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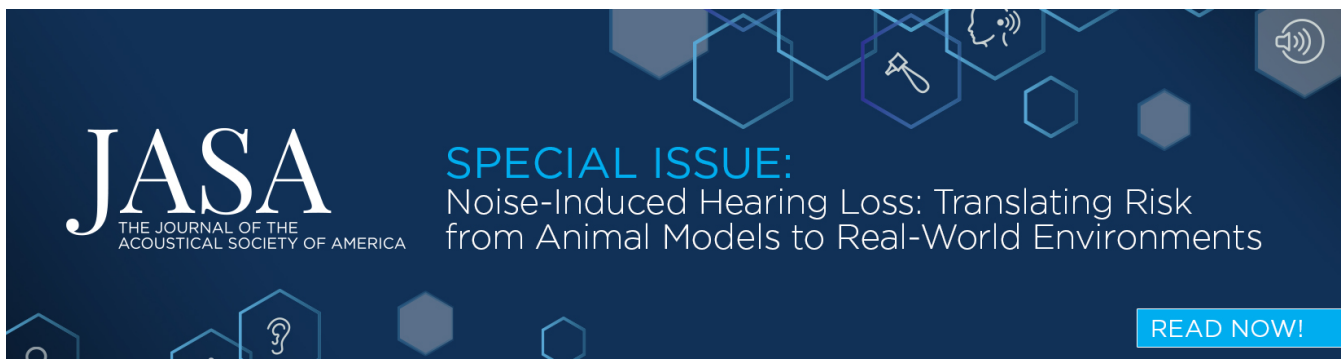
Comment on "Temporal and spatial variation in harbor seal (*Phoca vitulina* L.) roar calls from southern Scandinavia" [J. Acoust. Soc. Am. 141, 1824−1834 (2017)] (L)

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In their recent article, Sabinsky and colleagues investigated heterogeneity in harbor seals' vocalizations. The authors found seasonal and geographical variation in acoustic parameters, warning readers that recording conditions might account for some of their results. This paper expands on the temporal aspect of the encountered heterogeneity in harbor seals' vocalizations. Temporal information is the least susceptible to variable recording conditions. Hence geographical and seasonal variability in roar timing constitutes the most robust finding in the target article. In pinnipeds, evidence of timing and rhythm in the millisecond range—as opposed to circadian and seasonal rhythms—has theoretical and interdisciplinary relevance. In fact, the study of rhythm and timing in harbor seals is particularly decisive to support or confute a cross-species hypothesis, causally linking the evolution of vocal production learning and rhythm. The results by Sabinsky and colleagues can shed light on current scientific questions beyond pinniped bioacoustics, and help formulate empirically testable predictions. © *2018 Acoustical Society of America.*
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A recent article published in the *Journal of the Acoustical Society of America* (Sabinsky *et al.*, 2017) investigated sound production in adult harbor seals (*Phoca vitulina*). The research employed passive acoustic monitoring to record vocalizations in different geographic areas of the Eastern Atlantic. In one of the three study sites, recordings were performed over two consecutive years. Data collection was aimed at testing the presence and drivers of call heterogeneity. Established findings in the ethology and ecology of harbor seals enabled the authors to infer that recorded vocalizations were produced by sexually mature males. The authors found an impressive amount of variation over time and geographical areas, which could not be simply explained by geographical and genetic segregation (Sabinsky *et al.*, 2017). This piece of research is exemplar for its methodological rigor, breadth of scope, and unexpected results. One of the results of the paper concerns the patterning of temporal structure in seals' vocalizations. This was touched upon by the authors, but deserves a more in-depth discussion.

In the title of the paper, and often throughout the manuscript, the word "temporal variation" is used to mean monthly, seasonal, or yearly variation. An alternative meaning of "temporal" is the fine-grained variability in durational parameters of calls in the *millisecond-second range*. While the paper by Sabinsky and colleagues provides interesting data on both these meanings of "temporal patterning," emphasis—here as in previous studies (Van Parijs *et al.*, 1999; Van Parijs *et al.*, 2003)—seems to lay upon monthly, seasonal, or yearly variation. However, this research (Sabinsky *et al.*, 2017) also provides important insights into the temporal behavior of harbor seals in the millisecond-second range (Buhusi and Meck, 2005). In other words, this paper offers a first step in characterizing *rhythmic* properties (defined as pertaining to temporal structure) of harbor seals' natural vocalizations (Ravignani *et al.*, 2016).

