Title: Flexible control of vocal timing in bats enables escape from acoustic interference

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Abstract: In natural environments, background noise can degrade the integrity of acoustic signals, posing a problem for animals that rely on their vocalizations for communication and navigation. A simple behavioral strategy to combat acoustic interference would be to restrict call emissions to periods of low-amplitude or no noise. Using audio playback and computational tools for the automated detection of over 2.5 million vocalizations from groups of freely vocalizing bats, we show that bats (*Carollia perspicillata*) can dynamically adapt the timing of their calls to avoid acoustic jamming in both predictably and unpredictably patterned noise. This study demonstrates that bats spontaneously seek out temporal windows of opportunity for vocalizing in acoustically crowded environments, providing a mechanism for efficient echolocation and communication in cluttered acoustic landscapes.

One Sentence Summary: Bats avoid acoustic interference by rapidly adjusting the timing of vocalizations to the temporal pattern of varying noise.

Main Text:

The capacity for short-term vocal plasticity is advantageous in contexts where ambient noise is abundant, as it can enable acoustic jamming avoidance (*1*). Ambient noise presents a special challenge to echolocating bats, who rely on the returning echoes of their sonar pulses for navigation and in addition maintain social dynamics in part through the exchange of communication calls.

It is well established that bats possess impressive vocal plasticity, freely modifying various parameters of their vocalizations (*2*) such as the amplitude (known as the "Lombard effect") (*3–7*), duration (*4, 8–10*), repetition or emission pattern (*8, 9, 11*), complexity (*8*), and spectral content (*6, 12, 13*) (but see (*14–16*)) in response to playback of interfering noise. Yet, how bats overcome interference from moment-to-moment fluctuations in the amplitude of continuous background noise, a situation analogous to their natural environment, has received less attention. *Carollia perspicillata* bats live in colonies of up to hundreds of individuals where the acoustic landscape is densely populated by vocalizations which all share overlapping spectral and temporal properties.

In this study, we investigated the ability of bats to adapt the timing of their vocalizations to overcome acoustic jamming, using temporally predictable and unpredictable noise, across two experiments. We hypothesized that bats would preferentially vocalize in periods of low amplitude in amplitude modulated noise, in line with a metabolically efficient signal optimization strategy. Humans

regularly employ a similar strategy, such as when a pair of speakers pause their conversation so as not to be drowned out by the blaring siren of a passing ambulance.

We observed that freely vocalizing bats flexibly adapt the timing and rate of their calling to be inversely proportional to dynamically-changing background amplitude levels. This temporal jamming avoidance behavior emerged in the presence of both predictably and unpredictably patterned noise, implying an underlying auditory-vocal circuit that does not require entrainment for optimizing call timing. In addition, calling behavior is modulated not only by instantaneous amplitude levels but also by more global sound statistics (i.e., second-order temporal patterns), suggesting that bats learn and exploit properties of the acoustic environment which unfold over time.

Bats cluster call onsets toward amplitude troughs in broadband masking noise

In *experiment 1*, we recorded vocalizations from groups of bats during a silent baseline and during playback of two types of broadband white noise featuring different carrier frequencies (a 10-96 kHz "full-band masker", which overlaps with both communication and echolocation call frequencies, and a 50-96 kHz "half-band masker", which overlaps in frequency only with echolocation calls) (Fig. 1a-b). Audio recordings from our colony of captive bats showed that spontaneous vocalizations feature a prominent rhythm at approximately 11 Hz (fig. S1). Thus, we amplitude modulated the two maskers at 8 Hz and 15 Hz to see if the bats could adjust to slower or faster rates, respectively (Fig. 1c). We labelled detected vocalization onsets with the instantaneous phase of the modulation cycle at the corresponding time point (Fig. 1e). For the silent baseline, we labelled vocalizations according to a cosine model of a fictitious amplitude modulation with the same rate as the corresponding masking noise. Based on visual inspection of a subsample of our data (table S1), and the fact that these calls were primarily short in duration (median $= 3.4\ ms$, IQR $= 3.3\ ms$, 75% of calls $< 5\ ms$, across both experiments), we estimate that most (~ 90%) of detected vocalizations were echolocation pulses.

