Vocal learning in elephants: neural bases and adaptive context

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In the last decade clear evidence has accumulated that elephants are capable of vocal production learning. Examples of vocal imitation are documented in African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants, but little is known about the function of vocal learning within the natural communication systems of either species. We are also just starting to identify the neural basis of elephant vocalizations. The African elephant diencephalon and brainstem possess specializations related to aspects of neural information processing in the motor system (affecting the timing and learning of trunk movements) and the auditory and vocalization system. Comparative interdisciplinary (from behavioral to neuroanatomical) studies are strongly warranted to increase our understanding of both vocal learning and vocal behavior in elephants.

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Introduction

The first evidence of vocal imitation in African elephants (*Loxodonta africana*) was published in 2005 [1•]. No follow-up research on elephant vocal learning was conducted until a report about a speech-imitating Asian elephant (*Elephas maximus*) in 2012 [2•], expanding our knowledge of vocal learning ability to both living genera of Elephantidae. Both papers document vocal imitation produced by captive elephants, some kept in socially abnormal conditions. To date, no information is available on vocal learning or the relevance of vocal learning within the natural communication system of either species. Elephants, like humans, are terrestrial, long-lived and social mammals. Accordingly, the adaptive function of

their vocal learning can help reveal the original selective advantage of vocal learning in our human ancestors (because the adaptive function in modern human language, e.g. creating an extensive vocabulary, might not necessarily conform to the original function [3]).

Until recently, our knowledge of the elephant brain was limited [4]. Central to the current review are recent observations related to infrasound production and reception, as well as the control of the musculature involved. In the context of vocal learning, the most pressing question is whether elephants possess direct connections between telencephalic neurons and the primary vocal motor neurons in the brainstem controlling the vocal apparatus (following the Kuypers/Jürgens hypothesis) [5–9]. The required tract tracer studies to address this issue have not been conducted in elephants.

This review provides a synthesis of previous studies on elephant vocal learning and associated work from 1982 to 2014, along with new results and future perspectives.

Vocal flexibility and sound invention

African and Asian elephants use vocalizations with fundamental frequencies in the infrasonic range ('rumbles') for short-distance and long-distance communication [10,11]. The most remarkable species-specific difference in the vocal repertoire is the high-pitched, repetitive vocalizations (chirps/squeaks and squeals) of Asian elephants, which are typically absent in the African species [12]. The vocal repertoire of African and Asian elephants, with about 8–10 distinct call types [13–17] is not particularly large, but exhibits an interesting vocal plasticity (grading between call types, call type combinations [15,17], and sophisticated, context-dependent within-call type flexibility affecting all parameters including formant frequencies [18–22]). Sound visualization experiments revealed that elephants can control the vocal path from oral to nasal rumble production [12,23]. The nasal vocal tract is strongly elongated (un-extended trunk length of adult females: 1.7–1.8 m [24]). By using the nasal path during rumbling, an elephant lowers its formants by about threefold [23].

In addition, previously undocumented vocalizations sometimes emerge — mostly documented in captive elephants. These sounds appear to be vocally inventive because they are structurally unique and not socially relevant: they include trunk squelching sounds (Figure 1a, Audio Supplemental 1), croaking, creaking, and humming sounds (Figure 1b, Audio Supplemental 2)

Figure 1
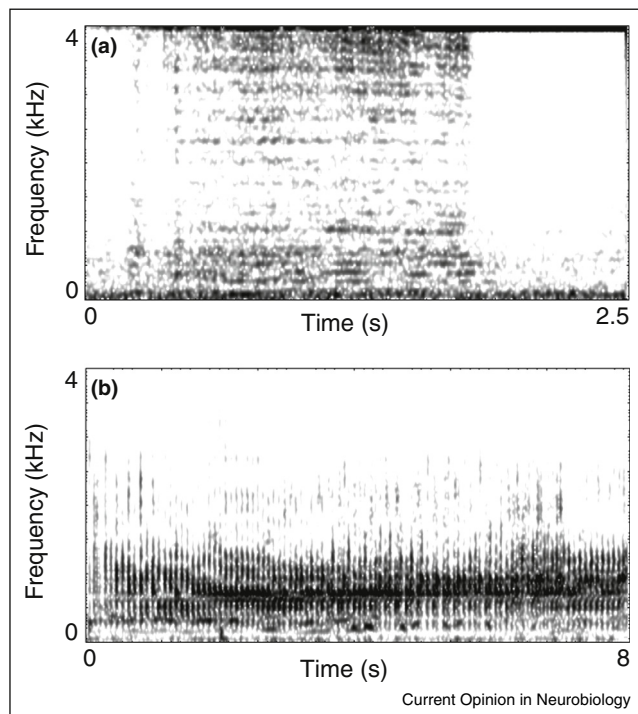
Spectrograms exemplifying idiosyncratic elephant vocalizations. A trunk-squelching sound produced by a five-year-old male African elephant at Vienna Zoo **(a)**. During sound production, the elephant twined the trunk while pressing air through the squeezed trunk tips. A pulsated creak-like sound **(b)** produced by a captive, 18-year-old female elephant in South Africa.

