1 **Informational Masking Can Constrain Acoustically Guided Mating Behavior**

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9 **Abstract**

10 Noisy social environments constrain human speech intelligibility in two primary ways: spectro-

11 temporal overlap between signals and noise reduces speech audibility ("energetic masking")

12 and noise interferes with processing the informative features of otherwise audible speech

13 ("informational masking"). To date, informational masking has not been investigated in studies

14 of vocal communication in nonhuman animals, even though their behavioral decisions frequently

15 depend on extracting information from vocalizations in noisy aggregations. In this study of a

16 treefrog, in which females chose mates in noisy breeding choruses, we investigated whether

17 informational masking can disrupt the processing of signal information in the contexts of species

18 recognition and sexual selection. We observed significant reductions in response to the

19 vocalizations of a potential mate when they were broadcast concurrently with other biologically

20 relevant sounds designed to reduce or eliminate energetic masking. These effects were more

21 pronounced when competing sounds were present in a particularly salient frequency range for

22 processing vocalizations. Among responsive subjects, however, performance in signal

23 recognition and discrimination tasks remained largely unchanged. These results confirm that

24 informational masking is a general communication problem among humans and other animals

25 and suggest it may be a crucial yet understudied source of selection shaping the evolution of

26 animal communication.

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Introduction

Noise is ubiquitous in natural environments and profoundly impacts all animals that rely on auditory perception for communication and other essential activities (Brumm, 2013; Brumm & Slabbekoorn, 2005; Wiley, 2015). In humans, competing sounds from multiple talkers and other sources can make conversations in crowded social settings difficult (Bronkhorst, 2015; Dimitrijevic et al., 2019; Middlebrooks et al., 2017) and can negatively affect cognitive performance in children (Klatte et al., 2013). In comparison, the consequences of noise-induced perceptual impairments are potentially more severe in nonhuman animals. Biotic and abiotic sounds in the environment potentially impact an animal's survival and reproduction by impairing its ability to detect (Lohr et al., 2003; Pohl et al., 2009), localize (Lee and Mason, 2017), recognize (Lee et al., 2017), and discriminate (Tanner and Bee, 2020; Wollerman and Wiley, 2002) among biologically important sounds in a variety of evolutionarily consequential contexts, such as mate choice (Bent et al., 2021; Gurule-Small and Tinghitella, 2018), prey detection (Schaub et al., 2008; Siemers and Schaub, 2011), and threat evasion (Simpson et al., 2016). However, our current knowledge of how nonhuman animals solve problems related to hearing and communicating in noise remains limited. To discover the diversity of evolutionary adaptations that allow animals to mitigate the impacts of noise, we must first understand the myriad ways noise imposes constraints on acoustic signal perception.

In a noisy environment where multiple sound sources are present, sound pressure waves from distinct sources combine to form one composite waveform that impinges on each tympanum. To recognize a target signal in this mixture, the auditory system must decompose the composite waveform into representations of discrete sounds and analyze each sound to extract features that convey relevant information (Bregman, 1990; McDermott, 2009). In vertebrates, the crucial first step of decomposition occurs in the inner ears, where different frequencies in the complex mixture are segregated by tonotopically organized auditory filters, each responding to a specific frequency range (Dooling et al., 2000; Lewis and Narins, 1999; Oxenham, 2013). When the sound energy of the signal and noise stimulates the same auditory filter at the same time, the two sounds directly compete on the auditory nerve (Recio-Spinoso and Cooper, 2013). In such cases, if the response of the auditory nerve in the presence of a signal does not change from its response to noise alone, the signal is rendered undetectable, and "energetic masking" is said to occur (Kidd et al., 2008; Middlebrooks et al., 2017). In the sensory ecology literature, energetic masking is so frequently used to explain the detrimental effects of extraneous noise on auditory perception that the general term "masking" is frequently

69   used synonymously with energetic masking (Barber et al., 2010; Erbe et al., 2016; Luther and

70   Gentry, 2013). However, a unitary concept of masking based on signal detection at the

71   periphery ignores the tremendous potential for noise to interfere with mechanisms operating at

72   central levels of the auditory system responsible for processing the biologically informative

73   features of otherwise audible signals (Rosa & Koper, 2018).

74   Research on human hearing demonstrates how noise can interfere with signal

75   processing at both peripheral and central levels of the nervous system (Amiri & Jarollahi, 2020;

76   Durlach et al., 2003; Kidd, 1994; Kidd et al., 2008; Shinn-Cunningham, 2013). Even when

77   signals and noise differ sufficiently in frequency so as to produce little or no competing

78   excitation in the periphery, noise can still make it difficult for the listeners to focus on the target

79   signal when it shares other features with the signal, such as similar temporal patterns (Kidd,

80   1994), common spatial origin (Freyman et al., 2001; Ihlefeld and Shinn-Cunningham, 2008), and

81   common onset/offset times (Neff & Dethlefs, 1995). This form of feature-based masking —

82   termed "informational masking" — does not result from an impaired ability to detect signals in

83   noise at the periphery but from an inability of central mechanisms to accurately process the

84   informative features of audible signals. Mechanistically, informational masking is thought to

85   occur because the simultaneous processing of signals and noise sharing similar features

86   interferes with a listener's ability to extract relevant information from signals (Gutschalk et al.,

87   2008; Scott et al., 2004; Shinn-Cunningham, 2013). Studies of speech perception suggest

88   informational masking may be a primary contributor to the so-called "cocktail party problem,"

89   which refers to the difficulty we have understanding speech in noisy social environments (Best

90   et al., 2020; Bronkhorst, 2015; Brungart et al., 2006; Carlile & Corkhill, 2015; Freyman et al.,

91   2005; Lidestam et al., 2014).

92   As in humans (McDermott, 2009; Middlebrooks et al., 2017), many other animals, such

93   as insects (Römer, 2013; Schmidt and Balakrishnan, 2015), frogs (Bee, 2015; Schwartz and

94   Bee, 2013; Vélez et al., 2013b), and birds (Aubin and Jouventin, 1998; Klump, 1996), also

95   communicate in cocktail-party-like scenarios where multiple individuals simultaneously produce

96   acoustic signals in large social groups (reviewed in Bee & Micheyl, 2008; Hulse, 2002).

97   However, ecological and evolutionary studies of animal communication in noise typically focus

98   on understanding how animals are adapted to reduce the effects of energetic masking in their

99   natural environments (Feng et al., 2006; Hage et al., 2013; Hotchkin & Parks, 2013; Lee et al.,

100 2021). Compared with our current understanding of how informational masking impacts human

101 speech perception, we have limited knowledge of the extent to which informational masking

102 impacts communication in other animals (Rosa and Koper, 2018). Consequently, the extent to

103   which informational masking represents a general communication problem shared by humans

104   and other animals that acts as a potent source of natural selection on animal communication

105   systems remains unknown.

106   Here, we tested the hypothesis that informational masking can disrupt the processing of

107   biologically informative features in the vocal signals of a nonhuman animal. Specifically, we

108   asked whether, in conditions of reduced energetic masking, a potential informational masker

109   could disrupt the ability of females of Cope's gray treefrog, *Hyla chrysoscelis*, to process

110   temporal features in a male's sexual advertisement calls related to species identity (Experiment

111   1) and mate quality (Experiment 2). Auditory perception in this species has been well studied in

112   the contexts of acoustically-mediated mate choice and communication in noisy environments

113   (reviews in Bee, 2015; Bee & Christensen-Dalsgaard, 2016; Gerhardt, 2001; Gerhardt & Huber,

114   2002). Male gray treefrogs aggregate in mixed-species breeding choruses each spring where

115   they attract mates by producing sequences of loud advertisement calls (~85 dB SPL at 1 m)

116   consisting of a short train of pulses (Fig 1; Gerhardt, 1975; Nityananda & Bee, 2011; Ward et

117   al., 2013a). High levels of background noise and extensive call overlap — both by conspecific

118   males and by males of other species that also produce pulsatile calls at different spectral

119   frequencies — are commonplace in mixed species choruses (Kuczynski et al., 2010;

120   Nityananda & Bee, 2011; Tanner & Bee, 2019). In these environments, females recognize and

121   discriminate among potential males using information encoded by temporal features of

122   advertisement calls (Bush et al., 2002; Gerhardt, 1994; Gupta & Bee, 2021; Nityananda & Bee,

123   2011; Schul & Bush, 2002; Ward et al., 2013a). However, chorus noise and overlapping calls

124   can interfere with signal recognition and discrimination (Bee, 2008; Bee & Schwartz, 2009; Lee

125   et al., 2017; Vélez et al., 2013a; Vélez & Bee, 2010).

126   Like most frogs, female gray treefrogs initiate mating by exhibiting phonotaxis toward

127   sounds recognized as an advertisement calls of their own species, and they exhibit

128   discrimination among potential mates with different call properties via selective phonotaxis

129   toward one calling male over one or more competing males (Gerhardt, 1995; Gerhardt & Huber,

130   2002). According to the informational masking hypothesis, we predicted that, even under

131   conditions designed to reduce energetic masking, concurrent pulsatile sounds would disrupt call

132   recognition and discrimination, as evidenced by changes in phonotaxis behavior. We tested this

133   prediction by exploiting the following key features of gray treefrog hearing and communication.

134   Each pulse in the male's pulsatile advertisement call consist of two harmonically related spectral

135   components with frequencies of about 1.25 and 2.5 kHz (Fig.1; Ward et al., 2013a). However,

136   females do not require both frequencies to recognize and discriminate between calls, and they

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137 readily respond to artificial signals having just one of the two spectral components (Bee, 2010;

138 Gerhardt et al., 2007; Nityananda & Bee, 2011). The key to our experimental design stems from

139 the fact that the two spectral components are primarily transduced by different sensory organs

140 in the frog inner ear. Frogs and other amphibians are unique among vertebrates in having two

141 sensory organs, the amphibian papilla (AP) and the basilar papilla (BP), that transduce airborne

142 sounds of different frequencies (Lewis and Narins, 1999; Simmons et al., 2006). In gray

143 treefrogs, the lower spectral component (~1.25 kHz) is transduced primarily by the AP (range of

144 sensitivity ~0.5 to 1.8 kHz), and the higher component (~2.5 kHz) is transduced primarily by the

145 BP (range of sensitivity ~1.4 to 4.0 kHz) (Fig 1; Hillery, 1984; Schrode et al., 2014). Together,

146 these features allowed us to test the informational masking hypothesis by delivering target

147 signals and potential maskers in different frequency regions transduced by different inner ear

148 papillae, thereby reducing the potential influence of peripheral energetic masking on behavioral

149 responses.

