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The role of auditory feedback on vocal pattern generation in marmoset monkeys

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Marmoset monkeys are known for their rich vocal repertoire. However, the underlying call production mechanisms remain unclear. By showing that marmoset monkeys are capable of interrupting and modulating ongoing vocalizations, recent studies in marmoset monkeys challenged the decades-old concepts of primate vocal pattern generation that suggested that monkey calls consist of one discrete call pattern. The current article will present a revised version of the brainstem vocal pattern-generating network in marmoset monkeys that is capable of responding to perturbing auditory stimuli with rapid modulatory changes of the acoustic call structure during ongoing calls. These audio-vocal integration processes might potentially happen at both the cortical and subcortical brain level.

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Introduction

The evolution of the human speech and language system is one of the most difficult and controversial biological questions to answer, mainly because human speech considerably surpasses primate vocal communication systems in scope and flexibility with seemingly no counterpart in the animal kingdom, even among hominids [1,2,3]. While human speech is above all a learned vocal pattern [4], the vocal repertoire of our closest relatives, non-human primates, consists mainly of stereotyped and largely innate calls that are uttered affectively in most contexts [3,5–7]. These assumptions were primarily supported by previous studies showing that monkeys that were deaf-born or deafened [8], raised in social isolation [8], or cross-fostered [9] developed the full adult species-

specific call repertoire with only minor differences in call structure from the vocal utterances of their normally raised conspecifics. Furthermore, specific call features, such as duration and frequency, remain surprisingly robust and stable in adult monkeys, resulting in rather stereotyped and discrete call patterns [10]. For example, behavioral experiments have shown that monkeys can stop sequences of calls immediately after acoustic perturbation, but cannot interrupt the acoustic structure of ongoing vocalizations [11,12]. These findings suggested that calls consist of single discrete pulses [11,12] and that the vocal motor plan is already present before vocal onset [13]. In accordance with neurophysiological and anatomical studies, these vocalizations were found to be produced by a vocal pattern-generating network (VPGN) situated in the brainstem [2,6,14] that is capable of producing rather fixed, inflexible, and discrete utterances.

In the last few years, however, a number of studies have observed several types of vocal flexibility allowing monkeys to cognitively control when [15,16], where [17], and what to vocalize [18–20]. In addition, it has been revealed that marmoset monkeys are able to modulate call patterns during ongoing calls in response to perturbing acoustic feedback [21,22,23,24]. These findings challenge previous assumptions that monkey vocalizations are discrete and inflexible patterns and question the idea of a VPGN that produces fixed-action vocal patterns.

In the present article, I will first review recent neuroethological insights suggesting that monkeys exhibit distinct types of vocal flexibility enabling them to modulate the acoustic structure in ongoing calls in response to acoustic perturbation. I will also introduce the VPGN as it has been thought to be until recently. Taking into consideration recent neurophysiological and neuroethological findings, I will then propose necessary alterations to the VPGN that can explain how it might be capable of generating the observed changes in call structure and present a revised version of the VPGN. Finally, I will summarize the potential cortical and subcortical brain levels at which the auditory system and the vocal motor network might interfere to exhibit the observed modulatory effects during ongoing calls.

Rapid vocal flexibility in response to perturbing auditory feedback

Very recently, several labs were able to reveal that monkeys are capable of modulating ongoing vocalizations rapidly after perturbing auditory feedback [21,22,23,24]. These

findings challenged the decades-old concepts of primate vocal pattern generation, indicating that vocalizations do not consist of one discrete call pattern.

