

Correlations across timing cues in natural vocalizations predict biases in judging synthetic sound burst durations.

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10 **Acknowledgements:** H.L.R. acknowledges support from National Science Foundation NSF grant 1355065
11 (HLR, PI), National Institute of Health NIH DC015138 01 (HLR, Co-I), and the University of Connecticut
12 Brain-Computer Interface Core. Grant support from the Deutsche Forschungsgemeinschaft are acknowl-
13 edge fro L.M. (ME4197/2 and ME4197/3) and M.W. (WO1732/4). L.C-T acknowledges support from a
14 CAPES Brazilian foundation grant.

15 **Conflict of interest statement:** H.L.R. has ownership interest in Elemind Technologies, Inc. and this private
16 company did not sponsor this research.

17 **Reproducibility:** Code and datasets from this manuscript are available as a standalone executable at
18 <https://doi.org/10.24433/CO.8495056.v1>

19 **Abstract**

20 It is well known that animals rely on multiple sources of information in order to successfully identify sounds
21 in natural environments, to make decisions that are optimal for their survival. For example, rats use duration
22 and pitch cues to respond appropriately to prosocial and distress vocalizations (Saito et al., 2019). Vo-
23 calization duration cues are known to co-vary with other temporal cues (Khatami et al., 2018), yet little
24 is known about whether animals rely upon such co-variations to successfully discriminate sounds. In the
25 current study, we find natural alarm vocalizations in rats have onset and offset slopes that are correlated
26 with their duration. Accordingly, vocalizations with faster onset slopes are more likely to have shorter dura-
27 tions. Given that vocalization slopes begin and end within milliseconds, they could provide rapid perceptual
28 cues for predicting and discriminating vocalization duration. To examine this possibility, we train rodents
29 to discriminate duration differences in sequences of synthetic vocalizations and examine how artificially
30 changing the slope impacts duration judgments. We find animals are biased to misjudge a range of synthetic
31 vocalizations as being shorter in duration when the onset and offset slopes are artificially fast. Moreover,
32 this bias is reduced when rats are exposed to multiple synthetic vocalization bursts. The observed perceptual
33 bias is accurately captured by a Bayesian decision-theoretic model that utilizes the empirical joint distribu-
34 tion of duration and onset slopes in natural vocalizations as a prior during duration judgements of synthetic
35 vocalizations. This model also explains why the bias is reduced when more evidence is accumulated across
36 multiple bursts, reducing the prior's influence. These results support the theory that animals are sensitive
37 to fine-grained statistical co-variations in auditory timing cues and integrate this information optimally with
38 incoming sensory evidence to guide their decisions.

39 **Introduction**

40 When someone jams their toe on a door and belts out an expression of, “oww, oww, oww”, how do
41 you judge whether they are truly hurt or just mildly annoyed? Certainly, the duration, loudness, and pitch
42 of each “oww” will help you judge the expression (Belin et al., 2008; Jürgens et al., 2018; Lausen and
43 Hammerschmidt, 2020). The slope of sound level increase with the onset and offset of each “oww” is

44 also an important cue (Cumming et al., 2015; Paquette and Peretz, 1997; Stecker and Hafter, 2000; Grassi
45 and Darwin, 2006; Friedrich and Heil, 2017). To make an accurate judgment, it could be important to hear
46 “oww” repeated multiple times to accumulate sound feature information (Brunton et al., 2013). Finally,
47 there can be unique combinations of temporal features in sounds that convey the information needed to
48 properly judge and categorize them (Bizley and Cohen, 2013). Accordingly, the effective judgment of such
49 expressions could require detecting a combination of acoustic features and their co-variations on multiple
50 timescales.

51 Though much is known about how acoustic features themselves shape perception, far less is known about
52 how their statistical variations may do so. Previously, we observed a physical limit in vocalization sequences
53 that humans and other animals generate where longer vocalizations cannot be repeated faster than the dura-
54 tion allows (Khatami et al., 2018). This results in an increase in the statistical probability that long-duration
55 vocalizations will have slower repetition rates than short-duration vocalizations. In other words, the repeti-
56 tion rate could be predictive of vocalization duration or vice versa. Indeed, mathematically, the combination
57 of vocalization duration and repetition rate objectively differentiates vocalization type or category across a
58 wide range of animals including humans (Khatami et al., 2018). On shorter timescales, humans rely heavily
59 on the rate or slope of sound onset to judge the duration or loudness of sound (Stecker and Hafter, 2000;
60 Grassi and Darwin, 2006; Friedrich and Heil, 2017). Indeed, it has been suggested that the sound onset
61 slope is a more informative cue for sound duration than the sustained sound duration itself (Friedrich and
62 Heil, 2017)! However, there are no theories for how such cue interactions come about. One well-supported
63 theory is that perception is strongly influenced by statistical variations of acoustical cues found in natural
64 sounds (Elliott and Theunissen, 2009; Geffen et al., 2011; McDermott and Simoncelli, 2011; Zhai et al.,
65 2020) Along these lines, we propose that statistical co-variations between onset and duration in natural
66 sounds could explain why sound onsets strongly influence the perception of sound duration.

67 Here we explore and computationally model how animals judge sound durations with independent
68 variation in sound slope. We examine these perceptual interactions in rodents, as they share similar brain
69 organization and sound duration perception with other mammals including humans (Kelly et al., 2006; Read
70 and Reyes, 2018). Here, rodents are trained to judge duration differences in large sets of synthetic sound
71 burst sequences with durations ranging from 100 to 250 ms. The durations of these sound burst sequences

72 are similar to those found in natural rodent vocalizations. However, our sound design allows us to artificially
73 impose fast slopes on longer-duration sounds to explore how sound slope impacts the perception of duration.
74 Intriguingly, we find long-duration sounds with faster than normal slopes are systematically misjudged as
75 being shorter in duration. This perceptual misjudgment or bias dominates when only a single sound burst
76 is heard; whereas, a more accurate judgment prevails when multiple sound bursts are heard. We find that
77 the observed misjudgments are well explained by a Bayesian model of decision-making that incorporates
78 “prior experience” with natural vocalization statistics into synthetic vocalization judgements. Specifically,
79 since the onset and duration are negatively correlated in natural vocalizations, incorporating this prior into
80 duration judgements about synthetic vocalizations introduces a bias towards shorter durations when slopes
81 are artificially fast. This model also accurately captures the improved performance and decreased bias seen
82 in the behavior when more sensory evidence is accumulated over repeated sound bursts. These results
83 support the idea that sound duration judgments reflect optimal integration of prior experience with ongoing
84 accumulation of sensory information.

85 **Materials and Methods**

86 **Quantifying Statistical Variations of Temporal Cues in Natural Alarm Vocalizations**

87 Prior studies found that rats and humans readily discriminated sound durations greater than 100 milliseconds
88 long ([Kelly et al., 2006](#)) and that the slope of sound onset altered duration perception ([Cumming et al., 2015](#);
89 [Paquette and Peretz, 1997](#); [Stecker and Hafter, 2000](#); [Grassi and Darwin, 2006](#); [Friedrich and Heil, 2017](#)).
90 However, the statistical variations and relationships between slope and duration temporal cues have not
91 been described for natural sounds. Here, we examined the statistical distributions of onset, offset, and
92 duration temporal cues found in natural rodent alarm vocalizations (Fig. 1). Alarm vocalizations were
93 generated by rodents in a conditioning paradigm as described previously ([Melo-Thomas et al., 2020](#)). and
94 the vocalizations made in the absence of haloperidol were used and are available in an online data repository
95 (DOI: 10.5281/zenodo.5762778). Here, 1330 vocalizations were selected for analysis based on having a
96 spectral center of mass around 22kHz ($24.7, \pm 0.87$), as is characteristic of alarm vocalizations (Fig. 1A).
97 Additionally, two raters screened each vocalization to make sure all artifacts were removed from the analysis.
98 Both raters, who were blind to the decisions of the other rater, showed high levels of agreement (intra-

99 rater percent agreement = 99.4%, inter-rater percent agreement = 98.0%). The onset, offset and intervening
100 duration cues of each vocalization were determined using an approach detailed previously (Khatami et al.,
101 2018). Briefly, a Hilbert transform was performed to recover the positive sound envelope (Fig. 1B, Teal
102 line). Vocalization onset was defined as that point where the envelope sound level rose to 10 standard
103 deviations above the noise floor (Fig. 1C, t_{onset}). Vocalization offset was determined as a return to the noise
104 floor or baseline sound level (Fig. 1C, t_{offset}). The amplitude of each call was set as a ratio of the area under
105 the curve (AUC) of the envelope ($Y(t)$) of the respective call such that,

$$AUC = \int_{t_{\text{onset}}}^{t_{\text{offset}}} Y(t) dt$$

106 In order to calculate onset and offset slope, we first calculated the change in amplitude and the change in
107 time for each vocalization in the data set. The change in relative amplitude value was mathematically be
108 defined as:

$$\Delta Y = \frac{Y(t_{\text{half-max}}) - Y(t_{\text{onset/offset}})}{AUC}$$

109 Vocalization “plateau” duration was quantified as the time between the vocalization half-maximum follow-
110 ing onset and the vocalization half-maximum prior to offset (Fig. 1C). In our set of 1330 vocalizations,
111 plateau duration varied from 28 to 1467ms with a median and mean duration of 581 and 586ms. The vocal-
112 ization onset slope was quantified by calculating the absolute amplitude rate of change between vocalization
113 onset (t_{onset}) and the first half-maximum peak ($Y(t_{\text{half-max}})$). Likewise, the vocalization offset slope was
114 quantified as the amplitude change between vocalization offset (t_{offset}) and the first half-maximum peak
115 ($t_{\text{half-max}}$). Finally, the absolute values were used to quantify the average onset and offset slope for each
116 vocalization as summarized (Fig. 1E).

$$s_{\text{slope}} = \frac{\Delta Y}{\Delta t}, \quad \Delta t = |t_{\text{onset/offset}} - t_{\text{half-max}}|$$

$$s_{\text{duration}} = t_{\text{half-max}}^{(2)} - t_{\text{half-max}}^{(1)}$$

117 **Synthetic Vocalizations for Perceptual Testing**

118 To behaviorally test the effects of sound slope on duration perception, we generated synthetic vocalizations
119 with a subset of slope and duration temporal cues observed in natural vocalizations (Fig. 1). In behavioral
120 tests (Fig. 2), animals judged a set of seven synthetic vocalizations durations as being short or long in
121 duration (Fig. 2C). The seven synthetic vocalizations ranged in duration from 100 to 250 milliseconds (Fig.
122 2C) and fell within the range of alarm vocalization plateau durations reported above and summarized as a
123 joint scatter plot (Fig. 1 C1). For synthetic vocalizations, the onset and offset slopes were the same
124 (symmetric) for all 7 sound durations used in behavioral testing. Synthetic vocalization durations were
125 defined by a square wave sound pressure waveform envelope. Accordingly, square wave sound pulses
126 defined 7 different plateau durations (100, 130, 160, 175, 190, 220, and 250 ms) spanning the lower end of
127 the natural vocalization duration range of 100 to 250 ms.