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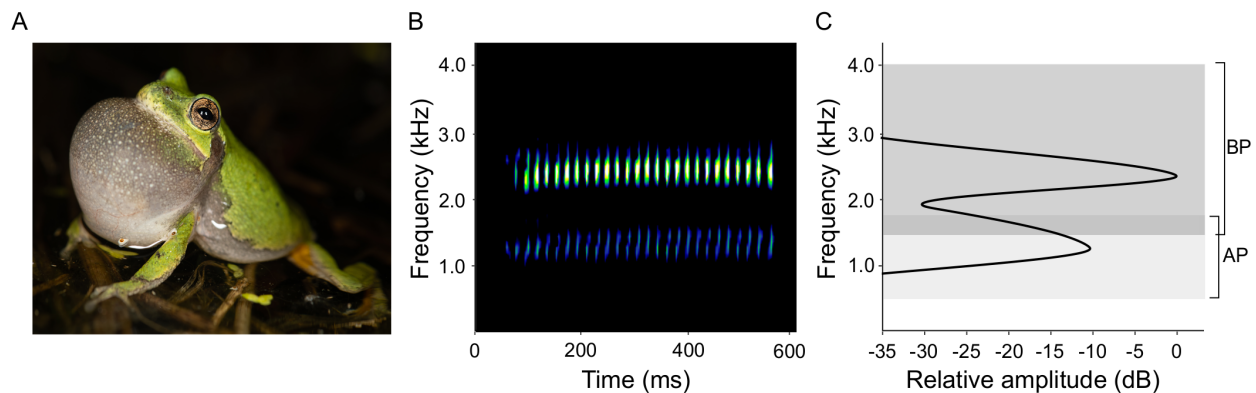
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Fig. 1: Natural advertisement call of male *H. chrysoscelis*. (A) Picture of a calling male *Hyla chrysoscelis* (photo credit: Alex Baugh). (B) Spectrogram illustrating the pulsatile temporal pattern and frequency composition of a natural advertisement call. (C) Power spectrum illustrating the high and the low spectral peaks of the advertisement call depicted in (B) relative to the approximate frequency ranges of the basilar papilla (BP; dark gray) and amphibian papilla (AP; light gray), respectively (after Hillery, 1984; Schrode et al., 2014).

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153 **Results**

154 **Experiment 1: Informational Masking and Signal Recognition**

155 In Cope's gray treefrog, females must correctly perceive the pulsed structure of a call to

156 recognize it as that of a male of her species (Schul & Bush 2002; Kuczynski et al. 2010). The

157 male's advertisement call consists of a pulse train of 12 to 43 pulses (mean = 30 pulses/call)

158 produced at an average pulse rate of 50 pulses/s (Ward et al., 2013a). Females must hear a

159 threshold number of pulses produced at a conspecific pulse rate before exhibiting a phonotaxis

160   response indicating recognition of the call (Gupta et al., 2021; Vélez & Bee, 2011). In

161   Experiment 1, we used an adaptive tracking procedure (Gupta et al., 2021) to test the prediction

162   that pulsatile sounds at remote frequencies impair signal recognition, as evidenced by lower

163   response rates, elevated pulse number thresholds, and longer response latencies compared

164   with quiet and a control masking condition lacking pulsatile sounds. Target signals were

165   presented in quiet (Fig. 2A) and in one of two masking conditions (Fig. 2B, C). The target signal

166   consisted of a train of up to 20 identical pulses, each with a species-typical amplitude envelope

167   and a frequency that was fixed at either 1.25 kHz (AP range) or 2.5 kHz (BP range). In the

168   informational masking condition (Fig. 2B), the target signal was presented concurrently with a

169   separate train of random-frequency pulses produced at a rate (25 pulses/s) that was half that of

170   the target signal (50 pulses/s). Each pulse of the informational masker had the same amplitude

171   envelope as each pulse in the target signal but was restricted to the opposite frequency range

172   with respect to the frequency tuning of the AP and BP (Fig. 2B). The slower pulse rate of the

173   informational masker was chosen to approximate the relatively unattractive pulse rate typical of

174   the spectrally similar calls of the closely related eastern gray treefrog (*Hyla versicolor*), which *H.*

175   *chrysoscelis* females frequently hear in mixed-species choruses but find far less attractive than

176   conspecific calls (Bee 2008; Nityananda & Bee 2011; Bush et al. 2002; Schul & Bush 2002).

177   Each pulse in the informational masker was temporally centered in the interval following every

178   other pulse in the target signal such that there was no spectral or temporal overlap between the

179   pulses of the target signal and informational masker. The non-overlapping spectral and temporal

180   relationships between the target signal and informational masker were chosen specifically to

181   minimize the potential for the informational masker to cause energetic masking through both

182   simultaneous spectro-temporal overlap and non-simultaneous effects, such as forward masking

183   (Hillery & Fay 1982). In a separate masking condition (Fig. 2C), the target signal was presented

184   concurrently with a band-limited noise having the same amplitude and long-term spectrum as

185   the informational masker. By also testing this masking condition, we attempted to control for any

186   possible effects of energetic masking because it stimulated the auditory system with the same

187   overall acoustic energy as the informational masker but was unlikely to interfere with call

188   recognition due to its lack of information-carrying temporal features. Thus, we generally

189   expected performance in the informational masking condition to be reduced relative to quiet and

190   the control masking condition, which we expected to be similar.

191   Across different groups of subjects, we used two stimulus configurations to examine how

192   signal information processed through different peripheral channels might be differentially

193   susceptible to informational masking (left and right panels of Fig. 2). In the "low-signal/high-
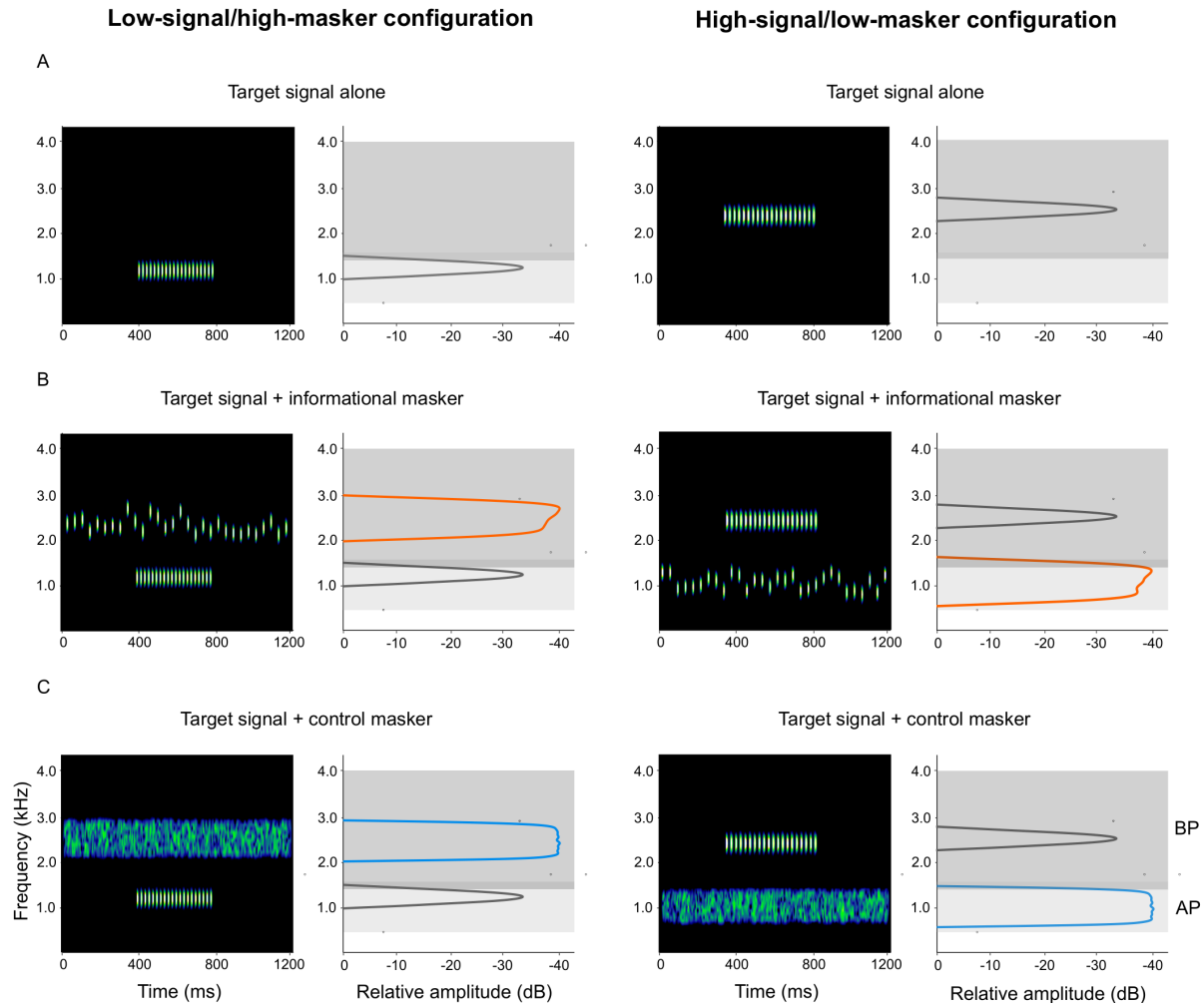
Fig. 2: The three masking conditions. Left and right panels illustrate spectrograms and power spectra of target signals and maskers in the low-signal/high-masker and high-signal/low-masker stimulus configurations, respectively. In the low-signal/high-masker configuration, target signals were in the AP range (light gray) and maskers were in the BP range (dark gray). In the high-signal/low-masker configuration, target signals were in the BP range and maskers were in the AP range. (A) Quiet condition in which a target signal with a pulse rate of 50 pulses/s was presented alone. The carrier frequency of the target signal was fixed at either 1.25 kHz (low-signal/high-masker configuration) or 2.5 kHz (high-signal/low-masker configuration) so that it would primarily stimulate one of the two papillae. (B) Informational masking condition in which the target signal was presented concurrently with a spectrally separated and temporally interleaved random-frequency pulse train (informational masker) with a pulse rate of 25 pulses/s. The frequency range of this informational masker fell within the sensitivity range of the papilla that was opposite to the one that was primarily stimulated by the target signal. (C) Control masking condition in which the target signal was presented concurrently with a band-limited noise (control masker) that had a frequency spectrum similar to that of the informational masker and was presented for the same duration. Gray, orange, and blue curves on the power spectra depict the frequencies in the target signals, informational maskers, and control maskers, respectively.

194   masker" configuration, the target signal was fixed at 1.25 kHz (AP range), and frequencies in

195   the maskers ranged between 2.1 to 2.8 kHz (BP range). In the "high-signal/low-masker"

196   configuration, the target signal was fixed at 2.5 kHz (BP range), and frequencies in the maskers

197   ranged between 0.7 to 1.4 kHz (AP range). All three conditions (quiet, informational masking,

198   and control masking) and both stimulus configurations were replicated factorially at signal-to-

199   noise ratios (SNRs; or equivalent signal levels in quiet) of -12 dB, -6 dB, and 0 dB. Masker

200   levels were fixed at 75 dB SPL (LC_{eq} re 20 μPa), and the amplitude of the target signal was

201   varied. Because response rates (χ^2 = 16.5, p < 0.001), pulse number thresholds (χ^2 = 28.9, p <

202   0.001), and response latencies (χ^2 = 28.9, p < 0.001) differed significantly between the two

203   stimulus configurations, we analyzed results for each configuration separately.

