1 **Sex-specific speed-accuracy tradeoffs shape neural processing of acoustic signals in a**
2 **grasshopper**

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24 Designed experiments and collected the behavioral data – BR, MR
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1

Abstract

Speed-accuracy tradeoffs – being fast at the risk of being wrong – are fundamental to many decisions and natural selection is expected to resolve these tradeoffs according to the costs and benefits of behavior. We here test the prediction that females and males should integrate information from courtship signals differently because they experience different payoffs along the speed-accuracy continuum. We fitted a neural model of decision making (a drift-diffusion model of integration to threshold) to behavioral data from the grasshopper *Chorthippus biguttulus* to determine the parameters of temporal integration of acoustic directional information used by male grasshoppers to locate receptive females. The model revealed that males had a low threshold for initiating a turning response, yet a large integration time constant enabled them to continue to gather information when cues were weak. This contrasts with parameters estimated for females of the same species when evaluating potential mates, in which response thresholds were much higher and behavior was strongly influenced by unattractive stimuli. Our results reveal differences in neural integration consistent with the sex-specific costs of mate search: Males often face competition and need to be fast, while females often pay high error costs and need to be deliberate.

Introduction

Sensory information is inherently noisy. Repeated sampling and integration of information over time reduces noise, and is a ubiquitous strategy in information processing and decision making [1-3]. The neural algorithm by which ecologically-relevant sensory information is integrated is expected to be shaped by a fundamental tradeoff between the speed of decision making and the accuracy of the inferred sensory input [1,4,5]. Studies of animals trained in artificial decision-making tasks show that the resolution of the speed-accuracy tradeoff depends on the relative costs of delaying the decision to accumulate more information compared to the costs of making an error based on insufficient information, the signal-to-noise ratio, and the stability of the sensory information over time [6-12]. However, all of these factors vary in natural environments, and among individuals, sexes and species [3,13,14]. While variation in speed-accuracy tradeoffs with condition or experience has been reported for naturalistic tasks [15-19], there exists little direct evidence that natural integration processes are shaped by selection, for instance from comparisons across groups expected to face different costs [3,20].

The processing of signals related to mate choice presents a clear instance in which selection likely favors different resolutions of the speed-accuracy tradeoff in the two sexes, which in turn are expected to result in sex differences in temporal integration: Integration processes in males should facilitate the fast decisions required for successful competition, while integration in females should be slower, but enable more accurate decisions about male quality. The existence of sex-specific circuits in the nervous system suggests that temporal integration could indeed be implemented in a sex-specific manner [21,22], but whether the characteristics of temporal integration differ between males and females in a natural task is unclear. Here we combine an existing behavioral data set [23] with new data and fit a drift-diffusion model [5] to characterize how the nervous system accumulates sensory cues and triggers decisions in mate searching. Based on the expected costs and benefits of different integration strategies under sexual selection theory, we test predictions for how integration may differ between males and females evaluating acoustic signals of the opposite sex.

The grasshopper *Chorthippus biguttulus* provides an excellent model for studies of temporal integration because both males and females produce and respond to acoustic signals during mate searching (Fig. 1A) [24], but integration and decision making strategies are expected to differ between the sexes because they are subject to different selection pressures [25]. Males produce calling songs to find females; receptive females are stationary but respond with songs that facilitate mate localization by the male [26]. In *C. biguttulus*, females pay high costs from making errors [25,27,28], because they are egg-limited and mating with a male of another species or of low genetic quality produces no or low-quality offspring. In addition, singing exposes females to predators and parasitoids. Females should therefore avoid responding to the song from males of another species or of low genetic quality. By contrast, females do not face competition from other females and therefore are not under pressure to be fast. Females are therefore expected to favor accuracy over speed when evaluating the male song pattern. This was confirmed by a drift-diffusion model for temporal integration based on female response behavior [29,30]. The model parameters indicated that females integrate information across the entire calling song of a male with a high threshold for response and very high negative