128 The fast and slow slopes were chosen to span the extreme ends of natural vocalization distribution (Fig.
129 2A, red and blue lines, respectively). To vary the slope of synthetic vocalizations, the square wave sound
130 pulses were smoothed with a Basis spline (B-spline) filter function, as detailed previously (Lee et al., 2016).
131 In two separate sets of sounds, the B-spline cutoff frequency was either 5 or 32 Hz to generate slow (83.7
132 A/s) versus fast (534.8 A/s) onset-offset slopes, respectively. The average slow onset-offset slope (Fig. 1E,
133 red bar, 83.7 A/m) used for behavioral testing fell within the range of onset slopes found in natural alarm
134 vocalizations (Fig. 1C1). In contrast, the fast onset-offset slopes were more than 2 fold faster than the
135 fastest onset slopes observed for comparable duration alarm vocalizations (Fig. 1E, blue bar; Fig. 1C1).
136 This allowed for high cue contrast with the average fast onset-offset slope (Fig. 1E, blue bar) being 6.4 fold
137 faster than the average slow onset-offset slope (Fig. 1E, red bar). The corresponding average fast and slow
138 slopes were 534.8 A/ms versus 83.7 A/ms, respectively (Fig. 1E). Synthetic onset and offset sound slopes
139 were estimated as the absolute approximate derivative at the first and second half-max points of the sound
140 envelope, respectively. Given that onset and offset slopes were symmetric, s_{slope} both slopes were defined
141 by the following equation.

$$s_{\text{slope}} = \left| \frac{dY}{dt_{\text{half-max}}} \right|$$

142 Accordingly, square wave sound pulses defined 7 different plateau durations (100, 130, 160, 175, 190,
143 220, and 250 ms) spanning the lower end of the natural vocalization duration range of 100 to 250 ms.
144 These square wave sound pulses were smoothed with a Basis spline (B-spline) filter function having a
145 cutoff frequency of either 5 or 32 Hz to generate slow (83.7 A/s) and fast (534.8 A/s) onset-offset slopes,
146 respectively. For each burst duration, the total energy of the sound was adjusted to be equal across the two
147 onset-offset sound conditions, to minimize the saliency of this cue. The onset times for any single sound
148 burst in a sequence were staggered over a 125 ms window to approximate the average 2 Hz sound burst rate
149 found in the 22 kHz vocalization sequences. The latter approach allowed us to minimize perceptual reliance
150 on periodicity cues. For the 7 different sound durations, there were 100 different sequence variations and a
151 total of 700 sound sequences for each onset-offset slope type. Thus, there were 1400 different sound burst
152 sequences for the two onset-offset slope conditions. For all sequence variations, each sound burst had a
153 unique random combination of tonal frequencies to reduce reliance on pitch perception for sound judgment.

154 Our synthetic vocalizations differed from natural vocalizations in several key ways. Our synthetic vocal-
155 izations were devoid of pitch cues, so we could probe temporal cue sensitivities. For all sequence variations,
156 each sound burst had a unique random combination of tonal frequencies to reduce reliance on pitch per-
157 ception for sound judgment. Thus, instead of having a fundamental frequency of 22 kHz with a harmonic
158 frequency at 44 kHz, the synthetic vocalizations were shaped white noise. Natural vocalizations had differ-
159 ent (asymmetric) onset versus offset slopes (Fig. 1B upper plot) but our synthetic vocalizations had the same
160 (symmetric) onset and offset slope (Fig. 1B, lower plot). With this symmetry, shorter inter-vocalization in-
161 tervals were possible allowing us to test sensitivity to slope and duration over more trials in a given block.
162 In natural vocalizations, the onset and offset slopes were negatively or positively correlated with vocaliza-
163 tion duration, respectively (Fig. 1C1 and C2, respectively). Moreover, onset slope and duration were more
164 strongly correlated than the offset slope and duration (Fig. 1C1). Accordingly, the onset slope versus dura-
165 tion correlation coefficient was -0.38 ($p < 0.0001$, $N = 1330$ vocalizations) and the offset slope versus duration
166 correlation coefficient was 0.12 ($p < 0.0001$, $N = 1330$). In our synthetic vocalizations, the slope and duration

167 did not co-vary (correlate) across the 7 different sound durations. Instead, for a given set of sounds (e.g. the
168 fast slope sounds) the slopes were the same across all 7 sound durations. This allowed us to determine if the
169 artificially imposed fast or slow sound slopes would uniformly shift the perception of duration.

170 **Using Natural Vocalization Statistics to Define the Prior of a Bayesian Model of Duration Judgement**

171 Though prior studies examined how sound onset slope impacts loudness and duration perception, no theory
172 for how such cue interactions come about had been formulated. Here, we hypothesized that onset slope
173 impacts sound duration perception because the two temporal cues co-vary in natural sounds such as alarm
174 vocalizations. To address this hypothesis, we developed computational models based on natural sound
175 statistics to predict shifts in duration judgment behavior observed with changes in slope. As detailed above,
176 we quantified the probabilities of three cue distributions found in natural alarm vocalizations including
177 onset, offset, and duration. Next, we quantified the co-variations or correlations in these cues including 1)
178 the joint distribution of onset slopes and durations ("onset" prior type), 2) joint distribution of offset slopes
179 and durations ("offset" prior type), and 3) the three-way joint distribution of onset slopes, offset slopes, and
180 durations ("both" prior type). Finally, we used the Gaussian approximations of the three joint probability
181 distributions as conditional priors in our Bayesian models to simulate the behavioral judgment of synthetic
182 vocalizations under our three task conditions.

183 Our first two steps to building our Bayesian model included quantifying the probabilities and correlations
184 between slope and duration temporal cues found in natural vocalizations. To quantify the joint distribution
185 of onset-offset slopes and duration cues found in natural alarm vocalizations, we fit a 2-D Gaussian to the
186 empirical joint distributions of slopes and duration for 22 kHz alarm calls. The μ (2d vector of means) and
187 Σ (2x2 covariance matrix) are the maximum likelihood estimates of slope and duration parameters in the
188 joint probability distribution. The mean probabilities of the fast and slow slope conditions were then used
189 as Gaussian priors in our Bayesian models (Fig. 1F). To incorporate these natural sound statistics into our
190 Bayesian model, the maximum likelihood estimation was utilized to fit a multivariate Gaussian (bivariate
191 for onset and offset prior types, trivariate for both prior type) as follows:

$$\mathcal{N}(s_{\text{duration}}, s_{\text{slope}}; \boldsymbol{\mu}, \Sigma) = \frac{1}{2\pi} |\Sigma|^{-1/2} \exp \left[-\frac{1}{2} (s_{\text{duration}} - \boldsymbol{\mu}) \Sigma^{-1} (s_{\text{duration}} - \boldsymbol{\mu})^T \right]$$

192 To calculate conditional prior distributions, the slope (s_{slope}) is set to the experimental slope conditions for
193 slow (83.7 A/ms) and fast (534.8 A/ms).

$$p(s_{\text{duration}}, s_{\text{slope}} | s_{\text{slope}}) = \mathcal{N}(\mu_{\text{prior}}, \sigma_{\text{prior}}^2)$$

$$\sigma_{\text{prior}}^2 = \Sigma_{11} - \Sigma_{12} \Sigma_{22}^{-1} \Sigma_{21}$$

$$\mu_{\text{prior}} = \mu_1 + \Sigma_{12} \Sigma_{22}^{-1} (s_{\text{slope}} - \mu_2)$$

194 These two Gaussians served as priors in our Bayesian Decision theoretic model used to simulate and in a
195 sense predict the sound duration judgement behavior, as detailed below.

196

197 **Automated Behavioral Training and Testing System**

198 Rats performed all behavioral tasks inside an acrylic crate located within a single-walled sound isolation
199 chamber. Three nose ports containing photodiode sensors were located on the back wall of the acrylic box.
200 An ultrasonic speaker (Avisoft Bioacoustics) was located along the back wall of the sound isolation chamber
201 at approximately 7 cm above and 18 cm in front of the center nose port. Based on nose-poke behavior
202 and computer-generated task conditionals, water reward was delivered automatically at a rate of 6 mL/min
203 through Teflon tubing (17 gauge) located at the center-left and right nose ports. Reward volume varied with
204 the phase of training but was approximately 25-50 μL for each correct choice. Behavior was monitored,
205 sound, light, and water delivery was controlled by custom MATLAB software (Mathworks, Natick MA), in
206 conjunction with Arduino-based pulse generator and state machines (Sanworks).

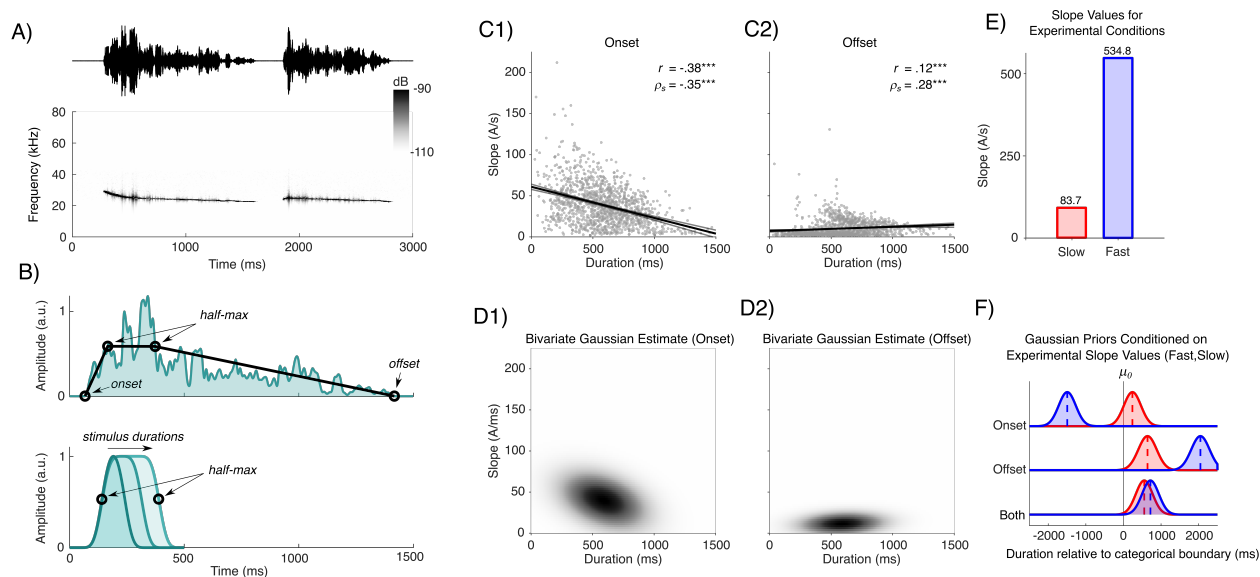
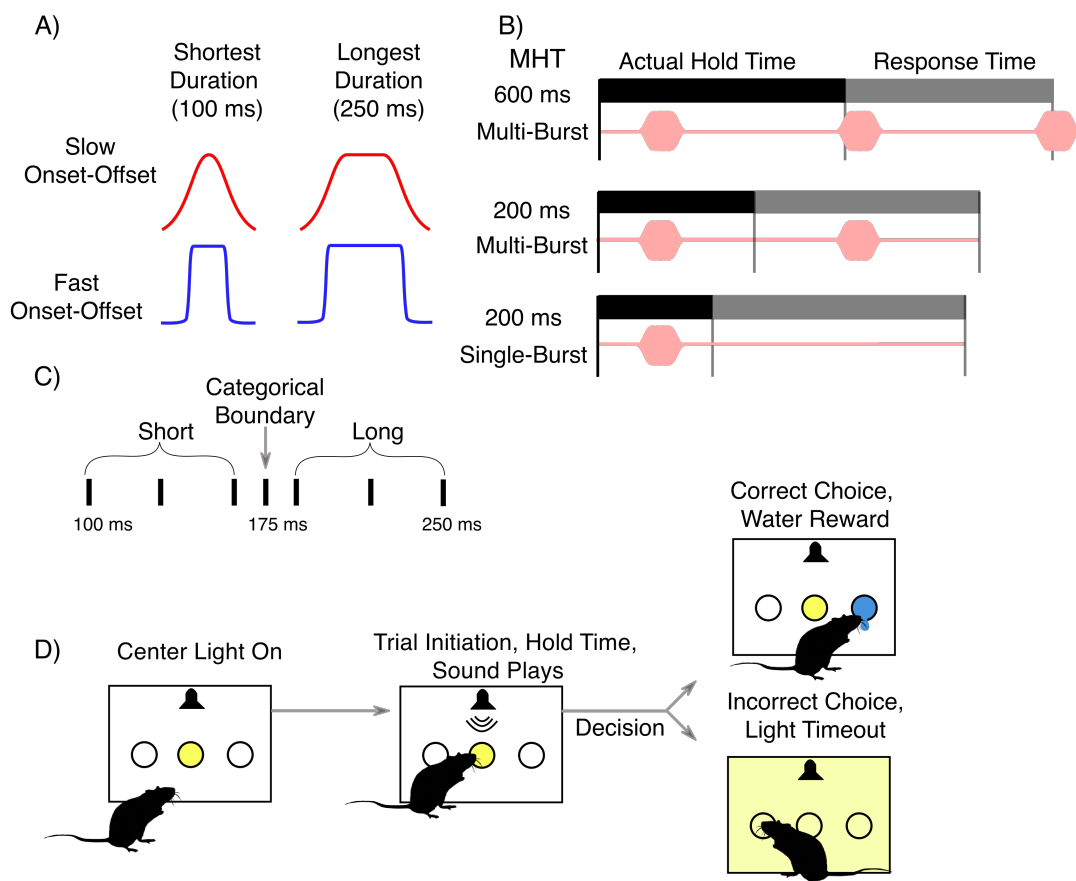