204   In the low-signal/high-masker configuration, 95.1% of subjects (136 of 143) tested in

205   quiet and 89.5% of subjects (51 of 57) tested in control masking conditions responded to a

206   target signal having 20 or fewer pulses (Fig. 3A). In contrast, only 54.7% of subjects (47 of 86)

207   tested in the informational masking condition did so (Fig. 3A). The response rate in the

208   informational masking condition was significantly lower compared with that in both quiet (GEE: β

209   = -2.72, p < 0.001) and the control masking condition (GEE: β = -1.74, p < 0.001). The

210   difference in response rate between quiet and the control masking condition, while much

211   smaller than that between quiet and the informational masking condition, was also statistically

212   significant (β = -0.97, p = 0.032). Neither SNR (χ^2 = 1.30, p = 0.520) nor the interaction of

213   masking condition and SNR (χ^2 = 1.08, p = 0.900) had significant effects on response rate based

214   on comparing models with these effects to one with masking condition as the only predictor

215   variable. Differences in response rates were not due to treatment order effects (χ^2 = 1.30, p =

216   0.520). We did not investigate responses to target signals with more than 20 pulses because

217   this value already exceeded both the minimum number of pulses per call (12 pulses) we have

218   recorded in local populations (Ward et al., 2013) and the maximum pulse number threshold (16

219   pulses) we have measured in response to target signals with both spectral peaks (Gupta et al.

220   2021).

221   Among those subjects that responded to target signals in both quiet and a masking

222   condition in the low-signal/high-masker configuration, the informational masker had little impact

223   on pulse number thresholds (Fig. 3B; Table 1) and no impact on response latency (Fig. 3C;

224   Table 1). We analyzed these data using a series of paired and independent-sample Wilcoxon

225   tests (with corrections for multiple comparisons) because the distributions of pulse number

226   threshold and response latency were non-normal; paired tests were used to compare responses

227   obtained from the same subject in quiet and in one of the masking conditions. At an SNR of -6

228   dB, we found a significant increase in pulse number threshold in the informational masking

229   condition compared with both quiet (Paired Wilcoxon test: V = 4, p = 0.021) and the control
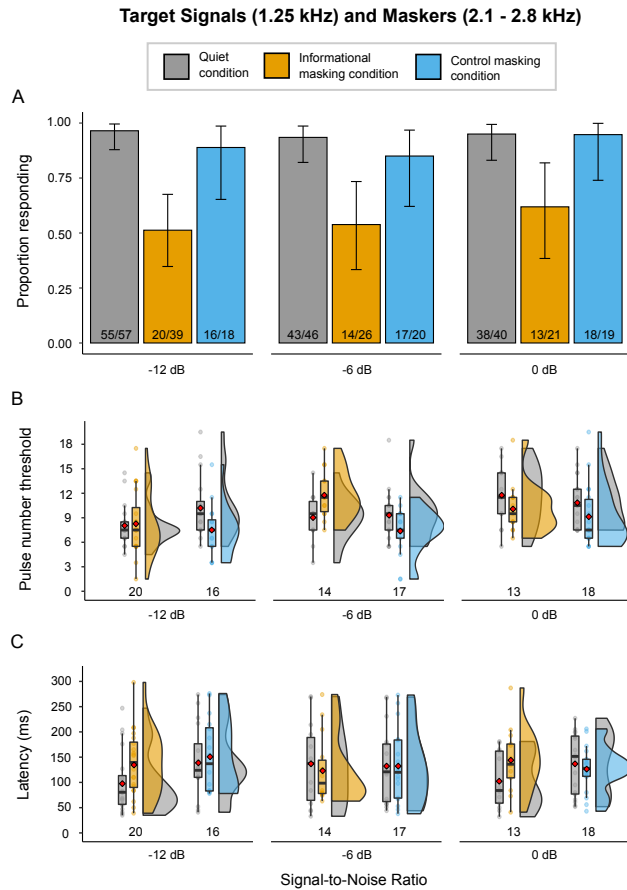
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Fig. 3: In Experiment 1, informational masking reduced the ability to recognize species-specific calls when the target signal was presented in the AP range and the masker was presented in the BP range. Gray, orange, and blue shaded regions depict the quiet, informational masking, and control masking conditions, respectively. (A) Response rate showing the proportion (± 95% exact binomial confidence intervals) of subjects that responded to target signals having 20 or fewer pulses at signal-to-noise ratios (SNRs) of -12 dB, -6 dB, and 0 dB. The base of each bar shows the numbers of subjects responding (numerator) and tested (denominator) in each condition. (B) Pulse number thresholds and (C) response latencies of subjects that responded to target signals in both quiet condition and in one of the two masking conditions. At each SNR, the paired box plots on the left depict the first, second (median), and third quartiles, and the mean (red diamond) values in quiet and the informational masking conditions, whereas the paired box plots on the right depict these values in quiet and the control masking conditions. The whiskers depict 1.5 times the interquartile range. The transparent points superimposed on the paired box plots depict individual data points obtained in quiet and in each masking condition. The two overlapping distributions are kernel density representations of the data that are depicted in the corresponding box plots. Sample sizes are indicated at the base of each dataset.

230 masking condition (Independent sample Wilcoxon test: W = 211, *p* < 0.001); the quiet and ns

231 did not differ (Paired Wilcoxon test: V = 103, *p* = 0.073). Differences in pulse number thresholds

232 at SNRs of -12 dB and 0 dB were not statistically different across the three conditions (Table 1).

233 Across all SNRs, the median (IQR) pulse number threshold of females was 9.5 pulses (7.5 –

234 11.5 pulses) in quiet, 9.5 pulses (7.5 – 12.0 pulses) in the informational masking condition, and

235 7.5 pulses (6.5 – 9.5 pulses) in the control masking condition (Fig. 3B). There were no

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Table 1: Outcomes of Wilcoxon signed rank tests comparing pulse number thresholds and response latencies between the three conditions when signals and maskers were in configuration 1. Significant results (after correcting α for multiple comparisons) are highlighted in bold. The informational masking condition is denoted as IM and the control masking condition is denoted as CM.

Response	SNR	Comparison	Statistic	*P*-value
Pulse number threshold	-12 dB	Quiet vs. IM (*N* = 20)	Paired Wilcoxon: V = 88.5	0.807
		Quiet vs. CM (*N* = 16)	Paired Wilcoxon: V = 111	0.027
		CM vs. IM (*N* = 16, 20)	Independent-sample Wilcoxon: W = 172.5	0.700
	-6 dB	**Quiet vs. IM (*N* = 14)**	**Paired Wilcoxon: V = 4.5**	**0.021**
		Quiet vs. CM (*N* = 17)	Paired Wilcoxon: V = 103	0.073
		CM vs. IM (*N* = 17,14)	**Independent-sample Wilcoxon: W = 211**	**< 0.001**
	0 dB	Quiet vs. IM (*N* = 13)	Paired Wilcoxon: V = 65	0.182
		Quiet vs. CM (*N* = 18)	Paired Wilcoxon: V = 93.5	0.060
		CM vs. IM (*N* = 18,13)	Independent-sample Wilcoxon: W = 148.5	0.211
Latency	-12 dB	Quiet vs. IM (*N* = 20)	Paired Wilcoxon: V = 55.5	0.067
		Quiet vs. CM (*N* = 16)	Paired Wilcoxon: V = 63	0.821
		CM vs. IM (*N* = 16,20)	Independent-sample Wilcoxon: W = 152	0.811
	-6 dB	Quiet vs. IM (*N* = 14)	Paired Wilcoxon: V = 62	0.583
		Quiet vs. CM (*N* = 17)	Paired Wilcoxon: V = 68	0.712
		CM vs. IM (*N* = 17,14)	Independent-sample Wilcoxon: W = 117	0.953
	0 dB	Quiet vs. IM (*N* = 13)	Paired Wilcoxon: V = 21	0.170
		Quiet vs. CM (*N* = 18)	Paired Wilcoxon: V = 91	0.507
		CM vs. IM (*N* = 18,13)	Independent-sample Wilcoxon: W = 135.5	0.471

236 significant differences between any of the three conditions in the latency to respond to the target

237 signal having the lowest number of pulses that elicited phonotaxis (Fig. 3C; Table1). Across all

238 SNRs, the median (IQR) response latencies were 113.5 s (62.75 – 176 s) in quiet, 126 s (84 –

239 176.5 s) in the informational masking condition, and 120 s (83 –178 s) in the control masking

240 condition (Fig. 3C).

241   In the high-signal/low-masker configuration, nearly all females responded to target

242 signals having 20 or fewer pulses in all three masking conditions and across all three SNRs

243 (Fig. 4A). Averaged across SNR, the response rates were 98.5% (130 of 132) in quiet, 94.2%

244 (65 of 69) in the informational masking condition, and 100% (63 of 63) in the control masking

245 condition. Differences in response rates across masking conditions and SNRs were not

246 analyzed statistically because of the high and nearly uniform response rates close to 100%,

247 including a 100% response rate in the control masking condition across all three SNRs (Fig.

248 4A).

249   The informational masker had little consistent impact on pulse number thresholds for

250 subjects that responded in the high-signal/low masker configuration (Fig. 4B; Table 2). Across

251 all SNRs, the median (IQR) pulse number threshold was 7.5 pulses (6.5 – 9.5 pulses) in quiet,

252 7.5 pulses (6.5 – 10.5 pulses) in the informational masking condition, and 6.5 pulses (5.5 – 8.5

253 pulses) in the control masking condition (Fig. 4B). At an SNR of 0 dB, pulse number thresholds

254 were significantly higher in the informational masking condition relative to both quiet (Paired

255 Wilcoxon test: V = 26, *p* = 0.009) and the control masking condition (Independent sample

256 Wilcoxon test: W = 329, *p* = 0.037). However, pulse number thresholds were also significantly

257 lower in the control masking condition relative to quiet (V = 180.5 V =26, *p* < 0.001). Broadly
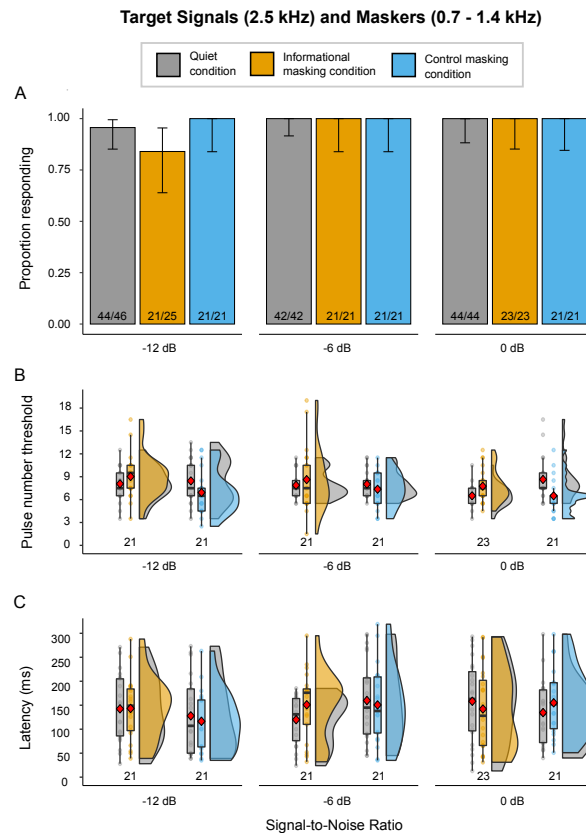

Fig. 4: In Experiment 1, informational masking did not reduce the ability to recognize species-specific calls when the target signal was presented in the BP range and the masker was presented in the AP range. Gray, orange, and blue shaded regions depict the quiet, informational masking, and control masking conditions, respectively. (A) Response rate showing the proportion (± 95% exact binomial confidence intervals) of subjects that responded to target signals having 20 or fewer pulses at signal-to-noise ratios (SNRs) of -12 dB, -6 dB, and 0 dB. The base of each bar shows the numbers of subjects responding (numerator) and tested (denominator) in each condition. (B) Pulse number thresholds and (C) response latencies of subjects that responded to target signals in both quiet condition and in one of the two masking conditions. At each SNR, the paired box plots on the left depict the first, second (median), and third quartiles, and the mean (red diamond) values in quiet and the informational masking conditions, whereas the paired box plots on the right depict these values in quiet and the control masking conditions. The whiskers depict 1.5 times the interquartile range. The transparent points superimposed on the paired box plots depict individual data points obtained in quiet and in each masking condition. The two overlapping distributions are kernel density representations of the data that are depicted in the corresponding box plots. Sample sizes are indicated at the base of each dataset.