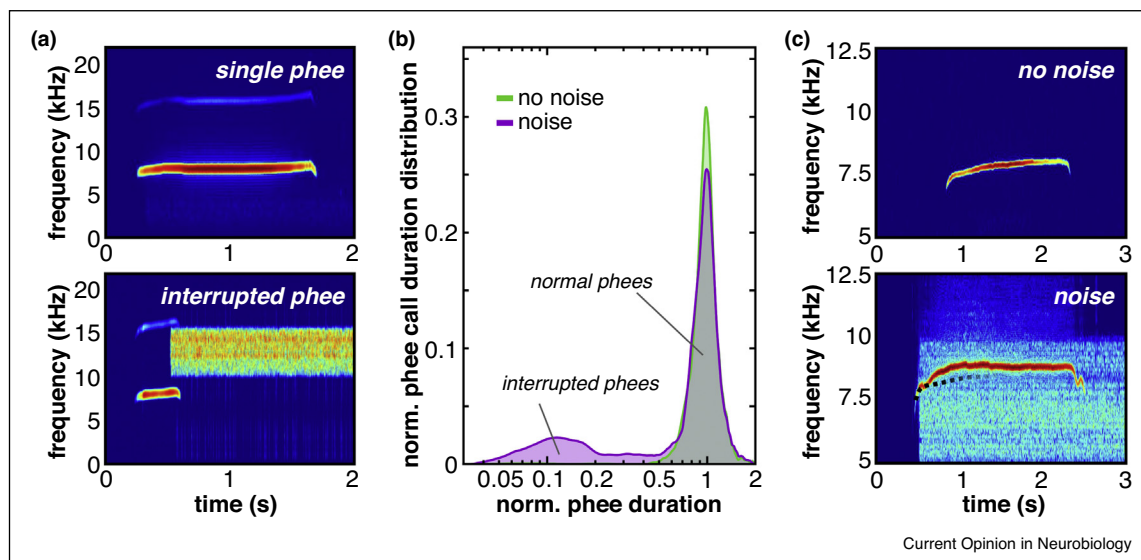
In a recent study, my group was able to show that marmoset monkeys are capable of truncating calls in response to vocalization-triggered noise [21**]. As in previous studies in other primate species [11,12], we used acoustic perturbation triggered by the vocal behavior itself and quantitatively measured the resulting vocal adjustments of marmoset monkeys during phee call production (Figure 1a). During perturbation, the duration of most uttered phee vocalizations was not affected by the interfering noise stimuli and uttered within the normal phee duration range (between 1 and 2 s of duration). However, a small yet distinct number of vocalizations (around 3% of all uttered phees in the noise conditions) were interrupted by the noise stimuli resulting in phee calls with durations well below 0.5 s (Figure 1a and b). These findings suggest that marmoset monkeys are capable of interfering with vocal pattern production after call onset and producing calls being shorter than the natural range of call durations. Calls were interrupted approximately already 80 ms after noise perturbation onset resulting in truncated calls being much shorter than vocalizations uttered under normal conditions, indicating a direct audio-vocal integration mechanism underlies this behavior.

In another study, my group investigated whether the marmoset phee calls that do not show any apparent differences in call duration exhibit changes in call

structure when the perturbing noise starts after call onset [23]. We found that marmoset monkeys are capable of rapidly (<100 ms) modulating call frequency in response to these perturbing noise stimuli (Figure 1c). Phee vocalizations swiftly increased in call frequency after noise perturbation in a rapid way, similar to the occasional interruptions of their calls in response to these perturbing stimuli (<100 ms). These findings are supported by another recent study using a similar neuroethological approach where marmoset monkeys were confronted with perturbing band pass filtered noise starting after call onset and with frequencies directly above or below the fundamental frequency of the phee calls [24]. Here, the monkeys shifted the fundamental frequencies of their vocalizations away from the spectrum of the interfering noise bursts. The findings of these studies also indicate a rapid effect of perturbing noise on vocal motor pattern production.

Finally, recent work revealed that marmoset monkeys exhibit feedback-dependent vocal control [22**]. Here, the frequency of the uttered vocalization was shifted in real-time and directly played back to the monkeys during ongoing calls. In response to the altered vocal feedback, the marmoset monkeys showed compensatory changes in vocal production with significantly increased call frequencies during negative frequency shifts and significantly decreased frequencies during positive shifts [22**]. Again, the observed changes in call structure were exhibited with short response latencies of approximately 150 ms after playback alteration, which are comparable to

Figure 1



Noise-induced interruption of phee call production in marmoset monkeys.