Figure 1: Analysis of natural vocalizations and correlation of sound onset/offset slope and plateau duration. A) Example of raw 22kHz vocalizations collected from one rat recording with the corresponding spectrogram. The examples shown have a center of mass at 25.0 kHz. B) [upper panel] Envelope of the first vocalization in panel A. Points show the time of sound onset, time of offset, and the time at the half-max values. [lower panel] Synthetic vocalizations used in discrimination task for the slow condition (short, middle, longest duration conditions). C1 and C2) Onset and offset slopes systematically co-vary with vocalization duration. Scatter plots illustrate the vocalization duration and slopes for each of the 1330 vocalizations analyzed (Methods). Vocalization durations ranged from 28 to 1467ms. C1) Onset slope decreases as vocalization duration increases following resulting in a strong negative (inverse) correlation. Pearson product-moment (r) and spearman rank-order (ρ_s) correlations are displayed with a significance level ($*** p < .0001$). C2) Offset slope increases as vocalization duration increases resulting in a weak positive correlation. D) [panel 1] Estimated bivariate Gaussian for duration and onset slope based on data from panel C1. [panel 2] Estimated bivariate Gaussian for duration and offset slope based on data from panel C2. E) Showing the slope values of the experimental slope conditions based on the stimulus duration at the categorical boundary (175 ms). F). Conditional univariate Gaussians derived from multivariate Gaussians. Conditional values come from the slope values in panel E. The distributions corresponding to “joint” are derived via a trivariate gaussian where duration, onset slope, and offset slope comprise the three axes.

207 Flexible Perceptual Categorization Task: Initial Training

208 To determine how onset-offset slope and task conditions impact perception of sound duration, we trained
 209 male Long Evans rats (from Envigo) to perform a flexible perceptual categorization in a binomial choice
 210 task (Jaramillo and Zador, 2014). All animal procedures were approved by the Institutional Animal Care
 211 and Use Committee (IACUC) at the University of Connecticut.



212 First, animals were acclimated to a reverse day-night cycle for training and testing and learned to obtain
 213 daily water by poking their nose into the nose ports to receive water reward. Animal weights were monitored

214 so that they did not fall below 80% of the individual's baseline.

215 To learn the binomial choice task, animals were progressed through six training phases. In phase 1,
216 animals were acclimated to hearing sound stimuli and obtaining their daily water allotment by poking their
217 nose in any one of the three nose ports to release a water reward. In phase 2, sequences of the shortest (100
218 ms) or longest (250 ms) duration sound bursts were played each time animals held their nose in the center
219 nose port for 150 ms. The sound sequence for that trial would continue to play until the animal by chance
220 poked their nose in the appropriate left or right side-port associated with long and short duration sounds,
221 respectively. In Phase 3, the required minimum hold time (MHT) for holding and hearing sound at the
222 center nose port was increased from 150 ms to 600 ms in 2 ms increments per trial. A bright overhead light
223 delivered a cue for a 6-second timeout when animals failed to hold for the MHT. During this timeout, rats
224 were unable to initiate a new trial in the center port. Phase 4, additionally required that rats respond (choose
225 a side port) within 4 seconds after the MHT. In phase 5, the overhead light was a cue for a 30-second timeout
226 when animals choose the incorrect side port for the 100 and 250 ms duration sounds. This ended the trial
227 and required rats to start a new trial b. Phase 5 was completed when animals correctly judged long (250 ms)
228 and short (100 ms) duration sounds with an average percent correct of 77%. In Phase 6, animals learned
229 to judge 100 and 250 ms sound durations as well as 5 additional intermediate sound durations. Generally,
230 throughout all phases, rats were moved to each new phase following sessions of ≥ 115 correct hold trials.

231 Since animals can develop motor biases toward choosing the left or right side, several anti-biasing
232 measures were employed throughout all phases of training. First, no more than 3 trials of the same plateau
233 duration were presented in a row. Additionally, after every 25 trials, a custom-written Matlab program
234 automatically evaluated the animals' bias and increased trial numbers as well as the reward volume (by 50
235 uL) or correct choices on the side opposite of the bias.

236 **Final Training & Testing**

237 In Phase 6, our goal was to compare the ability to judge sound durations with either fast or slow
238 onset-offset cues under similar conditions. During phase 6, animals judged sound durations with fast versus
239 slow onset-offset slopes in alternating blocks or "test sessions" with a fixed onset-offset slope condition.
240 For inclusion in our final analysis, a single session needed to have ≥ 115 correct hold trials, $\geq 77\%$ correct

241 choice performance on the cardinal duration sound bursts, and show no significant bias. Rats completed 8
242 sessions meeting the criteria (4 at each onset-offset slope condition) with a required hold time of 600 ms.

243 To test the impact of reducing the accumulation of sound bursts heard, we introduced two additional
244 conditions. First, we reduced the MHT from 600 to 200 milliseconds and animals continued to hear multiple
245 sound bursts until they made a choice. Next, the hold time was maintained at 200 ms and only a single burst
246 sound burst was played for animals to judge duration. On average, 21 and 23 training sessions (days) were
247 required for animals to meet the criteria for the 600 and 200 hold time conditions, respectively. On average,
248 37 sessions (days) were required for animals to reach the training criterion to judge the single burst sound
249 condition.

250 **Estimated sound bursts accumulated based on hold time**

251 Since the sound sequences continue to play throughout the MHT until animals make a choice, the total
252 number of sound bursts heard during the hold time was reduced by reducing the MHT from 600 to 200 ms
253 and from multiple bursts to a single burst (Fig. 3). In our binomial choice task, animals were free to remain
254 at the center port for longer before making their side port choice and sound continues to play until they
255 made a choice. Thus, animals accumulated sound evidence during the “hold time” between initiating and
256 completing a trial with a final choice at a side port. The actual hold times were all longer than the MHT
257 and varied with the multi-burst versus single burst conditions (Fig. 3D) but minimally with the sound slope
258 conditions (Fig. 3D, red vs blue symbols). We estimated the proportion of sound bursts heard for each task
259 condition as illustrated for the 200 ms MHT, multi-burst condition (Fig. 3C). For this condition, the number
260 of sound bursts played during the actual hold time was determined for each individual trial across all animals
261 (e.g., Fig. 3C, x-axis, red dots). Using a linear piece-wise regression, we fit this data (Fig. 3C, black line)
262 and estimated the proportion of sound bursts at the median hold time (Fig. 3C, black dot), as shown for this
263 example condition (Fig. 3C). The proportion of sound bursts heard was estimated for all median hold times
264 and sound conditions (Fig. 3E) using the same approach.

265

266 **Descriptive model of psychometric function**

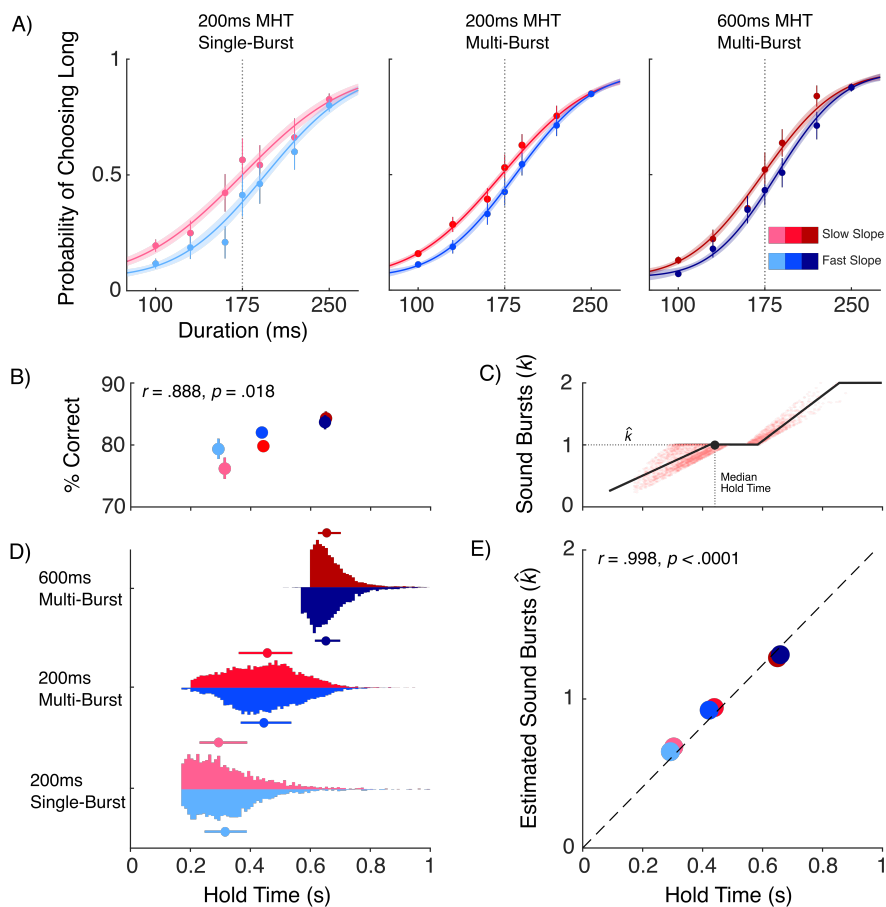


Figure 3: *Sound onset-offset slopes and the number of sound bursts heard both impact perceptual judgment of sound duration*. A) Judgment of sound duration varies as a function of sound onset-offset slope (slow versus fast, blue versus red) and MHT (left, middle and right panels). The mean choice probability (filled circles) and S.E.M. (vertical bars) for judging sound duration as “long” are plotted for each of the seven sound durations tested. To quantify the effect of sound onset-offset slope on sound duration judgment, maximum likelihood psychometric fits are generated for all MHT and sound slope conditions. Lighter colors indicate less evidence accumulation (correspondent with the MHT condition). Translucent bands indicate 95% confidence intervals (non-parametric bootstrap iterations = 400). B) Illustration of the estimated number of bursts (\hat{k}) heard during a given trial with respect to the actual median hold time (based on piecewise regression, METHODS and supplementary material). C) Percent correct (%Correct) sound duration judgment increases as the MHT is increased and the two are positively correlated ($r = 0.888$, $p = 0.018$). The mean and S.E.M. of the percent correct responses are plotted as a function of the MHT (x-axis) for all task and sound conditions. D) Violin histograms of the probability distribution of actual hold times for every trial (total trials= 22,756). E) The proportion and number of sound bursts heard increases with the actual median hold time (see supplementary material). Data shows a near absolute correlation ($r \approx 1$).