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Table 2: Outcomes of Wilcoxon signed rank tests comparing pulse number thresholds and response latencies between the three conditions when signals and makers were in configuration 2. Significant results (after correcting α for multiple comparisons) are highlighted in bold. The informational masking condition is denoted as IM and the control masking condition is denoted as CM.

Response	SNR	Comparison	Statistic	*P*-value
Pulse number threshold	-12 dB	Quiet vs. IM (*N* = 21)	Paired Wilcoxon: V = 40.5	0.158
		Quiet vs. CM (*N* = 21)	Paired Wilcoxon: V = 147.5	0.035
		CM vs. IM (*N* = 21,21)	Independent-sample Wilcoxon: W = 314.5	0.018
	-6 dB	Quiet vs. IM (*N* = 21)	Paired Wilcoxon: V = 69.5	0.495
		Quiet vs. CM (*N* = 21)	Paired Wilcoxon: V = 141	0.376
		CM vs. IM (*N* = 21,21)	Independent-sample Wilcoxon: W = 250	0.463
	0 dB	**Quiet vs. IM (*N* = 23)**	**Paired Wilcoxon: V = 26**	**0.009**
		Quiet vs. CM (*N* = 21)	**Paired Wilcoxon: V = 180**	**< 0.001**
		CM vs. IM (*N* = 21,23)	**Independent-sample Wilcoxon: W = 329**	**0.037**
Latency	-12 dB	Quiet vs. IM (*N* = 21)	Paired Wilcoxon: V = 101	0.896
		Quiet vs. CM (*N* = 21)	Paired Wilcoxon: V = 118	0.641
		CM vs. IM (*N* = 21,21)	Independent-sample Wilcoxon: W = 278	0.152
	-6 dB	Quiet vs. IM (*N* = 21)	Paired Wilcoxon: V = 63	0.071
		Quiet vs. CM (*N* = 21)	Paired Wilcoxon: V = 118	0.945
		CM vs. IM (*N* = 21,21)	Independent-sample Wilcoxon: W = 230	0.821
	0 dB	Quiet vs. IM (*N* = 23)	Paired Wilcoxon: V = 153	0.659
		Quiet vs. CM (*N* = 21)	Paired Wilcoxon: V = 82	0.251
		CM vs. IM (*N* =21,23)	Independent-sample Wilcoxon: W = 207	0.424

259   similar patterns of differences in pulse number thresholds were also observed at SNRs of -12
260   dB and -6 dB (Fig. 4B), but none of these differences was statistically significant after correcting
261   for multiple comparisons (Table 2). The informational masker had no impact on response
262   latencies for subjects that responded in the high-signal/low masker configuration (Fig. 4C; Table
263   2). Across all SNRs, the median (IQR) response latencies were 139.5 s (76.75 – 187.0 s) in
264   quiet, 152 s (73.0 – 188.0 s) in the informational masking conditions, and 133 s (90.50 –185.0 s)
265   in the control masking condition (Fig. 4C).

266

267   **Experiment 2: Informational Masking and Signal Discrimination**
268   Female frogs and other animals frequently prefer to mate with males bearing certain phenotypic
269   traits, such as sexual displays with more elaborate or exaggerated features, which can reflect
270   aspects of higher male quality (Gerhardt & Huber 2002; Rosenthal 2017). In both Cope's and
271   eastern gray treefrogs, females discriminate among the calls of different conspecific males
272   based on differences in call duration; they prefer males that produce longer calls consisting of
273   more pulses (Bee, 2008; Gerhardt, 1994; Lee et al., 2017; Ward et al., 2013a). In eastern gray

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274   treefrogs, pulse number is heritable (Welch et al., 2014), and males producing longer calls sire

275   offspring with higher fitness (Welch et al., 1998). In Experiment 2, we used two-alternative

276   choice tests (Gerhardt 1995) to test the prediction that pulsatile sounds at remote frequencies

277   impair signal discrimination, as evidenced by reduced expression of female preferences for

278   longer calls, compared with quiet and a control masking condition lacking pulsatile sounds.

279   We conducted a series of four, two-alternative choice tests in which we presented

280   subjects with a choice between two alternating target signals that differed in pulse number but

281   were otherwise identical. The shorter alternative had an absolute pulse number of either 8, 12,

282   16, or 24 pulses, and the longer alternative had 25% more pulses, corresponding to absolute

283   pulse numbers of 10, 15, 20, or 30 pulses, respectively. The two target signals were alternated

284   in time to simulate two calling males. Each two-alternative choice test was replicated at all six

285   factorial combinations of the two signal-masker configurations and three masking conditions

286   (quiet, informational masking, and control masking) (see Fig. 2). In each masking condition, the

287   same rendition of the masker was presented concurrently with each of the target signals within

288   each successive pair of alternating target signals but varied randomly between successive pairs

289   of the two signals over the duration of the choice test. Because we did not observe systematic

290   differences in response rate, pulse number threshold, or response latency as a function of SNR

291   in Experiment 1, we conducted Experiment 2 at a single SNR (-6 dB; maskers at 75 dB SPL and

292   target signals at 69 dB SPL). In each choice test, we recorded whether a subject made a choice

293   by selectively responding to one of the two target signals and scored its response as binary

294   (shorter or longer) when a choice was made. Across all four choice tests and across both

295   stimulus-masker configurations, 78.5% (113 of 144) of subjects that made a choice in quiet

296   chose the longer call, resulting in an overall preference ratio of 3.6:1 in favor of the longer call in

297   the absence of a masker. This result corroborates preferences for longer calls demonstrated in

298   earlier studies (Bee, 2008; Gerhardt, 1994; Lee et al., 2017; Ward et al., 2013a) and established

299   a baseline for the expectation that informational masking would lead to reduced preferences for

300   longer calls. Stimulus configuration influenced response rate, defined as the proportion of

301   subjects that made a choice (χ^2 = 42.6, p < 0.001), and the proportion of responsive subjects

302   that chose the longer target signal (χ^2 = 3.96, p = 0.047); therefore, as in Experiment 1, we

303   analyzed responses in the two stimulus configurations separately.

304   In the low-signal/high-masker configuration (Fig. 5A), neither the absolute pulse

305   numbers of the two alternative target signals in a choice test (χ^2 = 3.78, p = 0.290), nor the

306   interaction of absolute pulse number with masking condition (χ^2 = 10.00, p = 0.120) had

307   significant effects on subject response rates. Averaged across all four choice tests, subjects

13

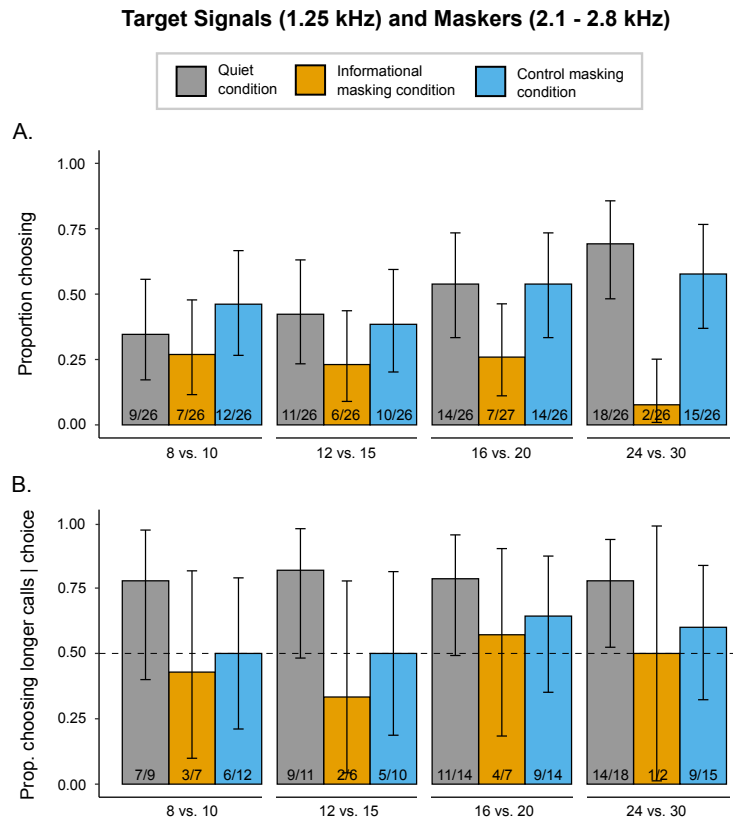**Target Signals (1.25 kHz) and Maskers (2.1 - 2.8 kHz)**

Fig. 5: In Experiment 2, informational masking reduced response rates and impaired pulse number discrimination when target signals were presented in the AP range and maskers were presented in the BP range. Gray, orange, and blue shaded regions depict the quiet, informational masking, and control masking conditions, respectively. (A) Response rates showing the proportions (± 95% exact binomial confidence intervals) of subjects tested that chose between two alternating target signals differing in pulse number. The base of each bar shows the numbers of subjects choosing (numerator) and tested (denominator) in each condition. (B) Probability of choosing the longer call depicted by the proportions (± 95% exact binomial confidence intervals) of subjects that chose the longer call over the shorter alternative. The base of each bar shows the numbers of subjects choosing the longer signal (numerator) and the total number that made a choice (denominator) in each condition.