(a) Example spectrogram of a normal, single phee and a phee interrupted by noise perturbation, respectively. (b) Normalized phee duration distribution for calls that were (noise) and were not perturbed (no noise) for five monkeys (adapted from Ref. [21**]). (c) Example spectrogram of a call that was not and was perturbed by noise. The black dotted line in the lower spectrogram indicates the trajectory of the unperturbed phee shown above (adapted from Ref. [23]).

response latencies being observed for human subjects in a similar experiment (228 ms) [25], again indicating a rather direct modulation of the vocal pattern-generating network from the auditory side (see also explanations regarding Figure 2 below).

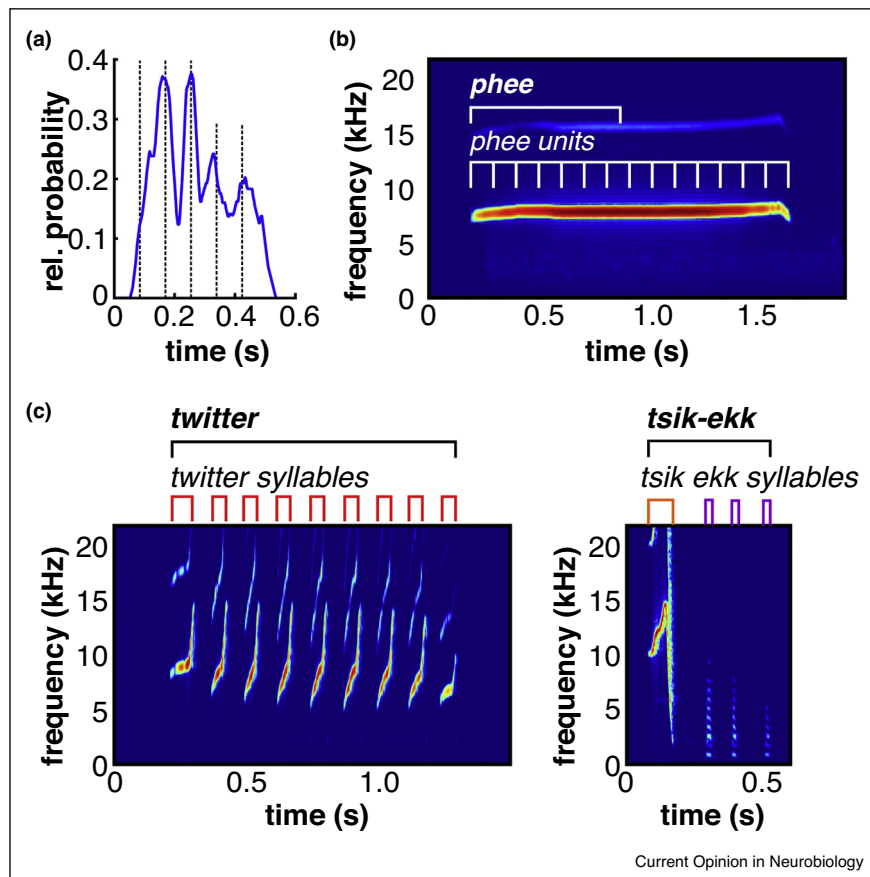
Overall, these recent studies suggest rapid audio-vocal integration mechanisms can directly modulate ongoing vocal pattern generating processes and challenge the concept of primate vocal pattern generation that vocal utterances are discrete call patterns.

