

Constraints and flexibility during vocal development: insights from marmoset monkeys

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Human vocal development is typically conceived as a sequence of two processes — an early maturation phase where vocal sounds change as a function of body growth ('constraints') followed by a period during which social experience can influence vocal sound production ('flexibility'). However, studies of other behaviors (e.g., locomotion) reveal that growth and experience are interactive throughout development. As it turns out, vocal development is not exceptional; it is also the on-going result of the interplay between an infant's growing biological system of production (the body and the nervous system) and experience with caregivers. Here, we review work on developing marmoset monkeys — a species that exhibits strikingly similar vocal developmental processes to those of prelinguistic human infants — that demonstrates how constraints and flexibility are parallel and interactive processes.

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Introduction

In human infants, much attention has been focused on the babbling period, where spontaneous streams of well-formed consonant-vowel syllables are the scaffold for simple words. While important, it is often overlooked that babbling is itself the culmination of the complex processes that make up prelinguistic vocal development. Early vocalizations, like cries, laughter, fussing, and cooing, are the infrastructure for babbling [1]. From a purely acoustic perspective, the increase in complexity from early to later vocalizations is continuous [2], and feedback

from caregivers is an instrumental driving force that can influence the maturation rate of prelinguistic vocalizations [3]. For example, the volubility of infants is influenced by social context [4], and caregivers who contingently respond to infant vocalizations spur the development of more complex vocalizations from those infants [5,6**]. Importantly, during prelinguistic vocal development, there is also growth of the vocal apparatus (the larynx, the vocal tract, and lungs) [7–9] (Figure 1a).

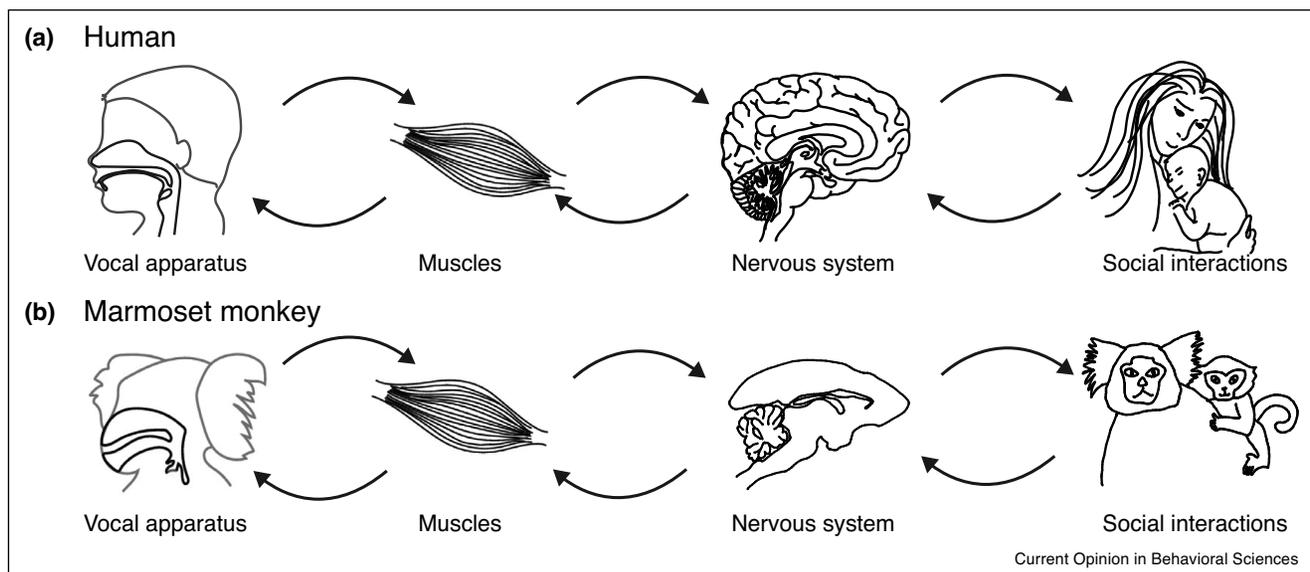
Models of vocal development that focus solely on the neural bases of learning often ignore these latter constraints. In order to understand the mechanisms underlying these parallel and interactive vocal developmental processes of growth and experience, we need an animal model system that shares these features with human development.

The marmoset monkey model system

Marmoset monkeys are a New World primate species and are cooperative breeders. Both parents, as well as older siblings and non-kin, will help care for offspring. This type of behavior is very rare among primates: only humans and members of the taxonomic group that includes marmosets (the Callitrichid family) exhibit this cooperative reproductive strategy. Thus, in terms of comparative developmental studies among human and nonhuman primates, marmoset monkeys (and other members of the callitrichid family) are a more compelling model system than the phylogenetically closer, but socially dissimilar, Old World apes and monkeys [10]. These cooperative breeding behaviors by humans and marmosets pave the way for more general prosocial cognitive processes [11,12], including those related to vocal communication [13].