Understanding temporal information in harbor seals' calls is of particular interest for a number of reasons. Apart from field-specific motivations, harbor seals' timing is a—yet untested—potential cornerstone (Patel, 2014; Ravignani and Cook, 2016) of a cross-species hypothesis formulated in cognitive neuroscience. The "vocal learning—beat perception and synchronization hypothesis" states that species capable of vocal production learning have direct neural connections between auditory and motor areas of the brain, in turn allowing fine rhythmic production skills (Patel, 2006). Cross-species support for this hypothesis comes from joint presence of vocal learning and rhythm in several bird species and humans, and joint absence of vocal learning and rhythm in other non-human primates (Patel *et al.*, 2009; Schachner *et al.*, 2009). Vocal production learning is a rare trait, but at least four taxonomic groups of mammals show this capacity (Janik and Slater, 1997; Schusterman, 2008). Pinnipeds are one of these clades (Reichmuth and Casey, 2014). On the one hand, harbor seals (Ralls *et al.*, 1985), and other pinniped species (Sanvito *et al.*, 2007; Stansbury, 2015) are capable of vocal production learning. On the other hand, there is evidence for rhythm in California sea lions (Cook *et al.*, 2013; Rouse *et al.*, 2016) and northern elephant seals (Mathevon *et al.*, 2017). This makes testing rhythm capacities in harbor seals (and vocal production learning in sea lions) quite crucial to support or refute the vocal learning—beat perception and synchronization hypothesis (Ravignani

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et al., 2016; Wilson and Cook, 2016). If harbor seals were shown capable of fine-grained acoustic rhythmic capacities, the hypothesis would be supported (Ravignani and Cook, 2016; Ravignani *et al.*, 2016). If, instead, timing were relatively unimportant for harbor seals, while sea lions were shown incapable of vocal production learning, the hypothesis would be confuted and would need to be reformulated (Patel, 2014; Wilson and Cook, 2016).

Evidence from a range of pinniped species suggests research on timing, rhythm, and vocal learning in this taxonomic group is promising. Northern elephant seals were recently found to rely on both rhythmic and timbral features in vocal agonistic encounters (Mathevon *et al.*, 2017). California sea lions produce series of barks that are quite stereotyped in spectral features, but exhibit rhythmic isochrony and heterogeneity (Schusterman, 1977), i.e., patterns of barks and silences repeat themselves metronomically, but their tempos differ across social situations and individuals. In addition, the same species can be trained to produce fine-tuned timed behavior (Cook *et al.*, 2013; Rouse *et al.*, 2016). Within this overall picture, no suggestive evidence for vocal timing in adult harbor seals was available until this recent paper in the *Journal of the Acoustical Society of America* (Sabinsky *et al.*, 2017).

Among the whole recorded acoustic data, the analyses focused on one vocalization type: underwater roars. A number of methodological precautions ensured robustness of the results. For instance, "individual roars were analyzed in a randomized order, rather than location by location, to reduce the risk of bias arising from a possible gradual change in classification criteria over the course of the analysis" (Sabinsky *et al.*, 2017, pp. 1826−1827). Based on the waveform and spectrogram, the roars were segmented in four parts: a pulse train, a start growl, a roar burst, and an end groan. While the roar burst was present in all annotated roars, the other three segment types were not systematically present in all roars. Apart from extracting a large number of spectral features, the *duration of the whole roar* and the *duration of the roar burst* segment were computed and entered in successive analyses.

Descriptive statistics from this dataset (Table I in Sabinsky *et al.*, 2017) already suggest interesting temporal properties of harbor seals' roars. First of all, the total

duration of the roars exhibits yearly and geographical heterogeneity. Likewise, duration of roar bursts appears to vary across location and year of sampling. In addition, although the number of independent data points (four, corresponding to the number of seasons or locations) prevents performing a meta-statistical test, longer calls do not appear to correspond to longer roar bursts (at least on average, see Fig. 1). If this intuition is correct, it implies that heterogeneity in total roar duration is attributable not only to roar bursts (vertical dimension in Fig. 1), but also to heterogeneity in the length of pulse trains, start growls, and end groans taken together (horizontal dimension in Fig. 1).

