

Timing of Antisynchronous Calling: A Case Study in a Harbor Seal Pup (*Phoca vitulina*)

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Alternative mathematical models predict differences in how animals adjust the timing of their calls. Differences can be measured as the effect of the timing of a conspecific call on the rate and period of calling of a focal animal, and the lag between the two. Here, I test these alternative hypotheses by tapping into harbor seals' (*Phoca vitulina*) mechanisms for spontaneous timing. Both socioecology and vocal behavior of harbor seals make them an interesting model species to study call rhythm and timing. Here, a wild-born seal pup was tested in controlled laboratory conditions. Based on previous recordings of her vocalizations and those of others, I designed playback experiments adapted to that specific animal. The call onsets of the animal were measured as a function of tempo, rhythmic regularity, and spectral properties of the playbacks. The pup adapted the timing of her calls in response to conspecifics' calls. Rather than responding at a fixed time delay, the pup adjusted her calls' onset to occur at a fraction of the playback tempo, showing a relative-phase antisynchrony. Experimental results were confirmed via computational modeling. This case study lends preliminary support to a classic mathematical model of animal behavior—Hamilton's selfish herd—in the acoustic domain.

Keywords: rhythm, vocal communication, synchrony, selfish herd, timing

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Precise timing of signals is an important dimension in animal communication. Studies on temporal structure have historically focused on individual timing. In contrast, timing can play a role in group interaction by coordinating calls between different individuals (Wilson & Cook, 2016). Across animal species, mechanisms for call timing are often shaped by the species' socioecology (Greenfield & Roizen, 1993; Mathevon, Casey, Reichmuth, & Charrier, 2017). In some species, individuals adjust their timing to vocalize before nearby conspecifics and increase their conspicuousness (Greenfield & Roizen, 1993). Other species show forms of contagious calling (reacting to conspecifics' calls), full synchronization, partial overlap, antisynchrony, and so forth (Ravnani, Bowling, & Fitch, 2014). In particular, antisynchrony consists of

an animal adjusting its next call onset to be a fraction of the *previous* calling period of the conspecific (Hamilton, 1971; Ravnani, 2014).

Harbor seals are very vocal in the first few weeks after birth (Sauvé, Beauplet, Hammill, & Charrier, 2015). During this time, seal pups live in large mother–pup groups; there, pups call to be noticed by adult females (Perry & Renouf, 1988). Calling concurrently in large groups poses a strategic problem: Many calls at approximately the same time can acoustically mask each other. Individual seal pups could solve this problem of overlap by adjusting the timing of their call onset. Such call adjustment would allow an animal to maintain conspicuousness, if it avoids overlap with a neighbor, and hear the neighbor more clearly (Grafe, 1999; Greenfield, 2015).

In harbor seals, a vocally flexible species (Ralls, Fiorelli, & Gish, 1985), call timing is relevant to understanding the dynamics of communication in a potentially crowded dimension: time. Here, I test the hypothesis that a harbor seal pup possesses timing capacities enabling antisynchronous alternation (Hamilton, 1971; Ravnani, 2014). In other words, I hypothesize the time lag between focal and conspecific call onsets to be a fraction of the conspecific's previous interonset interval (IOI). This is equivalent to an IOI-adjusted lag, that is, a constant phase, so that the focal animal's onset avoids overlap with the conspecific. If so, the expected acoustic outcome in a chorus of harbor seal pups would be antisynchronous alternation of calls over time.

Before the experiment, computational models served to understand behavioral mechanisms underlying seals' timing (Greenfield & Roizen, 1993). Alternative hypotheses (Table S1 in the online supplemental materials) were explored by simulated agents that

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would vocalize in response to conspecifics' calls according to different behavioral strategies (Figure 1A and Equations 1–4 in the online supplemental materials). I hypothesized that a seal pup would vocalize according to the simulated *antisynchronous* seal (Figure 1A, in turn following the formulation of Hamilton's selfish herd model: Hamilton, 1971; Ravignani, 2014), testing whether the call onset corresponded to a fraction of the previous playback period. Experimental data were then collected and compared with the simulated seals.

