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Strange Seal Sounds: Claps, Slaps, and Multimodal Pinniped Rhythms

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BEYOND VOCAL COMMUNICATION

Within mammalian bioacoustics, vocal communication has received much attention. Efforts to understand sound production often focus on sounds generated *via* apparatuses that specifically evolved to phonate, such as the larynx. However, while mammals mostly perceive sounds *via* one organ, the ear, they can produce sounds *via* limbs, tails, flippers, tools, and several other mechanisms which, at first, may not seem to have primarily evolved for sonation (Tyack and Miller, 2002; Frankel, 2009; Clark, 2016). For example, kangaroo rats drum their foot to communicate (Randall, 1984), while non-human primates drum using artificial tools (Remedios et al., 2009), resonant surfaces (Ravignani et al., 2013), and their hands (e.g., Dufour et al., 2015). Also aquatic mammals can produce a variety of non-vocal sounds (such as whistles, snorts, and others; Tyack and Miller, 2002). These sound production modes may enable communication even when laryngeal phonation is ineffective or impaired (Munoz and Blumstein, 2012; Partan, 2017). Research on sound production *beyond phonation* is key to properly characterise the richness of animal communication.

Recent exploratory work (Hocking et al., 2020) provides an example of non-vocal sound production in a pinniped: grey seals (*Halichoerus grypus*) clapping their fore flippers underwater, a signalling behaviour previously attributed to vocalising. While Hocking et al.'s observation is limited to few events, it is reminiscent of previous, seemingly unrelated work reporting water-slapping behaviour in other species, including a close relative, the harbour seal (*Phoca vitulina*) (Venables and Venables, 1957; Newby, 1973; Hanlan, 1998; Hayes et al., 2004; see also humpback whales: Dunlop et al., 2010). The preliminary data reported by Hocking et al. naturally invite a host of questions, whose answers rely on a characterisation of when, how often, and under what circumstances these claps occur. Are they a frequent or seasonal phenomenon? Are they modulated by social context? Furthermore, the mechanism of knock production should be considered: while clapping the fore flippers can generate loud knock-like sounds, other mechanisms have also been proposed (e.g., in walruses: teeth clacking, tongue movement, or suction; Sjare and Stirling, 1981; Sjare et al., 2003; Reichmuth et al., 2009; Larsen and Reichmuth, 2012). This is a good starting place for future research, though, clearly, more observations are required to answer these questions. In particular, the field should perform more empirical, foundational work. This should (1) provide robust observations and descriptions in addition to anecdotes, (2) evaluate context, timing and seasonality in the production of percussive sounds, (3) determine which sex produces these signals and potential sexually dimorphic characteristics, and (4) design rigorous experiments that test potential function of percussive sounds. Once these absolutely necessary foundations are established, we suggest exploring more complex topics related to bioenergetics, signal evolution, multimodality, and rhythm production/perception. In this Opinion piece, we discuss these more hypothetical research directions, which however can only be performed after more thorough biological descriptions of the basic phenomena.

MECHANISMS FOR (DIS)HONEST SIGNALLING?

If replicated, this research may encourage to re-evaluate previous evidence. Could previously recorded "vocalisations [which] sounded like a loud piercing clap" (pg. 61, McCulloch, 2000) and "knocks" (pg. 2213, Asselin et al., 1993) in grey seals have been actual underwater claps? A hypothetical reassessment of the production mechanism underlying a sound would entail several implications. Awareness of the sound source could be helpful to test potential sound-body allometric links.

One testable hypothesis is that claps may be a partly dishonest signal as they give away limited information about body size while their source level is surprisingly high, especially compared to captive individuals (Wahlberg et al., 2002). This hypothesis dovetails with some empirical evidence of water claps functioning as aggressive and territorial behaviours in harbour seals (Hayes et al., 2004), since claps have been so far observed mostly in males and in presence of other seals (for example in Weddell seals: Russell et al., 2016). Furthermore, limited underwater visibility, as reported by Hocking et al. (2020), would promote a signalling strategy concealing body size. To test whether clapping is a dishonest signal, field studies should investigate the conditions under which underwater claps take place (e.g., water visibility, social context).