Especially when compared to Old World primates like macaques, marmoset monkeys are quite agile in their vocal output. They and other closely related species readily adjust the timing of their contact calls to the timing of conspecific calls [14–16]; they also cooperatively modify the amplitude of their calls during vocal exchanges in accord with the perceived distance from conspecifics [17]. Marmosets also take turns when they vocalize, exhibiting contingent and repeated exchanges of vocalizations between any two individuals — related or unrelated — for an extended period of time (a behavior distinct from simple call-and-response behaviors observed among mates or competitors in other vertebrate species) [16]. Thus, while other nonhuman primates may

Figure 1



Vocal development in both humans (a) and marmoset monkeys (b) is an on-going, interactive process between the developing body, nervous system and social experience. One cannot 'explain' any aspect of vocal development without accounting for this interplay.

exhibit call-and-response behaviors with mates or specific group members (e.g., gibbons [18]; squirrel monkeys [19]; capuchins: [20]), this is not the same as turn-taking. Turn-taking is an on-going interaction with any conspecific involving multiple bouts of call-and-response exchanges. The turn-taking behavior by marmosets has the same coupled oscillator properties as human conversational turn-taking (but on a different time scale) [21,22]. In humans, this turn-taking behavior serves as a learning mechanism during prelinguistic vocal development: parents provide contingent responses to their offspring to spur the development of an infant's vocalizations [5,6^{**}]. As we will describe below, marmoset monkeys have also adopted this social reinforcement strategy during their vocal development.

Vocal development in marmoset monkeys

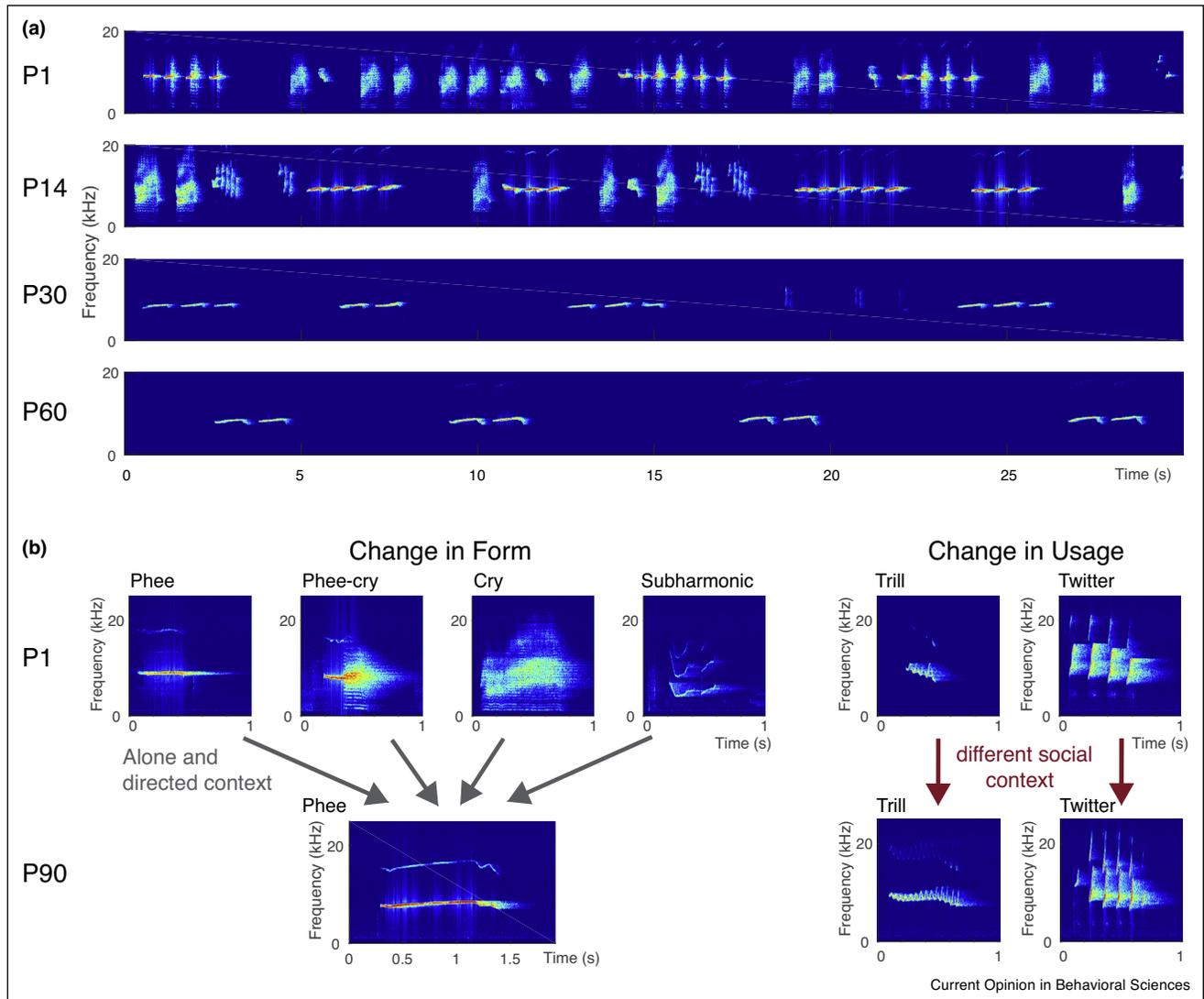
Contrary to what is known so far for other nonhuman primates [23], marmoset infants exhibit vocal learning in the first few months of postnatal life [24–26]. Similar to human infants [1,27] and juvenile songbirds [28^{*}], infant marmosets produce bouts of mature ('twitters', 'trills', and the contact call 'phee') and immature ('cries', 'subharmonic phee', 'phee-cries') vocalizations [24,25]. By two months of age, however, they only produce the appropriate contact calls ('phee') in both the undirected (alone) and directed contexts (vocally interacting with an out-of-sight conspecific) (Figure 2a). This suggests that two different vocal learning processes are at work: change in usage [26,29] and transformation of immature calls into mature versions [25] (Figure 2b). Twitters and trills are

