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of episodic memory may not be unique to vertebrates. Because the hypothetical common ancestor of cephalopods and vertebrates dates back to about one billion years ago [9], the evolution of episodic-like memory may provide a genuine case of evolutionary convergence. Perhaps the result of the live fast/die young lifestyle has been an important selective pressure for the evolution of What-Where-When memory in cephalopods, given that these animals need to optimize their foraging time while minimizing the risk of predation. Whatever the reason, these results provide a novel evolutionary insight into the emergence of complex cognition.

Supplemental Information

Supplemental Information includes experimental procedures, and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2013.10.021>.

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Koalas use a novel vocal organ to produce unusually low-pitched mating calls

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During the breeding season, male koalas produce ‘bellow’ vocalisations that are characterised by a continuous series of inhalation and exhalation sections, and an extremely low fundamental frequency (the main acoustic correlate of perceived pitch) [1]. Remarkably, the fundamental frequency (F0) of bellow inhalation sections averages 27.1 Hz (range: 9.8–61.5 Hz [1]), which is 20 times lower than would be expected for an animal weighing 8 kg [2] and more typical of an animal the size of an elephant (Supplemental figure S1A). Here, we demonstrate that koalas use a novel vocal organ to produce their unusually low-pitched mating calls.

Examination of 10 male koala larynges failed to identify any obvious specialisations for low frequency sound production. The laryngeal vocal folds were sharp-edged, thin structures that were mean 9.8 ± 0.9 mm long, 1.0 ± 0.1 mm wide and 0.8 ± 0.2 mm in depth. As a first approximation, the vocal fold can be assumed to behave like a simple string, whose rate of vibration (F0) is linearly and inversely related to its length [3]. According to this theoretical string model, a 9.8 mm fold should not be able to produce frequencies below 51.0 Hz (Supplemental information). In addition, if we use an empirical model based on the co-variation of vocal fold length and mean F0 across mammals (Supplemental figure S1B), the predicted mean F0 for a 9.8 mm fold should be around 389 Hz, which is far higher than the 27.1 Hz mean F0 of bellow inhalation sections [4]. Thus, the dimensions of the male koala’s vocal folds appear to be incompatible with the production of the extremely low F0 of male bellows.

Further detailed dissections revealed a pair of much larger, and previously undocumented folds spanning the intra-pharyngeal ostium (IPO), an oval opening within the soft palate

(or velum) that connects the oral and nasal portions of the pharynx (Figure 1). The distinctive shape and the position of these ‘velar vocal folds’ indicate that they could be used to produce sound as air is sucked in through the nostrils during inhalation (Figure 1). The velar vocal folds were paired medial protrusions of the IPO edges that were oriented rostro-caudally and heavily wrinkled (Figure 1B,C), allowing them to be stretched and brought under tension for vocal production, and relaxed to allow the IPO to remain open during nasal respiration. Previous findings indicate that male koalas use their sternothyroid muscle to pull the larynx caudally when they vocalise [4]. Because the larynx is attached to the caudal end of the pharynx where the IPO is situated, laryngeal retraction brought about by the sternothyroid muscle will automatically put tension on the rostro-caudally oriented velar vocal folds, and could also induce length changes of the folds. Contractions of the palatopharyngeal muscles may also influence the length and shape of the velar vocal folds directly (inducing width changes of the IPO).

In their resting state the velar vocal folds ($n = 10$) were mean 32.8 ± 2.6 mm long, 15.1 ± 1.9 mm wide and 10.8 ± 1.4 mm in depth. According to the string model, a 32.8 mm fold should be able to produce frequencies as low as 15.2 Hz, which is compatible with the range of F0s observed in the inhalation sections of bellows (9.8–61.5 Hz) [1]. In addition, when fully elongated the velar vocal folds were 51.1 mm long, which would theoretically allow them to oscillate at frequencies as low as 9.8 Hz. Assuming a tissue density of 1.02 g cm³ [5] the mass of the velar vocal folds of around 5.46 g also makes them ~683 times heavier than the laryngeal vocal folds (at around 0.008 g), which should also help to increase the radiated power of the low F0 signal [6].

