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Current Opinion in Neurobiology

Vocal learning in seals, sea lions, and walruses

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The pinnipeds provide a variety of clues to those interested in the vocal learning capabilities of non-human animals. Observational and experimental studies of seals, sea lions, and walruses reveal elements of vocal development, contextual control, plasticity in expression and learning, and even imitation of complex sounds. Consideration of the factors that influence the expression of these capabilities informs understanding of the behavioral and structural mechanisms that support vocal learning in mammals and the evolutionary forces shaping these capabilities.

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Current Opinion in Neurobiology 2014, **28**:66–71

This review comes from a themed issue on **Communication and language**

Edited by **Michael Brainard** and **Tecumseh Fitch**

http://dx.doi.org/10.1016/j.conb.2014.06.011

0959-4388/Published by Elsevier Ltd.

Comparative studies of animal communication provide insight into the origins of language in our own species, including the ability to acquire new sounds on the basis of social or environmental experience. For this reason alone, the topic of vocal learning — concerned with exploring how plasticity in sound production supports complex communication abilities — is important. Beyond their anthropocentric value, comparative studies of vocal learning clarify the proximal mechanisms that enable plasticity in sound production and usage in different species. They also offer clues as to how these mechanisms are linked to evolutionary pressures shaping neurobiological and anatomical function. Given the predominant interest in specialized human language acquisition, the search for rudimentary vocal learning abilities in other animals has turned up puzzling gaps in the emergence and existence of these capabilities. Although some distantly related birds (parrots, songbirds, and hummingbirds) are capable of sound modification associated with learning and auditory exposure, comparable capabilities have only recently been identified in mammals. These include some terrestrial (bats, elephants) and marine (cetaceans, pinnipeds) mammals with quite divergent evolutionary histories, ecological niches, and social constraints. Among these, the pinnipeds enable a unique view of the proximate and ultimate bases of vocal learning.

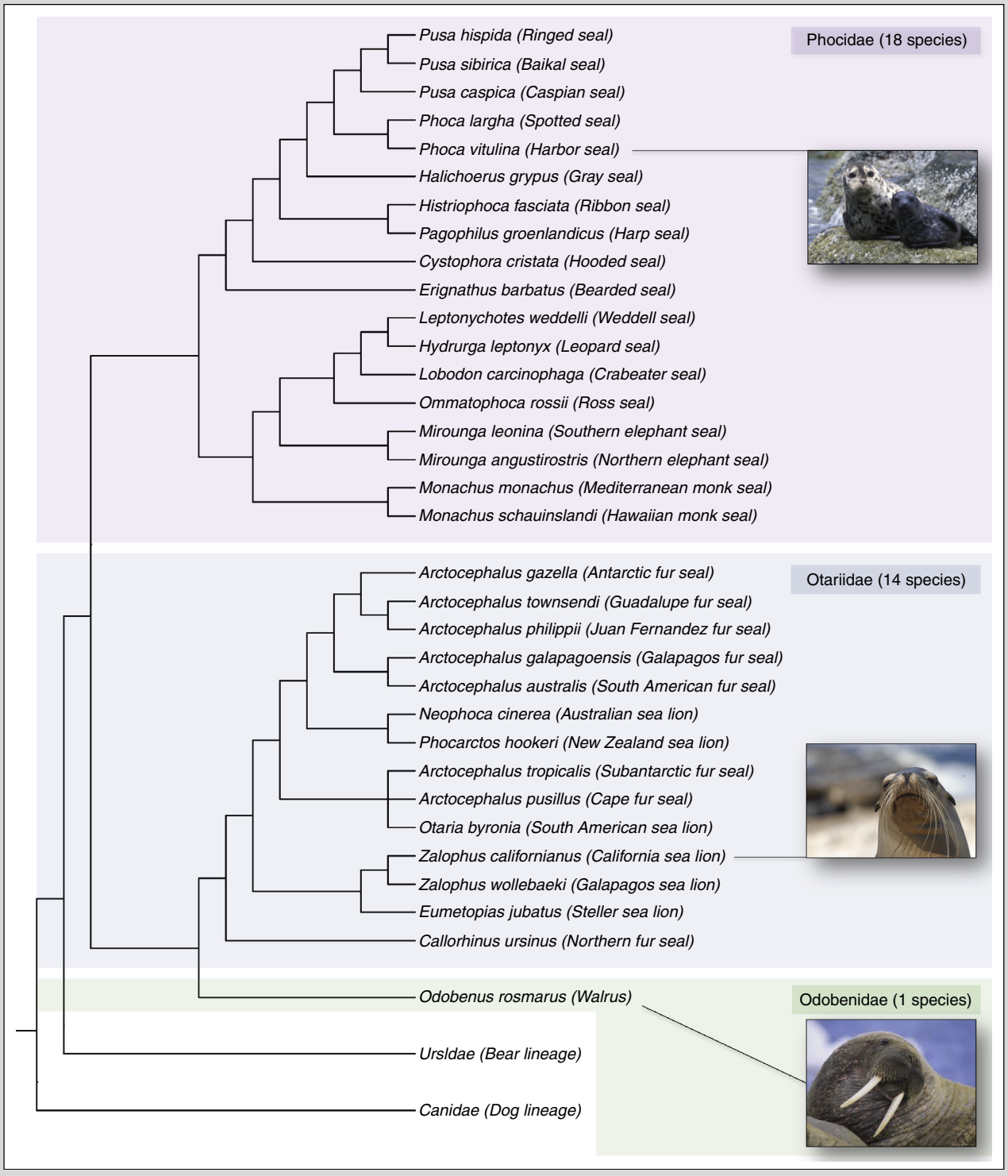
The pinnipeds are notable for their truly amphibious lifestyles — while they forage exclusively under water, they rest, give birth, and care for their young while hauled out on land or ice, often dividing their time equally between land and sea. There are three distinct lineages of extant pinnipeds (Box 1). The true seals (*Phocidae*), sea lions (*Otariidae*), and walruses (*Odobendiae*) share many adaptations as a result of their semi-aquatic habits, including fusiform body shape and flippered appendages [3]. The three clades also share characteristics — independent of those related to growth and maturation — that support the ability to acquire new sounds.