Vocal pattern generating network revisited: a neuroethological approach

In non-human primates, the genetically predetermined vocalizations are produced by the primary vocal motor network [2*]. This network consists of two structurally and functionally distinct parts, the VPGN in the brainstem and an upstream limbic vocal-initiating network driving the pattern generator based on affective state

[6,7]. The core of the primary vocal motor network is the VPGN in the brainstem, which is highly conserved in all vertebrate taxa [26]. This network consists mainly of the interconnected areas of the periaqueductal grey (PAG), parabrachial nucleus (PB), and ventrolateral pontine reticular formation. The latter contains the vocal pattern generator, which controls all phonatory motoneuron pools (nuclei of cranial nerves V, VII, and XII, and the ambiguus nucleus) that innervate the muscles of the larynx, oral cavity, tongue, and respiratory system to produce the actual acoustic structure of the calls [6,27,28*,29]. The role of these brainstem structures in vocal pattern generation has been deciphered based on a large number of electrophysiological recording, stimulation, and lesion studies in monkeys (for review: Ref. [2*]). The PAG and PB have a more general function in gating the type of vocalization, call duration, and timing of the vocal onset on the basis of the momentary respiratory status [2*,6]. The vocal pattern generator in the ventrolateral pontine brainstem itself is activated by these

Figure 2



Phee vocalizations share common principles in call pattern production with other call types.

(a) Multi-modal phee distribution of interrupted phees in an individual marmoset monkey. Vertical lines are multiple of each other. (b) and (c) Example spectrograms for phee, twitter, and tsik-ekks. Phee calls consist of phee units of similar duration (b), twitters of twitter syllables, and tsik-ekks of tsik and ekk syllables (c) (adapted from Ref. [21*]).

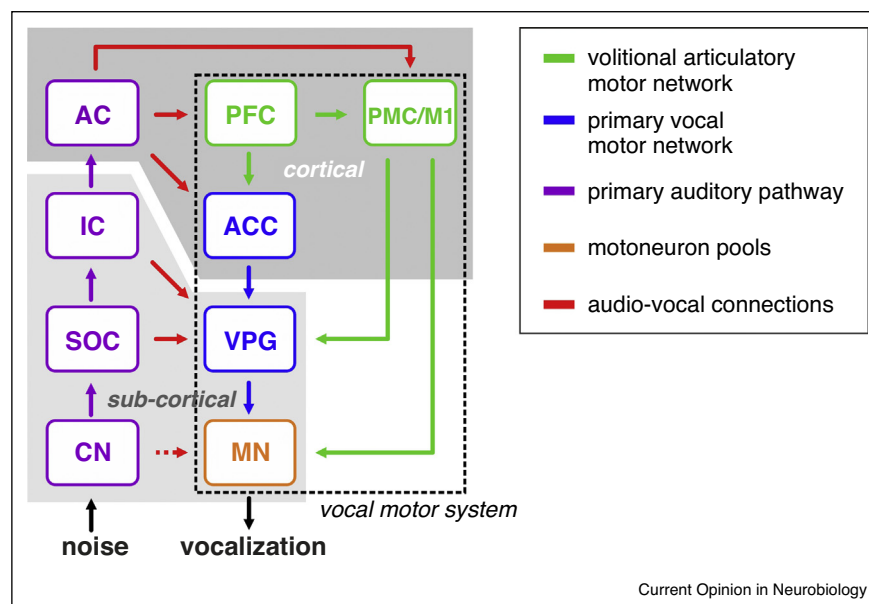
structures and generates the neural patterns that are driving the motoneuron pools to produce the acoustic structure of the entire calls. Earlier studies have suggested that the vocal pattern generating system consists of a network of dedicated pattern generators [30], each for each call type, since inactivation of distinct areas in the ventrolateral pontine brainstem led to the inhibition of just a few call types and not the entire vocal repertoire [31].

The recent studies discussed above suggest that marmoset vocalizations are not generated as a fixed action pattern, that is, predetermined before call onset, but rather in a more flexible way, allowing immediate modulation of the acoustic structure during ongoing call production. Therefore, these recent findings seem to be in contrast to the predominant concept of vocal pattern production in primates [2^{*},6,7,14]. However, recent findings might help to sufficiently revise this current concept and suggest an improved general principle of pattern generation in primate vocalization. As discussed above, a recent study revealed that marmoset monkeys were able to interrupt phee call production in response to perturbing noise [21^{**}]. Interestingly, interrupted phee distributions exhibited a multimodal distribution with distinct sharp peaks at multiples

of a smaller fraction (Figure 2a). These observations and further investigations suggest that the phee call is not a discrete call pattern by itself but that it is built of many sequentially uttered stereotyped brief units, just like other marmoset call types (Figure 2b and c).