[14,17], or whistling sounds produced by, for example, pressing the trunk against the lower lip [25[•],26].

Supplementary Audios 1 and 2 related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.conb.2014.07.001.

We know very little about how elephants generate their distinct vocalizations [12,27], but recent experiments on low-frequency rumbles suggest flow-induced vocal fold vibration (similar to human speech) [28,29].

Likewise, elephant sound perception has received little research attention, apart from early behavioral experiments revealing good low-frequency hearing [30]. Behavioral experiments further suggest that elephants may sense ground vibrations, including the seismic components of their rumbling vocalizations [31,32].

Examples of vocal imitation

Poole *et al.* [1[•]] documented two cases of vocal imitation in African savannah elephants: a 10-year-old female imitated the sounds of trucks, and a 23-year-old male named Calimero, who had spent a long time as the only African elephant in a zoo among Asian elephants, imitated the high-pitched chirping sounds typically produced by Asian elephants, but not by African elephants.

Stoeger *et al.* [2[•]] documented a male Asian elephant (Koshik) who imitates five human words in Korean with such precision that native Korean speakers could readily understand and transcribe his imitations. Koshik accurately imitates speech formant frequencies by placing his trunk inside his mouth, modulating the shape of the vocal tract during controlled phonation (Figures 2 and 3, Audio Supplemental 3 and 4).

Supplementary Audios 3 and 4 related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.conb.2014.07.001.

Koshik was captive-born and, as a juvenile, the only elephant for five years at the Everland Zoo in South Korea. This suggests that his speech imitation may have been driven by social deprivation from conspecifics during an important period of bonding and development, when humans were his only social contact.

Vocal learning and rhythmical entrainment

The vocal learning and rhythmical entrainment hypothesis raised by Patel [33[•]] suggests that a direct connection between the auditory centers and the motor planning regions (typical for vocal learners) is a prerequisite for the ability to synchronize with an auditory beat. This implies that *only* vocal learning species should be capable of rhythmical entrainment [33[•],34,35]. However, recent research revealed that even some non-vocal learners show evidence for beat synchronization or natural percussive behavior [36[•],37–40].

Elephants might also be capable of rhythmical entrainment [34]. An Asian elephant has been observed drumming a stable beat [41], and elephants in Asian tourist shows move rhythmically to music. Nonetheless, it remains unclear how much training was involved, whether the elephants spontaneously match their movements to the beat, or whether the accompanying music was chosen advantageously.

Untangling the evolutionarily relationship between vocal learning and rhythmical entrainment requires testing multiple species including non-vocal learners, alongside investigating whether all vocal learners indeed possess the ability for rhythmical entrainment. This should be *systematically* tested in both elephant species.

Elephant neuroanatomy

In recent years, an increasing number of studies have begun to unravel the structure of the elephant brain, the largest of any terrestrial mammal [42–55]. Regarding vocalizations, there are two important aspects: vocal