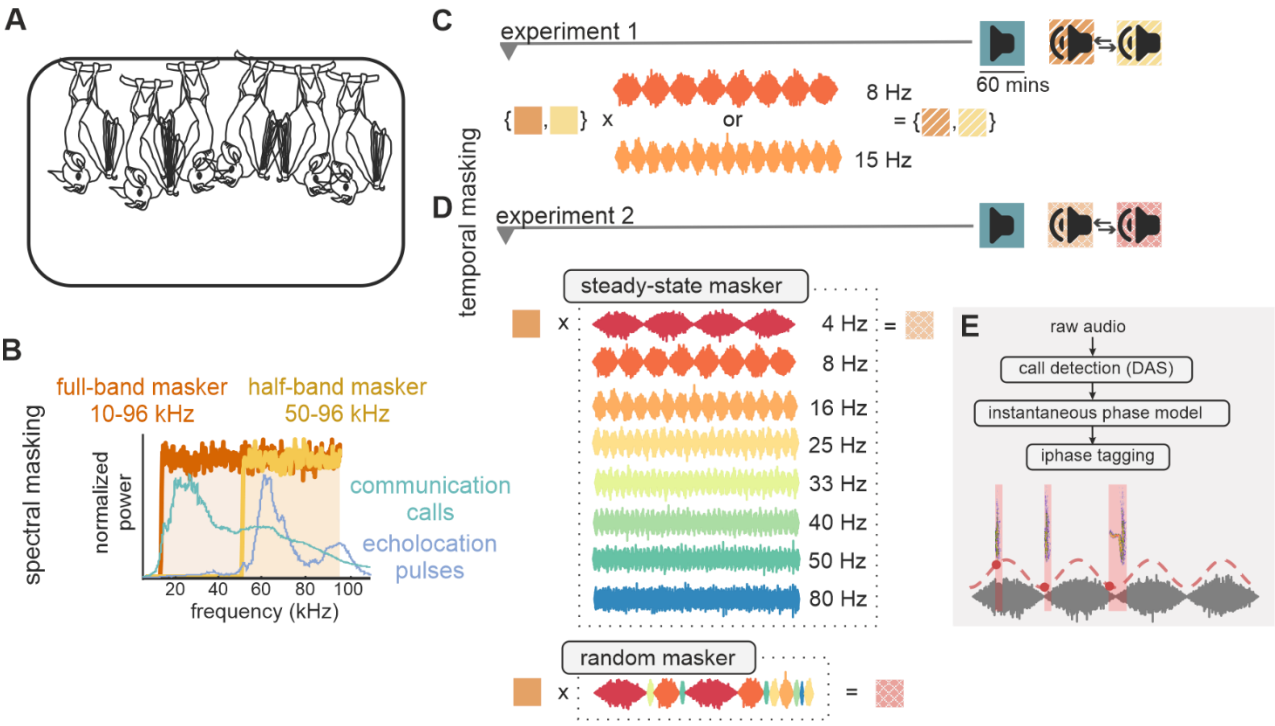

Fig. 1. Schematic of experiments. (A) Each group of bats (12) consisted of 6 adults (4 male) that could flit and socialize freely in a cage placed within the recording chamber. (**B)** Stimuli were broadband white noise with 10-96 kHz (full-band masker) and 50-96 kHz (half-band masker) carrier frequencies. Teal and violet traces indicate normalized power spectra of *C. perspicillata* communication and echolocation calls, respectively. (**C)** In experiment 1, maskers were amplitude modulated at 8 or 15 Hz for each group. Procedure (right): Recording days (5) consisting of three one-hour blocks: a silent baseline, then playback of the full-band and half-band masking noise. (**D)** In experiment 2, full-band masking noise was amplitude modulated at eight amplitude modulation (AM) rates (4-80Hz). A random condition consisted of a randomly permuted sequence of the eight AM cycles. Procedure (right): Recording days (5) consisted of a silent block , playback of the steady-state, consisting of continuous playback of each modulation rate for 7.5 minutes before switching rates until all rates were heard, and random masking noise. (**E)** Data analysis: Call events (pink shaded areas) were detected using Deep Audio Segmenter (DAS). Calls were tagged with the instantaneous phase (red dots) of the amplitude envelope (red dashed line).

The distribution of call onsets within the modulation cycle was inversely proportional to the amplitude level of the playback noise (Fig. 2a). These call onset density distributions were strongly unimodally clustered toward the amplitude downstate (Fig. 2a insets, right hemispheres) in the presence of the full-band masking noise for both modulation rates (Rayleigh's test: 8 Hz: $r = 0.06, p < 0.001$; 15 Hz: $r = 0.03, p < 0.001$, Bonferroni adjusted). However, call onsets emitted amidst the half-band masking noise more closely followed a uniform circular distribution (8 Hz: $r = -0.001, p = 1$; 15 Hz: $r = 0.001, p = 1$), possibly because less energetic masking resulted in a reduced need to adapt vocal timings. No bias towards vocalizing at either rate was observed in the silent baseline (8 Hz: $r = -0.001, p = 1$; 15 Hz: $r = -0.001, p = 1$). This preference for calling in the downstate of the amplitude cycle in the full-band masking condition was present for all groups tested (4 for each modulation rate) and on all five recording days (fig. S2).