According to these findings, I hypothesize that the vocal pattern generator in the ventrolateral reticular formation is not generating the acoustic structure of phee vocalizations as a whole, but rather generating highly stereotyped and more elementary vocal motor units. The number of vocal motor units that are produced by the vocal pattern generator and, therefore, determine phee call duration, is dependent on the duration of the excitatory input originating from the PAG, which serves a main gating function and is reciprocally connected with the vocal pattern generator within the ventrolateral pontine reticular formation [31,32]. This hypothesis is supported by single-unit recordings in macaques and squirrel monkeys [33,34] where neuronal activity observed in the PAG was closely correlated to call duration, while single-unit recordings in the putative vocal pattern generator of squirrel monkeys revealed syllable-correlated activity during trill vocalizations (comparable to twitter calls in marmosets; Figure 2c) [35].

Figure 3



Audio-vocal integration mechanisms exist at cortical and subcortical levels.

Call production might be affected by ambient noise at different brain levels. Audio-vocal integration mechanisms are known to exist between cortical and subcortical structures, as well as via corticofugal projections. See text for further explanation. Simplified circuit diagram summarizing the most relevant structures for vocal production and the auditory pathway in monkeys. Arrows indicate anatomically verified and relevant direct connections. The volitional articulatory motor network (indicated in green) is capable of modulating the primary vocal motor network (indicated in blue) and the motoneuron pools (indicated in orange) involved in call production. External auditory stimuli are perceived via the auditory pathway (indicated in purple), which is capable of modulating the vocal motor system via direct connections (indicated in red) at cortical and subcortical levels (adapted from Refs. [2^{*},23,36^{*},50]). Abbreviations: AC, primary auditory cortex; ACC, anterior cingulate cortex; CN, cochlear nucleus; IC, inferior colliculus; M1, ventral primary motor cortex; MN, motoneuron pools involved in call production; PFC, prefrontal cortex; PMC, ventral premotor cortex; SOC, superior olivary complex; VPG, vocal pattern generating network in the brainstem encompassing the periaqueductal gray, retroambigular nucleus, and parabrachial nucleus.

In contrast to the previous version of the vocal motor network, the proposed revision of the vocal motor network now allows rapid modulations of the acoustic structure during ongoing calls and abruptions of vocalizations in response to perturbing auditory stimuli. Interestingly, perturbing acoustic stimuli are capable of interrupting vocalizations or modulating the acoustic call structure with latencies within a range of the duration of one to two vocal motor units, that is, 80–160 ms, suggesting a rather direct interaction between the auditory system and vocal motor network [21^{••},22^{••},23]. Such connections from the auditory to vocal motor side are present at several cortical and subcortical levels, any or all of which might be capable in eliciting the observed audio-vocal interactions discussed above.

Considering the current literature, there are several anatomically and physiologically verified circuits that are capable of mediating audio-vocal integration processes between the auditory system and vocal motor network within the primate brainstem (Luo *et al.* [36[•]]). The first connection between the auditory and vocal motor side is the direct projections from the cochlear nucleus to the laryngeal and respiratory motor neuron pools involved in vocal production [36[•]]. This connection seems to be solely responsible for the laryngeal reflex, an extremely rapid reflexive activation of the recurrent laryngeal nerve in response to external acoustical stimulation in humans and bats [37,38]. Its potential role in audio-vocal integration processes in non-human primates is yet unknown. Two more likely connections between the primary auditory pathway and vocal motor network can be found at the brainstem level (Figure 3). One is between the superior olivary complex and the putative vocal pattern generator within the ventrolateral pontine reticular formation, and one is between the inferior colliculus and the putative vocal pattern generator in the brainstem [36[•]], which contains single neurons that respond to external acoustic stimuli and also show changes in neural activity before and during vocal production [39].

