RELATIONSHIPS BETWEEN VOCAL ONTOGENY AND VOCAL TRACT ANATOMY IN HARBOUR SEALS (PHOCA VITULINA)

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Understanding the origins and evolution of human speech benefits from a multidisciplinary and comparative approach. Research on animal models has already provided some valuable insight into the biological underpinnings of vocal communication. One important focus in the field of animal communication is sound production. The current literature on this topic hosts a great number of studies on avian species and our closer relatives, non-human primates. However, many pinniped species have been reported to have wide vocal repertoires, often producing call types in specific behavioral contexts (Ralls et al., 1985; Mathevon et al., 2017; Charrier et al., 2009). In fact, the vocal abilities of pinnipeds are better than was historically believed (Ravignani et al., 2016). Moreover, pinnipeds are phylogenetically closer to humans than the well-studied birds (O'Leary et al, 2013) and share some anatomical similarities to the human vocal apparatus (Fitch, 2000). Here, we: (i) report on longitudinal data on vocal ontogeny in harbor seal

pups, (ii) complement the bioacoustic findings with results from a large anatomical data set of larynges, and (iii) critically compare our findings with available literature on harbor seal sound production. Taken together, they suggest that phocids are good candidates for animal models in future research on the evolution of human speech. In harbor seals (*Phoca vitulina*), young pups produce mother attraction calls which play an important role in parent-offspring recognition. Female reproductive success relies almost entirely on the accurate identification of offspring within the colony after foraging trips (Insley et al., 2003). Studies conducted on harbor seal mother attraction calls found that these calls are individually distinctive (Renouf, 1984; Perry & Renouf, 1988) and that mothers can recognize the calls of their offspring shortly after birth (Renouf, 1985). It is still uncertain which call parameters are used by the mother to recognize the pup and whether she regularly needs to update her acoustic template of the pup vocalisations. In fact, previous studies on the ontogeny of mother attraction calls have shown that this call type changes in acoustic (Khan et al., 2006; Sauvé et al., 2015) and temporal structure (Ravignani et al., 2018), with potential for vocal production learning. Using longitudinal call data, we found that many call features covary with age and sex, but not with body length. Our findings also further provide evidence for the importance of the fundamental frequency and its modulation as individualised call parameters that could play an important role in successful parent-offspring recognition. As pups grow, the development of the anatomical structures making up the vocal tract will impose constraints on the acoustic signals produced. The acoustic allometry framework suggests that vocal tract length is constrained by body size, but vocal fold length is not (confirmed in seals using anatomical data; Ravignani et al. 2017). In light of the source-filter theory, acoustic parameters shaped by the filter such as formants would then be better at conveying body size information than the fundamental frequency, a source parameter (Fant, 1960). Our anatomical measurements of harbor seal vocal tract and larynx indicate that neither vocal tract nor vocal fold length correlate with body size. Body size may be a fundamental driver of acoustic signals (Martin et al., 2017), but future allometry studies will shed more light on which call features accurately encode size information and how these interact with vocal development, plasticity and learning.

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References

- Charrier, I., Pitcher, B. J., & Harcourt, R. G. (2009). Vocal recognition of mothers by Australian sea lion pups: individual signature and environmental constraints. *Animal Behaviour*, 78(5), 1127-1134.
- Fant G. (1960). Acoustic Theory of Speech Production. The Hague, The Netherlands: Mouton & Co. Publishers.
- Fitch, W. T. (2000). The evolution of speech: A comparative review. *Trends in Cognitive Sciences*, 4, 258-267.
- Insley, S. J., Phillips, A. V., & Charrier, I. (2003). A review of social recognition in pinnipeds. *Aquatic Mammals*, 29(2), 181-201.
- Khan, C. B., Markowitz, H., & McCowan, B. (2006). Vocal development in captive harbor seal pups, Phoca vitulina richardii: Age, sex, and individual differences. *The Journal of the Acoustical Society of America*, 120(3), 1684-1694.
- Martin, K., Tucker, M. A., & Rogers, T. L. (2017). Does size matter? Examining the drivers of mammalian vocalizations. *Evolution*, 71(2), 249-260.
- Mathevon, N., Casey, C., Reichmuth, C., & Charrier, I. (2017). Northern elephant seals memorize the rhythm and timbre of their rivals' voices. *Current Biology*, 27(15), 2352-2356.
- O'Leary, M.A., Bloch, J.I., Flynn, J.J., Gaudin, T.J., Giallombardo, A., Giannini, N.P., Goldberg, S.L., Kraatz, B.P., Luo, Z.X., Meng, J. and Ni, X. (2013). The placental mammal ancestor and the post–K-Pg radiation of placentals. *Science*, *339*(6120), 662-667.
- Perry, E. A., & Renouf, D. (1988). Further studies of the role of harbour seal (Phoca vitulina) pup vocalizations in preventing separation of mother–pup pairs. *Canadian Journal of Zoology*, 66(4), 934-938.
- Ralls, K., Fiorelli, P., & Gish, S. (1985). Vocalizations and vocal mimicry in captive harbor seals, Phoca vitulina. *Canadian Journal of Zoology*, 63(5), 1050-1056.
- Ravignani, A., Fitch, W., Hanke, F. D., Heinrich, T., Hurgitsch, B., Kotz, S. A., Scharff, C., Stoeger, A. & de Boer, B. (2016). What pinnipeds have to say about human speech, music, and the evolution of rhythm. *Frontiers in Neuroscience*, 10, 274.
- Ravignani, A., Gross, S., Garcia, M., Rubio-Garcia, A., & de Boer, B. (2017). How small could a pup sound? The physical bases of signaling body size in harbor seals. *Current Zoology*, 63(4), 457-465.
- Ravignani, A., Kello, C. T., de Reus, K., Kotz, S. A., Dalla Bella, S., Méndez-Aróstegui, M., Rapado, B., Rubio-Garcia, A. & de Boer, B. (2018). Ontogeny of vocal rhythms in harbor seal pups: an exploratory study. *Current Zoology*, 65(1), 107-120

- Renouf, D. (1984). The vocalization of the harbour seal pup (Phoca vitulina) and its role in the maintenance of contact with the mother. *Journal of Zoology*, 202(4), 583-590.
- Renouf, D. (1985). A demonstration of the ability of the harbour seal PhocaVitulina (L.) to discriminate among pup vocalizations. *Journal of Experimental Marine Biology and Ecology*, 87(1), 41-46.
- Sauvé, C. C., Beauplet, G., Hammill, M. O., & Charrier, I. (2015). Acoustic analysis of airborne, underwater, and amphibious mother attraction calls by wild harbor seal pups (Phoca vitulina). *Journal of Mammalogy*, 96(3), 591-602.