Because koalas produce the low F0 sections of bellows on inhalation [7], we reproduced natural sound production in three male koala cadavers by sucking air through the pharynx and the larynx via the trachea, mimicking inhalation of air using the lungs (Supplemental figure S2). This allowed us to investigate whether an ingressive flow of air can induce self-sustained oscillation of the velar vocal folds and produce low frequency sounds. An endoscopic video camera was attached to a tube leading from the suction pump and placed

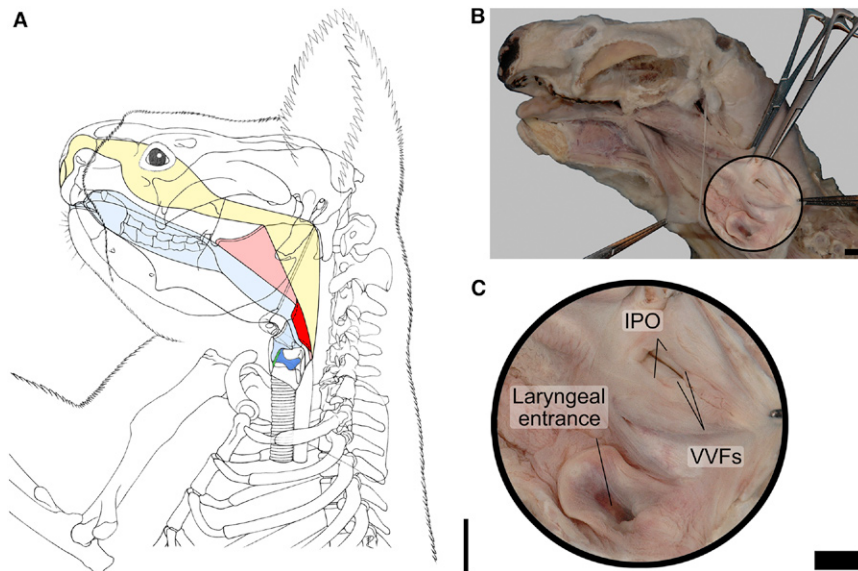


Figure 1. The velar vocal folds of male koalas. (A) The velar vocal folds (VVF) are located at the intersection between the oral and nasal portions of the pharynx just opposite to the laryngeal entrance. Oral tract in light blue, nasal tract in yellow, soft palate in light red, VVF in red, laryngeal vocal folds in green, arytenoid cartilage in blue. (B) Photograph of the pharynx opened along its left lateral wall with the soft palate pulled dorsally. (C) Close up view of the entrance to the larynx, the IPO and velar vocal folds.

inside the trachea using a ring-tie to make the seal airtight (Supplemental figure S2A). This *in situ* placement of the video camera just below the larynx allowed us to visualize the velar vocal folds through the space between the arytenoid cartilages (to which the laryngeal vocal folds are attached) and visually document their role in sound production, whilst ruling out the involvement of the laryngeal vocal folds (Supplemental figure S2B). High quality sound recordings were captured at the same time.

Using this approach, we induced and documented the production of periodic sound signals caused by velar vocal fold vibration during 250 separate phonation events. Video and acoustic data show that the velar vocal folds can produce F₀s ranging from 6–133 Hz (mean: 22.7 Hz), which covers the reported minimum and maximum F₀s of male bellow inhalation sections of 9.8–61.5 Hz [1] (Supplemental movie S1). In addition, the sharp pulses produced by the velar vocal folds in our experiment look and sound remarkably like those produced by live animals (Supplemental figure S2C, Audio S1 and S2). Taken together, these observations confirm that male koalas use their velar vocal folds to produce the extremely low F₀ sections of bellows.

To our knowledge, the only other example of a specialised sound

producing organ in mammals that is independent of the larynx are the phonic lips used by toothed whales to generate echolocation clicks [8]. We suggest that the koala's newly described velar vocal folds may reflect a specialisation to efficiently produce low F₀ either because it enhances the salience of vocal tract resonances (thereby facilitating the communication of cues to identity or body size [1,9]) or because F₀ itself acts as a direct cue to male quality. Female koalas have also been reported to bellow [7], but do so much more rarely than males. Investigations of female koala vocal anatomy, therefore, are now needed to determine whether they also possess velar vocal folds. In addition, because koalas produce a range of other high-pitched vocalizations [7] that may be compatible with the dimensions of the laryngeal vocal folds, future work could also determine how the F₀ of these calls relates to the F₀ range predicted when applying the string equation to this species' laryngeal vocal fold length.

Other adaptations that allow mammals to produce disproportionately low F₀s include hypertrophied larynges [10] or specialisations of the vocal folds that increase their vibrating mass [6]. The combination of morphological, video

and acoustic data presented here documents the first evidence in a terrestrial mammal of an organ other than the larynx that is specialised for sound production. Further studies are now warranted to investigate whether this remarkable adaptation is shared with other mammals, or whether it is unique to koalas.

Supplemental Information

Supplemental Information including a movie, two audio recordings, experimental procedures and two figures can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2013.10.069>.

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