308   made choices in 50.0% of tests (52 of 104) in quiet and 49.0% of tests (51 of 104) in the control

309   masking condition, and response rates in these two conditions did not differ (GEE: β = -0.04, *p* =

310   0.884). In contrast, the response rate was just 20.9% (22 of 105) in the informational masking

311   condition, which was significantly lower than response rates in quiet (GEE: β = -1.36, *p* < 0.001)

312   and in the control masking condition (GEE: β = -1.32, *p* < 0.001).

313   Among those subjects that made a choice in the low-signal/high-masker configuration

314   (Fig. 5B), the ratio of choices favoring the longer alternative (i.e., longer:shorter) was highest in

315   quiet (3.7:1), lowest in the informational masking condition (0.8:1), and intermediate in the

316   control masking condition (1.3:1), after combining data across the four different choice tests.

317   This general pattern – that of diminished preferences in the presence of an informational

318   masker compared with quiet and the control masker – was consistent across all four choice

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319   tests, as choice outcome did not depend on absolute pulse number (χ^2 = 0.90, p = 0.830) or its

320   interaction with masking condition (χ^2 = 0.92, p = 0.988). Subjects were significantly less likely to

321   choose longer calls over shorter calls in the informational masking condition compared with

322   quiet (GEE: β = -1.50, p = 0.011; Fig. 5B) but not compared with the control masking condition

323   (GEE: β = -0.46, p = 0.454; Fig. 5B); the probability of choosing the longer signal was not

324   significantly different between quiet and the control masking condition (GEE: β = -1.04, p =

325   0.046; Fig. 5B). It is worth noting that the sample sizes in these choice tests were small ($\leq$ 12 in

326   most tests) due to the low rate of responding in the low-signal/high-masker configuration.

327   Response rates were higher in the high-signal/low-masker configuration (cf. Figs. 5A &

328   6A) and depended on both masking condition (χ^2 = 6.76, p = 0.034) and absolute pulse number

329   (χ^2 = 12.3, p = 0.007), but not their interaction (χ^2 = 9.46, p = 0.150). Averaged across all four

330   choice tests, the response rate in the high-signal/low-masker configuration was highest in quiet

331   (80.0%, 92 of 115), lowest in the informational masking condition (67.3%, 76 of 113), and

332   intermediate in the control masking condition (76.7%, 89 of 116). After controlling for the effects

333   of absolute pulse number, response rate in the informational masking condition was significantly

334   lower compared with quiet (GEE: β = -0.68, p = 0.010), but not compared with the control

335   masking condition (GEE: β = -0.48, p = 0.160). Response rate did not differ between quiet and

336   the control masking condition (GEE: β = 0.20, p = 0.519). After controlling for the effects of

337   masking condition, subjects were less likely to respond (Fig. 5A) by making a choice in tests in

338   which the shorter alternative had 8 pulses compared with those with shorter alternatives having

339   16 pulses (GEE: β = -1.06, p = 0.001) but not 12 pulses (GEE: β = -0.48, p = 0.097) or 24

340   pulses (GEE: β = -0.55, p = 0.174).

341   In the high-signal/low-masker configuration, the probability of choosing the longer call

342   varied as a function of the absolute pulse numbers used in a given choice test (χ^2 = 13.5, p =

343   0.004). However, there was no clear pattern across tests: after controlling for differences in

344   masking condition, subjects were less likely to choose the longer target signal (Fig. 5B) in tests

345   in which the shorter alternative had 12 pulses compared with those with shorter alternatives

346   having 8 pulses (GEE: β = -1.12, p = 0.003) or 24 pulses (GEE: β = -1.09, p = 0.007) but not 16

347   pulses (GEE: β = -0.74, p = 0.088). There was no interaction between masking condition and

348   absolute pulse number (χ^2 = 2.94, p = 0.820). Among subjects that made a choice in this

349   configuration (Fig. 6B), and after combining data across different choice tests, the ratio of

350   choices favoring the longer alternative was highest in quiet (3.6:1), lowest in the informational

351   masking condition (2.0:1), and intermediate in the control masking condition (3.0:1). However,

352   after controlling for the effect of absolute pulse number, there were no significant differences in

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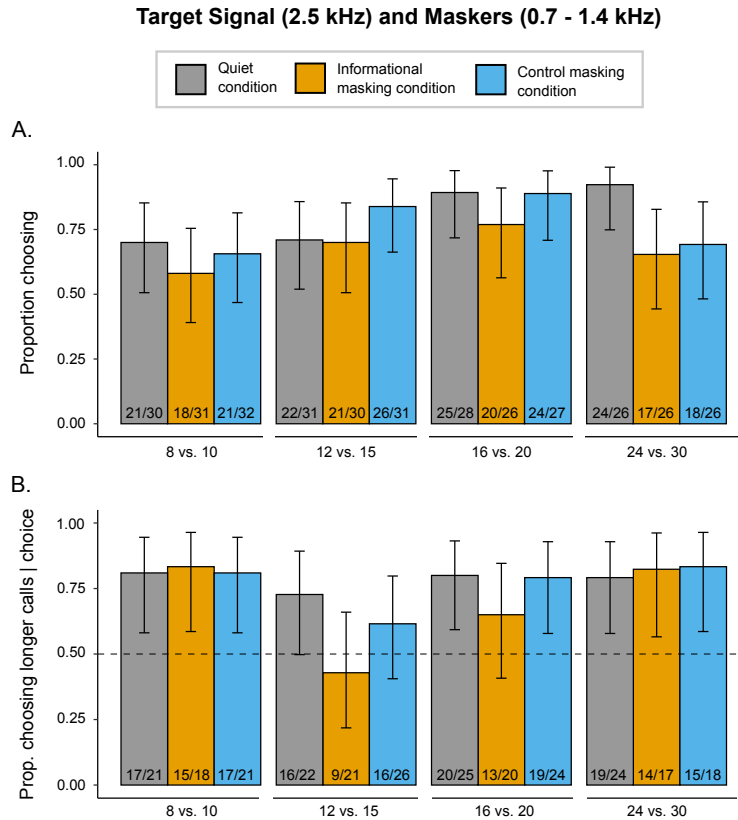**Target Signal (2.5 kHz) and Maskers (0.7 - 1.4 kHz)**

Fig. 6: In Experiment 2, informational masking did not reduce response rates or impair pulse-number discrimination when target signals were presented in the BP range and maskers were presented in the AP range. Gray, orange, and blue shaded regions depict the quiet, informational masking, and control masking conditions, respectively. (A) Response rates showing the proportions (± 95% exact binomial confidence intervals) of subjects tested that chose between two alternating target signals differing in pulse number. The base of each bar shows the numbers of subjects choosing (numerator) and tested (denominator) in each condition. (B) Probability of choosing the longer call depicted by the proportions (± 95% exact binomial confidence intervals) of subjects that chose the longer call over the shorter alternative. The base of each bar shows the numbers of subjects choosing the longer signal (numerator) and the total number that made a choice (denominator) in each condition.

353   the probability of choosing longer over shorter target signals between the informational masking

354   condition and quiet (GEE: β = -0.55, p = 0.116), between the informational masking and control

355   masking condition (GEE: β = -0.44, p = 0.175), or between the control masking condition and

356   quiet (GEE: β = -0.11, p = 0.757).

357

358   **Discussion**

359   Results from this study of a treefrog are consistent with the hypothesis that informational

360   masking can disrupt the processing of biologically informative features in the vocal signals of a

361   nonhuman animal. This outcome highlights informational masking as a general communication

362   problem shared by humans and other animals and suggests it may be a heretofore

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363   unrecognized source of selection acting on animal communication systems. The present study,

364   for example, confirms informational masking can disrupt acoustically guided choice of a mate,

365   one of the most evolutionarily consequential choices many animals will ever make (Rosenthal,

366   2017). In frogs, as in many other animals (Bee & Micheyl 2008), mate choice decisions depend

367   on a female's ability, under noisy social conditions, to recognize and respond appropriately to

368   the acoustic signals of a future mate based on correctly evaluating his signals, as well as

369   discriminating between his signals and those of other courters. Phonotaxis toward a sound

370   source constitutes behavioral evidence that a female frog has recognized a sound as that of an

371   appropriate mate (Gerhardt 1995; Gerhardt & Huber 2002; Ryan & Rand 2001). In the low-

372   signal/high-masker configuration, phonotaxis response rates were markedly reduced in the

373   informational masking conditions compared with both quiet and the control masking conditions,

374   which themselves did not differ. Moreover, this key result was robust: it was replicated across a

375   12-dB range of SNRs and across both Experiment 1 (signal recognition; Fig. 3A) and

376   Experiment 2 (signal discrimination; Fig. 5A). We interpret these findings as evidence that

377   central mechanisms for recognizing and responding to temporally structured vocalizations were

378   disrupted due to informational masking when other temporally structured sounds were present

379   at remote frequencies. Consistent with this interpretation are the data from responsive subjects.

380   Whenever statistically significant differences were observed, they were consistently in the

381   direction of degraded performance – that is, elevated pulse number thresholds (Experiment 1,

382   Fig. 3B) or reduced preference for longer calls (Experiment 2, Fig. 5B) – in the presence of the

383   informational masker relative to quiet, the control masking condition, or both. However, our

384   results also highlight two important features of informational masking in treefrogs: not all

385   individuals were equally susceptible to informational masking, and informational masking was

386   asymmetric between sounds transduced by the frog's two inner ear sensory papillae. We return

387   to a discussion of these two features after considering the possible mechanistic basis of

388   informational masking in treefrogs.

389   In humans, informational masking can occur when similarity between sounds of interest

390   and other concurrent sounds leads to failures of auditory stream segregation or impairments of

391   selective attention to audible and well segregated signals (Best et al., 2020; Ihlefeld and Shinn-

392   Cunningham, 2008; Shinn-Cunningham, 2013). We believe a reduced ability to segregate target

393   signals from informational maskers is unlikely to have contributed significantly to our results.

394   Recall that the spectro-temporal relationships between the pulses of target signals and

395   informational maskers – namely, wide frequency separation and a complete lack of temporal

396   overlap – were specified to reduce energetic masking. These same spectro-temporal

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397 relationships almost certainly promoted the segregation of signals and maskers into different

398 auditory streams. Some of the most potent cues promoting the segregation of sounds into

399 different auditory streams in humans and other animals are frequency separation, temporal

400 incoherence (e.g., differences in onset times and patterns of amplitude modulation), and spatial

401 separation (Bee, 2012; Dent et al., 2016; Dolležal et al., 2012; Lu et al., 2017; MacDougall-

402 Shackleton et al., 1998; Micheyl et al., 2010; Middlebrooks & Onsan, 2012; Nie & Nelson, 2015;

403 Oxenham, 2008; Shamma et al., 2013). Gray treefrogs are known to perceptually segregate

404 overlapping sounds (e.g., call-like sounds) into different auditory streams based on frequency

405 separation (Nityananda & Bee 2011), temporal incoherence (Gupta & Bee 2020), and spatial

406 separation (Bee & Riemersma 2008; Schwartz & Gerhardt 1995; Schwartz & Del Monte 2019).

407 Based on considerations of this earlier work, we suggest that the effects of informational

408 masking observed here are unlikely due to a breakdown of auditory stream segregation, but

409 instead reflect constraints on bottom-up attentional processing of biologically informative

410 temporal features of signals.