Experimental Methods

Subject

The female harbor seal pup was born in the wild. At the estimated age of 7 days, she was brought into rehabilitation (cause: orphanage) at Sealcenter Pieterburen, the Netherlands. Playback experiments were performed between the 29th and 37th day of life. The animal was individually housed in a pool situated in a one-room cabin. Whereas seals are usually housed in pairs, this experiment took advantage of the rare occurrence of individual housing.

Stimuli

The experiment comprised six *sessions*, each separated by 24 to 48 hr. Each session, lasting approximately 15 min, consisted of 18 *sequences*, concatenated in random order and separated by 12 s of silence. Each sequence was one of all possible $3 \times 2 \times 3$ combinations of the three factors described in the following text (see predictions in Table 1 and Table S2 in the online supplemental materials). Each sequence consisted of 21 identical single calls, concatenated and interleaved with silence of variable length according to different rhythmic patterns (tempo and rhythmicity conditions in the following text), resulting in 20 IOIs. Sequences varied along three experimentally manipulated factors (Figure 1B). *Tempo* corresponded to the average IOI of a sequence: slow = 2,418 ms, medium = 1,983 ms, and fast = 1,548 ms (Cook, Rouse, Wilson, & Reichmuth, 2013). The "medium tempo" condition equaled the mean spontaneous call rate of this animal recorded and analyzed 24 hr before the experiment (see the online supplemental materials; Ravignani, 2018). *Rhythmicity* corresponded to interval regularity. Sequences were either perfectly isochronous, with call onsets occurring metronomically in time, or random, with IOIs sampled (every session) from a normal distribution with average IOI as in the isochronous condition, and standard deviation equaling 20% of that IOI (Patel, Iversen, Bregman, & Schulz, 2009a, 2009b). *Identity* was the identity of the pup whose call was concatenated and broadcasted to the focal pup. The three calls used as tokens had been previously recorded from three 3-week-old pups: one from the focal pup, one from a coetaneous pup from the same coastal region but different area, and a third one from a pup from a different region. As geography may affect call features in this species (Sabinsky, Larsen, Wahlberg, & Tougaard, 2017; Sauv   et al., 2015), this design tried to ensure that the pup would respond to at least one call type (either very similar or dissimilar to hers), while attempting to minimize habituation (Perry & Renouf, 1988). Mean power intensity was normalized across calls.

Apparatus and Experimental Procedure

Vocalizations and playbacks were recorded in air with a unidirectional microphone Sennheiser ME-66 (frequency response: 40 Hz–20 kHz; Sennheiser electronic GmbH & Co. KG, Wedemark, Germany see the online supplemental materials). Playbacks were broadcasted from a JBL Flip 2 bluetooth speaker (JBL, Los Angeles, CA; frequency response: 100 Hz–20 kHz) hidden from the seal's sight and connected to an iPhone 5S (Apple, Cupertino, CA). Matching previous measurements in harbor seal pups (Sauv   et al., 2015), Sound Pressure Level (SPL) at 2 m (the seal's approximate location) reached 87 dB (C-weighted; silence: 48 dB). After all equipment was in place and working, playback was triggered remotely.

Data Processing and Statistics

The recorded audio file, containing playbacks and calls, was annotated in Praat on two separate tiers (see the online supplemental materials). Data were imported (Buschmeier & Wlodarczak, 2013; Ravignani, 2018) via Python, processed in Parselmouth (Jadoul, Thompson, & de Boer, 2018), and analyzed in R. Independent variables were session, sequence, rhythmicity, tempo, and playback identity. Dependent variables were number of vocalizations, calls/s, mean and variance of vocalization period, lag, and phase of calls. Individual analyses of variance (ANOVAs) tested the effect of playback variables on calls/s, mean and variance of call period, and lag. ANOVAs were only performed on the lowest-Akaike Information Criterion model, that is, the model surviving stepwise model selection (see the online supplemental materials). Circular statistics (Cook et al., 2013) tested the effect of experimental playback variables on call phase. The Rayleigh test tested phase uniformity and whether call onsets had a systematic, possibly synchronous, relation with playback onsets. Circular ANOVAs tested whether circular distributions of phases differed between experimental conditions. Statistical tests showing significance appear in Table 1 and S2 in the online supplemental materials and are contrasted with hypotheses.