frequently produced by marmosets of all ages [30,31], but in adults they are typically produced when in visual contact with conspecifics and not in the undirected context. Thus, twitters and trills undergo a change in usage. It is worth noting, however, that this process has not been systematically and quantitatively examined in marmosets of any age and thus no specific pattern of vocal ontogeny for these calls have been identified.

Conversely, cries, phee-cries and subharmonic-phees are only produced by infants and are immature versions of the contact call [24,25]. Like the vocal transformations observed in preverbal human infants [2,32] and songbirds [28^{*}], these immature calls eventually become mature-sounding contact calls [24,25]. Measurements of several acoustic features [28^{*}] — duration, dominant frequency, amplitude modulation (AM) frequency, and Wiener entropy (a measure of noisiness) — revealed that marmoset monkeys go through this vocal transformation of their contact calls within their first two months of postnatal life [25]. During this time, contact calls lengthen in duration, decrease in dominant and AM frequencies, and decrease in entropy (i.e., they get more tonal).

Infants, in general, experience massive changes to their body morphology. Human infants, for example, double in weight within the first six months of their life (Center For Disease Control Data, USA); infant marmosets double their weight in about one month [25]. As the infants grow generally, so too do their vocal folds. Bigger vocal folds tend to oscillate slower leading to the

Figure 2



Infant marmoset vocalizations undergo dramatic acoustic changes. **(a)** Spectrograms of the vocalizations from one infant over two months of postnatal development. **(b)** Cries, phee-cries, and subharmonic-pees transform into mature contact calls whereas trills and twitters undergo a change in usage.

production of lower frequency vocalizations. Concurrently, the vocal tract (the mouth and nasal cavities) is lengthening, changing its resonance properties and affecting which frequency bands are amplified relative others in vocalizations [33,34^{*}]. Can these growth related changes account for the developmental trajectory of marmoset contact calls (as measured by the four acoustic parameters)? A comparison of the body weight curve of marmoset infants with the trajectory of acoustic change revealed that growth could explain a portion of the change in each acoustic parameter but none in its entirety [25]. Thus, growth constraints are important to marmoset vocal development, but are not the complete story.

Turn-taking as the developmental system upon which infant marmoset vocalizations are learned

The timing of when immature contact calls transform into mature-sounding versions is also influenced by how often parents provide contingent vocal feedback to those infant calls [25,35^{**}]. 'Contingent feedback' consists of those calls produced by marmoset parents that follow their infant's vocalization by a few seconds (similar to the contingent turn-taking pattern used by two adult marmosets during vocal exchanges). Parent-infant vocal interactions in marmosets recorded and quantified in the directed context (where infants and their mother or father were in auditory, but not visual, contact) revealed that the

timing of the transition varied substantially across infants (~10 to 40 days) [25]. A parental influence to account for this variability could be via the number of adult vocalizations the infant has heard (an exposure account) or via the number of contingent responses from parents. The latter turned out to be the case: the number of contingent vocal responses from parents correlated with the timing of the infants' phee-cry transition [25].