Collectively, pinnipeds produce a variety of sounds, both in air and in water [4,5•]. Many vocalizations have specialized functions related individual recognition [6] or reproductive displays [7••,8,9]; however, the proximal mechanisms supporting sound production are not well described [10•]. Primary adaptations associated with underwater foraging afford a high degree of voluntary breath control to all pinnipeds. In some species, air cycling occurs within the respiratory system and vocal tract, which may include specialized tracheal, pharyngeal, or nasal air sacs, or hypertrophied tracheal membranes, thought to be involved in sound production [10•]. These structures are particularly compliant and able to withstand significant changes in volume under hydrostatic pressure [11]. Although the larynx may be involved in underwater sound production, many species produce typical underwater calls without the release of air [10] that remain constant with changes in depth and corresponding pressures [12]. In addition, the walrus [13,14] and many seals [15–17] have especially fleshy and labile oral tissues used for underwater suction feeding (and in some cases, underwater nursing [18,19]) that further enhance the diversity of their sound emissions through vibration or manipulation of supralaryngeal structures [7••,10•].

Talking harbor seals

The most well-known and popularized account of any mammal modifying its vocalizations on the basis of social experience comes from Hoover, a captive male harbor seal that, as an adult, produced a variety of human expressions including the phases '*Hoova! Hoova! Hey!*',

Box 1 Phylogenetic relationships among the pinnipeds. Three families of the order Carnivora are highlighted and shown in reference to the *Canidae* (canine) and *Ursidae* (bear) outgroups. The *Phocidae* (true seal) lineage has been isolated from other pinnipeds for at least 24 million years. The *Otariidae* (sea lion and fur seal) and *Odobenidae* (walrus) lineages have been separated for at least 18 million years. The evolutionary distances between the clades are noted to emphasize the point that similar traits among these lineages are often the result of convergent adaptations. The species mentioned in the text, including the three examples depicted to the right side of the figure, can be cross-referenced to the phylogenetic tree. The figure is redrawn from [1,2] with divergence dates from [2]. Branch lengths are not scaled to divergence dates. Photos: A. Friedlaender (harbor seal), C. Reichmuth (sea lion), P. Nicklen (walrus).