Figure 2
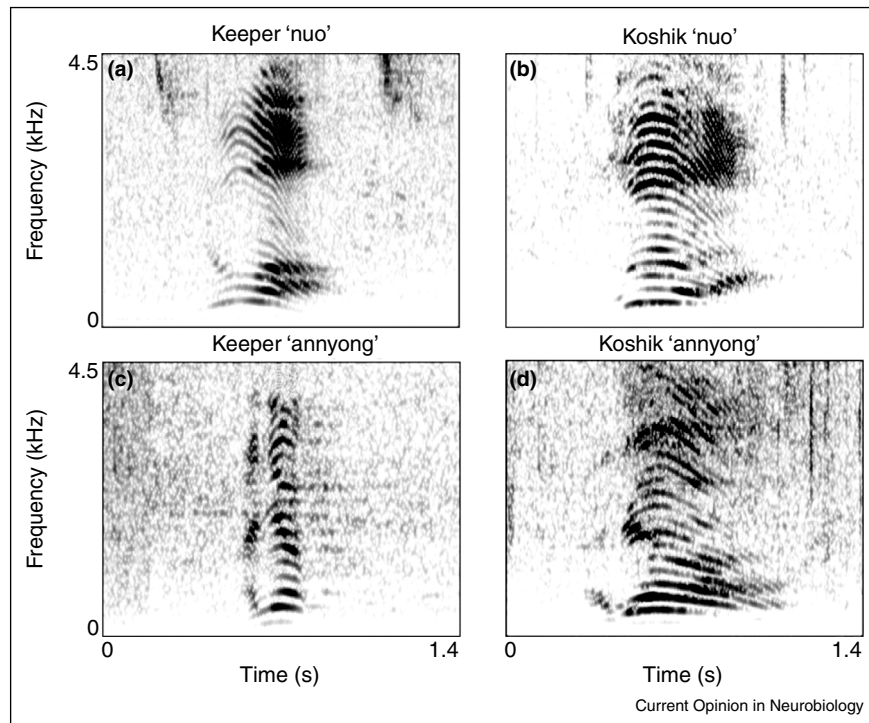
Spectral comparison of Koshik's speech imitations in Korean compared to those of a keeper. Spectrograms **(a,b)** show the utterance 'nuo' ('lie down'), and **(c,d)** show 'annyong' ('hello') by a keeper and Koshik, respectively. In **(d)**, Koshik protracts the '-nyong' part of 'annyong' compared to this human example.

production, including vocal pattern generation and muscular control, and vocal reception, including detection and extraction of information that appear to have distinct neural correlates (Figure 4). For infrasound production, the large nucleus ellipticus of the midbrain, found only in elephants, elephant seals and cetaceans, may act as a specialized vocal pattern generator [51•]. In terms of muscular control, several factors suggest that the timing

Figure 3

Koshik's posture during speech imitation. Koshik accurately imitates human formant frequencies by placing his trunk tip into his mouth (always from the right side) at the onset of phonation. During phonation, he raises the lower jaw while keeping the trunk inside the mouth, thus modulating the shape of his vocal tract.

Figure 4
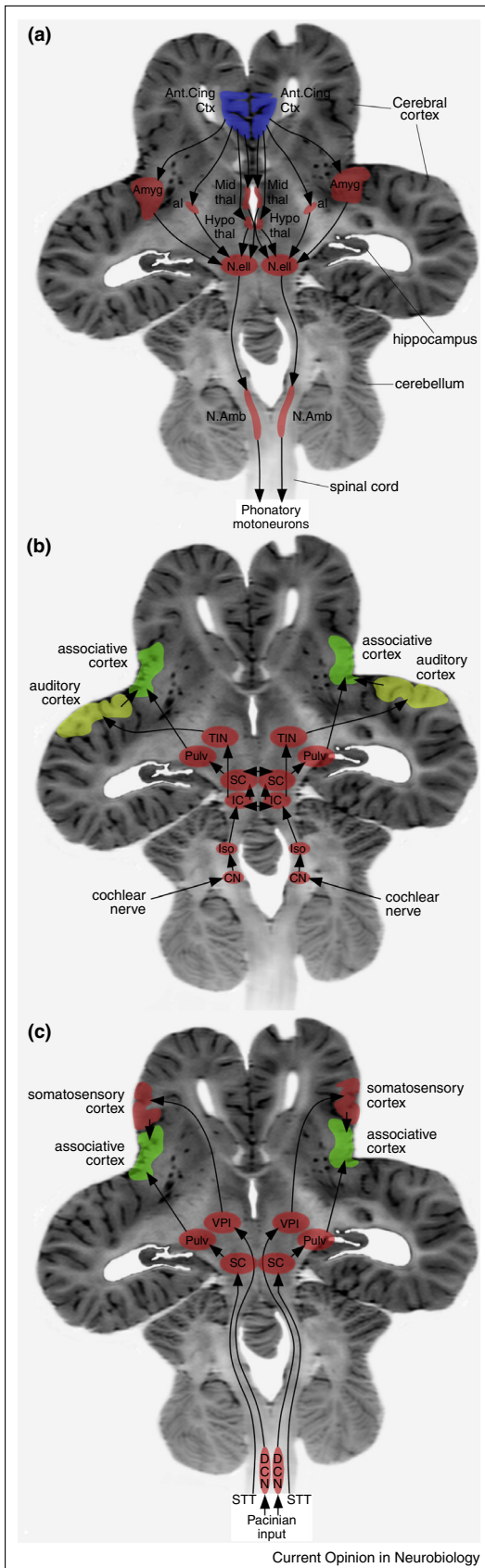
and learning of movements related to trunk control are very important for elephant vocalizations. These include a relatively and absolutely large cerebellum [48] containing larger and more complex neurons than other mammals [49,50], along with a specialized substantia nigra pars compacta, facial nerve motor nucleus and inferior olivary complex [51[•]], with a human-sized hippocampal formation (in both absolute and relative terms) [52,53], all suggesting that the timing and learning of movements related to control of the trunk are very important for elephant vocalizations.