Computer Simulations and Alternative Mechanisms

Four mechanisms were compared. The *arousal* mechanism exemplifies how hearing more calls triggers production of more calls (feature not shown in Figure 1A, but incorporated in the simulation). Apart from an equal number of calls, the call onsets of the focal animal (square) and that of the conspecific or playback (circle) have no systematic relation (Figure 1A). The *antisynchrony* mechanism shows how the call occurs shortly after the conspecific's call, and at a fraction k of its call period. This mechanism might be mostly reactive (see supplementary Discussion in the online supplemental materials). This model predicts that, in an experiment, timing of playbacks will affect absolute call timing (lag) but not relative call timing (phase) to avoid overlap (Hamilton, 1971; Ravignani et al., 2014). In the *phase-reset* mechanism, the focal animal "resets its internal clock" in response to a conspecific's call, to anticipate the next call of the conspecific (Greenfield & Roizen, 1993). This model predicts a constant, stable relation between the calls' onsets of playback and focal. Equivalently, this model predicts that the lag is fixed and equals

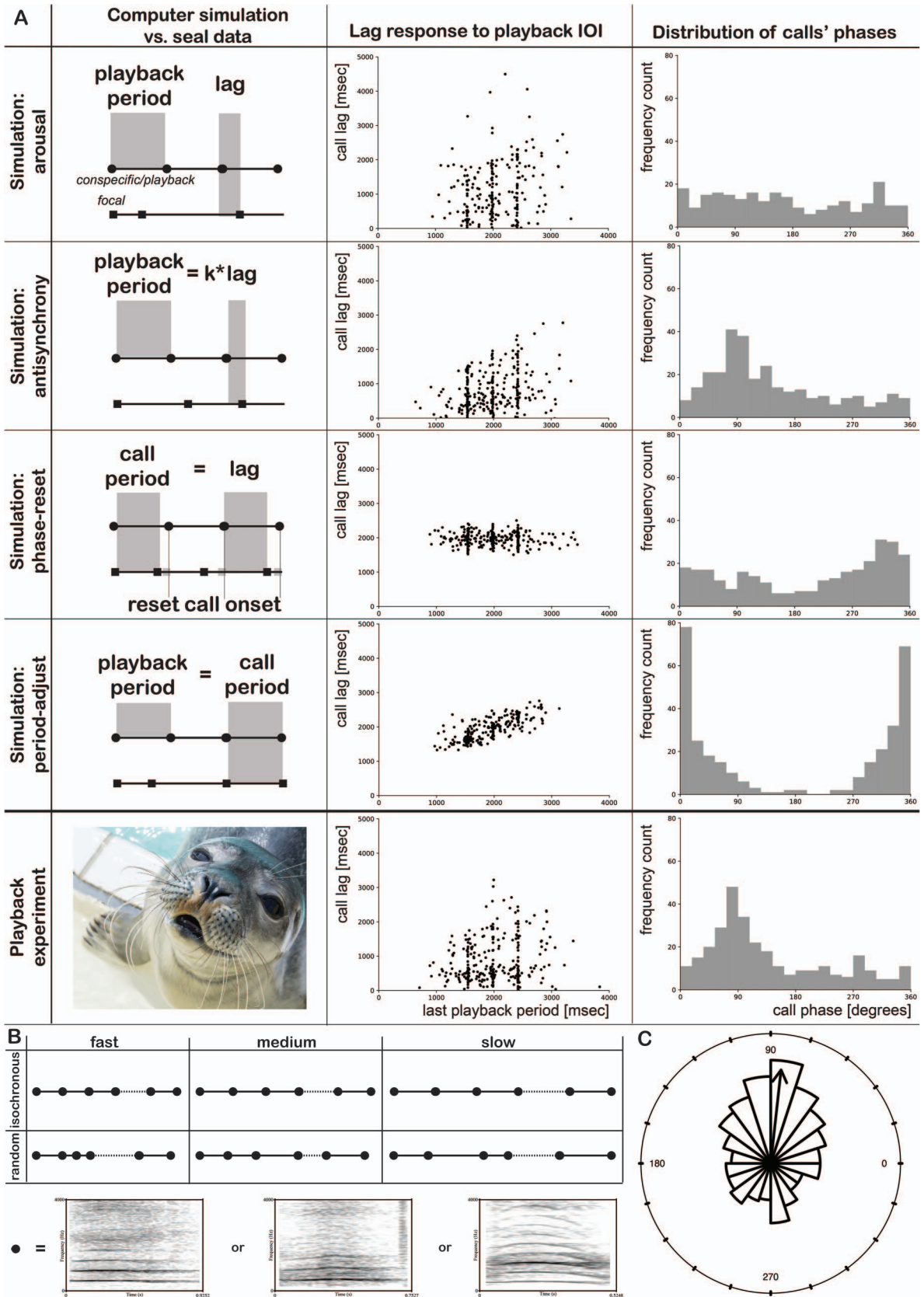


Figure 1 (opposite)

Table 1
Predictions and Results on How Experimentally Manipulated (Figure 1B) and Recorded Variables Relate to the Antisynchrony Hypothesis

Measured (dependent) variables	Predicted effect of experimentally-manipulated (independent) variables	Experimental outcome: Results of the statistical models consistent or inconsistent with the antisynchrony hypothesis
Number of vocalizations	Tempo	Number of vocalizations = playback identity (ANOVA, $F = 4.8, p < .05$) + session number ($F = 6.2, p < .001$)
Calls/s	Tempo	Calls/s = playback identity ($F = 3.7, p < .05$) + tempo ($F = 5.6, p < .01$)
Mean and variance of vocalization's interonset interval	None	None
Lag	Tempo	Lag = tempo (ANOVA: $F = 9.8, p < .001$) + playback identity ($F = 3.2, p < .05$)