Angular vectors for call onset distributions in the full-band masking conditions pointed toward the amplitude downstate and angular means had narrow confidence intervals (95% maximum likelihood estimated (MLE) parameters from a von Mises distribution), indicating that call onsets were prominently clustered near the amplitude trough (table S2). Bootstrapped von Mises parameters, circular mean (μ) and concentration (κ), revealed that the clustering of call onsets on the falling edge of the amplitude cycle was consistent throughout the dataset. Meanwhile, circular means were more dispersed, and concentrations were modest for the half-band masking condition, and both parameters had negligible magnitudes in the silent condition (Fig. 2c, fig. S3a).

Call onset phases varied significantly between playback conditions for each modulation rate (Mardia-Watson-Wheeler test: 8 Hz: $1228, p < 0.001$; 15 Hz: $369, p < 0.001$, Bonferroni adjusted). Angular dispersions, but not the angular means, were significantly modulated by the type of masking noise (Rao's test: full- vs. half-band maskers, $p < 0.001$, table S3), highlighting the difference in the circular concentration of call onsets between masking conditions.

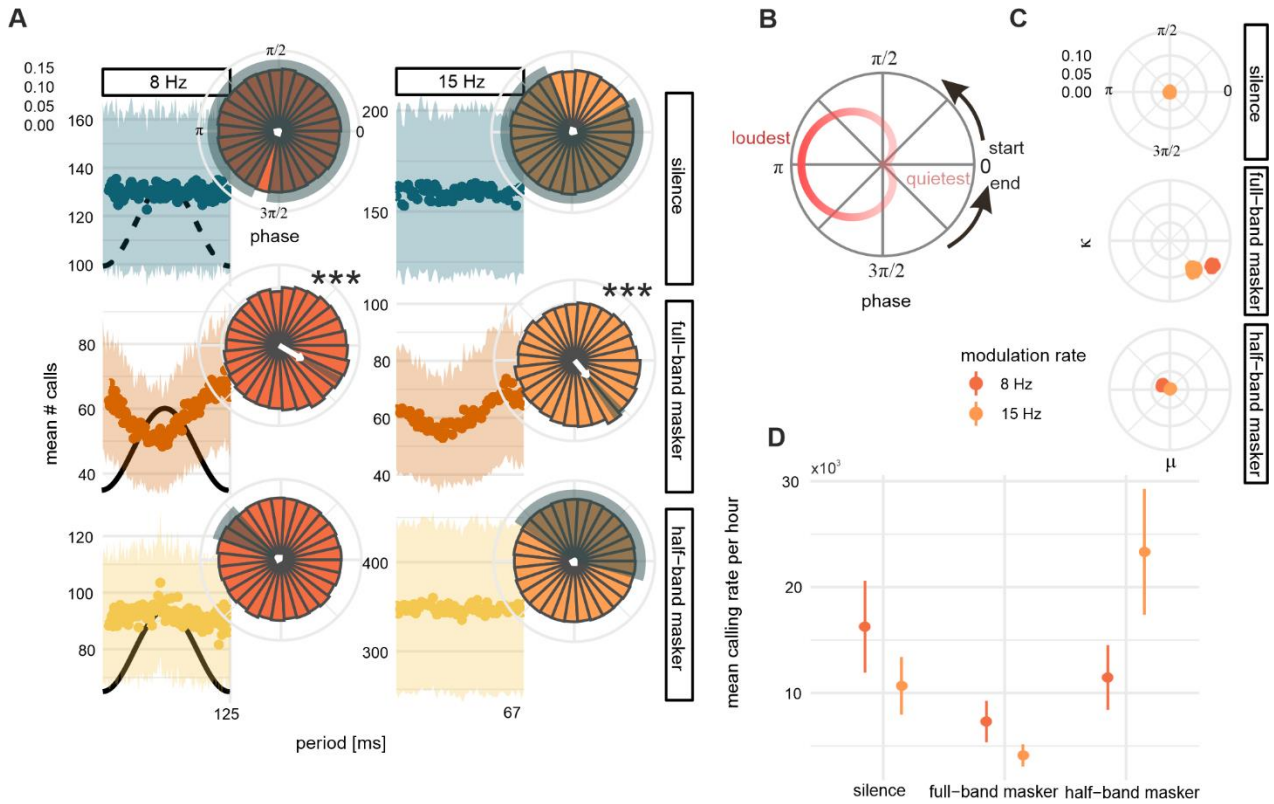

Fig. 2. Anti-phase preference for call onset timing in broadband noise. (**A**) Average call onset distributions within the modulation cycle track the inverse of the amplitude phase in full-band masker conditions, but not in silent and half-band masker conditions (1 ms bins). Shaded areas indicate standard error of the mean (SEM). Black curves: schematic of amplitude envelope (not to scale). Insets: Circular density histograms of call onsets (30 bins). White arrows indicate mean vectors: arrows indicate angular means; arrow lengths indicate resultant lengths (concentration). Shaded areas indicate maximum likelihood (MLE) bootstrapped 95% confidence intervals for angular means. *** $p < 0.001$, Rayleigh's test. (**B**) Schematic representing the translation from the cartesian to polar coordinates. 0 position (right) corresponds to the amplitude trough. Red trace represents amplitude change over a cycle. (**C**) Bootstrapped MLE von Mises mean (μ) and concentration (κ) parameters indicating robust pattern of call onset clustering in the full-band masking condition for both modulation rates. (**D**) Mean number of calls observed in each condition show a predictable drop in calling induced by acoustic masking, except for the 15Hz context in the half-band masking condition. Error bars indicate SEM.