Conversely, claps could be honest signals, since the strength of the animal or the size of its flipper may determine the intensity of the clap and the perceived loudness. This second hypothesis would comply with allometric scaling (e.g. Garcia et al., 2017): if sound-producing structures scale with body size, honest signalling ensues (Garcia and Ravignani, 2020). Larger individuals should also be able to produce stronger or (visually) larger claps (Partan, 2013). Anatomical observations in, and tests of allometry across, individuals producing underwater claps might contribute to disentangling these contrasting hypotheses.

EXAPTATION AND REPURPOSING OF BIOMECHANICAL PROCESSES

This research underlines the process of evolutionary exaptations for communicative purposes (Gould and Lewontin, 1979; Buss et al., 1998). Seal clapping "may be a ritualised version of a swimming stroke" (pg. 1, Hocking et al., 2020). In other words, a movement evolved for essential in-water displacement (Fish, 2000; Kuhn and Frey, 2012) may have been repurposed for acoustic communication (see also Clark, 2016). As a parallel, the tree drumming of woodpeckers is now a purely communicative signal, probably repurposed from what originally was a simpler foraging behaviour (Dodenhoff et al., 2001; Miles et al., 2018, 2020; Garcia et al., 2020). Both seals and woodpeckers may provide fascinating examples of the evolution and repurposing of biomechanical processes. At what point in pinniped phylogeny may swimming strokes have been recruited for communication, and did this happen in multiple pinniped species? Communicative non-vocal sounds have been observed in several pinnipeds (Schusterman and Van Parijs, 2003; Russell et al., 2016[1]); more specifically, claps have been reported, to our knowledge, in grey seals (e.g., Hocking et al., 2020), harbour seals (Venables and Venables, 1957; Newby, 1973; Hanlan, 1998; Hayes et al., 2004), and walruses (e.g., Reichmuth et al., 2009). Underwater recordings of similar non-vocal sounds in other pinnipeds might contribute to answering this question. With limited evidence it is difficult and unwise to generalise to all pinnipeds. However, one may hypothesise that the swimming style of phocids, propelled by their hindflippers, may free up their foreflippers for communicative purposes, while the swimming style of otariids, using their foreflippers to "fly" underwater, may have hindered their exaptation for communication (Kuhn and Frey, 2012).

MULTIMODALITY AND ENERGETICS

Most work mentioned above advocates multimodal approaches to communication. Multimodality is sometimes neglected, with some research programs only focusing on one production and one perception channel (Slocombe et al., 2011). Grey seals exhibit a communicative behaviour that is motorically produced (bypassing specialised laryngeal neurons) and might be perceived acoustically at long ranges and visually at short ranges (Wahlberg et al., 2002; Ravignani et al., 2016; Hocking et al., 2020). As the larynx is hidden from sight, the act of mammalian vocalisation is invisible to the receiver (cf. Fitch and Reby, 2001; Higham and Hebets, 2013; Nowak, 2020). A clap, instead, could potentially reach the receiver visually, acoustically, or haptically, also allowing for multisensory integration.

Multimodality also entails energetic considerations. While laryngeal phonation is relatively cheap, other modes of controlled sound production may be more energy-expensive. Indeed, research on the energetic costs of communication generally assumes higher expenditure for multi-modal as compared to uni-modal interactions (Partan, 2013). For example, in sympatric wolf spiders, multi-modal displays (as in *Schizocosa ocreata*) require higher energy levels than unimodal displays (as in *S. Rovneri*) (Cady et al., 2011). Rather than being disadvantageous, such a costly display might serve as an honest signal indicating a male's good condition (Zahavi, 1975; Byers et al., 2010; Mitoyen et al., 2019). Yet, questions concerning the relative costs and benefits of pinniped sound production *via* clapping and slapping (Beier and Wartzok, 1979; Wahlberg et al., 2002; Gillooly and Ophir, 2010) remain open, as well as their function (e.g., territorial, reproductive, etc.; Russell et al., 2016). If they indeed relate to mating, one may expect a variation in clapping/slapping abilities due to ontogeny (Rado et al., 1991), an increase at puberty onset, a cyclical variation entrained with mating seasonality or a decline due to senescence (Soulsbury and

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[1] We are here referring to jaw claps, which the authors originally grouped as vocalisations for methodological reasons.

Halsey, 2018). The reliable evidence of such seasonal and developmental trends in the vocal displays of seals (e.g., Van Parijs et al., 1999; Galimberti et al., 2008; Reichmuth and Schusterman, 2009) may invite comparisons with non-vocal displays and facilitate the understanding of their function. By combining quantitative techniques (e.g., Gillooly and Ophir, 2010), allometric considerations (Garcia and Ravignani, 2020), and field observations (Hocking et al., 2020), some of these questions may be addressed.