At the cortical level, the auditory cortex (AC) is reciprocally interconnected with all cortical structures of the vocal motor network, such as the prefrontal cortex (PFC), premotor and motor cortices (PMC and M1) of the volitional articulatory motor network, and anterior cingulate cortex of the primary vocal motor network [2[•],40–42]. While several studies have already highlighted the potential role of the AC in feedback-dependent vocal control [43,44], a recent study revealed the first evidence of a causal role of the AC in the modulation of vocal output [22^{••}]. As discussed above, marmoset monkeys showed compensatory changes in vocal production in response to real-time shifted playback. Interestingly, electrical microstimulation of the AC rapidly evoked similar changes during vocal output and the activity of

single neurons in the AC predicted the observed vocal changes in response to altered feedback [22^{••}].

Conclusion

Marmoset monkeys have been shown to be capable of modulating ongoing vocalizations rapidly after perturbing auditory feedback, which challenges the decades-old concepts of primate vocal pattern generation, indicating that vocalizations do not consist of one discrete call pattern. However, recent studies have also revealed that marmoset vocalizations are not a discrete call pattern in and of themselves but built of many sequentially uttered stereotyped brief units enabling audio-vocal integration processes to interfere within ongoing calls produced by the vocal pattern generating network. In the future, neurophysiological studies will have to elucidate at which level the auditory system interferes with the vocal motor network to modulate call production. The marmoset monkey will be a particularly suitable model system due to its rich vocal repertoire, produced either spontaneously [45] or under behavioral control [46], as well due to several neurophysiological techniques that have been established in recent years [47–49].

Conflict of interest statement

Nothing declared.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

1. Ghazanfar AA, Rendall D: **Evolution of human vocal production.** *Curr Biol* 2008, **18**:R457-R460.
2. Hage SR, Nieder A: **Dual neural network model for the evolution of speech and language.** *Trends Neurosci* 2016, **39**:813-829. •
3. Fischer J, Hage SR: **Primate vocalization as a model for human speech: scopes and limits.** In *Human Language: From Genes and Brains to Behavior*. Edited by Hagoort P. MIT Press; 2019:639-656.
4. Goldstein MH, King AP, West MJ: **Social interaction shapes babbling: testing parallels between birdsong and speech.** *Proc Natl Acad Sci U S A* 2003, **100**:8030-8035.
5. Hage SR: **Dual neural network model of speech and language evolution: new insights on flexibility of vocal production systems and involvement of frontal cortex.** *Curr Opin Behav Sci* 2018, **21**:80-87.
6. Jürgens U: **Neural pathways underlying vocal control.** *Neurosci Biobehav Rev* 2002, **26**:235-258.