411   Bottom-up attention involves stimulus-driven mechanisms in which information is

412 processed involuntarily based on salient stimulus features (Katsuki & Constantinidis, 2014;

413 Kaya & Elhilali, 2014). In Cope's gray treefrog, pulse rate is perhaps the most salient acoustic

414 feature mediating recognition of, and responses to, conspecific calls (Bush et al. 2002; Schul &

415 Bush, 2002; Gerhardt 2008; Tanner et al., 2017). Females respond to, and exhibit robust

416 selective phonotaxis toward, advertisement calls with conspecific pulse rates but respond

417 infrequently to calls with faster or slower pulse rates (e.g., Bush et al. 2002). Between the

418 periphery and the midbrain, the processing of amplitude modulated (AM) sounds undergoes a

419 transformation from synchronized spiking activity in auditory nerve fibers to highly selective AM

420 tuning in the inferior colliculus (IC; also known as the torus semicircularis; Rose & Gooler 2007).

421 Electrophysiological recordings of neurons in the IC of awake gray treefrogs show pulse-rate

422 selectivity mirroring that observed in behavioral phonotaxis experiments with gravid females

423 (Rose et al. 1985; 2015; Gupta et al. 2021). The vertebrate IC is a key auditory processing and

424 audio-motor integration area thought to function in mediating acoustically guided behaviors with

425 short latencies, such as responding to prey, predators, or conspecifics (Casseday & Covey,

426 1996), including phonotaxis in female frogs (Endepols et al., 2003; Hoke et al., 2007, 2004).

427 Small lesions of the gray treefrog IC nearly eliminate phonotaxis behavior (Endepols et al.

428 2003). In stark contrast, even extensive lesions of the thalamus, a brain area implicated in top-

429 down attention to acoustic signals in frogs (Endepols et al. 2003; Ponnath and Farris 2013), fail

430 to eliminate selective phonotaxis based on differences in pulse rate (Endepols et al. 2003).

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431 Together, these data suggest temporal information related to pulse rate is processed through

432 bottom-up mechanisms that operate along the frog's ascending auditory pathway and that

433 ultimately drive adaptive behavioral responses to biologically relevant signals.

434 We hypothesize that informational masking may have occurred in the present study due

435 to the disruption of the precise, time-dependent integration of excitation and inhibition performed

436 by a subclass of pulse-rate selective IC neurons known as interval-counting neurons. These

437 neurons only fire after they are presented with a threshold number of pulses occurring at an

438 optimal pulse rate that typically coincides with the species-specific pulse rate of advertisement

439 calls (Edwards et al., 2002; Rose, 2014). In addition, the pulse number thresholds of interval-

440 counting neurons closely match those measured behaviorally, indicating these neurons play a

441 key functional role in processing biologically informative temporal features in pulsatile sounds

442 (Gupta et al., 2021; Rose et al., 2015). Interval-counting neurons respond to the first pulse of a

443 pulsatile sound with a brief excitatory postsynaptic potential (EPSP) followed by a large

444 inhibitory postsynaptic potential (IPSP). Upon stimulation by subsequent pulses at the optimal

445 pulse rate, excitation progressively overcomes inhibition, and action potentials are elicited

446 following a threshold number of pulses. However, when a sound having a slower or faster pulse

447 rate is presented, each pulse elicits an IPSP that disrupts the normal processes underlying

448 interval counting (Edwards et al., 2007; Rose et al., 2011). Most neurons in the frog IC have V-

449 shaped excitatory tuning functions that coincide with the tuning of one of the two inner ear

450 papillae and that are encompassed by a broader range of inhibitory tuning (Hall, 1999). We

451 speculate that an informational masker composed of slow-rate pulses in the range of the

452 opposite inner ear papilla elicit additional inhibition in the form of masker-driven IPSPs that

453 disrupt the precisely timed integration of excitation and inhibition underlying the interval counting

454 process (Edwards et al. 2007; Rose et al. 2015), at least in some individuals and in a frequency-

455 dependent manner.

456 One key outcome from this study is the documentation of considerable individual

457 differences in susceptibility to informational masking. For example, in Experiment 1 (signal

458 recognition), most subjects tested using the low-signal/high-masker configuration either failed to

459 respond at all or they responded at pulse number thresholds and with response latencies that

460 were similar to those of subjects tested in quiet. Studies of human subjects have also reported

461 large individual variation in susceptibility to informational masking. Thresholds for detecting pure

462 tones under informational masking conditions, for example, can vary by 20-30 dB and, in some

463 extreme cases, up to 50 dB among human listeners (Lutfi et al., 2003; Neff and Dethlefs, 1995).

464 Other studies have reported similarly large individual differences in speech recognition

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465   thresholds in the presence of competing speech or speech-shaped noise (Swaminathan et al.,

466   2015; Wightman et al., 2010; Zhang et al., 2021). Large individual differences among humans in

467   susceptibility to informational masking have been attributed to several possible factors, including

468   differences in sensory coding, neural processing, and attentional or cognitive strategies (Lutfi et

469   al., 2003; Swaminathan et al., 2015). At present, the mechanisms responsible for individual

470   differences in susceptibility to informational masking in frogs remain completely unknown.

471   Compared with, for example, songbirds and mammals, vocal communication in frogs is not

472   known for involving complex, top-down cognitive processing; thus, individual differences in

473   sensory coding and low-level, bottom-up neural processing may be more likely explanations for

474   individual differences in susceptibility to informational masking.

475   A second key outcome from this study was the demonstration of a stark asymmetry in

476   informational masking related to the relative frequency relationships between target signals and

477   maskers. Evidence of informational masking was most pronounced in the low-signal/high-

478   masker condition, in which the signal was primarily transduced by the AP and the masker was

479   transduced by the BP. At present, we lack a suitable mechanistic explanation for this

480   asymmetry. Gray treefrogs can process temporal information related to pulse rate in sounds

481   transduced in the inner ear by either the low-frequency (AP) or high-frequency (BP) peripheral

482   channels (Gerhardt 2008; Bee, 2010; Nityananda & Bee, 2011, 2012). Although thresholds for

483   responding to single-frequency target signals transduced by the two peripheral channels do not

484   differ (Nityananda & Bee, 2012), there is nevertheless a frequency-dependent processing bias

485   that favors signals transduced through one or the other peripheral channel. This bias varies

486   across geographic populations and evolutionary lineages within the gray treefrog species

487   complex (Gerhardt et al., 2007; Bee, 2010; Reichert & Höbel, 2017). In Minnesota, where this

488   study was conducted, female phonotaxis is biased toward sounds transduced by the high-

489   frequency (BP) peripheral channel (Bee 2010; Gupta & Bee unpublished data). It is tempting to

490   speculate that a bias toward processing temporal information in the BP range is in some way

491   responsible for the greater susceptibility to informational masking observed when the masker

492   was in this frequency range. Such speculation, however, would seem to be at odds with

493   previous work showing that target signals in the range of the BP are more, not less, susceptible

494   to interference from distracting sounds compared with signals in the range of the AP, even when

495   distractors are presented at 12-15 semitones away in frequency (Nityananda & Bee, 2011).

496   Additional research will be needed to resolve this issue.

497   Results from this study significantly broaden current views on the effects of noise on

498   animals. Studies of masking in the context of acoustic signaling typically focus (either explicitly

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499   or implicitly) on energetic masking, even though informational masking is potentially more

500   detrimental (Rosa & Koper, 2018). A few psychoacoustic studies have parsed informational

501   from energetic masking in nonhuman animals (Branstetter et al., 2016; Cai and Dent, 2020;

502   Eipert and Klump, 2020), and a few ecological studies have explored the idea that noise

503   (primarily anthropogenic noise) acts as a distractor that causes animals to shift their attention

504   away from behaviorally important tasks (Allen et al., 2021; Chan et al., 2010a; Chan et al.,

505   2010b; Hubbard et al., 2015; Rochais et al., 2017). To the best of our knowledge, however, all

506   such studies have evaluated the potential for informational masking outside the context of

507   communication. By highlighting informational masking as a heretofore understudied source of

508   potential selection on communication systems, this study opens several avenues for future

509   research that could further advance our understanding of hearing and acoustic communication.

510   Future studies, for example, should investigate the relative contributions of energetic and

511   informational masking in imposing constraints on communicative interactions in animals that,

512   like humans and frogs, frequently communicate in noisy social aggregations. It will be important

513   to determine the extent to which energetic and informational masking impose similar or different

514   constraints on communication and how those constraints independently and synergistically

515   impact signal reception and decision making in noise. Given the recent and growing awareness

516   of the negative effects of anthropogenic noise on animals (Barber et al. 2010; Rosa & Koper,

517   2018; Slabbekoorn et al., 2018; Gomes et al. 2021), it seems clear that any impacts related to

518   masking communication sounds should be examined through dual lenses of energetic and

519   informational masking. Finally, because frogs are a well-established vertebrate model in

520   research on vocal communication and auditory neuroethology (Gerhardt & Huber 2002; Narins

521   et al. 2007), this study suggests future work on frogs could address the existing dearth of

522   studies investigating the neural basis of informational masking at a cellular level in subcortical

523   areas of the vertebrate brain (Snyder and Elhilali, 2017).

524

525   **Materials and Methods**

526

527   **Subjects**

528   Wild-caught gravid females of the western *H. chrysoscelis* lineage (Booker et al. 2022) were

529   used as subjects for this study. All subjects were captured in amplexus at night (2200-0100 h)

530   between mid-May and early July in 2018, 2019, and 2021 from wetlands at the Carver Park

531   Reserve (Carver County, MN, USA), Richardson Nature Center (Hennepin County, MN, USA),

532   and Tamarack Nature Center (Ramsey County, MN, USA). Previous studies of a congeneric

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533   species (*Hyla gratiosa*) have established that gravid females captured in amplexus are as

534   discriminating as those captured prior to choosing a mate (Murphy and Gerhardt, 1996). Pairs

535   were collected in small plastic containers and returned to the laboratory on the St. Paul campus

536   of the University of Minnesota, where phonotaxis experiments were conducted. Each pair was

537   provided with aged tap water and maintained at approximately 4°C for up to 72 hours to delay

538   oviposition. This is a common procedure used with temperate zone frogs that delays oviposition

539   and extends a female's responsiveness in behavioral tests (Gerhardt, 1995). Approximately 30

540   minutes before testing, pairs were transferred to a temperature-controlled incubator so that their

541   body temperature could reach 20 $\pm$ 1°C. All experiments were conducted at this temperature

542   because female preferences are often temperature-dependent (Gerhardt, 1978), and 20°C is

543   close to the average nighttime temperature at the local field sites during the gray treefrog

544   breeding season (Ward et al., 2013a). Pairs were released at the site of their capture after the

545   completion of testing. All animal procedures were approved by the University of Minnesota's

546   Institutional Animal Care and Use Committee (1701-34456A and 2001-37746A) and adhered to

547   the *Guidelines for the Treatment of Animals in Behavioural Research and Teaching*, jointly

548   published by the Animal Behavior Society and the Association for the Study of Animal

549   Behaviour.

550

551   **Acoustic Stimuli**

552   All signals and maskers were synthesized in MATLAB R2018a (Mathworks, Natick, MA, USA) at

553   a sampling rate of 44.1 kHz (16 bit). Each target signal (Fig. 2A) was a pulse train consisting of

554   between 1 and 30 identical, equally spaced pulses that were modeled after a typical pulse in

555   natural advertisement calls recorded from our study populations (Fig. 1; Ward et al., 2013a).