In terms of infrasound reception, specializations of the medial geniculate body of the dorsal thalamus and the lateral superior olivary nucleus within the pons appear to be related to the aerial aspect of infrasound [51[•]]. The specialized transverse infrageniculate nucleus within the medial geniculate body of the dorsal thalamus, which appears to have no homologue in other mammals, is likely to interact with the cerebral cortex to extract semantic information from the infrasonic vocalizations. The enlarged lateral superior olivary nucleus appears to be involved in sound source localization using interaural intensity differences. Specializations of the ventrolateral nuclei of the dorsal thalamus and the dorsal column nuclei of the medulla appear to be related to the seismic component of infrasound [51[•]]. The seismic component of the infrasonic vocalizations appears to be detected through Pacinian corpuscles in the feet and trunk [55], which then pass through enlarged dorsal column nuclei in the medulla and onto the ventral posterior inferior nucleus of the dorsal thalamus, a nucleus specialized for the processing of vibratory tactile stimuli that is not present in all mammals.

Elephants: terrestrial, long-lived and social vocal learners

Like humans, elephants are long-lived, terrestrial mammals with a complex social system, where individuals possess different levels of association [56,57]. Female African elephants use acoustic signals to maintain individual-specific bonds and have an extensive network of vocal recognition, that is distinguishing the calls of family and bond group members from those of outsiders [58,59].

Neural pathways involved with vocalizations in the elephant. Images depicting the possible pathways involved in producing vocalizations **(a)**, the reception of the aerial component of infrasonic vocalizations **(b)** and the reception of the seismic component of infrasonic vocalizations **(c)**, superimposed on a horizontal magnetic resonance image of the elephant brain. In each of these three aspects of vocalization processing, specific specializations within the brain have been observed (see text). **al** — ansa lenticularis; **Amyg** — amygdaloid body; **Ant. Cing Ctx** — anterior cingulate cortex; **CN** — cochlear nuclear complex; **DCN** — dorsal column nuclei; **Hypothal** — hypothalamus; **IC** — inferior colliculus; **Iso** — lateral superior olivary nucleus; **Mid thal** — midline nuclei of dorsal thalamus; **N. amb** — nucleus ambiguus; **N.ell** — nucleus ellipticus; **Pulv** — pulvinar nucleus of dorsal thalamus; **SC** — superior colliculus; **STT** — spinothalamic tract; **TIN** — transverse infrageniculate nucleus; **VPI** — ventral posterior inferior nucleus of dorsal thalamus.

Forming and recalling social memories of their life history is a key cognitive challenge helping ensure survival [60–62]. Vocal learning in elephants might be used to facilitate vocal recognition within their fission-fusion society by increasing the similarity between related or socially affiliated individuals (males also use vocalizations to negotiate within the social network). Call convergence in socially bonded animals also occurs in other vocal learning species (e.g. [63–66]), and regional dialects have been detected in the songs of male rock hyraxes (*Procavia capensis*) [67] (suggesting vocal learning in another Afrotherian mammal).

Moreover, the mechanisms that lead to the development of novel sounds in captive elephants should be verified, since vocal invention might be a form of vocal learning used to develop signals that differ from others (e.g. to increase vocal individuality) rather than converging to a model [68–71]. Identifying the function *or functions* of vocal learning within the natural communication system of elephants clearly provides an exciting avenue for future research.

Conclusions

This review summarized the accumulating evidence for vocal learning in elephants.

A fascinating aspect of elephant vocalizations — most striking in Koshik, the speech-imitating elephant — is that elephants use their trunk, and evolutionary highly specialized appendage, to modulate sound production in a very sophisticated manner. Notwithstanding, this review reveals that research on elephant vocal learning is still in a fledgling stage regarding context, function and neural information processing. By combining behavioral, anatomical and neuroanatomical studies, a clearer picture of elephant vocal capacities and how they relate to the life history of these iconic species should emerge.

Conflict of interest statement

Nothing declared.

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