7. Ackermann H, Hage SR, Ziegler W: **Brain mechanisms of acoustic communication in humans and nonhuman primates: an evolutionary perspective.** *Behav Brain Sci* 2014, **37**:529-546.
8. Hammerschmidt K, Freudenstein T, Jürgens U: **Vocal development in squirrel monkeys.** *Behaviour* 2001, **138**:1179-1204.
9. Owren MJ, Dieter JA, Seyfarth RM, Cheney DL: **Vocalizations of rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques cross-fostered between species show evidence of only limited modification.** *Dev Psychobiol* 1993, **26**:389-406.
10. Agamaite JA, Chang C-J, Osmanski MS, Wang X: **A quantitative acoustic analysis of the vocal repertoire of the common marmoset (*Callithrix jacchus*).** *J Acoust Soc Am* 2015, **138**:2906-2928.
11. Miller CT, Flusberg S, Hauser MD: **Interruptibility of long call production in tamarins: implications for vocal control.** *J Exp Biol* 2003, **206**:2629-2639.
12. Egnor SER, Iguina CG, Hauser MD: **Perturbation of auditory feedback causes systematic perturbation in vocal structure in adult cotton-top tamarins.** *J Exp Biol* 2006, **209**:3652-3663.
13. Miller CT, Eliades SJ, Wang X: **Motor planning for vocal production in common marmosets.** *Anim Behav* 2009, **78**:1195-1203.
14. Loh KK, Petrides M, Hopkins WD, Procyk E, Amiez C: **Cognitive control of vocalizations in the primate ventrolateral-dorsomedial frontal (VLF-DMF) brain network.** *Neurosci Biobehav Rev* 2017, **82**:32-44.
15. Roy S, Miller CT, Gottsch D, Wang X: **Vocal control by the common marmoset in the presence of interfering noise.** *J Exp Biol* 2011, **214**:3619-3629.
16. Hage SR, Nieder A: **Single neurons in monkey prefrontal cortex encode volitional initiation of vocalizations.** *Nat Commun* 2013, **4**:2409.
17. Choi JY, Takahashi DY, Ghazanfar AA: **Cooperative vocal control in marmoset monkeys via vocal feedback.** *J Neurophysiol* 2015, **114**:274-283.
18. Hage SR, Gavrilov N, Nieder A: **Cognitive control of distinct vocalizations in rhesus monkeys.** *J Cogn Neurosci* 2013, **25**:1692-1701.
19. Seyfarth R, Cheney D, Marler P: **Monkey responses to three different alarm calls: evidence of predator classification and semantic communication.** *Science (80-)* 1980, **210**:801-803.
20. Price T, Wadewitz P, Cheney D, Seyfarth R, Hammerschmidt K, Fischer J: **Vervets revisited: a quantitative analysis of alarm call structure and context specificity.** *Sci Rep* 2015, **5**:1-11.
21. Pomberger T, Risueno-Segovia C, Löschner J, Hage SR: **Precise motor control enables rapid flexibility in vocal behavior of marmoset monkeys.** *Curr Biol* 2018, **28**:788-794.
This study provides the first evidence that monkeys are capable of interrupting vocalizations only at periodic time points, indicating that these calls do not consist of one discrete call pattern but are built of many sequentially uttered units.
22. Eliades SJ, Tsunada J: **Auditory cortical activity drives feedback-dependent vocal control in marmosets.** *Nat Commun* 2018, **9**:2540.
This is the first study providing behavioral and neurophysiological evidence for the causal role of the auditory cortex in feedback control during vocal output in marmoset monkeys.
23. Pomberger T, Löschner J, Hage SR: **Compensatory mechanisms affect sensorimotor integration during ongoing vocal-motor acts in marmoset monkeys.** *bioRxiv* 2019 <http://dx.doi.org/10.1101/696989>.
24. Zhao L, Rad BB, Wang X, Wang X: **Long-lasting vocal plasticity in adult marmoset monkeys.** *Proc R Soc B Biol Sci* 2019, **286**:20190817.
25. Burnett TA, Freedland MB, Larson CR, Hain TC: **Voice F0 responses to manipulations in pitch feedback.** *J Acoust Soc Am* 1998, **103**:3153-3161.
26. Bass aH, Chagnaud BP: **Shared developmental and evolutionary origins for neural basis of vocal-acoustic and pectoral-gestural signaling.** *Proc Natl Acad Sci U S A* 2012, **109**:10677-10684.
27. Jürgens U, Hage SR: **On the role of the reticular formation in vocal pattern generation.** *Behav Brain Res* 2007, **182**:308-314.