556   The carrier frequency of each pulse within a target signal was fixed at either 1.25 kHz ("low-

557   signal"; AP range) or 2.5 kHz ("high-signal"; BP range), which are close to the average values of

558   the two harmonically related spectral components present in natural calls (Ward et al., 2013a).

559   Pulses within each target signal were shaped to have species typical rise and fall times (3.1-ms

560   inverse exponential rise time; 5.4-ms exponential fall time) and were delivered at a rate of 50

561   pulses/s (10-ms pulse duration, 20-ms pulse period, and 50% pulse duty cycle). During a

562   phonotaxis test, each target signal was repeated at a rate of 11 signals/min, which

563   approximates the average call rate in local populations (Ward et al. 2013a).

564   In the informational masking conditions (Fig. 2B), each masker consisted of a repeated

565   sequence of 30 pulses produced at a rate of 25 pulses/s (10-ms pulse duration, 40-ms pulse

566   period, and 25% pulse duty cycle). The temporal features of each pulse were identical to those

22

567   used in the target signal. The carrier frequency of each pulse in the informational masker was

568   randomly chosen from among 13 frequencies spaced one semitone apart between 0.7 kHz and

569   1.4 kHz ("low-masker"; AP range) or from 13 frequencies between 2.1 and 2.8 kHz ("high-

570   masker"; BP range) having the same absolute spacing (in Hz) as the frequencies between 0.7

571   kHz and 1.4 kHz. The pulses of the informational masker were interleaved with those of the

572   target signal such that each masker pulse occurred precisely between consecutive pairs of

573   signal pulses. In the control masking conditions (Fig. 2C), each masker consisted of an

574   independently generated, band-limited noise having the same duration and bandwidth (0.7 kHz

575   to 1.4 kHz or 2.1 kHz to 2.8 kHz) as the informational masker. In both masking conditions, a

576   masker was gated on and off with each presentation of a target signal at a rate of 11

577   maskers/min, and each presentation of a target signal was temporally centered in a masker.

578   Each separate rendition of a masker was randomized in the sense that the frequency of its

579   pulses (for the informational masker) or its temporal envelop (for the control masker) was

580   determined randomly so that the same masker never repeated in the same test of a given

581   subject. The sound pressure level (SPL re 20 μPa) of all maskers used in this study were

582   calibrated to 75 dB (LC$_{eq}$) at 1 m. This value falls within the range of background noise levels

583   measured in gray treefrog choruses (Tanner & Bee, 2019).

584   It is important to note that the informational masking condition was designed to blend

585   elements of classic experiments on informational masking in humans (e.g., the multitone

586   masking paradigm; Neff & Green 1987; Kidd et al. 2008) with elements of biological realism

587   pertinent to a female gray treefrog choosing a mate, such as a high degree of temporal overlap

588   between the pulsatile calls of multiple individuals or species in a chorus (Schwartz et al. 2001;

589   Nityananda & Bee 2011). A pulsatile informational masker was used because pulses (or trills)

590   are common in animal vocalizations, including frog calls (Gerhardt & Huber 2002), and thus

591   represent a natural sound for many animal species. The masker's slower pulse rate (relative to

592   the target signal) was chosen for three reasons: (1) several other frog species that breed

593   syntopically with *H. chrysoscelis* produce calls with relatively slower pulse rates, thus rendering

594   sounds with slower pulse rates biologically relevant in a mixed-species chorus environment

595   (Bee et al. 2010; Howard & Young 1998; Gupta et al. 2021); (2) a pulse rate of 25 pulses/s is

596   close to that of the eastern gray treefrog (*H. versicolor*), which often breeds in the same

597   choruses with, and whose calls are generally unattractive to, females of *H. chrysoscelis* (Bush

598   et al. 2002; Ward et al. 2013b); and (3) a pulse rate exactly half as fast as that of the target

599   signal allowed us to temporally interleave signal and masker pulses, thereby reducing the

600   potential for energetic masking. The frequency ranges selected for the informational maskers

23

601   coincide with frequencies present in the calls of other syntopically breeding frogs in mixed

602   species choruses (Nityananda & Bee 2011). We randomized the frequency of the pulses within

603   and between renditions of each masker to introduce an element of uncertainty into the testing

604   paradigm, which has been shown in studies of humans to contribute to informational masking

605   (Neff & Green 1987; Kidd et al. 2008).

606

607   **General Protocol**

608   We conducted experiments inside a circular phonotaxis arena (Fig. 7; 2-m diameter, 60-cm

609   height) setup inside a custom-built, temperature-controlled (20 ± 1°C), semi-anechoic chamber

610   (length x width x height: 2.8 x 2.3 x 2.1 m; Industrial Acoustics Company, IAC, North Aurora, IL,

611   USA). The chamber walls and ceiling were lined with dark gray acoustic absorber panels (IAC's

612   Planarchoic^{TM} system), and the floor was covered with dark gray, low-pile carpet. The arena

613   itself was made from hardware cloth and covered with black fabric. On the floor outside the

614   circular arena wall, we positioned two Mod1 Orb speakers (Orb Audio, Sherman Oaks, CA,

615   USA) separated by an angle of 90°, with both speakers directed toward the center of the arena.

616   Using this arena design and speaker placement allowed us to present acoustic stimuli to

617   subjects who could not see the speakers.

618   Signals and maskers were broadcast using Adobe Audition 3.0 (Adobe Systems Inc.,

619   San Jose, CA, USA) running on a Dell Optiplex 980 or 5050 PC (Dell Computer Corporation,

620   Round Rock, TX, USA). We used a MOTU model 16A sound card (MOTU, Inc., Cambridge,

621   MA, USA) interfaced with Crown XLS 1000 High-Density Power Amplifier (Crown International,

622   Los Angeles, CA, USA) to broadcast sounds. Stimuli were calibrated to their target sound

623   pressure levels (SPL; LCF, re 20 µPa) by placing a Bruël and Kjær Type 4950 microphone

624   connected to a Bruël and Kjær Type 2250-L sound level meter (Bruël and Kjær, Nærum,

625   Denmark) 1 m away from the speaker at the approximate position of a subject's head at the

626   release point. The frequency response of the playback system was ± 2 dB across the frequency

627   range of interest (0.7 kHz to 2.8 kHz) when measured at this position.

628   At the beginning of a phonotaxis test, we separated the subject from her mate and

629   placed her in a small acoustically transparent release cage (9-cm diameter, 2-cm height)

630   located on the center of the arena floor. We allowed the subject to acclimate in the chamber for

631   30 sec, after which we started the playback. At this time, we remotely lifted the lid of the release

632   cage using a rope-and-pulley system and allowed the subjects to move freely in the arena. A

633   test continued until the subject responded to a stimulus by entering a response zone consisting

634   of a 10-cm semi-circle in front of a playback speaker or until the subject was considered to have

24

635 failed to respond to a stimulus. Our criteria for determining failure to respond were the following:

636 (1) if the subject did not exit the release cage within 3 min; (2) if the subject did not enter a

637 response zone within 5 minutes; (3) if the subject's first physical contact with the arena wall was

638 in the semi-circle opposite the speaker in a single-stimulus test or in the quadrant opposite that

639 formed by the two speakers in a choice test. Movements of subjects inside the arena were

640 observed under infrared (IR) light (Tracksys, Ltd., Nottingham, UK) and scored in real-time by

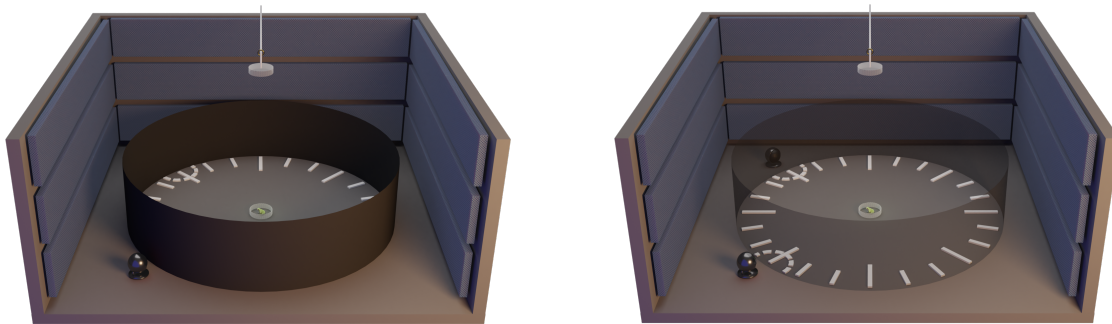641 an observer outside the chamber by means of a video monitor.

Fig. 7: Schematic 3D diagram of the experimental setup. Left panel depicts the circular phonotaxis arena inside a semi-anechoic chamber. Acoustic stimuli were broadcast from two speakers positioned on the floor outside the arena wall. In the right panel, the arena wall has been made visually transparent so that the two speakers and the marked response zones on the arena floor in front of the speakers are visible. At the center of the arena floor is a release cage in which subjects were placed at the start of each test.

642

Experiment 1: Signal Recognition

644 Experiment 1 tested the prediction that informational masking can impair signal recognition. We

645 assessed signal recognition using a series of single-stimulus, no-choice tests (Gerhardt 1995;

646 Ryan & Rand 2001) and an adaptive tracking procedure (Bee & Schwartz, 2009; Gupta et al.

647 2021) to measure pulse number thresholds, which we operationally defined as the minimum

648 number of pulses required to elicit positive phonotaxis. We measured two pulse number

649 thresholds for each subject, one in quiet and one in a masking condition, with the order of

650 threshold determination determined randomly. Subjects were assigned randomly to one of the

651 two masking conditions (Fig. 2; informational masker or control masker), one of the two stimulus

652 configurations (Fig. 2; low-signal/high-masker or high-signal/low-masker), and to one of three

653 SNRs (-12 dB, -6 dB, or 0 dB). The amplitude of the masker was fixed at 75 dB SPL, and signal

654 levels of 63, 69, and 75 dB SPL were used, respectively, to achieve nominal SNRs of -12 dB, -6

655 dB, and 0 dB.

25

656   The first phonotaxis test of each subject was considered a "reference test" and consisted

657   of broadcasting a sequence of attractive synthetic call having the average properties of

658   conspecific (*H. chrysoscelis*) calls recorded in local populations (see Ward et al. 2013a). For

659   females collected from ponds where the closely related and morphologically indistinguishable

660   eastern gray treefrog (*Hyla versicolor*) were also breeding, we alternated broadcasts of this

661   conspecific call with broadcasts of synthetic *H. versicolor* calls. Signals were calibrated to 85 dB

662   SPL in reference tests. Gravid females exhibit robust selective phonotaxis toward synthetically-

663   generated conspecific calls (Gerhardt, 1994; Gerhardt & Doherty, 1988; Bee 2008; Gall et al.