Rate of calling is modulated by the degree of spectral masking

Playback noise impacted not only the timing, but also the number of vocalizations emitted by the bats. The presence of masking noise resulted in a reduction in the rate of vocalization between silent (528,155 calls) and full-band masking conditions (224,384). Surprisingly, the rate of calling increased relative to the silent baseline in the presence of the half-band masker (672,528).

Playback condition significantly accounted for the variation in the hourly rate of calling for the 15 Hz context ($\chi^2 = 21.34(2), p < 0.001$), but not in the 8 Hz context ($\chi^2 = 4.37(2), p = 0.11$), as modelled by a negative binomial distribution. Nonetheless, in the 8 Hz context, the rate of calling dropped between silent and full-band masking conditions ($\mathrm{B} = .45, \mathrm{SEB} = 0.38, p = 0.034$ 95% CI$[0.21 - 0.95]$), and silent and half-band masking conditions. In the 15 Hz context, the rate of calling dropped between silent and full-band masking conditions ($\mathrm{B} = .39, \mathrm{SEB} = 0.36, p < 0.01$, 95% CI$[0.19 - 0.79]$), but increased between baseline and the half-band masker ($\mathrm{B} = 2.19, \mathrm{SEB} = 0.36, p = 0.03$, 95% CI$[1.07 - 4.46]$, table S3-7, Fig. 2d). Between modulation rate contexts, calling rates were only significantly different in the half-band masking condition ($z = -1.85$, $p = 0.06$), due to the greater number of calls in the 15 Hz context.

Bats can adapt call timings to both predictably and unpredictably patterned noise

In *experiment 1*, we observed that bats exhibit an untrained and flexible adaptation of vocalization timing and rate when presented with rhythmic masking noise. In *experiment 2*, we further probed this behavior by asking: First, what is the upper temporal limit for this anti-phase calling behavior? And second, can the bats still perform this feat if the temporal pattern of the masking noise is unpredictable? To this end, we played the full-band masker noise to four additional groups of bats, this time amplitude modulated at eight different rates (4, 8, 16, 25, 33, 40, 50, and 80 Hz) for 7.5 minutes each (steady-state condition), as well as in a randomly permuted sequence of modulation cycles sampled from those eight rates for 60 minutes (random condition) (Fig. 1d).

Call onsets tracked the inverse of the modulation envelope up to 16 Hz (Rayleigh's test: 4, 8 and 16 Hz, $p < 0.001$, Bonferroni adjusted, Fig. 3a). Call onset clustering was negligible for rates of 25 Hz and above (table S8). Importantly, as this anti-phase clustering pattern was present in both steady-state and random temporal conditions, the bats evidently did not need to be able to predict the time-of-arrival of the upcoming amplitude downstate to be able to adapt call timings (Fig. 3a). This call pattern was present for all groups of bats tested (fig. S4).

Bootstrapped von Mises parameters showed that this temporal "targeting" of the falling edge of the amplitude modulation does not display a step change above 16 Hz, but rather a gradual decrease in tracking fidelity (Fig. 3b, fig. S3b). Call onset phases varied significantly between playback conditions for modulation rates from 4 to 40 Hz (Mardia-Watson-Wheeler test: $p < 0.001$, Bonferroni adjusted, table S9). Angular dispersions were significantly modulated by playback condition for 4 to 25 Hz (Rao's test: $p < 0.001$) and more modestly in the 33 and 40 Hz contexts ($p < 0.05$). Angular means were only markedly different between playback conditions for the 8 Hz context ($p < 0.001$, table S10).

Rate of calling depends on local and global acoustic context

In line with our hypothesis that "noisier" acoustic environments incur greater suppression of vocalization, most calls detected in *experiment 2* were emitted in the silent condition (539,086), with fewer calls emitted in the presence of the steady-state masker (312,728), and the fewest calls emitted during playback of the random masker (237,180). However, the precise pattern of suppression was sensitive to the temporal structure of the acoustic masker.

Most notably, while playback of the random masker reduced the overall number of vocalizations, there was significant variation in the rate of calling observed in cycles of each modulation rate in this condition ($\chi^2 = 81.08(7), p < 0.001$, Fig. 3b, table S14). More calls were observed in 4 Hz cycles embedded in the random stream of amplitude modulation cycles than were observed in the 4 Hz steady-state condition ($p = 0.01$, Fig. 3b, table S13), possibly because the unpredictable stream posed a significant challenge to the bats which could be partially overcome by exploiting the comparably long periods of low amplitude noise (the slow rise and decay) provided by recurring 4 Hz cycles.