28. Tschida K, Michael V, Takato J, Han B-X, Zhao S, Sakurai K, Mooney R, Wang F: **A specialized neural circuit gates social vocalizations in the mouse.** *Neuron* 2019, **103**:459-472.e4.
Using genetic and neurophysiological methods, this study provides insights into the vocal motor system in rodents highlighting the gating function of the PAG, giving rise to a descending vocal pattern generating circuit.
29. Hage SR, Jürgens U: **On the role of the pontine brainstem in vocal pattern generation: a telemetric single-unit recording study in the squirrel monkey.** *J Neurosci* 2006, **26**:7105-7115.
30. Barlow SM, Estep M: **Central pattern generation and the motor infrastructure for suck, respiration, and speech.** *J Commun Disord* 2006, **39**:366-380.
31. Jürgens U: **Localization of a pontine vocalization-controlling area.** *J Acoust Soc Am* 2000, **108**:1393-1396.
32. Hannig S, Jürgens U: **Projections of the ventrolateral pontine vocalization area in the squirrel monkey.** *Exp Brain Res* 2006, **169**:92-105.
33. Larson CR, Kistler MK: **Periaqueductal gray neuronal activity associated with laryngeal EMG and vocalization in the awake monkey.** *Neurosci Lett* 1984, **46**:261-266.
34. Düsterhöft F, Häusler U, Jürgens U: **Neuronal activity in the periaqueductal gray and bordering structures during vocal communication in the squirrel monkey.** *Neuroscience* 2004, **123**:53-60.
35. Hage SR, Jürgens U: **Localization of a vocal pattern generator in the pontine brainstem of the squirrel monkey.** *Eur J Neurosci* 2006, **23**:840-844.
36. Luo J, Hage SR, Moss CF: **The Lombard effect: from acoustics to neural mechanisms.** *Trends Neurosci* 2018, **41**(12):938-949 <http://dx.doi.org/10.1016/j.tins.2018.07.011>.
A detailed review of behavioral and neurophysiological data proposing that the Lombard effect, as the most prominent example for audio-vocal integration processes, is driven by a subcortical neural network that can be modulated by cortical processes.
37. Jen PH-S, Suga N: **Coordinated activities of middle-ear and laryngeal muscles in echolocating bats.** *Science (80-)* 1976, **191**:950-952.
38. Sapis S, McClean MD, Larson CR: **Human laryngeal responses to auditory stimulation.** *J Acoust Soc Am* 1983, **73**:315-321.
39. Hage SR, Jürgens U, Ehret G: **Audio-vocal interaction in the pontine brainstem during self-initiated vocalization in the squirrel monkey.** *Eur J Neurosci* 2006, **23**:3297-3308.
40. Hickok G, Poeppel D: **The cortical organization of speech processing.** *Nat Neurosci* 2007, **8**:393-402.
41. Rauschecker JP, Scott SK: **Maps and streams in the auditory cortex: nonhuman primates illuminate human speech processing.** *Nat Neurosci* 2009, **12**:718-724.
42. Simonyan K, Jürgens U: **Afferent cortical connections of the motor cortical larynx area in the rhesus monkey.** *Neuroscience* 2005, **130**:133-149.
43. Müller-Preuss P, Ploog D: **Inhibition of auditory cortical neurons during phonation.** *Brain Res* 1981, **215**:61-76.
44. Eliades SJ, Wang X: **Neural substrates of vocalization feedback monitoring in primate auditory cortex.** *Nature* 2008, **453**:1102-1106.
45. Liao DA, Zhang YS, Cai LX, Ghazanfar AA: **Internal states and extrinsic factors both determine monkey vocal production.** *Proc Natl Acad Sci U S A* 2018, **115**:201722426.
46. Pomberger T, Risueno-Segovia C, Gultekin YB, Dohmen D, Hage SR: **Cognitive control of complex motor behavior in marmoset monkeys.** *Nat Commun* 2019, **10**:1-8.

47. Roy S, Wang X: **Wireless multi-channel single unit recording in freely moving and vocalizing primates.** *J Neurosci Methods* 2012, **203**:28-40.
48. Eliades SJ, Wang X: **Chronic multi-electrode neural recording in free-roaming monkeys.** *J Neurosci Methods* 2008, **172**:201-214.
49. Pomberger T, Hage SR: **Semi-chronic laminar recordings in the brainstem of behaving marmoset monkeys.** *J Neurosci Methods* 2019, **311**:186-192.
50. Eliades SJ, Wang X: **Corollary discharge mechanisms during vocal production in marmoset monkeys.** *Biol Psychiatry Cogn Neurosci Neuroimaging* 2019, **4**:805-812.