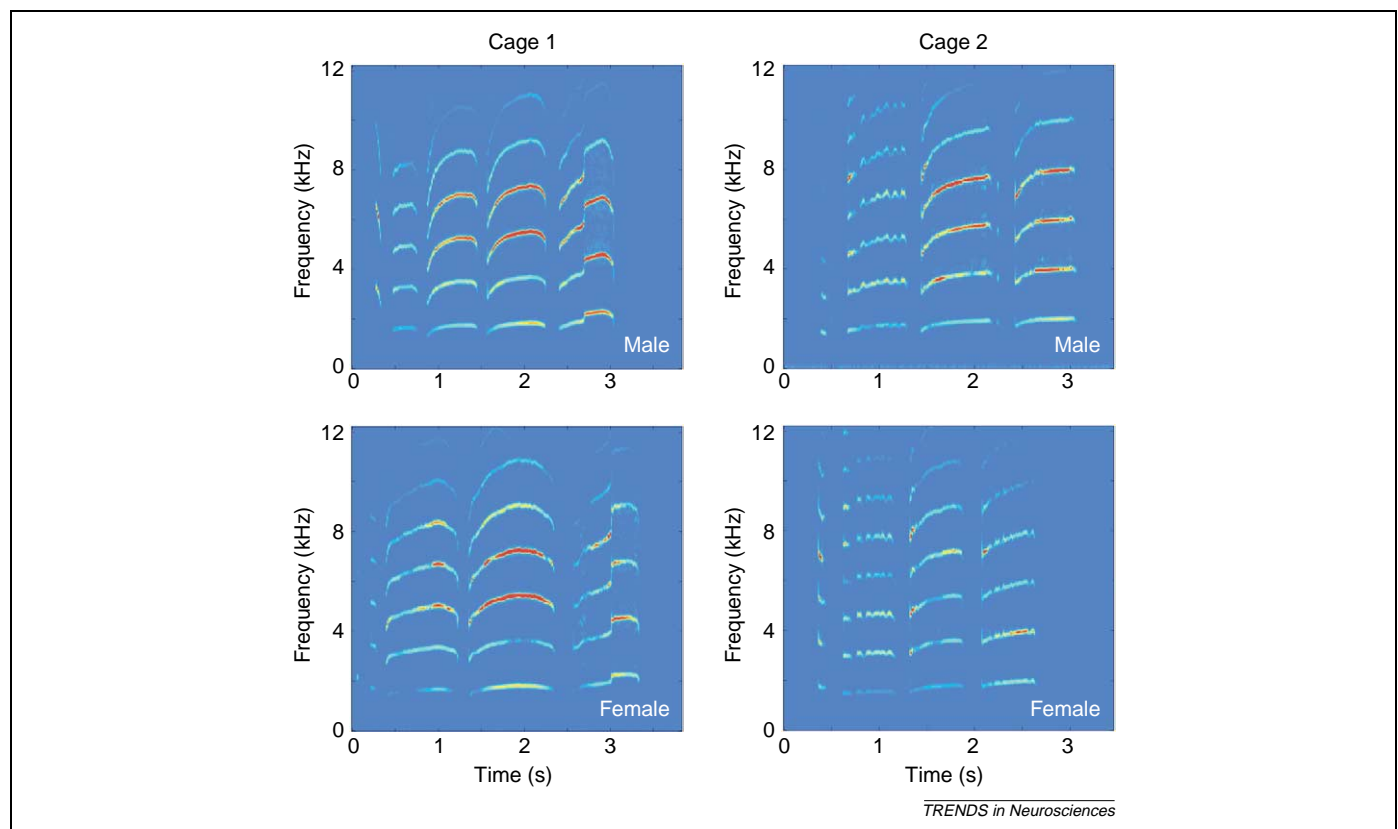
### Changes in vocal signals in adulthood

Contrary to the paucity of evidence for vocal plasticity in development, a wide variety of studies have presented evidence that adult vocalizations undergo modification as a function of social context. This evidence falls into two major categories: demonstration

of acoustic variation between social groups and observation of acoustic convergence.

#### 'Dialects': acoustic variation between social groups

Green [28] demonstrated a difference in the acoustic structure of 'coo' vocalizations elicited by provisioning in three geographically distant populations of Japanese macaques. Gouzoules and Gouzoules [12] examined recruitment screams from pigtail macaques and found matriline-specific acoustic features, which they referred to as a 'matrilineal signature'. Hauser [29] also found evidence for a matrilineal signature in the coo vocalizations of rhesus macaques. Further insight into these matrilineal dialects came from observations of a particularly distinctive coo variant in the same study area [30]. Female members of one matriline produced a coo vocalization that sounded 'nasal' to human listeners. The possibility of a learned component in this matrilineal dialect came from observing the pattern of expression of this coo variant – two females that had migrated out of the matriline did not show the acoustically distinctive signature, and an additional female reduced the frequency of production of the distinctive coo variant after emigration. Acoustic variation has also been observed in several studies of wild chimpanzee pant hoots [31,32]. Mitani and colleagues [31] recorded two geographically distinct populations, compared a variety of acoustic features and showed that there were significant acoustic differences