Inferential statistics, by means of discriminant function analysis, reveal a similar picture (Table II in Sabinsky *et al.*, 2017). First, as the authors observe, the two durational variables (total roar and roar burst) exhibit the highest canonical loadings. In other words, temporal features are what make roars most discriminable. In addition, each of the two variables loads on a different canonical component. In particular, total roar duration (corresponding to the sum of the horizontal and the vertical coordinate of each data point in Fig. 1) has a high loading on the first canonical function, but little on the second or third canonical functions. Conversely, the duration of roar bursts loads negatively on the first canonical function, but positively and strongly on the second and third canonical functions. In other words, roars' and roar bursts' durations seem to vary relatively independently from each other (see Fig. 1). This offers some preliminary support of rhythmic structuring of roar sequences, at least from the production perspective (as opposed to the perception perspective). To better understand this point, suppose that both durational variables had instead similar loadings on the same canonical function. This would mean that they covaried across sampled roars, so that a longer roar would feature a proportionally longer roar burst. (In this scenario, the squares in Fig. 1 would lie on a diagonal.) In turn, this would mean that duration of pulse trains, start growls, and end groans taken together would carry little potential for information encoding. As this is not the case, we can speculate that all combinations of short/long sections of a roar are in principle possible (corresponding to an even distribution of squares in the Cartesian plane in Fig. 1), dramatically increasing the
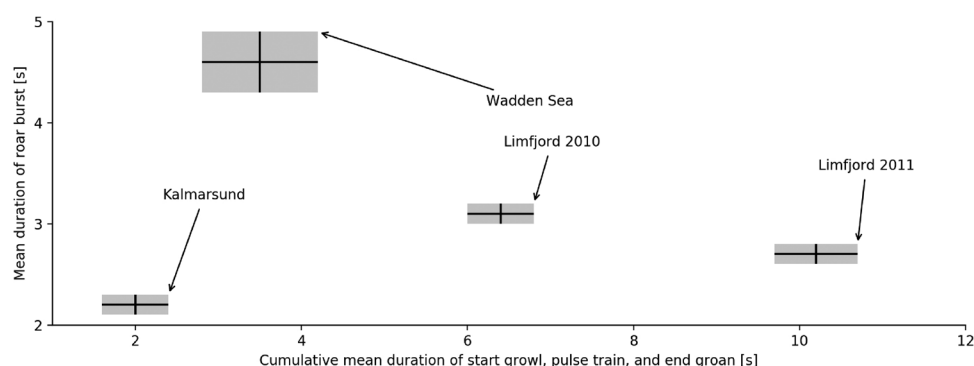

FIG. 1. Joint variability of duration of roar bursts (vertical axis) and cumulative duration of start growls, pulse trains, and end groans (horizontal axis). Black crosses indicate means, which were obtained by reporting (vertical axis) and transforming (horizontal axis) the originally reported data (Table I in Sabinsky *et al.*, 2017). Grey shadings indicate 1 SE as originally reported (vertical axis) and the sum of SE between durational variables (horizontal axis).

number of ways durational intervals can be potentially combined to communicate (see Fig. 2 and Ravignani and Madison, 2017).

Temporal information in harbor seal vocalizations might have an important communicative role from puppyhood. From the production side, harbor seal pups emit mother attraction calls during the first weeks of life (Renouf, 1984). The duration of these calls: (1) exhibits inter-individual variability, (2) increases with age, and (3) is modulated by the sex of the animal (Perry and Renouf, 1988; Khan *et al.*, 2006; Sauvé *et al.*, 2015a; Ravignani, 2018). Evidence from the perception side is quite indirect. No study to date has investigated how harbor seal pups perceive temporal features in coetaneous calls, or how they react to them. However, indirect evidence suggests that adult females might use temporal information in distinguishing among pups. An adult female was trained to discriminate pairs of alien pup calls which differed both in temporal and spectral features (Renouf, 1985). The experiment was successful, but left an open question: did the female seal rely more on spectral or on durational features to correctly discriminate calls (compare with the more refined design in Mathevon *et al.*, 2017)? Likewise, playback experiments provided strong evidence that mothers spontaneously recognize the sound of their own pup vs other pups (Sauvé *et al.*, 2015b). However, no *post hoc* analysis of the calls used for playbacks was performed; such analyses could have exactly tested which acoustic characteristics (e.g., timbral, rhythmic, harmonic) had enabled successful individual recognition.