'*Hello there!*', and '*Hey! Hey! Come over here!*' in a recognizable New England accent. Remarkably, Hoover's speech sounds not only replicated English words, but also the tone, accent, and attitude of a particular individual [20•,21••,22]. Although similar in frequency range to the guttural growls of harbor seals, these vocalizations contained at least twelve appropriately ordered words that were readily discernable to human listeners [7••,23]. The origin of Hoover's imitative vocal behavior is uncertain, but likely stems from his early rearing in a household in Maine [22]. This mysterious but well documented case of a 'talking' seal inspired several subsequent attempts to teach other harbor seals to produce speech-like sounds [7••,21••,23] including Hoover's descendants [K. Streeter, personal communication]. These efforts showed that novel variants of species-typical sounds could be induced through operant conditioning, and learned and repeated by the seals that were trained. However, despite some interesting findings of vocal plasticity and learning produced by these teaching attempts, Hoover's rendition of human speech remains the sole convincing evidence of vocal imitation by a pinniped.

Vocal learning in the laboratory

Pinnipeds can be readily trained and studied in captivity. As a result, much has been learned about their vocal behavior and capabilities [24,25]. Early observational studies showed strong seasonal trends in sound production associated with reproductive cycles in sea lions, and social suppression of this vocal behavior by dominant individuals [26]. Subsequent behavioral conditioning studies demonstrated volitional control of vocalizations in sea lions, seals, and walruses: individuals could be systematically trained using food rewards to produce species-typical vocalizations — and to inhibit these vocalizations — in response to specific arbitrary cues [7••,27–30,31•]. Adret [32•] advocated that the understanding of vocal learning abilities in animals would benefit from the focused application of operant conditioning techniques, and this viewpoint has been supported by empirical studies conducted with pinnipeds. Sea lions [33], gray seals [31•], harbor seals [7••], and walruses [7••] can all learn to produce sounds from their own repertoire in response to different discriminative stimuli, regardless of emotional context, seasonality, or social conditions. Although there have been no findings from the laboratory to rival the vocal mimicry ability demonstrated by Hoover, there is evidence that adult harbor seals [7••] and walruses [34•] can be taught to produce novel sounds and novel sound combinations through reinforcement training that selects for variability in responses. Such training reveals plasticity in sound production that may be modified by social or environmental consequences under natural conditions.

Vocal learning in nature

Several field studies support the hypothesis that vocal learning occurs in free-ranging pinnipeds. Geographic differences in call types or repertoires have been described for underwater rutting vocalizations of Weddell seals [35–37], leopard seals [38], harbor seals [39,40], harp seals [41], and bearded seals [42], raising the possibility that social learning alters sound production in these species [43,44]. With respect to the social transmission of more complex sounds, there is also evidence that male walruses can modify their patterned underwater songs and adopt new song variants over the course of a few breeding seasons [45•]. This finding is reminiscent of the regional song transmission exhibited by humpback whales [46–48], which is often cited as a classic example of mammalian vocal learning [44]. Despite accumulating evidence of geographic or temporal shifts in the vocalizations of some pinnipeds, it remains difficult to attribute these cases to social transmission because of the possible confounds of genetic, developmental, and other contributing factors.

One case that might clarify the bases of regional differences in vocalizations is that of the northern elephant seal. Among the largest of seals, this species was reduced to 10–30 individuals after exhaustive commercial exploitation in the 1800s [49]. Genetic homogeneity due to inbreeding among descendants of the few surviving seals [50] provided the opportunity to assess whether social learning contributes to geographic variability in vocalizations. Le Boeuf and Peterson recorded the breeding displays of male elephant seals from distant colonies after the population had substantially recovered in numbers and expanded in range [51]. These investigators found similarities in the calls of males recorded at particular breeding sites and differences in calls between breeding sites. They asserted these findings as evidence of vocal dialects, and concluded that in the absence of strong genetic variation, that male seals most likely acquired their site-specific vocalizations by learning the calls of surrounding males and adopting the vocal peculiarities of their geographic region.