Meanwhile, vocalization rates in 8 and 16 Hz contexts were comparable across all conditions (Fig. 3b, table S11-12), possibly due to the relative ease of shifting call timing at rates close to the spontaneous ~ 11 Hz vocalization rate.

For all other modulation rates, playback condition was a significant predictor of the variance in the number of observed vocalizations ($p < 0.05$, Fig. 3b, table S11-12), which dropped significantly

between the silent baseline and random masker conditions (25 - 50 Hz: $p \leq 0.01$, table S13) or monotonically between all conditions (80 Hz: $p < 0.001$, table S13).

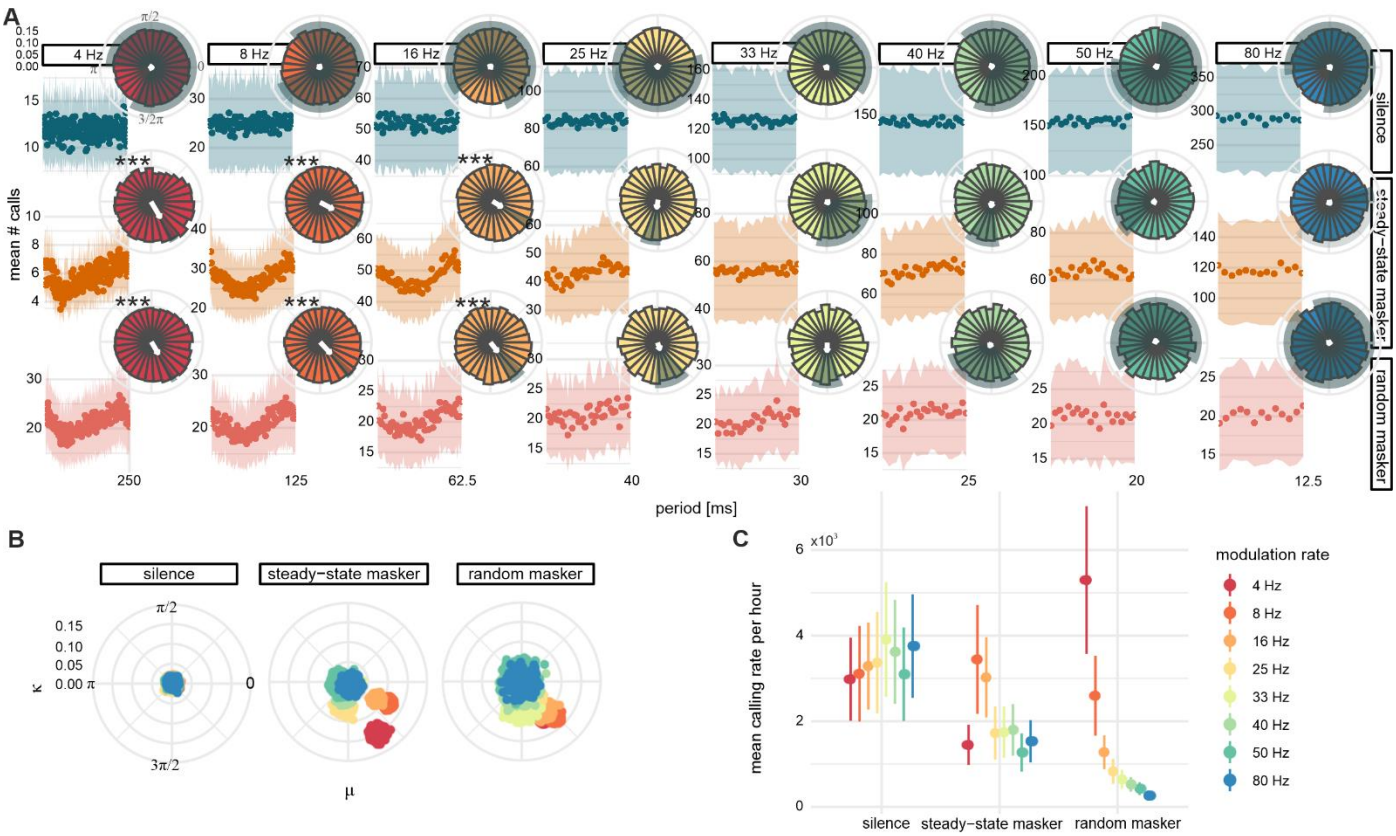

Fig. 3. Call timing adaptation to amplitude modulated noise is independent of predictability but sensitive to rate. (**A**) Average call onset distributions show call timings follow the inverse of the amplitude modulation cycle in both predictable (steady-state) and unpredictable (random) temporal contexts, but only do so reliably up to 16 Hz. *** *p < 0.001*, Rayleigh's test. (**B**) MLE von Mises mean and concentration parameters indicate that the call clustering pattern is robust but graded, with the greatest anti-phase concentration of call onsets occurring in slowest rate contexts and the clustering becoming less extreme with increasing rate. (**C**) The mean rate of calling is suppressed by masking noise, but the degree of suppression is determined by modulation rate. All indicators are the same as in Fig. 2.