**Figure 2.** Home-cage 'dialect' in cotton-top tamarins (*Saguinus oedipus*). All calls are combination long calls produced spontaneously in isolation by the reproductively active male (upper two panels) and female (lower two panels) members of two different social groups (left panels versus right panels). Mated pairs are unrelated. Although basic structure (a short downward frequency-modulated sweep followed by three or four longer syllables) is conserved across cages, there are similarities in fine spectrotemporal structure within cages.

between the two groups. This observation has been confirmed and extended by Crockford and colleagues [32].

Differences in the acoustic properties of vocalizations have also been shown between captive groups in: Barbary macaques (*M. sylvanus*) [33], chimpanzees [34], cotton-top tamarins (*Saguinus oedipus*) [35] (Figure 2), Wied's black tufted-ear marmosets (*Callithrix kuhlii*) [36] and mouse lemurs (*Microcebus murinus*) [37].

The observation of acoustic differences between social groups is consistent with vocal plasticity and is clearly a prerequisite. It is not, however, diagnostic, as many studies have shown that such differences can have a genetic basis [38]. Most of the studies cited are unlikely to have a genetic basis because vocal behavior was predicted by current group membership or social context, rather than by genetic relatedness. For example, in Weiss and colleagues' [35] study of tamarins, although the breeding adult males in two family groups were dizygotic twins, their acoustic signatures were less like each other than like the members of their respective cage groups. Marshall and colleagues [34] also stated that the acoustic similarity they observed in call structure was unlikely to have a genetic basis, as the males with similar calls within each facility were unrelated. Zimmermann and Hafen [37] attempted to address the genetic confound more directly through DNA fingerprinting; they state that the acoustic variation between the colonies can be only partly explained by the genetic variation. However, because we know very little about how genetics informs the development and expression of acoustic structure, it is difficult to rule out a genetic basis for this acoustic variation.

### Acoustic convergence

Although group-level similarity in acoustics might be evidence for vocal learning, it is difficult to rule out genetic factors. This is not the case if convergence of

acoustic features is observed in the vocalizations of unrelated individuals.

Mitani and Gros-Louis [39] investigated the acoustic structure of pant hoots in a pair of free-living chimpanzees that chorused together. They showed that the calls of both members of this dyad were more similar to each other when they were chorusing together than when they were chorusing with other individuals. Sugiura [5] has shown that free-living female Japanese macaques match the acoustic features of response 'coo' vocalizations to the eliciting stimulus 'coo'. Both observations suggest that the subjects are matching their vocal behavior to that of a conspecific on a short timescale.

Vocal convergence can also occur over longer timescales. Marshall and colleagues [34] have described the presence of a spectrally distinct syllable (the 'Bronx cheer variant') in the pant hoots of males in a captive colony of chimpanzees. This distinct syllable was introduced to the colony by a single individual. Snowdon and Elowson [6] have also shown that the trill vocalizations of pygmy marmosets converged in acoustic structure following pairing.

Spectral and temporal changes have been observed in every major primate group, in both sexes, and in a wide variety of call types: from sexual advertisement calls [37] to contact calls [35] to alarm vocalizations [33]. This plasticity appears to be restricted to subtle changes within call types, rather than apply to the generation of novel calls. Results of studies of vocal production learning in infants and adults are summarized in Table 1.

### Concluding remarks

Early researchers were looking for the kind of large-scale dependence of overall vocal repertoire structure on species-typical auditory experience that characterizes

**Table 1. Studies investigating vocal production learning**

Method	Learning observed (Refs)	No learning observed (Refs)	Caveats
<b>Infant studies</b>			
Prevent auditory experience by deafening, muting social partners and social isolation	[17,23]	[15,18,19]	(i) Some auditory experience might be necessary for vocal development, even if there is no production learning (permissive rather than instructive) (ii) Social isolation might produce social abnormalities that are expressed as vocal deficits but are not specific to auditory experience
Cross-foster infants between species with different vocal behavior	[24]	[3]	The vocal repertoire of the two species must be sufficiently different that changes, or the lack thereof, can be detected
<b>Adult studies</b>			
Compare the spectrotemporal features of two conspecific groups	[10,25,26,28-31]	Not applicable	(i) Genetic factors (especially founder effects) (ii) Social factors: differential selective reinforcement by conspecifics; differential selective reinforcement by human caretakers or providers (iii) Environmental factors: differences in habitat acoustics or demands; differences in stress level or motivation
Determine whether the vocalizations of two individuals converge to a common acoustic form	[5,6,31,35]	Not applicable	As above