To quantify how sound onset-offset slope and task conditions impact sound duration judgement, choice response data were fit with a standard modified sigmoid function using the Palamedes toolbox (Prins and

Kingdom, 2018). The generic form of this psychometric function is a sigmoid link function scaled to lie between asymptotic lapse rates:

$$\psi(x; \theta) = \gamma + (1 - \gamma - \lambda)\phi(x; \mu, \sigma) \quad (1)$$

267 Where θ denotes the set of parameters $\{\mu, \sigma, \gamma, \lambda\}$, and ϕ denotes the cumulative normal function.
268 For equation 1, x refers to the sound plateau duration, ψ refers to probability a choice classifying the
269 sound as long, σ corresponds to the standard deviation of the cumulative normal function. The standard
270 deviation, σ , is linearly and inversely related to the sigmoid function slope. Thus, the sigma (σ) parameter
271 and slope quantify perceptual variance and sensitivity, respectively, for judging short versus long sound
272 durations. Accordingly, the sigma parameter indexes “sensory noise” or variation. The μ parameter
273 corresponds to the mean of the cumulative normal distribution of choice probabilities. If we assume uniform
274 priors and equal rewards for long versus short durations, μ defines the x -intercept and the point of subjective
275 equality ($p_x = 0.5$), also known as the bias point, on the response function.

276 Rather than fitting all conditions (2 slope conditions x 3 hold time conditions) with independent sets of
277 4 parameters each, we sought to find the most constrained descriptive model that accounted for the data.
278 We did this using Palamedes’ model comparison feature, which only allows parameters to vary between
279 conditions if warranted by a model comparison (transformed likelihood ratio test), and constrains them to
280 be fixed across conditions otherwise. (Prins and Kingdom, 2018)

281 Normative (Bayesian decision-theoretic) model incorporating natural sound statistics

282 To examine whether natural co-variations in onset-offset slopes and durations can predict how onset-offset
283 cues impact sound duration judgement, we constructed a Bayesian decision-theoretic model of sound epoch
284 duration judgements.

285 Let the true onset-offset slope of a sound be s_{slope}^* and its duration be s_{duration}^* . We assume that animals
286 maintain a prior belief about the joint occurrence of these features $p(s_{\text{duration}}, s_{\text{slope}})$ based on natural statis-

287 tics. We estimated this “natural statistics prior” based on the joint probability distribution of onset-offset
288 slopes and durations found in natural alarm vocalizations, approximated by a bivariate Gaussian density
289 (Fig. 1). We tested three different possibilities - that animals’ duration decisions were affected by only
290 the onset slope, only the offset slope, or the joint distribution of onset and offset slopes - these correspond
291 to different assumptions about which slope dimensions are predictive of natural vocalizations, and hence
292 attended to. We assume that animals make duration judgements in accordance to Bayesian decision theory,
293 by combining this prior with noisy sound duration evidence, and picking decisions that maximize expected
294 utility, as follows:

295 We assume that noisy duration observations on any given trial x_{duration} is drawn from a Gaussian centered
296 around the true duration, with a standard deviation of σ_s .

$$p(x_{\text{duration}} | s_{\text{duration}}^*, s_{\text{slope}}^*) = \mathcal{N}(s_{\text{duration}}^*, \sigma_s^2)$$

297 We allow for the possibility of different levels of noise depending on the onset-offset slope: $\sigma_s \in$
298 $\{\sigma_s^{\text{slow}}, \sigma_s^{\text{fast}}\}$. Further, we assume that the true onset-offset slope on the trial is known: $s_{\text{slope}} = s_{\text{slope}}^* \in$
299 $\{\text{slow}, \text{fast}\}$, since “fast” and “slow” slopes were chosen to be at extreme ends of rats’ auditory neuron slope
300 response fields and discrimination performance, assessed previously (Lee et al., 2016; Osman et al., 2018).

301 Then the likelihood of the hypothesized duration s_{duration} on a given trial is a Gaussian function, centered
302 around the observation x_{duration}

$$\mathcal{L}(s_{\text{duration}}) = p(x_{\text{duration}} | s_{\text{duration}}, s_{\text{slope}})$$

303 We assume that rather than receiving just 1 observation, animals receive a constant rate of independent
304 observations over time i.e. $x_{\text{duration}} = \{x_1, x_2, \dots, x_k\}$. Assuming that animals integrate these optimally, this
305 yields a total likelihood that is the product of likelihoods for each individual observation, hence reducing
306 in width as an inverse function of the number (i.e., Fig. 3B the number of observed sound bursts, \hat{k}) or the
307 proportion (k) of observations in a given trial. We assume the proportion of observations (k) to be a linear

308 function of the hold time in a given trial (Fig. 3B and 3E): $k \propto t_{\text{hold}}$,

$$\mathcal{L}(s_{\text{duration}}) = \prod_k p(x_k | s_{\text{duration}}, s_{\text{slope}}) = \mathcal{N}(\bar{x}_{\text{duration}}, \sigma_s^2/k)$$

$$\bar{x}_{\text{duration}} = \frac{1}{k} \sum_{i=1}^k x_i$$

309 Let the conditional prior $p(s_{\text{duration}} | s_{\text{slope}})$ evaluated at the current trial's slope have a mean of μ_{prior} and
 310 a standard deviation of σ_{prior} . Then the posterior belief about duration, for a given set of noisy observations
 311 and slope condition is given by Bayes rule:

$$p(s_{\text{duration}} | x_{\text{duration}}, s_{\text{slope}}) \propto p(x_{\text{duration}} | s_{\text{duration}}, s_{\text{slope}}) p(s_{\text{duration}} | s_{\text{slope}})$$

$$p(s_{\text{duration}} | x_{\text{duration}}, s_{\text{slope}}) = \mathcal{N}(\mu_{\text{post}}, \sigma_{\text{post}}^2)$$

$$\mu_{\text{post}} = w_{\text{prior}} \mu_{\text{prior}} + w_s \bar{x}_{\text{duration}}, \quad \sigma_{\text{post}} = (\sigma_{\text{prior}}^{-2} + k \sigma_s^{-2})^{-1/2}$$

$$w_{\text{prior}} = \frac{\sigma_{\text{post}}^2}{\sigma_{\text{prior}}^2}, \quad w_s = \frac{k \sigma_{\text{post}}^2}{\sigma_s^2}$$

312 Note that as the animal receives more observations, the influence of the stimulus increases and the influence
 313 of the prior reduces.

314 The probability of a “long” duration is given by the integral of the posterior density beyond the true category
 315 boundary μ_0 , which we assume to be known. The maximum utility decision rule, assuming knowledge of
 316 rewards and priors, involves deterministically choosing “long” judgements when the posterior mean exceeds
 317 the category boundary, and “short” otherwise.

$$\begin{aligned}
 p(s_{\text{duration}} > \mu_0 | x_{\text{duration}}, s_{\text{slope}}) &= 1 - \phi(\mu_0; \mu_{\text{post}}, \sigma_{\text{post}}) \\
 \text{choice} = \text{long} &\text{ if } p(s_{\text{duration}} > \mu_0 | x_{\text{duration}}, s_{\text{slope}}) > p(s_{\text{duration}} < \mu_0 | x_{\text{duration}}, s_{\text{slope}}) \\
 &= \text{long if } \mu_{\text{post}} > \mu_0
 \end{aligned}$$

318 However, since the posterior mean depends on noisy observations, the probability of choosing a “long”
 319 judgement for a given true duration requires marginalizing over possible noisy values of x_{duration} (eq. 7, [Ma](#)
 320 [\(2019\)](#))

$$\begin{aligned}
 p(\text{choice} = \text{long} | s_{\text{duration}}^*) &= p(\mu_{\text{post}} > \mu_0 | s_{\text{duration}}^*) \\
 &= 1 - \phi(\mu_0; \mu, \sigma)
 \end{aligned}$$

$$\mu = \mu_{\text{prior}}(\sigma_{\text{prior}}^{-2} + \sigma_s^{-2}) / \sigma_{\text{prior}}^2 + s_{\text{duration}}^* \cdot k(\sigma_{\text{prior}}^{-2} + \sigma_s^{-2}) / \sigma_s^{-2} \quad (2)$$

$$\sigma = \sqrt{k} \cdot \sigma_s^{-1/2} / (\sigma_{\text{prior}}^{-2} + k\sigma_s^{-2}) \quad (3)$$

321 This yields a cumulative normal psychometric function (eq. 6) with midpoint μ and inverse slope σ . We
 322 augment this psychometric function with lapse rates, assuming that animals occasionally lapse due to fixed
 323 motor errors or inattention ([Pisupati et al., 2021](#)).

324 In the inattention model, p_{lapse} is the probability of not attending, and p_{guess} is assumed to be proportional to
 325 the prior probabilities of each category i.e. $p_{\text{guess}} = p(s_{\text{duration}} > \mu_0 | s_{\text{slope}})$, while in the motor error model
 326 p_{lapse} is the probability of motor error, and p_{guess} is assumed to be 0.5

$$p(\text{choice} = \text{long} | s_{\text{duration}}^*) = p_{\text{lapse}} \cdot p_{\text{guess}} + (1 - p_{\text{lapse}})(1 - \phi(\mu_0; \mu, \sigma)) \quad (4)$$

327 This yields a psychometric function that can be fit to the behavior in any given condition, with 2 free
328 parameters: σ_s and p_{lapse} for both “inattention” and “motor error” lapse models. Across conditions, we
329 force p_{lapse} to be the same, based on a preliminary analysis that showed empirical lapse rates to be the same
330 across conditions. The sensory noise parameter σ_s is either fixed across conditions (“fixed” noise models)
331 or allowed to vary between different slope conditions (“variable” noise models). We fix $k = 1$ for the single
332 burst 200ms hold time condition, allowing the k on other conditions to reflect relative integration times (fig.
333 3). For the “perfect integration” model, k is fixed to be proportional to the empirical hold times, yielding
334 no extra free parameters. We also entertain an “imperfect integration” model, that allows $t_{\text{integration}} < t_{\text{hold}}$,
335 yielding 2 extra free parameters.

336 For each of the three prior types (onset, offset, and both), 8 model variants (2 lapse models \times 2 noise
337 models \times 2 integration models) were fit using maximum likelihood fitting, using MATLAB’s `fmincon`
338 function. Thus, all together we compared 24 different models (3 prior types \times 8 model variants). Model
339 comparison was performed using Bayesian Information Criterion (BIC) and Akaike Information Criterion
340 (AIC) as detailed (figure 5B, supplementary table 2). We also fit synthetic data generated from each model
341 and performed a similar model comparison, in order to assess model recovery.