Phase	-Tempo	Phase = playback identity (circular analysis of variance: $\chi^2 = 6.8, p < .05$); phase = -tempo (circular analysis of variance: $\chi^2 = .7, p > .68$)
Relation between playback and call onset: test if phase equals a uniform—as opposed to a unimodal—distribution on a circle, and if lag equals 0	Unimodal	Unimodal (Rayleigh test of uniformity with unspecified mean direction; $z = .36, p < .001$)
	≠0	≠0 (Rayleigh test with specified mean $\mu = 0$; $z = .03, p > .16$)

Note. ANOVA = analysis of variance. Negation sign “-” denotes a lack of effect—hypothesized or experimentally found. Bold font indicates similarities between predictions and experimental data. ANOVAs' degrees of freedom were as follows: two for tempo and playback identity and four for session number (residuals' degrees of freedom in the [online supplemental materials](#)). Two possible cases of trend ($p \sim .079$) are not reported in the table but may deserve future investigation, namely, the effect of tempo on mean and variance of vocalization's interonset interval.

the focal call period. The *period-adjust* mechanism predicts the focal animal to adjust its phase and period to those of the conspecific (Merker et al., 2009; Wing et al., 2014), so that the periods of the focal and conspecific coincide. This mechanism predicts a measurable difference between rhythmicity conditions: Isochronous stimuli are predictable, whereas random stimuli sequences are not.

Results

Amount, Rate, and Period of Calling

Playback identity and session significantly predicted the number of vocalizations (Table 1). Playback identity and tempo significantly predicted the number of calls/s, consistent with antisynchrony and all other hypotheses. No experimentally manipulated variable had a significant effect on vocalization period (playback

period on vocalization period: $F = 2.6, p > .07$) or its variance (session, sequence, and identity on vocalization period: all $F < 2.9, p > .07$), refuting the period-adjust hypothesis.