COMMUNICATIVE RHYTHMS IN THE MILLISECOND-SECOND RANGE

More observations on the clapping behaviour of grey seals, their characteristics, and context of use are needed: Are these sounds produced occasionally or routinely? Do they contain rhythmic components? The presence of rhythmic features in claps would allow to link Hocking et al.'s (2020) finding to research on communicative rhythms and could spur a subfield of ecologically-relevant percussive rhythms in mammals. Recently, cross-species evidence has shown rhythmic capacities, sometimes employed for communication, in pinnipeds (Cook et al., 2013; Rouse et al., 2016; Mathevon et al., 2017; Ravignani, 2019). "Rhythm" is not meant here in its circadian sense, studied for instance in ecology, but instead as "temporal structure" at short timescales (de Reus et al., 2020). When little information is encoded in the frequency domain, as in seals' claps and slaps (Wahlberg et al., 2002; Hocking et al., 2020), this temporal structure could emerge in sound signals and serve to encode information. Within animal cognition and behaviour, evidence for rhythm in pinnipeds is particularly interesting (Ravignani et al., 2016; Wilson and Cook, 2016). In fact, pinnipeds constitute a key taxon to test a cross-species hypothesis which links rhythm and vocal learning capacities (Patel, 2006). Still, work on rhythm in mammals is relatively limited, especially when compared to the richness of rhythm production research, for instance, in insects and frogs (Greenfield, 1994; Hartbauer and Römer, 2016). While these species can produce extremely fast rhythms, the rate and complexity of non-vocal rhythms in mammals may be hampered by the physical limitations occurring when moving a limb (but see, for example, Randall, 1984 on the foot drumming behaviour of kangaroo rats). Mammalogists and comparative psychologists may still be inspired and benefit from decades of work on rhythm and percussive behaviour in arthropods and anurans (Ravignani et al., 2014). In particular, since the 1960's, entomologists and then herpetologists have been measuring the communicative rhythms of their species with almost millisecond accuracy (e.g., Buck and Buck, 1968). Avian researchers followed, while mammalogists and primatologists are slightly lagging behind (de Reus et al., 2020). Applying concepts such as phase resetting and period correction, for instance, to communicative rhythms in apes could also inform the evolution of rhythmic capacities in our own species (cf. Bittman, 2020).

CONCLUSIONS AND FUTURE WORK

Hocking et al.'s (2020) finding, albeit preliminary, can inspire at least six hypothetical strands of future work. First, to establish a base from psychophysics, *propagation* experiments could test how far the sound of grey seals clapping carries underwater (Wahlberg et al., 2002); this strand of research would help disentangle the role of claps as either honest or dishonest signals, as the latter may be more relevant at short distances (e.g., Tyack and Miller, 2002). Second, *biomechanics* and metabolic work could pinpoint the energetic costs and evolutionary benefits of clapping (Fish, 2000; Kuhn and Frey, 2012); this research should consider the context in which a signalling behaviour occurs (e.g., occasional vs. prolonged use; environmental and social conditions). Third, a larger dataset (McCulloch, 2000) would allow onset-to-onset temporal measurements to investigate whether claps may feature putative *rhythmic structures*, linking either claps within a series (e.g., based on their inter-onset intervals) or repeated series performed in succession. After that, to test for homologies and analogies, comparative analyses could be attempted with water slaps in harbour seals and other pinniped percussive behaviour (Wahlberg et al., 2002). Fourth, it would be important to test how nearby conspecifics perceive claps. Therefore, connecting to recent work on pinniped timing (Heinrich et al., 2016, 2020), one could explore how grey seals *perceive temporal information* in sequences of claps. Fifth, one could target the proximate and ultimate *function of clapping*, and its potential role in sexual or natural selection. Sixth, methodological advances in neuroimaging techniques (e.g., Cook et al., 2021) may be employed to inform on the neural underpinnings of cross-modality and their interface with the physiological and physical constraints imposed on flippers by their original function (i.e., swimming). All this work, we stress, can only come once more fundamental research is performed to tackle basic biological questions. For the time being, we will keep looking for more percussive performances by these fascinating mammals.

AUTHOR CONTRIBUTIONS

AR and LV developed the arguments and co-wrote the paper. All authors contributed to the article and approved the submitted version.

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