As the authors rightfully acknowledge (Sabinsky *et al.*, 2017), their recording methods were completely different across sites. Different sampling rates, in particular, could affect differences in measured spectral properties of the calls. However, the temporal properties of vocalizations should be quite comparable: even the recordings with the lowest sampling rate (20 kHz), and the successive down-sampling (5 kHz), provide a temporal resolution well above the timing detection capacities in mammals (Meck, 1996; Matell and Meck, 2000; Buhusi and Meck, 2005; Grondin, 2010). More in general, the authors provide several "killjoy explanations" to account for the seasonal and geographic variation in their data, such as different recording methods or equipment. However, while these potential confounds may apply to spectral properties of the signal, they should nonetheless leave their rhythmic properties unaffected.

While reviewing different hypotheses that could explain their results, the authors acknowledge that genetic and geographic factors cannot account alone for the variability in recorded roars (Sabinsky *et al.*, 2017). In particular, they
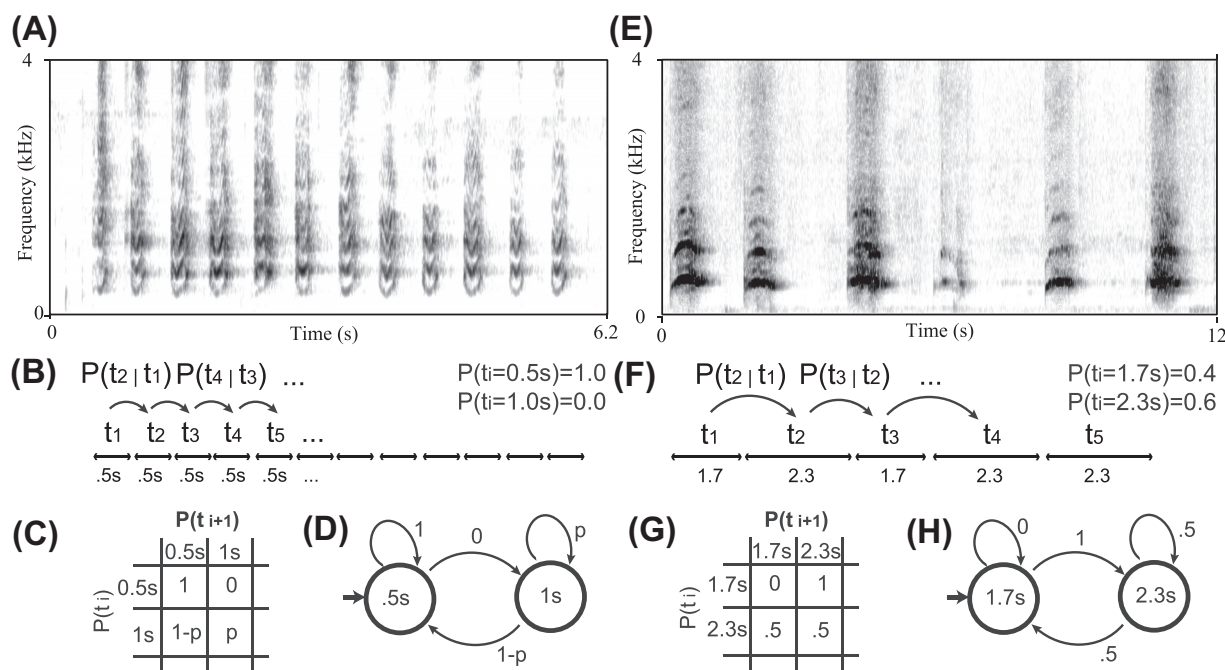

FIG. 2. Some possible approaches to represent temporal structure in pinniped calls. (A) Spectrogram of a California sea lion (*Zalophus californianus*) bark sequence, recorded with a Zoom H6 and visualized with a Fourier window length of 0.02 s (adapted from Fig. 5 in Ravignani and Madison, 2017). Notice the isochronous rhythm, i.e., how the inter-onset interval between adjacent barks is quite constant (see also Ravignani and Madison, 2017). (B) Time series of intervals ($t_1, t_2, \ldots$), corresponding to the recording visualized in (A). Intervals induce absolute probabilities—on the right side—and transition probabilities such as $P(t_2 \mid t_1)$, which is a shorthand for $P(t_2 = x \mid t_1 = y)$—on the left side. Computed durations in B (and F, see below) are only approximate and for illustrative purposes (see also Fig. 4 and details in Ravignani and Madison, 2017). (C) Transition matrix, which summarizes all the information obtained from computing transition probabilities. As the 1 s inter-onset interval was never observed in the data, probabilities in the second row are parameterized as (1-p, p), where p is a real number between 0 and 1. Previous literature would suggest that p in California sea lions is close to 1 (Schusterman, 1977). (D) A probabilistic finite state machine, an equivalent representation to transition matrices, can generate rhythmic patterns as those in panels (B) and (C). (E) Spectrogram of mother attraction calls produced by an Eastern Atlantic harbor seal pup (*Phoca vitulina vitulina*), recorded with a Zoom H6 (Fourier window length = 0.02 s). Notice how the temporal structure appears less isochronous than that of sea lion barks in (A) (see also Ravignani, 2018). (F) Time series of intervals ($t_1, t_2, \ldots$), corresponding to the call series visualized in (E). In this recording of a harbor seal pup inter-onset intervals belong roughly to two durational classes ($\approx$1.7 s and $\approx$2.3 s). (G) Transition matrix summarizing transitions between inter-onset intervals of harbor seal pups' calls. (H) A probabilistic finite state machine, depicting equivalent information to that summarized in (G).