humans and songbirds. Experiments and observations over the past 30 years have shown that this does not occur in non-human primates. However, as more recent data are beginning to show, subtle modification of a fixed template occurs in a wide variety of call types in every major primate group. This increases the expressive potential of a vocal communication system, and it might be crucial for advertising and maintaining social group membership, commitment to a current alliance or indicating receipt of distant calls. Although it is clear from numerous studies that such spectrotemporal changes occur in the vocalizations of adult non-human primates, evidence for such changes during vocal development is mixed. Some studies have shown changes in vocal production that are unlikely to result from purely maturational processes [26], but others have failed to show such changes [16,22]. An important unanswered question for the field of non-human primate vocal communication is the extent to which the variation in observed vocal plasticity during development results from methodological differences or reflects a true difference in the vocal abilities of different non-human primates. Regardless, it is clear that the case for vocal plasticity in adulthood is significantly stronger than that for developmental vocal plasticity. This is surprising, given that the opposite pattern holds for humans and most songbirds: vocal plasticity is stronger during development than in adulthood. One explanation for this paradoxical observation is that subtle spectrotemporal changes occur at all ages but are simply more difficult to detect in variable juvenile vocalizations. Another possibility, which has been suggested previously [8], is that much of the developmental work showing an absence of vocal production learning was carried out before the widespread availability of sophisticated data collection and analysis techniques. By contrast, much of the work showing adult vocal plasticity is more recent and has, therefore, taken advantage of these methods. However, the replication of the early developmental results using modern methods by Hammerschmidt and colleagues [16,22] makes this unlikely. Another, more intriguing, possibility is that vocal plasticity is actually confined to adulthood in non-human primates. Neurobiological investigation of the mechanisms underlying vocal production learning provides an ideal insight into this possibility.

#### Box 1. Questions for future research

- The various acoustic modifications observed in adult vocalizations occur at a variety of timescales, from seconds to weeks. Are these changes governed by multiple mechanisms or do they reflect the activity of a single general-purpose vocal production learning ability?
- Given that the basic structure of non-human primate vocal signals appears to be innately determined, whereas the fine spectrotemporal features can be modified based on auditory experience, how are these innate and learned components integrated in the CNS?
- Social context has been shown to modulate the acoustic morphology of non-human primate vocalizations. What neural pathways are responsible for this modulation?

#### Neural basis of vocal control in non-human primates

Various studies have implicated anterior cingulate cortex, the supplemental motor area, motor cortex and the cerebellum, as well as many subcortical structures (notably the periaqueductal gray), in vocal control in non-human primates [40–47]. The results of these studies have often been contradictory. For example, cerebellar lesions can change the pitch, duration and intensity of rhesus macaque vocalizations [47] but have no effect on the acoustic structure of squirrel monkey vocalizations [42]. Similarly, although bilateral anterior cingulate lesions eliminate both conditioned and spontaneous vocalizations in rhesus macaques [40], such lesions in squirrel monkeys eliminate only spontaneous vocalizations and spare vocal responses to the calls of conspecifics [44,46]. Of particular interest is the contrast in reports on the involvement of Broca's area and facial motor cortex. Lesions to these structures in humans produce severe speech production deficits, whereas lesions to their homologs do not produce similar deficits in vocal production in monkeys [40,41]. However, cerebellar lesions that disrupt field potentials in the Broca's area homolog can change the spectrotemporal structure of vocalizations in Japanese macaques [45]. What is responsible for this variability? One likely candidate is the variability in the methods used to elicit vocalizations, which have included operant conditioning, exposure to predator models, restraint, feeding and electrical stimulation.

If, as appears to be the case, vocal plasticity in non-human primates consists of a subtle acoustic change on top of an innately determined call structure, then the tendency of researchers to average calls across social situations and individuals might mask structural differences. When researchers have carefully controlled the social situation and identified individual callers, distinct acoustic differences in calls have often been noted, even in the early literature [48]. We believe the study of the neural basis of vocal control can benefit from similar attendance to individual identity, social situation and the fine spectrotemporal features of vocalizations. This is already beginning to be demonstrated: recent work has shown distinct differences between the neural control of spontaneous versus elicited vocalizations [49], and between self-produced vocalizations and the vocalizations of other conspecifics [50]. Given the importance of social situation in eliciting vocal behavior, investigation of the neural basis of non-human primate vocal behavior will benefit enormously from new advances in experimental methods – notably functional magnetic resonance imaging and telemetered, chronic, multi-electrode recording [51] – that allow neural recording in awake, freely behaving animals. Based on behavioral data from a wide range of species, we believe productive avenues of research exist in three areas (Box 1): (i) determining the effect of social context on vocal control, (ii) elucidating the mechanism(s) involved in vocal production learning and (iii) investigating how the innate mechanisms for learning constrain the nature of experientially plastic vocal behavior.

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