664   2019); therefore, this initial reference test allowed us to confirm both a female's species identity

665   (if necessary) and its motivation to respond in phonotaxis tests. Only responsive females

666   identified as *H. chrysoscelis* were used as subjects in subsequent tests.

667   We followed procedures described by Gupta et al. (2021) to measure pulse number

668   thresholds from 323 subjects. In the first of a sequence of single-speaker tests, we presented

669   subjects with a sequence of target signals consisting of 8 pulses. Depending on whether the

670   subject responded to the target signal, we either decreased or increased the number of pulses

671   in the target signal by two pulses in the subsequent test. If the subject responded to the

672   sequence of 8-pulse target signal on this test, they heard a sequence of 6-pulse signals in their

673   next test; subjects that failed to respond to the 8-pulse target signal heard a sequence of 10-

674   pulse target signals in their next test. This process continued until the subject's response

675   changed from a response to a no response or from no response to a response between two

676   consecutive tests. After this change in behavior, we performed a final test in which we reversed

677   the direction of change and either increased or decreased the pulse number by one pulse based

678   on whether it responded to the target signal in the immediately preceding test. The pulse

679   number threshold was calculated by averaging the lowest pulse number that elicited a response

680   and the highest pulse number that did not. The maximum number of pulses used in any target

681   signal was 20 pulses. If the subject did not respond to a target signal with 20 pulses, we did not

682   determine its pulse number threshold. As already noted, this maximum value was chosen

683   because it exceeds the minimum number of pulses per call (12 pulses; Ward et al., 2013a) and

684   the maximum pulse number threshold in response to target signals with both spectral peaks (16

685   pulses; Gupta et al. 2021). In addition, restricting the maximum number of pulses to 20 was

686   necessary to ensure we could measure two pulse number thresholds per subject, which

687   typically do not respond in more than about 15 to 20 phonotaxis tests before losing response

688   motivation. Response latencies were recorded for all tests in which the subject responded to a

689   target signal. After determining a subject's first pulse number threshold we immediately

690   restarted the adaptive tracking procedure to determine their second threshold. In addition, we

691   determined the latency to respond to each target signal having the lowest number of pulses that

692   elicited a response. If at any time during testing, a subject failed to respond in three consecutive

693   tests, we performed another reference test. Only subjects that exhibited positive phonotaxis in

694   this reference test were tested further; two subjects were excluded from the final dataset

695   because they did not meet this inclusion criterion. Procedures for determining pulse number

696   thresholds in quiet and in the two masking conditions were the same with the following

697   exception. In the masking condition, subjects experienced a "sham" test prior to commencing

698   the adaptative tracking procedure to determine their masked pulse number threshold. In this

699   sham condition, the masker was presented alone without the target signal. Responses to the

700   masker were not entirely unexpected given that some gravid females will, in the absence of a

701   target signal with conspecific call properties, respond to other types of sounds with the

702   appropriate spectral content, including bandlimited noise (Bee and Swanson, 2007; Vélez et al.

703   2017), unmodulated tones (Kuczynski et al. 2010), and signals with slower or faster pulse rate

704   typical of a heterospecific male (Gerhardt, 2001; Gerhardt and Doherty, 1988). It was, therefore,

705   desirable to exclude highly motivated subjects that responded to maskers to obtain accurate

706   pulse number thresholds using the adaptive tracking procedure. We excluded 46 subjects from

707   determination of a pulse number threshold because they responded to the masker in the

708   relevant sham condition; 43 of 186 subjects (23.1%) tested in the low-signal/high-masker

709   configuration responded to the high-masker sham and 3 of 135 subjects (2.2%) tested in the

710   high-signal/low-masker configuration responded to the low-masker sham. Our final sample size

711   in Experiment 1 was 275 subjects.

712   We measured response rate by coding each subject's response in quiet or a masking

713   condition as binary. If a subject's pulse number threshold was 20 or fewer pulses in a particular

714   condition, it was assigned a response score of 1. Otherwise, it was assigned a score of 0. We

715   used generalized estimating equations (GEE) with logit link functions and exchangeable

716   correlations to analyze this binary response variable. GEE is an extension of the generalized

717   linear model (GLM) that takes into account correlated measurements within a dataset. But

718   unlike GLMM, which produces estimates that are conditional on random effects, GEE is a better

719   alternative for producing estimates that are averaged over random effects (Hubbard et al.,

720   2010). An initial inspection of the data revealed large effects of stimulus configuration, which we

721   confirmed by comparing two GEE models with and without stimulus configuration as a predictor

722   variable for each of the three response variables — response rate, pulse number threshold, and

723   response latency (see Results section). Because these effects were of secondary interest, we

724   separately analyzed the effects of masking condition and SNR in the two configurations. For

725   analyses of response rate in the low-signal/high-masker configuration, the initial GEE model

726   included masking condition (quiet, informational masking, and control masking), SNR (-12 dB, -

727   6 dB, and 0 dB), and the masking condition × SNR interaction as predictor variables. Subject ID

728   was used for clustering to account for repeated measures. We fitted a second GEE model in

729   which we excluded the masking condition × SNR interaction. We compared the two models

730   using ANOVA and found that they were not statistically different. We fitted a third GEE model in

731   which we additionally excluded SNR as a predictor variable and compared this model with the

732   second model using ANOVA and found that they also were not statistically different. Using a

733   similar model comparison method, we investigated whether the order in which thresholds were

734   determined had any bearing on the outcome. For analyses of response rate in the high-

735   signal/low-masker configuration, we could not fit GEE models because the response rate of

736   subjects in the control masking condition was 100%. The lack of variance in the data led to the

737   problem of complete separation, producing spurious results for the main effects model. To

738   compare any two models using ANOVA, we used $\alpha = 0.05$ for hypothesis testing. But to test

739   differences between the three treatment conditions (quiet vs. informational masking, quiet vs.

740   control masking, and informational masking vs. control masking), we used Wald statistics and

741   the Holm-Šydák correction for multiple comparisons.

742   We determined pulse number thresholds and response latencies for each subject that

743   responded in both quiet and in the presence of their assigned masker. Subjects that did not

744   respond to target signals with 20 or fewer pulses in either quiet or in the presence of the masker

745   were excluded from this analysis (N = 50). This paired data allowed us to evaluate how the

746   presence of each masker influenced phonotaxis behavior relative to quiet in the same group of

747   subjects. To make pairwise comparisons, we used two separate paired-sample Wilcoxon tests

748   at each SNR to compare separately the pulse number thresholds and response latencies in

749   quiet and the paired condition with a masker. Because these data were not normally distributed

750   and could not be successfully transformed to follow a normal distribution, a non-parametric

751   version of paired t-test was used for hypothesis testing. An independent sample Wilcoxon test

752   was used to compare the pulse number thresholds and response latencies between subjects

753   that responded in the informational masking and control masking conditions at each SNR. In

754   this set of analyses also, we used the Holm-Šydák correction for multiple comparisons.

755

756   **Experiment 2: Signal Discrimination**

757   Experiment 2 tested the prediction that informational masking can impair signal discrimination.

758   We assessed signal discrimination using a series of two-alternative choice tests (Gerhardt 1995;

759   Ryan & Rand 2001) to measure the preferences of female *H. chrysoscelis* for longer calls with

760   more pulses. To create a choice scenario for subjects, different target signals were broadcast

761   from the two speakers separated by 90° around the test arena. These signals alternated in time

762   such that there were equal intervals of silence preceding and following each presentation. All

763   subjects were initially tested with a reference test in which we presented a choice between

764   synthetic *H. chrysoscelis* and *H. versicolor* calls. Only subjects that selectively responded to the

765   *H. chrysoscelis* call were tested further. As in Experiment 1, separate groups of subjects were

766   tested in the two stimulus configurations (Fig. 2). Within each configuration, subjects were given

767   a choice between a shorter target signal (with 8, 12, 16 pulses, or 24 pulses) and a longer target

768   signal having 25% more pulses (10, 15, 20, and 30 pulses, respectively). Tests of 8 versus 10,

769   12 versus 15, and 16 versus 20 were performed within subjects and replicated within subjects in

770   each masking condition (quiet, informational masker, control masker); a separate group of

771   subjects was tested with 24 versus 30 in all three masking conditions. The order of tests was

772   randomized for each subject. We scored a response when the subject made a choice by

773   entering the response zone in front of one of the two speakers, and we noted its choice as being

774   for either the longer or shorter signal. We used the criteria from Experiment 1 to determine when

775   no response had occurred. Also as in Experiment 1, we performed a reference test after three

776   consecutive no responses to confirm females were still motivated to respond. Subjects that lost

777   motivation during testing (7 of 111) were not tested further, but we included their data from all

778   tests that were completed before they exhibited their last response. To prevent side bias, we

779   randomized which speaker broadcast the shorter target signal. The shorter signal was always

780   the signal that started the alternating sequence of two target signals. To determine whether

781   females were significantly biased toward the first sound they heard, we performed a control

782   experiment in which we gave 20 subjects an additional choice between two identical versions of

783   the synthetic *H. chrysoscelis* calls used in reference tests; 12 of 20 subjects chose the speaker

784   that broadcast the first signal in the alternating sequence (two-tailed binomial test: p = 0.503).

785   The sound pressure levels of all target signals and maskers used in the pulse-number

786   discrimination tests were calibrated to 69 dB SPL and 75 dB SPL, respectively, to create a

787   nominal SNR of -6 dB; signals were calibrated to 85 dB SPL in references tests.

788   We measured response rate by coding each subject's response as binary: made a

789   choice (1) or did not make a choice (0). For the subset of subjects that responded in each

790   choice test, we also scored their choice as binary: longer signal (1) or shorter signal (0). As in

791 Experiment 1, we fitted two GEE models with and without stimulus configuration as a predictor

792 variable. Again, stimulus configuration had a significant effect; therefore we used separate GEE

793 models for each stimulus configuration to analyze response rate and the probability of choosing

794 the longer call. Each model was fitted using a logit link function and exchangeable correlation

795 structure. The first model included masking condition (quiet, informational masker, or control

796 masker), the number of pulses in the shorter signal ("absolute pulse number": 8, 12, 16, or 24

797 pulses), and the masking condition × absolute pulse number interaction as predictor variables.

798 We compared this model with a second model in which we excluded the interaction term. In

799 both stimulus configurations, we did not find any statistical difference between the two models.

800 We fitted a third model in which we additionally excluded absolute pulse number as a predictor

801 variable and compared the second and the third model. If absolute pulse number had a

802 significant effect on the outcome, we adopted the second model. Otherwise, we adopted the

803 third model with masking condition as the only predictor variable. We again used Wald statistics

804 and the Holm-Šydák correction for multiple comparisons to compare the outcomes across the

805 three masking conditions.

806

807 **Acknowledgments**

814

815 **Competing interests**

816 No competing interests declared

817

818 **References**

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