342 RESULTS

343 It is known that the slope of a sound’s onset can dramatically change how we perceive its duration (Stecker
344 and Hafter, 2000; Grassi and Darwin, 2006; Friedrich and Heil, 2017) and yet the basis for this percep-
345 tual interaction remains unknown. Here, we propose such cue interactions may reflect expectations based
346 on prior experience hearing co-variations in the onset slope and durations of natural sounds. To examine
347 this, we first quantify the statistical distributions of these cues in recordings of natural rodent alarm vocal-
348 ization sequences (Methods, Fig. 1). As the name implies, alarm vocalizations are used to communicate
349 an alarm to other rodents when they are distressed or alternately when they are defeated during rough and
350 tumble play (Wöhr and Schwarting, 2008; Thomas et al., 1983; Saito et al., 2019). When rodents hear syn-
351 thetic versions of these alarm vocalizations, they display stereotyped social responses provided the proper
352 combinations of pitch and temporal cues are incorporated (Wöhr and Schwarting, 2008; Saito et al., 2019).
353 Confirming prior studies, natural rodent alarm vocalizations examined here have a pitch or fundamental

354 frequency around 22 kHz (Fig. 1A1, A2) and durations ranging from 50 to 1500 ms (Fig. 1B, C). In
355 addition to these known acoustic features, we find the vocalizations with the shortest durations are statis-
356 tically more likely to have faster onset slopes (Fig. 1C1). Conversely, the vocalizations with the longest
357 duration are statistically more likely to have slower onset slopes (Fig. 1C1). Accordingly, the onset slope is
358 inversely correlated with vocalization duration (Fig. 1C1, Onset slope: $r = -.383$ and $p = 1e-47$). In contrast,
359 vocalization offset slopes have a weak positive correlation with duration (Fig. 1C2, Offset slope: $r = .125$ and
360 $p = 5e-6$). These correlations between onset, offset and duration extend the list of known timing cues that
361 identify vocalization type (Khatami et al., 2018; Saito et al., 2019).

362 Given the statistical co-variations reported here, we hypothesize that the slope of a sound would strongly
363 influence the perceptual judgment of its duration. To test our hypothesis, we create synthetic vocalizations
364 or sound bursts with plateau duration (Methods) ranging from 100 to 250 ms, which falls within the range
365 of natural alarm vocalizations (Fig. 1C). Our sound design allows us to symmetrically vary the sound
366 onset-offset slope independent of the sound duration (Methods). Thus, we are able to generate synthetic
367 vocalizations with a range of durations (100-150 ms) that all have the same symmetric onset and offset
368 slopes (Fig. 1B, bottom panel). To test the effects of the slope cue on duration perception, we generate
369 one set of synthetic vocalizations with slow onset-offset slopes and another set with fast onset-offset slopes
370 (Fig. 1E, red versus blue, respectively). Animals were trained initially on sound sequences with slow onset-
371 offset slopes until they reach a high-performance criterion (Methods). Importantly, the normalized slow
372 onset-offset slope used here is 84 A/s (Fig. 1E), which falls within the range we observe in the natural
373 alarm vocalizations with plateau durations ranging from 100 to 150 ms (Methods, Fig. 1C). In contrast,
374 the fast onset-offset slope used here is about two-fold faster than the fastest onset slope observed in the
375 natural vocalizations but still within the range of slopes evoking significant neural responses in rats (Lee
376 et al., 2016). Multivariate Gaussian fits of the joint distribution of natural vocalization slope and durations
377 (Fig. 1C1, C2) are used to quantify the co-occurrence of sound slope and duration cues (Methods, Fig. D1,
378 D2). In theory, prior experience hearing natural sounds such as alarm vocalizations and the statistical co-
379 variations therein could influence animals' inferences about sound duration. Moreover, co-variation of onset
380 or offset slopes alone or together could be used to infer duration. Accordingly, these three cue-combination
381 scenarios quantified with Gaussian distributions corresponding to fast and slow slopes are used to define the

382 1-dimensional priors over sound duration for the fast and slow slope conditions, respectively (Fig. 1F, blue
383 versus red, respectively, Methods).

384 Previous studies find sound judgment can improve with an accumulation of sensory information across
385 time and repetitions of acoustic events (Brunton et al., 2013; Liu et al., 2015; Raposo et al., 2012). This
386 principle applies to sound duration perception (Raposo et al., 2012), though most other prior studies have
387 probed duration perception of single sound bursts instead of sound burst sequences (Friedrich and Heil,
388 2017; Kelly et al., 2006). Here, we use a binomial choice task (Fig. 2) to test how animals judge
389 the duration of synthetic sounds when onset-offset slopes are fast versus slow (Fig. 2A). The duration
390 judgment is examined across three task conditions (Fig. 2B) using a reinforcement strategy (Fig. 2C) to
391 train animals to perform this bimodal two-alternative forced-choice behavioral task (Fig. 2D). Our three
392 task contingencies allow us to examine sound duration judgment as a function of the proportional number
393 of sound bursts heard (Fig. 3). Though the required minimum hold time (MHT) is fixed in the three task
394 contingencies, animals may hold longer than the MHT and the actual hold time varies on a trial-by-trial
395 basis (Methods, Fig. 3D, solid red and blue dots). For example, when MHT is 200 ms and multiple sound
396 bursts are played, the actual hold time is 445 ms (Fig. 3C, vertical dotted line). Under the latter condition,
397 animals hear on average 1 single sound burst before releasing from the center port (Fig. 3C, horizontal
398 dotted line). Conversely, when MHT is 600 ms and the actual median hold time is 652 ms (Fig. 3D, red
399 dot, top histogram), the number of sound bursts heard is 1.28 on average. Thus, the proportional number
400 of sound bursts heard increases when MHT is increased from 200 to 600 ms and multiple sound bursts are
401 heard (Fig. 3E). In the third task contingency where the MHT is 200 ms and only a single sound burst
402 is ever played, animals typically heard only a fraction (0.74) of one sound burst before making a duration
403 judgment (Fig. 3E). In all task conditions, animals judge 7 different sound durations as short versus long
404 (Fig. 2C) based on reward and time-out contingencies (Fig. 2D, Methods). Animals initially learn to hold
405 for a minimum of 600 ms while hearing a sequence of synthetic vocalizations with a varied but average
406 repetition rate of 2 Hz (Fig. 2B, 600 ms MHT, multi-burst). After reaching the task performance criteria
407 (Methods), duration judgment is tested for sounds with slow versus fast onset-offset slopes in alternating
408 test blocks (Fig. 2A). Animals then progressively learn to perform the sound duration judgment task while
409 holding for a minimum of 200 ms and hearing only one synthetic vocalization (Fig. 2B).

410 Though prior studies have demonstrated that sound slope cues alter duration perception none have ex-
411 amined how accumulating more sensory evidence impacts this cue interaction. Here, we find that sound
412 duration judgment is significantly impacted by both the sound slope cues and by hearing proportionally
413 more sound bursts (Figs. 3 and 4). Population performance for judging seven different sound durations is
414 quantified as the mean choice probability for judging sounds as long in duration (Fig. 3A, filled circles,
415 Methods). Initially, behavioral responses are fit with a standard sigmoidal response function (Methods, Fig.
416 3A, red and blue lines) in order to quantify performance metrics (Fig. 4). For all three MHT and task
417 conditions, there is a rightward shift in the perceptual boundary or "bias" (Fig. 3A, vertical dotted lines)
418 for sound duration judgment when sounds have fast (Fig. 3A, blue lines) versus slow (Fig. 3A, red lines)
419 onset-offset slope. This rightward bias indicates that animals are judging all sound durations as shorter when
420 their onset-offset slope is faster. This perceptual bias is most pronounced for the fast slope condition, and
421 when animals haven't accumulated much sensory information i.e. when they hear a maximum of one single
422 sound (Fig. 3A, left panel) and on average only a fraction of a single sound burst (Fig. 3E, light blue, and
423 pink dots). This perceptual effect is readily appreciated by comparing the bias parameter when hearing a
424 single burst with slow (Fig. 4A, SB) versus fast (Fig. 4B, SB) onset-offset slopes. Independent of the sound
425 onset-offset slope, sound duration judgment becomes sharper, and psychometric response functions steeper,
426 as more sound bursts are heard (Fig. 3A, 600 ms vs 200 ms MHT, right versus left panels). Accordingly,
427 there is a rank order decrease in the inverse sensitivity (Fig. 4C, D) which corresponds to an increase in
428 judgment accuracy across task conditions where animals hear proportionally more sound bursts. This effect
429 is observed for sounds with slow or fast onset-offset slopes suggesting that it is primarily related to the
430 accumulation of sensory information and not sound slope. Finally, changing the sound onset-offset slope
431 or number of sound bursts heard has no impact on the overall performance levels and relative performance
432 lapse for judging the shortest and longest duration sounds (Fig. 4E, F). Together, these results indicate that
433 sound slope cues can bias duration perception and that accumulating more sensory evidence can effectively
434 reduce this bias.

435 Although our behavioral results indicate that sound slope cues impact sound duration judgments, the
436 underlying principles driving this temporal cue and task interaction remain unclear. To examine whether

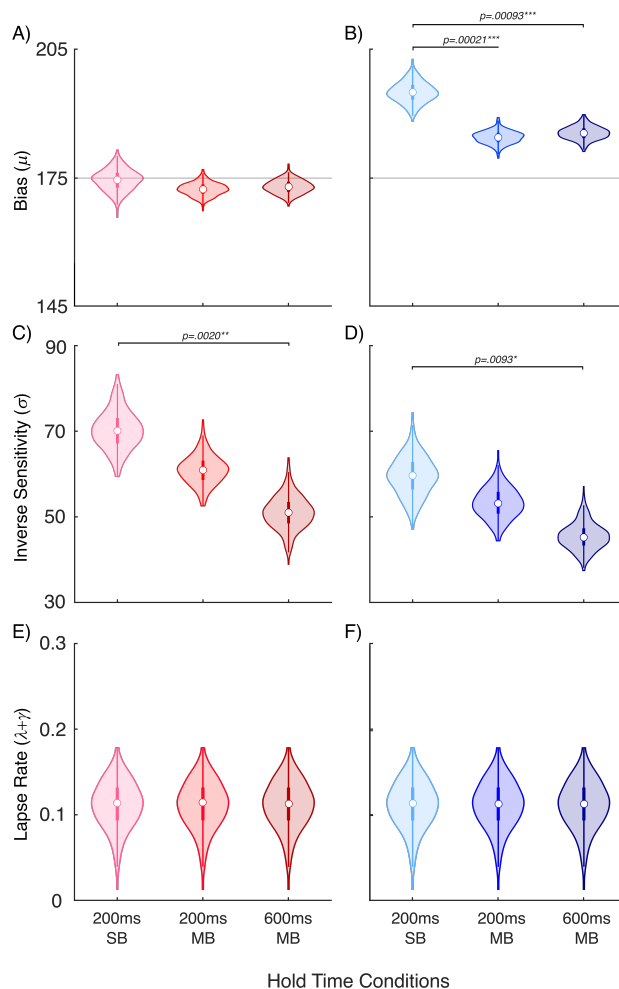


Figure 4: *Distinct shifts in perception with change in onset-offset slopes versus change in number of bursts heard.* Psychometric response function bias (μ), inverse sensitivity (σ) and lapse parameters ($\gamma+\lambda$) sampling distributions are shown for all task conditions (non-parametric bootstrap iterations = 400). A-B) The bias is shifted to higher values under all three MHT conditions when sound onset-offset slopes change from slow to fast (two-tailed z-test - 200ms SB: $p=9.5e-8$, $z=5.77$; 200ms MB: $p=1.4e-7$, $z=5.71$; 600ms MB: $p=2.2e-7$, $z=5.62$). C-D). Inverse sensitivity or σ shows a consistent decrease with respect to the hold time condition (z-test p-values shown in figure). E-D) Lapse rates are fixed across hold time and sound slope condition (mean [+/- SEM]= .113 [+/- .028]). * $p<.05$, ** $p<.01$, *** $p<.001$

437 such interactions stem from expectations based on prior experience hearing natural sounds, we fit the be-
 438 havioral responses using a normative, Bayesian decision-theoretic model of decision-making (Fig. 5). As
 439 illustrated in the joint probability distributions of durations and slopes, onset and offset slopes both co-vary
 440 with the duration of natural alarm vocalizations (Fig. 1). We utilized the Gaussian fits of these empirical
 441 joint distributions as parameter-free, “natural statistics priors” to infer duration in our Bayesian model (Fig.