Narrowing temporal windows of opportunity for vocalization leads paradoxically to fewer overlapping calls

In modulated noise, temporal windows of opportunity for vocalizing are sparse. If groups of bats begin collectively targeting narrow windows for vocalizing, this could lead to an increase in the number of temporally overlapping calls. Although our study design did not permit an evaluation of individual calling patterns, temporal overlaps in detected calls nonetheless signified multiple speakers. Overall, we found few overlapping calls (experiment 1: 42,618 of 1,425,067 calls, experiment 2: 31,942 of 1,088,994; < 3% in total; fig. S5b, d, table S15).

However, contrary to our predictions, the fewest number of overlaps were recorded in the masking conditions where acoustic interference was greatest and would have encouraged the greatest temporal clustering of calls (fig. S5b, d, table S16). Nonetheless, overlapping calls were clustered in the amplitude downstate for slower modulation rates (Rayleigh's test: experiment 1: 8 Hz full-band masker: $p < 0.001$, 15 Hz half-band masker: $p < 0.001$; experiment 2: 8 Hz steady-state masker, $p = 0.003$, 16 Hz steady-state masker, $p = 0.04$, Bonferroni adjusted; fig. S5a, c).

Evidence for temporal anchoring to terminal troughs across different temporal rates

The fact that vocal timing can be calibrated to occur in an anti-phase pattern within a single amplitude modulation cycle (Fig. 3a, random masker) implies that acoustic evidence in the first half of the cycle (the rising edge) is sufficient to inform the bats' decision of when to vocalize in the second half of the cycle (the falling edge). Yet, the rates for which we observed this adaptation (4, 8, 15 and 16 Hz) feature significantly different period lengths (250 to 62.5 ms), leaving open the question of whether bats achieve this timing adaptation by attempting to call after amplitude peaks or by targeting the terminal troughs. To answer this question, we computed two measures of call onset timing from bootstrapped mean phases (in radians): time relative to the amplitude peak, and time relative to the terminal amplitude trough (in ms) (Fig. 4a, c). If call onset timing within the modulation cycle scales isometrically as a function of rate, then call timings should be equidistant between peaks and terminal troughs across modulation rate contexts. Alternatively, if amplitude peaks (or terminal troughs) are used as acoustic landmarks for timing adaptation, then calls should arrive at roughly the same delay after the peak (or before the trough), independently of rate.

To adjudicate between two possibilities, we used a linear classifier to predict modulation rate classes for mean call onsets, using time-from-peak and time-to-trough measures of call onset timing as predictors. We evaluated three versions of this model to determine the classification performance for each measure separately and together (see Methods): the full model featured both time-to-trough and time-from-peak predictors, the "troughs model" included only the former, and the "peaks model" included only the latter.

Classification performance of an unseen validation set was lowest for troughs models for both experiments (Fig. 4b-e, Table 1). Timing relative to amplitude peaks provided perfect (*experiment 1*) or very good classification (*experiment 2*). Finally, a model that used both measures provided perfect performance when the classification task was binary (8 or 15 Hz, *experiment 1*), but performed worse than the peaks model when the task required distinguishing multiple classes (*experiment 2*, Fig. 4b-e, Table 1).

	Model	Accuracy (95% CI)	[Mean] F1
Experiment 1	**Full model**	1.0 (0.995, 1)	1.0
	Troughs model	0.815 (0.786, 0.841)	0.806
	Peaks model	1.0 (0.995, 1)	1.0
Experiment 2	**Full model**	0.517 (0.504, 0.529)	0.499
	Troughs model	0.386 (0.374, 0.398)	0.363
	Peaks model	0.709 (0.698, 0.721)	0.709

Table 1. Classification performance for models predicting modulate rate classes from call onset timing. For experiment 1, F1 scores (geometric mean of precision and recall) are computed based on 8 Hz class being the "positive class." For experiment 2, the multi-class F1 score is the average of F1 scores for all modulation rate classes.

Together, these results demonstrate that mean call onset timings relative to the terminal amplitude trough were much more similar across modulation rates than timings relative to amplitude peaks, which scaled with cycle length. This provides evidence that bats may have calibrated the shift in vocalization timings across modulation rates and temporal conditions (both predictable and unpredictable) by aiming to vocalize at or near terminal troughs of the modulation cycles when the noise level would have been at a minimum. Given the short duration of most detected calls (above), vocalizations would likely not have extended into the following cycle (table S17).