Lag and Phase

Playback identity and tempo significantly predicted lag, consistent with the antisynchrony and phase-reset hypotheses (though refuting the arousal hypothesis). In fact, both antisynchrony and phase-reset hypotheses predict that longer conspecific IOI (tempo) will lead to the focal animal further delaying her call with respect to the last playback (increased lag). The only significant predictor of phase was the identity of the playback. Notably, neither tempo nor rhythmic regularity (together with session and sequence, all $\chi^2 < 18, p > .12$) significantly predicted phase. Hence, tempo affected lag but not phase. This is consistent with antisynchrony, but inconsistent with all other hypotheses: If the lag of the focal is

Figure 1 (opposite). (A) Computer simulations (first four rows) and experimental data (last row) compared across mechanisms, lag-period plots, and phase histograms (columns). The first four rows describe and simulate the following timing mechanisms: arousal, antisynchrony, phase-reset, and period-adjust. The leftmost column sketches the timing mechanisms as functions of call onsets of the focal animal (square) and onsets of the conspecific or playback (circle). The central column plots the lag versus previous playback interonset interval, and the rightmost column plots the phase distribution, for each simulation and for the experimental data. Note the close match between the experimental (fifth row) and simulated antisynchrony data (second row). However, the antisynchrony simulation also contains a stochastic, arousal-based component: This additional mechanism may partly explain the observed behavior. Additional explanations are in Table S1 in the online supplemental materials. (B) Experimental conditions along which playback patterns varied: tempo (fast, medium, or slow), rhythmic regularity (isochronous or random), and identity of the pup (the three calls shown in the spectrograms). (C) Rose plot, showing the circular distribution of relative vocalization phases during the playback experiment. Every bin corresponds to 18° (Cook et al., 2013). The playback onset is denoted by 0° . Lag (not shown) is the time between call and previous playback. The black arrow denotes the focal animal's average phase, that is, the angular mean of vocalizations' onsets: This is the ratio of lag and the IOI of the previous playback, modulo this IOI times 360, resulting in a unit vector with an angle on the circle. See the online article for the color version of this figure.

a constant fraction of the playback period, equivalent to a fixed phase, altering the period (tempo) should affect the lag but not the phase. Contrasting these findings (Table 1), we can infer that the lag and number of calls are adjusted to the tempo, whereas the phase is not affected by tempo. In other words, the ratio between lag and IOI is constant on average, suggesting a form of adjustment to keep phase, rather than lag, constant.

Phase Distribution and Synchrony

I tested for the presence of a nonrandom relation between playback and call onsets. The distribution of relative phase angles differed from uniform circular, consistent with antisynchrony among others. I tested for presence of synchronization between playback and call, that is, phase statistically equal to 0: Playbacks and calls were not synchronized predictively. In fact, the mean angular phase of all pooled data was 83.69° (Figure 1C). A Rayleigh test with specified mean $\mu = 83.69^\circ$ confirmed this specific nonuniform phase ($z = 0.30, p < .001$), consistent with antisynchrony. These two tests, showing that the phase distribution is nonuniform with a mean different from 0 are consistent with antisynchrony, and inconsistent with the three alternative hypotheses.

Results of Computer Simulations

All computer-simulated seals produced the same number of calls as in the corresponding experimental sessions (see the [online supplemental materials](#)). Therefore, as in the experiments, only some randomly sampled playbacks elicited simulated calls. Figure 1A compares the data from experiment and antisynchrony simulation in a lag-period space (scatterplots) and the distributions of phases (histograms). In both visualizations, the antisynchronous simulated seal closely matches the experimental data. Moreover, among the simulations of alternative mechanisms (Figure 1A), the antisynchronous simulation is the closest match to the experimental data. A two-sample Kolmogorov–Smirnov test quantitatively compared the distributions of all experiment–simulation and simulation–simulation pairs of ratios (rightmost column in Figure 1A). Significance in this test implies a difference between distributions. All tests were significant (all $D > .17, p < .001$) except for the experimental–antisynchrony comparison ($D = 0.7, p = .36$): The distribution of the actual seal pup matches the simulated antisynchronous pup but statistically differs from all other simulated seals. Among alternative models, the antisynchronous seal behaves the closest to the real seal.