442 1E). To fit the data, we compare three different prior types (Fig. 5B, table with rows reflecting prior type)
443 derived from three different natural statistical joint distributions for duration and onset slope (onset, Fig. 1F,
444 top), duration and offset slope (offset, Fig. 1F, middle) or duration with both onset and offset slopes (both,
445 Fig. 1F, bottom). The model had free parameters to account for three potential sources of errors in deci-
446 sions: “noise” in sensory observations, “lapses” or random decisions (Pisupati et al., 2021), and suboptimal
447 “integration” strategies. Accounting for these three sources of noise in our models with different integration
448 constraints generates a total of 8 model variations tested (Methods, Fig. 5B, table with three types of column
449 subdivisions: lapse type, noise constraint, and integration type). The noise in duration observations could ei-
450 ther be the same across slope conditions (“fixed”, 1 parameter across conditions) or differ for different slope
451 conditions (“variable”, 2 parameters for the two slope conditions). Lapses, or decisions made irrespective
452 of duration evidence, could arise due to motor errors and hence be made randomly (choosing either decision
453 with a probability of 0.5), and occur with a fixed probability across conditions (“motor error”, 1 parameter
454 across conditions), or arise from inattention and hence be made with a bias reflecting that condition’s prior,
455 and occur with a variable probability across conditions, (“inattention”, 2 parameters for the two slope con-
456 ditions). The integration of evidence across multiple bursts was either perfectly optimal, with the number of
457 effective bursts being fixed to be equal to the empirical hold times (“perfect”, no extra free parameters), or
458 suboptimal, with the effective number of bursts being less than the empirical hold times (“imperfect”, with
459 2 additional free parameters). The different assumptions about these three sources of errors, combined with
460 the three different prior types gave rise to a total of 24 combinations, which we compared using factorial
461 model comparison (Ma, 2019).

462 When we fit the behavioral data with the twenty-four different models, we find the overall best-fitting
463 model according to Bayesian information criterion (BIC) and Akaike information criteria (AIC) used the
464 empirical prior based on sound onset slopes and durations, and required only three free parameters - variable
465 sensory noise parameters across slope conditions, and a fixed lapse probability due to motor errors across
466 conditions, with perfect integration of evidence determined by the empirical hold times (Fig. 5A, 5B,
467 diamond). In contrast, across all model variations, priors based on the offset slope alone or based on a
468 combination of onset and offset slope did not accurately predict shifts in sound duration judgment with
469 sound slope (Fig. 5B, offset and both). Additionally, sensory noise but not lapse probabilities must vary

470 to account for response differences across behavioral task conditions. Importantly, our model is highly
471 constrained, using an entirely parameter-free empirical prior to account for perceptual biases, and only 3
472 additional free parameters to account for other sources of errors. In comparison, the standard sigmoidal
473 model requires thirteen free parameters (with a total of 6 individual bias parameters) to accurately fit the
474 response data (Fig. 3A). Hence, incorporating natural sound statistics offers a parsimonious explanation
475 for the perceptual misjudgements in sound duration caused by varying sound slopes. Finally, our Bayesian
476 model captures the inverse relationship observed between the empirical hold times and the perceptual bias
477 as well as inverse sensitivity, since integrating more sensory evidence overcomes the influence of the prior,
478 leading to less biased and more accurate decisions (Fig. 5C). Since the best fitting model performed perfect
479 integration, it required no additional free parameters to capture this effect, directly using the empirical hold
480 times as a parameter-free proxy for the number of accumulated evidence bursts. In summary, model fits
481 indicate that two key factors account for (mis)judgments of sound duration - prior experiences with co-
482 variations in natural sound statistics, and the amount of accumulated sensory evidence. Together, these
483 results offer a principled and normative explanation for why and how one auditory temporal cue can bias
484 the perception of another, and how accumulating sensory information can overcome these biases.

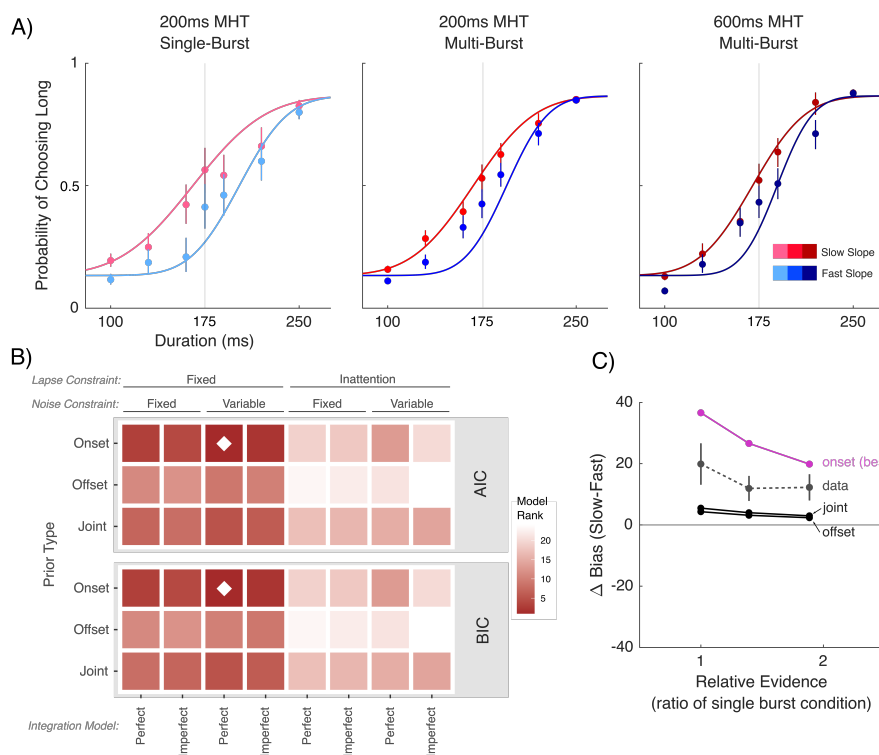


Figure 5: *Bayesian decision theoretic (BDT) model of observed bias.* A) Model fits from the best-fitting BDT model (solid lines) overlaid onto raw decision probabilities (points) from the behavioral experiment. B) Factorial model comparison of each of the three types of parameter constraints (lapse, noise and integration) for the three types of prior (onset, offset and both). Models are rank-ordered so that the model with the lowest information criterion (Akaike and Bayesian) is 1 (the best model, darkest color) and the one with the highest information criterion is 24 (the worst model, lightest color). Diamond denotes the best model. C) Line plot to demonstrating the change in bias across different prior types as a function of amount of accumulated evidence (prior models shown here are based on the lowest AIC model for each prior type; see supplementary materials for raw AIC/BIC values).

485

486 DISCUSSION

487 Previous studies find the rate of sound onset dramatically influences the perception of sound duration but
 488 the underlying principles for these cue interactions remain unknown (Cumming et al., 2015; Paquette and
 489 Peretz, 1997; Stecker and Hafter, 2000; Grassi and Darwin, 2006; Friedrich and Heil, 2017; Bizley and
 490 Cohen, 2013). We previously demonstrated that natural co-variations between duration and other temporal
 491 cues can be used to differentiate vocalization type across many animals including humans (Khatami et al.,
 492 2018). Using a similar approach here, we find a strong inverse correlation between the distribution of

493 onset slopes and durations of rodent alarm vocalizations (Fig 1). Accordingly, vocalizations with faster
494 onset slopes are more likely to be short in duration. Given this correlation, onset slopes could serve as a
495 predictive cue for vocalization duration. In contrast, offset slope and duration only have a weak positive
496 correlation. These observations lead us to hypothesize that perception of sound duration should be biased
497 by sound onset slopes, more so than offset slopes. Behaviorally, we find that rodents are perceptually biased
498 to judge synthetic vocalizations with fast onset-offset slopes as being shorter in duration (Fig. 3, 4). To
499 gain insight into this “mis-judgment” of duration and explore the potential contributions of onset and offset
500 slope statistics, we model the behavior with a normative, Bayesian decision-theoretic model. We find that
501 the behavioral data is best fit by a model that incorporates the joint statistics of durations and onset slopes of
502 natural vocalizations as a prior (Fig. 5A, blue curves; Fig. 5B, diamond). This supports our hypothesis that
503 onset slope more strongly biases the perception of duration than offset slope due to its natural co-variations
504 with duration, and accounts for the behavioral biases observed in the present study. Since our model accounts
505 for these biases by using empirical priors derived from natural vocalizations, and empirical hold times as
506 a proxy of accumulated evidence, it requires far fewer parameters than standard psychometric functions
507 to capture the observed biases (Fig. 3). Models that incorporate co-variations in onset slope and duration
508 perform better than similarly constrained models incorporating co-variations of offset and duration, or the
509 combined co-variations of onset and offset slopes with duration (Fig. 5B, offset and both). Moreover, our
510 Bayesian model captures the behaviorally observed decrease in bias (Fig. 5C) and improvement in sound
511 duration sensitivity (Fig. 3B) as animals listen to and integrate more sensory information across multiple
512 vocalizations, reducing the influence of the prior. In summary, our results demonstrate that prior experience
513 with the natural co-variations in onset, offset and duration cues can explain why onset slope cues heavily
514 bias perception of sound duration, with this perceptual bias reducing if perceptual evidence is integrated
515 over longer time windows.

516 Cue integration both within and across sensory modalities has been shown to follow principles of Bayesian
517 inference in a number of studies in humans (Trommershauser et al., 2011) as well as rodents (Raposo et
518 al., 2012; Madl et al., 2014; Nikbakht et al., 2018; Sheppard et al., 2013). According to these principles,
519 animals integrate information from multiple cues if they expect them to arise from a common source that
520 produces correlated measurements across cues. Such expectations can be formalized as a “coupling prior”

521 between cues, reflecting statistical regularities learned with prior experience (Spence, 2011). Such priors are
522 beneficial (i.e. lead to improved accuracy) in natural environments and tasks that respect these correlations,
523 and especially beneficial when sensory information about one or more cues is limited or noisy. However,
524 the same priors can be detrimental (i.e. lead to biases and impaired accuracy) in tasks that do not respect
525 these natural, learned regularities. Accordingly, in the present study when the synthetic vocalization du-
526 ration is the task-relevant cue and the onset-offset slopes are artificially fast compared to natural statistics,
527 duration judgment is biased and performance drops. In a similar vein, rats and mice performing a visual
528 rate-discrimination task (Odoemene et al., 2018) are influenced not just by the rewarded relevant variable
529 (i.e. event rate) but also by the total event count. While this may be beneficial on most trials when rate and
530 count are correlated, it can lead to incorrectly biased decisions on “catch” trials when the two are varied
531 independently. These findings support the idea that there are advantages and disadvantages to relying on en-
532 vironmental priors, especially when generalizing them to new environments, and decision-making systems
533 will need to flexibly tune how much they generalize in order to remain adaptive.