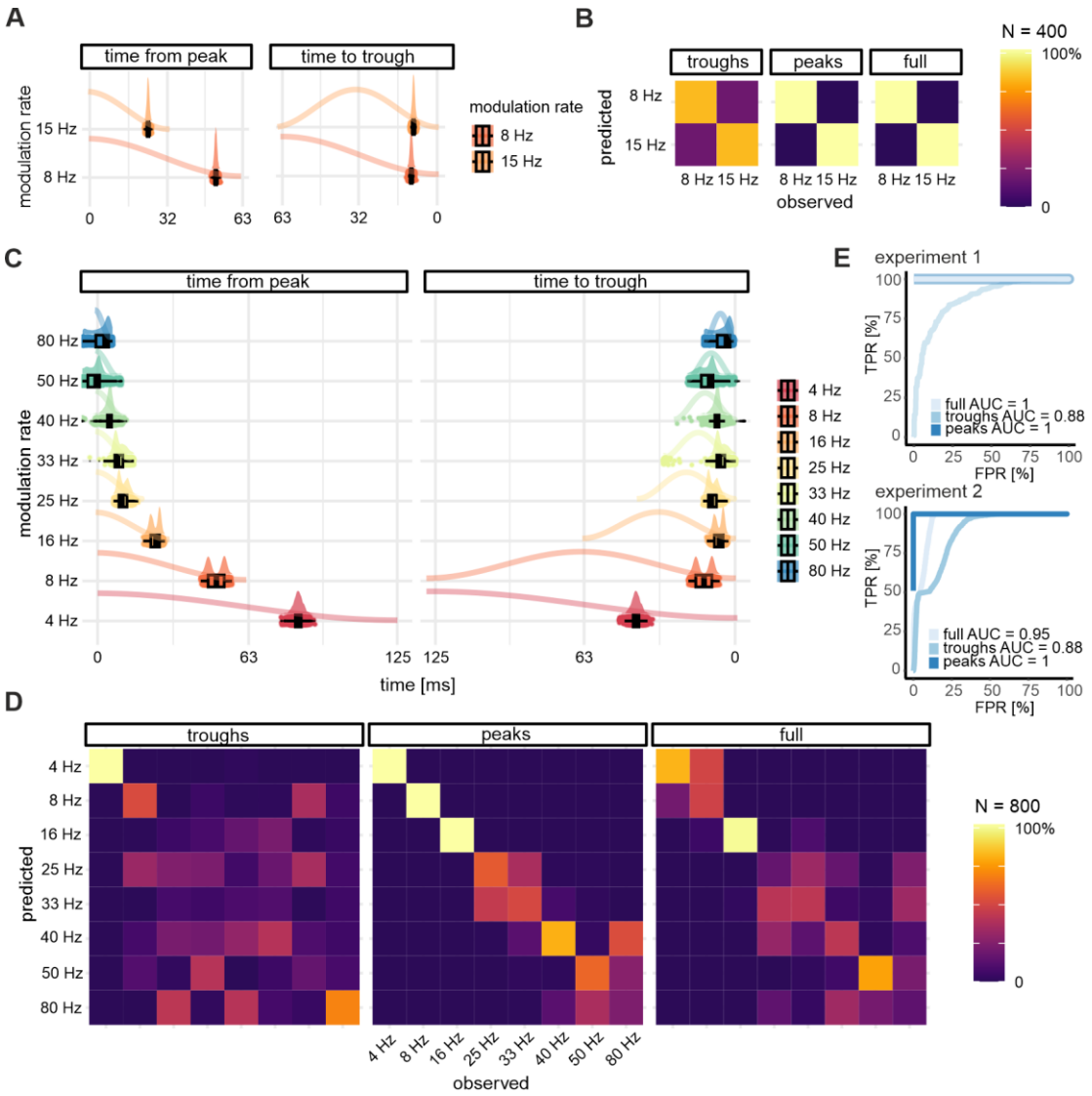

Fig. 4. Mean call onset timings measured relative to the amplitude trough and peak show distinct patterns. (**A**) and (**C**) Bootstrapped angular means (in radians) from the full-band masking condition (in (**A**), experiment 1) and both masking conditions (in (**C**), experiment 2) expressed as time (in ms) relative to the amplitude peak (left) and relative to the terminal trough (right). Mean call onsets occur in a scaled manner relative to the amplitude peak, but roughly concurrently relative to the terminal trough. Boxplots indicate median, 1st and 3rd quartiles. Whiskers indicate 1.5x the inter-quartile range from box edges. Small dots behind boxplots are raw data values. Half-violins above boxplots are indicate density distributions. Colored traces schematically represent the amplitude envelope. (**B**) and (**D**) Confusion matrices for predicted vs. observed modulation rate classes from three linear discriminant classifiers: a "troughs" model using only time-to-trough, a "peaks" models using only time-from-peak, or both. For experiment 1 (**B**) and experiment 2 (**D**), both peaks and full models or peaks models alone, respectively, offer the best classification, while troughs models offer the worst. (**E**) ROC curves showing the trade-off between false-positive and true-positive rate for classification by each model.