Further support for the influence of social learning on vocal production comes from southern elephant seals recorded during reproductive development. Similar to their northern counterpart, male southern elephant seals transition from possessing non-structured, variable threat vocalizations as sub-adults to producing stereotyped, fixed calls as adults [52,53••]. However, southern elephant seals are not genetically constrained [54]. Longitudinal recordings of individual southern elephant seal males showed that an adult's vocalization was most similar in type to that of the dominant male present during the sub-adult period of development [53••]. After confirming that shared call types could not be explained by relatedness, Sanvito *et al.* [53••] concluded that vocal learning as a result of auditory exposure best explained this finding. Interestingly, the shift from high plasticity to high specificity in the individual vocalizations of both

northern and southern male elephant seals during ontogeny can be compared to that of songbirds, the phylogenetic group that has most convincingly demonstrated advanced vocal learning capabilities [55].

Isolation experiments would be required to determine whether elephant seals and other pinniped species have a crucial periods of social learning that are important to vocal development. Although such social deprivation studies are not likely to be conducted intentionally, a few opportunistic observations are relevant to this issue. One female northern elephant seal raised in isolation from conspecifics spontaneously developed an unusual call, not present in wild populations, which persisted throughout her lifetime [56]. In another example, a male walrus calf, raised in captivity through adulthood with female but not male conspecifics, developed and seasonally emitted rhythmic components of adult song [57], but failed to produce the organized song structure characteristic of the species [8]. These anecdotes suggest the potential for vocal learning and indicate that further ontogenetic study of pinniped vocal development is warranted.

Comparative implications

Theoretical explanations for the ability of some birds and mammals to modify their calls through learning generally assume primary adaptation for communicative or cognitive function [58•]. It is not yet clear whether this assumption is correct for the pinniped lineages. Like other marine mammals, seals, sea lions, and walruses all demonstrate a high degree of voluntary control over their sound emissions, an ability that is likely related to respiratory adaptations for diving. Plasticity in sound production reported for walruses and seals is further enabled by adaptations of oral structures related to specialized suction feeding and underwater nursing. Such motor affordances enable supralaryngeal filtering of sounds through subtle movements of the mouth, lips, and tongue. The role of other specialized respiratory structures in sound production, including the pharyngeal air sacs of walruses, the tracheal air sacs of ribbon seals, and the enhanced tracheal structures of bearded seals, are intriguing but remain poorly understood [10•].

In a manner analogous to that of odontocete cetaceans, the patterned sequences of knocks, bells, and whistles emitted by male walruses during the breeding season show apparent modification by social experience while bypassing typical mammalian sound pathways entirely. This evidence of 'vocal' song learning in walruses through manipulation of non-laryngeal structures parallels that for 'vocal' learning in some odontocetes cetaceans, who produce socially relevant sounds with highly specialized respiratory structures [10•] and can acquire new sounds through mimicry [59]. Regardless of how communication signals are emitted, it is evident that — in addition to the social and cognitive drivers of vocal learning — environmental adaptations related to aquatic living have influenced the emergence of these capabilities in marine mammals.

Despite mounting evidence favoring their capacity for vocal learning, much remains to be learned about sound production and acoustic communication in seals, sea lions, and walruses. Presently, there is little data available on the natural acoustic repertoires of several species. Future work should further characterize species-typical sound types in the wild, in hopes of understanding the function and ontogeny of acoustic communication under natural conditions. Additionally, some of the rigorous approaches that have been fruitful in evaluating vocal learning capabilities in birds and primates could be further adapted for pinnipeds raised in captivity. Replicated, cross-socialization experiments would allow for control over environmental and genetic influences of vocal development. Operant conditioning of vocal behavior could provide more evidence on the extents and limits of vocal plasticity and learning in different species. The most convincing evidence of vocal learning would be provided by examples of individuals acquiring new sounds following novel auditory exposures. Finally, detailed studies of anatomical and neurobiological mechanisms are required to describe the physical and cognitive template that supports vocal learning capabilities. Based on the available evidence, seals, sea lions, and walruses are unique and productive models for studies of vocal learning. At present, our limited understanding remains insufficient to explain the extraordinary vocal behavior of Hoover the harbor seal.

Conflict of interest statement

Nothing declared.

Acknowledgements

This manuscript was inspired by many thoughtful and spirited discussions with Dr. R. Schusterman, whose studies of both primates and pinnipeds helped to shape our views about the mechanisms of vocal learning. We thank Dr. P. Cook for his comments during the preparation of this manuscript, and A. Rouse for assistance with Box 1.

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