534 How can one be sure that biases observed in a given task are the result of biased priors, rather than other
535 biasing influences on decisions? Unconstrained Bayesian models might be overly flexible and capable of
536 accounting for a vast range of erroneous behaviors through the use of mismatched priors, and hence difficult
537 to falsify (Rahnev and Denison, 2018). This is why we instead opt for the approach of constraining the
538 parameters of the prior in our model entirely based on empirical natural statistics, with the sole assumption
539 being that animals’ judgments about synthetic vocalizations are biased by their prior beliefs about sounds
540 such as vocalizations. Moreover, decisions in Bayesian models are made by combining priors with incoming
541 samples of sensory evidence, each weighted by their respective certainty. Hence prolonged sampling and
542 integration of sensory evidence can lead to more accurate decisions by offering more certain evidence and
543 correcting for any biases from the prior, a feature evident in the behavioral data and captured by our model
544 based on empirical sampling times. These results extend previous work in support of the ability to optimally
545 accumulate auditory information to improve perceptual accuracy (Brunton et al., 2013)

546 What neural substrates could underlie these Bayesian computations? In order to maximize efficiency,
547 neurons in the brain should utilize codes that match the statistics of the signals they represent (Gervain and
548 Geffen, 2019; Carruthers et al., 2013). Accordingly, theoretical work on efficient coding has proposed that

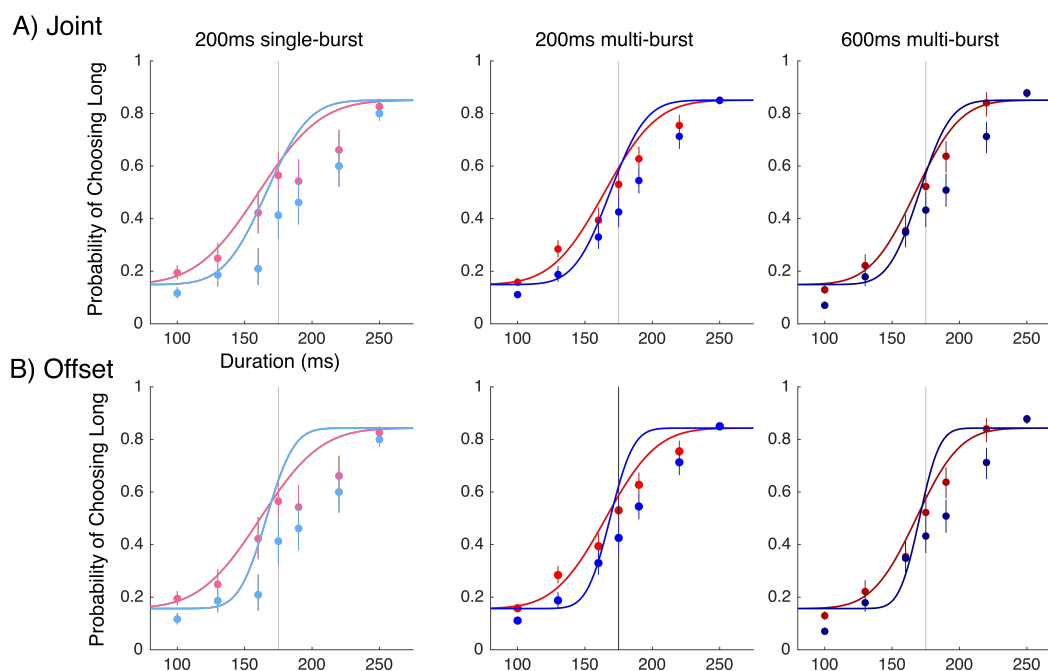
549 prior distributions could be implicitly represented in the distribution of tuning curves in neural populations,
550 with regions of higher prior probability being tiled more densely by more selective neurons (Ganguli and
551 Simoncelli, 2014a). Consequently, encoding a correlated “coupling prior” across multiple cues would entail
552 joint (rather than independent) encoding of these cues, with sharper and denser tuning to cue combinations
553 congruent with the prior (Yerxa et al., 2020a). Such joint encoding schemes would encourage integration,
554 prioritizing the efficient inference of common sources over the accurate reconstruction of component cues
555 (Zhang et al., 2019). At the same time, independent encoding schemes would remain advantageous when
556 no common source is detected and integration is not warranted (Zhang et al., 2019).

557 The simultaneously parallel and hierarchical structure of cortical pathways offers a possible candidate for a
558 flexible Bayesian inference (Rohe et al., 2019). Following a general rule observed in other sensory cortices,
559 as one transitions from primary to secondary auditory cortices, neurons respond to dynamically changing
560 sensory stimuli on increasingly longer timescales (Hamilton et al., 2018; Wang and Kennedy, 2016; Chaud-
561 huri et al., 2015; Lee et al., 2016; Johnson et al., 2020). We and others have shown previously that primary
562 and secondary auditory cortices encode multiple temporal cues including onset and offset timing, duration,
563 and rhythmicity cues in sound sequences (Lee et al., 2016; Read and Reyes, 2018). However, primary cortical
564 neurons respond to and encode sound onset-offset slope and sound rhythmicity independently (Lee et al.,
565 2016), and more accurately categorize the sound’s onset-offset slope and rhythmicity than those in secondary
566 auditory cortices (Osman et al., 2018). Likewise, primary auditory cortical neurons accurately encode vari-
567 ations in spectral and temporal cues in natural vocalization sequences (Lee et al., 2016; Storace et al., 2011;
568 Carruthers et al., 2013; Gervain and Geffen, 2019). In contrast, secondary auditory cortical neurons respond
569 to and encode these cues in a joint manner. For example, secondary auditory cortical neurons that respond
570 preferentially to sounds with slow onset-offset slopes tend to have more sustained spike-timing responses
571 and consequently a slower repetition rate or rhythmicity sensitivity (Lee et al., 2016). This co-variation in
572 neural sensitivity to the two temporal cues can be used to objectively differentiate sound sequences (Osman
573 et al., 2018). Thus, its neural spiking patterns, much like the natural sensory statistics themselves, can pro-
574 vide temporal cues that distinguish natural vocalizations (Khatami et al., 2018; Elie and Theunissen, 2019;
575 Carruthers et al., 2013). This raises the interesting possibility that the primary auditory cortical area pro-
576 vides a neural substrate for more accurate estimations of separate sources through independent encoding,

577 while secondary auditory cortical areas allow for more efficient probabilistic inference of common sources.
578 Accordingly, secondary auditory cortex might be expected to encode the joint statistical co-variations found
579 in natural sounds such as vocalizations, providing the “top-down” neural substrate for a “coupling prior”.
580 Though future studies are needed to establish this link, auditory cortices contain the neural code to represent
581 multiple temporal cues and support their optimal integration with prior experience. This neural code may in
582 turn be relayed to downstream areas such as the secondary motor cortex or striatum for further integration
583 over time (Erlich et al., 2015; Yartsev et al., 2018), or with value (Pisupati et al., 2021) to support optimal
584 decision-making.

585

586 Supplemental Materials



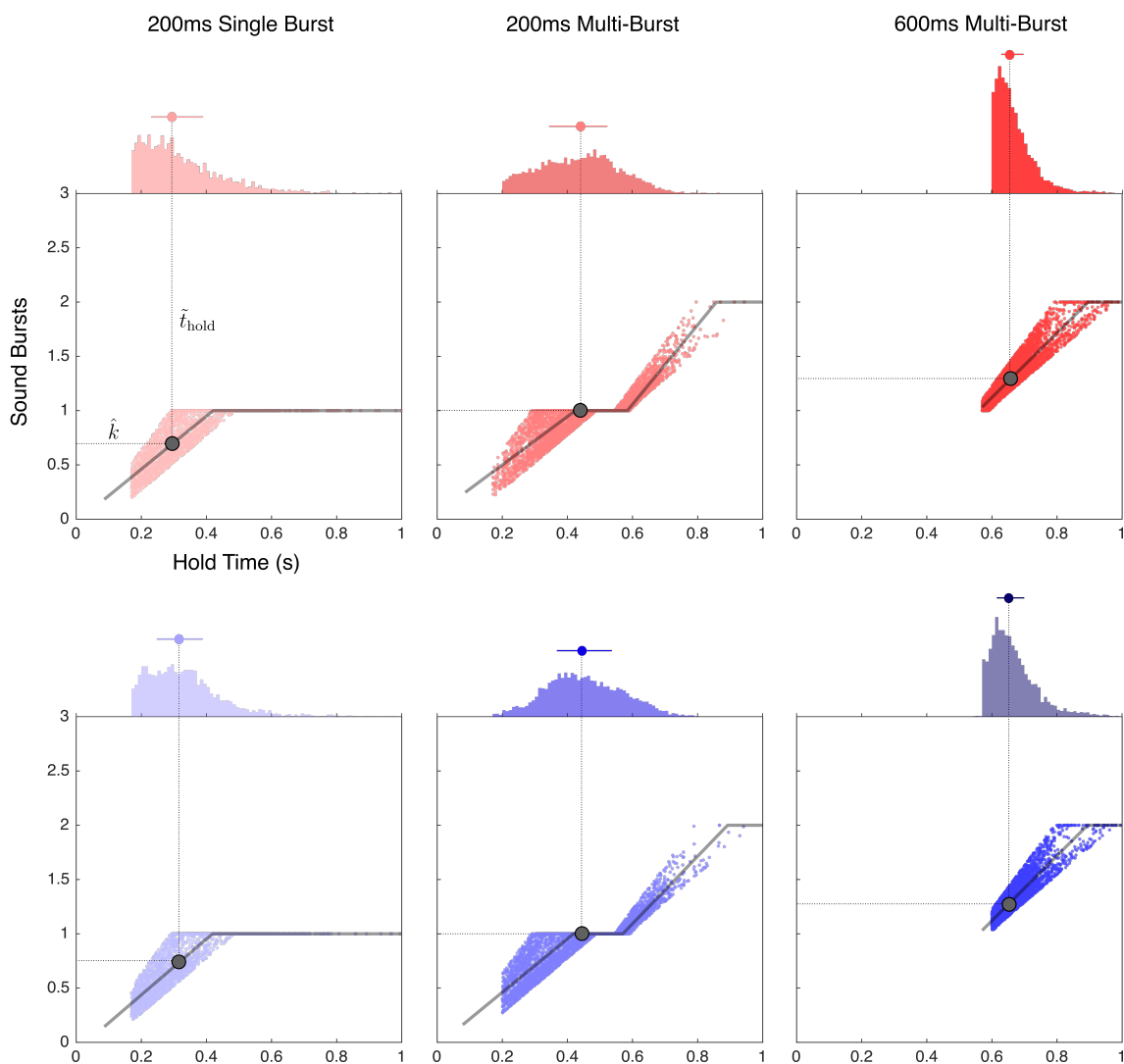
Supplemental Figure 1: Best model fits according to AIC for offset and joint prior types.

Prior Type	Noise Constraint	Integration Model	Lapse Constraint	Δ BIC	Δ AIC	nLL
onset	fixed	perfect	fixed	76.37	84.59	12834.83
onset	fixed	perfect	inattention	7271.68	7279.89	16432.48
onset	fixed	imperfect	fixed	95.55	87.33	12834.2
onset	fixed	imperfect	inattention	7220.65	7212.44	16396.75
onset	variable	perfect	fixed	0	0	12791.53
onset	variable	perfect	inattention	5706.65	5706.65	15644.86
onset	variable	imperfect	fixed	18.02	1.59	12790.33
onset	variable	imperfect	inattention	13243.25	13226.82	19402.94
offset	fixed	perfect	fixed	705.07	713.29	13149.18
offset	fixed	perfect	inattention	31603.35	31611.57	28598.32
offset	fixed	imperfect	fixed	854.48	846.27	13213.67
offset	fixed	imperfect	inattention	20168.25	20160.03	22870.55
offset	variable	perfect	fixed	698.15	698.15	13140.61
offset	variable	perfect	inattention	13535.87	13535.87	19559.47
offset	variable	imperfect	fixed	716.38	699.94	13139.5
offset	variable	imperfect	inattention	27684.32	27667.88	26623.47
joint	fixed	perfect	fixed	417.16	425.38	13005.22
joint	fixed	perfect	inattention	6873.15	6881.37	16233.22
joint	fixed	imperfect	fixed	431.05	422.83	13001.95
joint	fixed	imperfect	inattention	6701.02	6692.81	16136.94
joint	variable	perfect	fixed	373.03	373.03	12978.05
joint	variable	perfect	inattention	6640.6	6640.6	16111.83
joint	variable	imperfect	fixed	725.58	709.15	13144.11
joint	variable	imperfect	inattention	6486.2	6469.76	16024.41

Supplemental Table 1: Model fit metrics for all models compared in the study.

