

## RHYTHMIC PERCEPTION, PRODUCTION AND INTERACTIVITY IN HARBOUR AND GREY SEALS

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Comparative studies on rhythmic animal behaviour can help understand the evolutionary origins of rhythm cognition underlying many human behaviours, including speech (Kotz, Ravignani & Fitch, 2018) and conversational interaction (Pika, Wilkinson, Kendrick & Vernes, 2018). Pinnipeds are a particularly promising clade for comparative investigations in the vocal domain (Ravignani et al., 2016), showing remarkable vocal flexibility (Ralls et al., 1985; Reichmuth & Casey, 2014) as well as rhythmic capacities (Cook et al., 2013; Mathevon et al., 2017). The variability in these traits across species guides hypotheses from evolutionary neuroscience, that postulate mechanistic connections between vocal learning and rhythm (Kuypers, 1958a, 1958b; Jürgens, Kirzinger, & von Cramon, 1982; Patel & Iversen, 2014). In seal pups, who are born and weaned in large breeding colonies on land, vocal rhythmicity can be functionally explained by their socio-ecology: a pup calling for its mother's attention may avoid acoustic masking by vocalizing in turns with nearby conspecifics (Ravignani, 2018). Here we disentangle different aspects of seal pup rhythm cognition to better describe individual timing patterns in turn-taking choruses. We present data from four studies on harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*), testing rhythm perception, production, and interactivity.

In the first study, we tested 20 wild-born harbour seals regarding their capacity to distinguish rhythmic properties in a listening task. The experiment used a set-up inspired by the head-turn preference procedure from infant development studies (Nelson et al., 1995). We measured the number of looks and look duration of individual seals towards the playback stimulus, comparing experimental manipulations for 4 properties: rhythmic regularity (random vs. isochronous), tempo (slow vs. fast), duration (long vs. short calls) and sex (calls produced by a female vs. a male pup). Regularity, tempo, and duration significantly affected the behavioural measures. These results show the importance of rhythmicity as a call property affecting harbour seals' behavioural responses, and support their fine-grained perceptual discrimination capacities in the temporal domain.

The second study (Ravignani et al., 2018) examined rhythmicity in spontaneously produced calls by 3 individual wild-born harbour seal pups, exploring the ontogeny of temporal call organization over the course of several weeks. Analyses on call duration, inter-onset interval, and inter-peak interval showed that call rhythms evolve, with some properties becoming more categorically structured over time. These results demonstrate harbour seals' productive rhythmic flexibility in development and suggest a vocal production system particularly suitable for interactive settings.

Next, we tested the rhythmic interactivity of harbour seal pup vocalizations in a playback experiment eliciting vocal responses. Manipulating regularity, tempo, and identity of the playback calls, we measured the absolute time and relative phase of individual pups' responses. We contrasted the experimental data with results from agent-based simulations to compare several alternative call timing strategies. The results show that seal pups interactively time their vocal responses to conspecific calls, avoiding overlap by taking turns.

Our final study investigates rhythmic interactions in spontaneous settings, using similar analyses in a different species. We analyzed interactive call timing in multitrack recordings of grey seal pups housed in groups. By studying groups of multiple individuals, we applied the analysis techniques from the previous studies in a more ecological setting, and explored how individual call timing strategies contribute to a group-level chorus.

We conclude that seals both perceive and produce vocal rhythmicity, without explicit training. Our results suggest that seal pups interactively time their calls, such that they vocalize in turns, maximizing individual conspicuousness by minimizing acoustic masking. Both harbour and grey seal pup vocalizations are known to have individually distinctive spectral properties, which are used in mother-offspring recognition (Perry & Renouf, 1988; McCulloch & Boness, 1999). We argue that socio-ecological pressures for individual conspicuousness and distinguishability shape both the spectral and temporal dimensions of seal pup vocal communication. Pinnipeds provide a useful model for convergently evolved rhythmic traits, and our results might inform future cross-species work on timing in communicative behaviours — including human speech.

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