find that the seasonal variation in acoustic parameters is greater or equal than the geographical variation. This suggests behavioral flexibility, which could either be induced hormonally or through different social contexts experienced by the animals across seasons. Could vocal learning be a possible explanation for this vocal heterogeneity? A captive harbor seal and other pinnipeds have been shown capable of vocal production learning (Ralls et al., 1985; Sanvito et al., 2007; Reichmuth and Casey, 2014; Stansbury, 2015); although not the most parsimonious explanation in this case, vocal learning deserves proper empirical testing in wild harbor seals. Traditionally, research on vocal learning across species has focused more on spectral rather than temporal parameters of vocalizations. In fact, the majority of pinniped bioacoustics has neglected the temporal dimension of vocalizations. Recent findings in pinnipeds (Mathevon et al., 2017) and birds (Norton and Scharff, 2016) have highlighted the relevance of rhythm and timing in vocal learning. Sabinsky and colleagues' (2017) findings provide one more reason to focus on timing while investigating pinniped vocal learning.

Related to individual vocal flexibility, from the methods used in this study, one cannot ascertain whether the analyzed recordings encompassed several vocalizations from few seals or few vocalizations each from one of many seals. Until now, many published studies have employed passive acoustic monitoring to describe pinniped vocal repertoires (e.g., Nikolich et al., 2016). This was essential to provide, among others, indirect evidence for existence of temporal structure in harbor seals' roars (Sabinsky et al., 2017). After this first stage, the field would now need to prioritize collection of recordings from individuals of known identity. In particular, by following few individuals and tracking their vocalizations over time, two hypotheses could be tested. First, harbor seals are believed to be vocal learners, and longitudinal recordings of single individuals could test this in the wild, and map the vocal development and flexibility of these animals. Second, by recording not only individual seals' calls, but also those of other individuals within hearing range, one could test whether spatial and social proximity between individuals mutually shapes vocalizations. In addition, the source-filter theory framework has been rarely applied to harbor seal vocal production (Fant, 1960; Ohala, 1984; Ravignani et al., 2017). Analyzing vocalization using this framework will enable understanding which acoustic features are attributable to laryngeal mechanics, and which to upper vocal tract dynamics, and whether other phonation mechanisms are at play.

The authors put forward an intriguing hypothesis. They suggest that the duration of roars could be a biological signal of health state. In fact, harbor seals are susceptible to lungworm parasites, which might hinder their respiratory capacities, and hence shorten the duration of their vocal emissions (Sabinsky et al., 2017). This hypothesis is testable by performing spirometry (Fahlman et al., 2017) on lungworm patients and healthy animals, and comparing the duration of vocalizations between groups. Alternatively, roar duration in harbor seals could serve functions similar to those seen in other pinnipeds. In male leopard seals, for instance, temporal patterning of underwater call production is linked to indicators of body size (Rogers, 2017). In male Australian fur seals, temporal patterning instead partly subserves individual recognition (Tripovich et al., 2008). Population studies and playback experiments could enable testing whether longer roars predict higher mating success, and hence whether roar duration might be a sexually selected trait (Nowicki and Searcy, 2014).

To conclude, the study of rhythm, timing and vocal learning in harbor seals is an exciting, growing field. On the one hand, recent results of rhythmic variability (Sabinsky et al., 2017) provide cues for future playback experiments and focused recordings. On the other hand, hypotheses from neuroscience and evolutionary biology offer an interdisciplinary platform to put harbor seal research in the bigger picture of evolutionary bioacoustics.

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