	Duration	Onset Slope	Offset Slope
Duration	1	3.0e-39	2.0e-26
Onset Slope	-0.38	1	4.0e-06
Offset Slope	0.12	0.13	1
Mean	586.5	38.5	10.2
SD	245.6	24.5	9.9

Supplemental Table 2: Summary statistics used as the parameters for joint priors. Correlation matrix contains Pearson product-moment correlations below the diagonal and their corresponding p-values above the diagonal.



Supplemental Figure 2: Scatterplots demonstrating the relationship between the time the animal was holding in the center port and the number of bursts heard during that time period (all trials). The residual variability is due to varying duration and the intentional jittering of the presentation of the sound stimulus. A piecewise linear regression is fit to the data using robust least squares in order to account for heteroscedasticity. Plateaus represent the empty intervals in between sound bursts. The number of estimated bursts (\hat{k}) in a given condition is predicted based on the median hold time for the given condition (\tilde{t}_{hold}). As shown in figure 3, \hat{k} and \tilde{t}_{hold} are nearly perfectly correlated ($r = 0.998$, $p < 0.0001$).

587 **References**

- 588 Belin P, Fillion-Bilodeau S, Gosselin F (2008) The Montreal Affective Voices: a validated set of nonverbal
589 affect bursts for research on auditory affective processing. *Behavior research methods* 40:531–539.
- 590 Bizley JK, Cohen YE (2013) The what, where and how of auditory-object perception. *Nature Reviews*
591 *Neuroscience* 14:693–707.
- 592 Brunton BW, Botvinick MM, Brody CD (2013) Rats and humans can optimally accumulate evidence for
593 decision-making. *Science* 340:95–98.
- 594 Carruthers IM, Natan RG, Geffen MN (2013) Encoding of ultrasonic vocalizations in the auditory cortex.
595 *Journal of neurophysiology* 109:1912–1927.
- 596 Chaudhuri R, Knoblauch K, Gariel MA, Kennedy H, Wang XJ (2015) A large-scale circuit mechanism for
597 hierarchical dynamical processing in the primate cortex. *Neuron* 88:419–431.
- 598 Cumming R, Wilson A, Goswami U (2015) Basic auditory processing and sensitivity to prosodic structure
599 in children with specific language impairments: a new look at a perceptual hypothesis. *Frontiers in*
600 *Psychology* 6:972.
- 601 Elie JE, Theunissen FE (2019) Invariant neural responses for sensory categories revealed by the time-varying
602 information for communication calls. *PLoS computational biology* 15:e1006698.
- 603 Elliott TM, Theunissen FE (2009) The modulation transfer function for speech intelligibility. *PLoS compu-*
604 *tational biology* 5:e1000302.
- 605 Erlich J, Brunton B, Duan C, Hanks T, Brody C (2015) Distinct effects of prefrontal and parietal cortex
606 inactivations on an accumulation of evidence task in the rat. *Elife* 4.
- 607 Friedrich B, Heil P (2017) Onset-duration matching of acoustic stimuli revisited: conventional arithmetic
608 vs. proposed geometric measures of accuracy and precision. *Frontiers in psychology* 7:2013.
- 609 Ganguli D, Simoncelli E (2014a) Efficient sensory encoding and Bayesian inference with heterogeneous
610 neural populations. *Neural Comput* 26:2103–34.

- 611 Ganguli D, Simoncelli EP (2014b) Efficient sensory encoding and Bayesian inference with heterogeneous
612 neural populations. *Neural computation* 26:2103–2134.
- 613 Gaucher Q, Huetz C, Gourévitch B, Laudanski J, Ocelli F, Edeline JM (2013) How do auditory cortex
614 neurons represent communication sounds? *Hearing research* 305:102–112.
- 615 Geffen MN, Gervain J, Werker JF, Magnasco MO (2011) Auditory perception of self-similarity in water
616 sounds. *Frontiers in integrative neuroscience* 5:15.
- 617 Gervain J, Geffen MN (2019) Efficient neural coding in auditory and speech perception. *Trends in neuro-*
618 *sciences* 42:56–65.
- 619 Grassi M, Darwin CJ (2006) The subjective duration of ramped and damped sounds. *Perception & Psy-*
620 *chophysics* 68:1382–1392.
- 621 Hamilton LS, Edwards E, Chang EF (2018) A spatial map of onset and sustained responses to speech in the
622 human superior temporal gyrus. *Current Biology* 28:1860–1871.
- 623 Jaramillo S, Zador AM (2014) Mice and rats achieve similar levels of performance in an adaptive decision-
624 making task. *Frontiers in systems neuroscience* 8:173.
- 625 Johnson JS, Niwa M, O'Connor KN, Sutter ML (2020) Amplitude modulation encoding in the auditory
626 cortex: comparisons between the primary and middle lateral belt regions. *Journal of Neurophysiol-*
627 *ogy* 124:1706–1726.
- 628 Jürgens R, Fischer J, Schacht A (2018) Hot speech and exploding bombs: autonomic arousal during emotion
629 classification of prosodic utterances and affective sounds. *Frontiers in psychology* 9:228.
- 630 Kelly JB, Cooke JE, Gilbride PC, Mitchell C, Zhang H (2006) Behavioral limits of auditory temporal
631 resolution in the rat: amplitude modulation and duration discrimination. *Journal of Comparative Psy-*
632 *chology* 120:98.
- 633 Khatami F, Wöhr M, Read HL, Escabí MA (2018) Origins of scale invariance in vocalization sequences and
634 speech. *PLoS computational biology* 14:e1005996.

- 635 Lausen A, Hammerschmidt K (2020) Emotion recognition and confidence ratings predicted by vocal stim-
636 ulus type and prosodic parameters. *Humanities and Social Sciences Communications* 7:1–17.
- 637 Lee CM, Osman AF, Volgushev M, Escabí MA, Read HL (2016) Neural spike-timing patterns vary with
638 sound shape and periodicity in three auditory cortical fields. *Journal of neurophysiology* .
- 639 Liu AS, Tsunada J, Gold JJ, Cohen YE (2015) Temporal integration of auditory information is invariant to
640 temporal grouping cues. *ENeuro* 2.
- 641 Ma WJ (2019) Bayesian decision models: A primer. *Neuron* 104:164–175.
- 642 Madl T, Franklin S, Chen K, Montaldi D, Trapp R (2014) Bayesian integration of information in hippocam-
643 pal place cells. *PLOS one* 9:e89762.
- 644 McDermott JH, Simoncelli EP (2011) Sound texture perception via statistics of the auditory periphery:
645 evidence from sound synthesis. *Neuron* 71:926–940.
- 646 Melo-Thomas L, Tonelli LC, Müller CP, Wöhr M, Schwarting RK (2020) Playback of 50-khz ultrasonic
647 vocalizations overcomes psychomotor deficits induced by sub-chronic haloperidol treatment in rats. *Psy-
648 chopharmacology* 237:2043–2053.
- 649 Nikbakht N, Tafreshiha A, Zoccolan D, Diamond ME (2018) Supralinear and supramodal integration of
650 visual and tactile signals in rats: psychophysics and neuronal mechanisms. *Neuron* 97:626–639.
- 651 Odoemene O, Pisupati S, Nguyen H, Churchland AK (2018) Visual evidence accumulation guides decision-
652 making in unrestrained mice. *Journal of Neuroscience* 38:10143–10155.
- 653 Osman AF, Lee CM, Escabí MA, Read HL (2018) A hierarchy of time scales for discriminating and classify-
654 ing the temporal shape of sound in three auditory cortical fields. *Journal of Neuroscience* 38:6967–6982.
- 655 Paquette C, Peretz I (1997) Role of familiarity in auditory discrimination of musical instrument: a laterality
656 study. *Cortex* 33:689–696.
- 657 Pisupati S, Chartarifsky-Lynn L, Khanal A, Churchland A (2021) Lapses in perceptual decisions reflect
658 exploration. *Elife* 10.

- 659 Prins N, Kingdom FA (2018) Applying the model-comparison approach to test specific research hypotheses
660 in psychophysical research using the palamedes toolbox. *Frontiers in psychology* 9:1250.
- 661 Rahnev D, Denison R (2018) Suboptimality in Perceptual Decision Making. *Behav Brain Sci* pp. 1–107.
- 662 Raposo D, Sheppard JP, Schrater PR, Churchland AK (2012) Multisensory decision-making in rats and
663 humans. *Journal of neuroscience* 32:3726–3735.
- 664 Read HL, Reyes AD (2018) Sensing Sound Through Thalamocortical Afferent Architecture and Cortical
665 Microcircuits In *The Mammalian Auditory Pathways*, pp. 169–198. Springer.
- 666 Rohe T, Ehrlis A, Noppeney U (2019) The neural dynamics of hierarchical Bayesian causal inference in
667 multisensory perception. *Nat Commun* 10:1907.
- 668 Roth S, Black MJ (2007) On the spatial statistics of optical flow. *International Journal of Computer*
669 *Vision* 74:33–50.
- 670 Saito Y, Tachibana RO, Okanoya K (2019) Acoustical cues for perception of emotional vocalizations in rats.
671 *Scientific reports* 9:1–9.
- 672 Sheppard J, Raposo D, Churchland A (2013) Dynamic weighting of multisensory stimuli shapes decision-
673 making in rats and humans. *J Vis* 13.
- 674 Spence C (2011) Crossmodal correspondences: A tutorial review. *Attention, Perception, & Psy-*
675 *chophysics* 73:971–995.
- 676 Stecker GC, Hafter ER (2000) An effect of temporal asymmetry on loudness. *The Journal of the Acoustical*
677 *Society of America* 107:3358–3368.
- 678 Storace DA, Higgins NC, Read HL (2011) Thalamocortical pathway specialization for sound frequency
679 resolution. *Journal of Comparative Neurology* 519:177–193.
- 680 Thomas DA, Takahashi LK, Barfield RJ (1983) Analysis of ultrasonic vocalizations emitted by intruders
681 during aggressive encounters among rats (*Rattus norvegicus*). *Journal of comparative psychology* 97:201.
- 682 Trommershauser J, Kording K, Landy MS (2011) *Sensory cue integration* Oxford University Press.

- 683 Wang XJ, Kennedy H (2016) Brain structure and dynamics across scales: in search of rules. *Current opinion*
684 *in neurobiology* 37:92–98.
- 685 Wöhr M, Schwarting RK (2008) Maternal care, isolation-induced infant ultrasonic calling, and their rela-
686 tions to adult anxiety-related behavior in the rat. *Behavioral neuroscience* 122:310.
- 687 Yartsev M, Hanks T, Yoon A, Brody C (2018) Causal contribution and dynamical encoding in the striatum
688 during evidence accumulation. *Elife* 7.
- 689 Yerxa T, Kee E, DeWeese M, Cooper E (2020a) Efficient sensory coding of multidimensional stimuli. *PLoS*
690 *Comput Biol* 16:e1008146.
- 691 Yerxa TE, Kee E, DeWeese MR, Cooper EA (2020b) Efficient sensory coding of multidimensional stimuli.
692 *PLoS computational biology* 16:e1008146.
- 693 Zhai X, Khatami F, Sadeghi M, He F, Read HL, Stevenson IH, Escabí MA (2020) Distinct neural ensemble
694 response statistics are associated with recognition and discrimination of natural sound textures. *Proceed-*
695 *ings of the National Academy of Sciences* 117:31482–31493.
- 696 Zhang W, Wang H, Chen A, Gu Y, Lee T, Wong K, Wu S (2019) Complementary congruent and opposite
697 neurons achieve concurrent multisensory integration and segregation. *Elife* 8.