Discussion

We found that *Carollia perspicillata* bats adapt to background noise by dynamically adjusting their vocalization timing. Our study makes bats one of only a few mammals thus far observed to spontaneously adjust to jamming noise by exploiting temporal parameters of the acoustic landscape, alongside marmosets (*17*), cotton-top tamarins (*18*), and dolphins (*19*). (This capacity has previously also been found in weakly electric fish (*20*), some songbirds (*21*) and frogs (*22*) as well as numerous insects (*1*).) Call onsets tracked the inverse of the amplitude level for modulation rates between 4 and 16 Hz whether the temporal pattern of amplitude fluctuations was predicable or not. These results invite two interesting inferences.

First, vocal timing in bats is plastic but may be constrained by an intrinsic rate of vocalization, such as the ~11 Hz rate we observed from our colony. This inference is supported by a previous study which demonstrated that the auditory cortex of bats exhibits phase-locked spiking activity in response to amplitude modulated tones, but only up to ~22 Hz (*23*). In addition, while our study investigated vocal production behavior while bats were largely stationary, it has long been known that bat vocalizations are temporally linked with respiration and coordinated with the wingbeat during flight (*24*, *25*). Thus, both neural and metabolic constraints may play a role in limiting the range of vocal timing adaptations. However, given that bats of this species are expert echolocators, and Phyllostomid bats have previously been successfully trained to modify social vocalizations parameters (*26*), adaptation to faster rates may be possible under an operant conditioning paradigm. This hypothesis is consistent with our findings which showed diffuse call onset clustering patterns for rates of 25 Hz and above, indicating a gradual roll-off of temporal tracking, rather than a hard cutoff.

Second, the mechanism underlying short-term vocal plasticity is sufficiently fast and flexible to permit adaptation to a range of temporal rates without the need for strict predictability. This is a critical feature, as the natural environment presents numerous acoustic hurdles characterized by erratic temporal patterns, making it highly adaptive to be able to calibrate calling behavior to moment-to-moment fluctuations in amplitude level. In the wild, background noise may also be continuous over long periods of time. While a few studies on bat vocal adaptation have observed phasic vocal responses to playback noise (*27*), or changes in call interval (*28*) and pulse emission timing (*10*, *11*), these have mainly employed pulsatile or discrete stimuli, rather than continuous playback, to probe vocal production behavior.

An open question raised by our findings regards whether bats achieve jamming avoidance primarily by continuous, active online monitoring of the acoustic landscape, or whether they switch as needed between such a strategy and reference to an internal prediction model of the auditory scene. While an active online monitoring strategy would adequately explain our results, bats have recently been shown to build and act upon predictions of auditory targets (*29*). Future studies are needed to discern whether the bat brain switches between minimally costly approaches to the problem in a context-dependent manner.

Overall, the behavior we observed is consistent with the notion that bats vocalize like metabolically efficient signal optimizers: First, the vocal timing adaptation we observed is employed in a “lazy” manner, i.e. only when the degree of masking necessitates temporal shifting. Thus, we observed no anti-phase clustering of call onsets when we only partially masked the spectral frequencies used for vocalization. Second, consistent with previous studies, we found that overall rates of calling dropped during playback of masking noise, though this effect was strongly modulated by acoustic context, such that bats appear to evade acoustic jamming by learning global statistical patterns in ambient noise and then locally exploiting the windows of opportunity afforded by slower amplitude fluctuations. Finally, we found that while mean call onset times scaled with modulation period, call timing with respect to the end of the cycle was more similar between different temporal rates. providing evidence that bats are aligning call timings to the amplitude trough, where they would incur the least amount of interference.

Beyond its importance for maintaining signal quality, vocal flexibility in the temporal domain is a critical prerequisite for complex social communication, as it allows for the ability to respond to conspecific signals of arbitrary length and complexity (*30*). In addition to exquisite motor control of the noseleaf during sonar pulse generation (*31*, *32*), *Carollia perspicillata* bats possess a significant

repertoire of social calls (*33*, *34*) that are laryngeal in origin. Our study helps elucidate how these bats maintain sensitive temporal dynamics in social interactions.

In sum, our study demonstrates that the Phyllostomid bat *Carollia perspicillata* has a capacity for vocal flexibility in the temporal domain that is finely responsive to continuous and dynamically changing amplitude fluctuations, enabling this species to optimize calling behavior as needed, by integrating acoustic information at the millisecond timescale.

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Supplementary Materials

Materials and Methods
Figs. S1 to S7
Tables S1 to S17
References (33, 35-37)