Discussion

This experiment and model show that a seal adjusted her timing behavior depending on conspecifics' playbacks, and beyond simple arousal. Pups' calls are directed toward mostly silent mothers, who normally only nurse their own pup (Perry & Renouf, 1988; Sauv e et al., 2015). Hence, it is partly surprising that a pup, which is not the intended receiver of a signal, adjusts her call timing depending on a conspecific. In addition, the seal appears to time her calls to occur at approximately one-quarter of the playback period (83.69° , with 360° equaling the previous IOI; Figure 1C). This suggests a relative-duration, rather than an absolute-duration,

adjustment. Instead of performing predictive synchronization, the seal systematically desynchronizes—as in a musical canon. This flexibility in call timing suggests that this pup's calls are timed depending on conspecifics' call timing, possibly to enhance conspicuousness (see [supplementary Discussion](#) in the online supplemental materials). In this experiment, Hamilton's herd mechanism (Hamilton, 1971) is reversed and applied as a way of maximizing individual conspicuousness (Greenfield, 2015). The inverse mechanism, as actually intended in the original model of spatial clustering where each caller minimizes conspicuousness (Hamilton, 1971), leads instead to perfect synchrony in computer simulations (Ravignani et al., 2014). This hypothetical synchrony, not observed here but in several other species (Ravignani et al., 2014), would still constitute an epiphenomenon of competition among individuals (Greenfield & Roizen, 1993), rather than a group effort to synchronize.

Animal rhythm experiments often obtain evidence revealing animals' inability to synchronize (Kotz, Ravignani, & Fitch, 2018; Schachner, Brady, Pepperberg, & Hauser, 2009). In this case study, synchrony does not stand out as the most spontaneous form of vocal timing. Conversely, the harbor seal pup showed a consistent antisynchronous behavior. This may inform future research aimed at testing synchrony: Potential failure in *training* seals to synchronize could be attributable to other forms of temporal coordination being more *spontaneous* than synchrony for this species. Failure to reject hypotheses might arise from collateral factors, avertable by adapting experimental tasks to the particular species and individual. I tailored my experimental stimuli to the focal animal, by using her previously recorded natural vocalization period and broadcasting conspecifics' vocalizations instead of less ecologically relevant sounds (Greenfield & Roizen, 1993; Mathevon et al., 2017). Although this did not appear to introduce experimental confounds, it might have made the task easier to accomplish for the animal. This approach can potentially open up avenues for the comparative study of timing, also by departing from human-centered synchrony and embracing the richness of other temporal coordination patterns across species (Wilson & Cook, 2016).

Experimental stimuli included variation in spectral characteristics (the identity factor, bottom of Figure 1B) to try and slow down habituation to the signals. Indeed, the amount of calling did not decrease over sessions. These spectral characteristics also affected call timing. Although the effect of playback identity on the focal lag is not robust (see additional analyses in the [online supplemental materials](#)), similar spectro-temporal interactions were found in other species (Grafe, 1999), including pinnipeds (Mathevon et al., 2017). Future experiments should use a full factorial design to establish whether the (weak) effect of spectral features on call timing found here is due to individual or geographical variation in conspecific voices.

Future research should address some outstanding questions. First, as my results are limited to only one individual, playback experiments should test whether they generalize to more harbor seals and other pinnipeds. Second, multitrack group recordings should be collected to test whether pup choruses indeed follow, in their dynamical timing, the antisynchronous strategy found in the experiment and model. For instance, if antisynchronous timing generalized to group vocalizations beyond "duets," a four pups' chorus should show onsets at $0^\circ/90^\circ/180^\circ/270^\circ$. Third, audio–

motor synchronization experiments should be performed in harbor seals (Wilson & Cook, 2016). Success in synchronization will show that, even though one state of temporal coordination might be the default one, possibly because of ecological relevance, other states might be reached via cognitive or vocal flexibility.

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