These data suggest that developing marmoset monkeys — unlike every other nonhuman primate investigated thus far — may be vocal learners [36]. However, a viable alternative hypothesis is that marmoset parents are simply responding more to healthier infants who develop their vocalizations more quickly than others. To address this, an experiment was performed to explicitly test whether or not the amount of contingent vocal feedback can accelerate the rate at which marmoset infants begin producing mature-sounding contact calls [35**]. Since marmoset monkeys typically give birth to dizygotic twins [37], the influence of genetics and the perinatal environment on vocal development could be controlled for. Starting from the first postnatal day to two months of age, randomly assigned infants were provided different levels of contingent feedback using closed-loop, computer-driven playbacks of parental contact calls. Twins who received high levels of contingent feedback learned to produce mature-sounding contact calls faster than their twin receiving low feedback [35**]. These results unequivocally demonstrate that infant marmoset monkeys use social experience to learn how to produce their vocalizations.

While these data demonstrate that marmoset monkeys learn how to produce their contact calls via contingent feedback from parents, the study did not address whether there are any long-term consequences to more or less parental contact. To put it another way, it seems that while parental feedback could influence the rate of vocal development, all infants would eventually be able to produce normal vocal output (even if they had no feedback at all). This is the case for babbling in human infants — even deaf infants babble, but do so with a substantial developmental delay [38]. In marmoset monkeys, however, an investigation of the vocal output of two sets of offspring from the same parents — one set normally-reared, the other separated from parents — revealed that parental contact of some form is necessary for normal vocal development in marmosets [39**]. In contrast to normally-reared monkeys, marmosets with limited parental contact, and who were now over a year old (the developmental equivalent of a 12-year old human), still produced infant-like specific vocal behaviors [39**].

Vocal production is demanding, eliciting high metabolic costs [40]. In marmoset monkeys, mature contact call production is particularly energetically-demanding, as it

requires high tension of the vocal folds and strong and sustained respiratory power to produce long, multi-syllabic, loud, and tonal vocalizations [34*]. The data show that, as in humans, changes in bodily growth shape the acoustic change in developing vocalizations, and these acoustic changes, in turn, shape the communicative experience marmoset infants have with their parents (Figure 1b).

How does cooperative breeding relate to vocal learning?

In the evolution of human communication, a key transition occurred when humans began to interact cooperatively [41]. Care of infants is probably the most important context in which cooperation with unrelated individuals occurs, and there is a strong correlation between the reproductive success of mothers and the amount of infant care provided by others [42]. When caregiver attention is a limited resource, and when non-maternal caregivers may have higher threshold than mothers to provide care, evolution may select for vocal behaviors that help infants attract attention [43]. Babbling and other infant vocalizations attract caregivers and trigger contingent responses from them. It is been suggested that infant babbling evolved to exploit auditory predispositions in adult receivers [44]. The fact that parents of both human and marmoset infants are more likely to give contingent responses to infant vocalizations when those vocalizations sound more adult-like is consistent with this 'receiver predisposition' idea [45,46]. This suggests that a vocal learning mechanism may have evolved to speed up the production of mature-sounding vocalizations (i.e., those that exploit the receiver predispositions) using social feedback because such vocalizations are more likely to elicit caregiver attention.

An integrated account of flexibility and constraints during vocal development

Given that vocal development is a systems phenomenon, its understanding requires consideration at many levels: from the vocal apparatus and its many associated muscles to the nervous system and the differential sensory feedback from environmental and social interactions (Figure 1a,b). Each element modifies both itself and others over time [47]. To capture such adaptive coordination, theoretical methods can be used to place these phenomena in a quantitative framework. Data from developing marmoset monkeys combined with optimal control theory were used to generate a developmental landscape based on the Waddington metaphor [48]. The model progressively adds one factor (such as the biomechanics of the vocal apparatus) and infers what aspects of the behavior can or cannot be explained before adding another factor (e.g., the strengthening of the musculature). This approach underscores the fact that the nervous system and its interplay with experience does not function in isolation; they must typically process sensory data

and communicate with the developing body to generate appropriate behaviors. The resulting coupling with changing morphology and other physiological systems both constrains and enables the adaptive behaviors that such neural circuits can produce [49,50].

Conflict of interest statement

Nothing declared.

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This experimental study unequivocally demonstrates vocal production learning in infant nonhuman primates. It controls for genetics by using dizygotic twins and also shows that different acoustic parameters are more or less susceptible to contingent feedback from parents. This has the potential to better illuminate the underlying learning mechanisms.

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