90   weighting of unattractive song components (i.e., those of heterospecific or malformed males).
91   These integration parameters ensure the accurate detection of unsuitable males combined with
92   slow behavioral responses to attractive males.
93
94   Here, we extend the modelling approach to male mate localization, which is predicted to have
95   very different integration characteristics. Female density is low in the visually cluttered
96   environment and females lack conspicuous visual characteristics or long-range chemical cues
97   that would allow males to find them. Chance encounters are therefore rare and the female
98   response song is often the only possibility for localizing receptive females [28,31]. Furthermore,
99   the speed of approach is critical because females already engaged in close-range courtship
100 with faster arriving males will not continue to advertise their position, preventing slower males
101 from localizing those females. Thus, although males rarely directly interact with one another in
102 physical competitions, they nevertheless face high levels of competition to rapidly localize
103 responsive females in a crowded and noisy environment [32]. Males should therefore favor
104 speed over accuracy to a greater degree than females, although we do not expect males to
105 completely disfavor accuracy when integrating directional cues from the female song, since
106 localization errors increase the time exposed to predators and parasitoids, and will prevent them
107 from finding the female. We predict therefore that males will have higher sensory weightings (or
108 equivalently, a lower response threshold) than females, reflecting their speedier response. This
109 puts them at risk of making errors if early sensory information is wrong. Furthermore, to
110 maintain accuracy when directional cues are equivocal, we predict that integration times will be
111 at least as long as typical female songs so that males can maximize the chances of integrating
112 sufficient directional information from female signals.
113
114 To test these predictions, we used new and previously published behavioral data from a two-
115 speaker playback design that measured male localization of artificial female songs with
116 conflicting directional cues [23]. We applied a drift-diffusion model to the behavioral data to
117 determine the parameters of temporal integration in males. The drift-diffusion model
118 corresponded very well with males' decisions, and the model's parameters matched our
119 predictions of long temporal integration times and a low threshold for response, which contrasts
120 with the parameters determined for female behavior using the same model. This reveals sex-
121 specific differences in the neural processing of sexual signals consistent with predictions from
122 sexual selection theory.
123
124

125 **Methods**

126 **Animals**

127 Behavioral data were collected as described in [23]. We used lab-reared and wild-caught males
128 of the species *C. biguttulus*. Lab-reared males were the F1 offspring from wild-caught
129 individuals and were isolated by sex at the last instar nymph stage and reared in cages
130 separated by sex. Wild-caught males could have mated previously but were kept separate from
131 females for at least three days before the experiments, which is sufficient for them to regain
132 motivation to respond to female signals [33,34]. To further minimize variation in male motivation
133 to respond, we only tested males that responded to a test signal from an attractive female,
134 indicating high motivation to engage in courtship behavior. We did not systematically track male
135 age or exclude males based on their age. Both lab-reared and wild-caught males were group-
136 housed in male-only cages in similar conditions. In group housing, all males would have been
137 exposed to the song of other males, as well as the songs of female playbacks used to assess
138 male motivation and identify test subjects. We, as well as previous studies [35], did not observe
139 any systematic differences in the selectivity of lab-reared or wild-caught males, nor any effect of
140 previous experience on the integration of acoustic cues from females. There is also no evidence
141 for learning in this communication system.

142

143 **Behavioral experiments**

144 Motivated adult were placed between two speakers that broadcast an artificial female song
145 stimulus (Fig. 1B). A female song consists of subunits ("syllables") that are separated by
146 pauses. The syllables in our female model song were separated by a 17.5 ms pause; each
147 syllable consisted of 6 sound pulses (average pulse duration 10.7 ms). This stimulus pattern
148 was highly attractive and reliably elicited turning responses in males, allowing us to assess how
149 directional cues from the stimulus were integrated by the males. Syllables that lack a pause or
150 do not consist of distinct sound pulses are not attractive to males and fail to elicit male turning
151 responses [36-38]. Individual syllables were manipulated to have timing or level differences
152 between the speakers (see below). Stimuli were broadcast at 60 dB SPL at the position of the
153 male. Males were presented with ten repetitions of each stimulus. We tested a total of 204
154 males and most males were tested with more than one stimulus. The median number of
155 different stimuli tested per male (with 10 repetitions per stimulus) was 8 (inter-quartile range 5-
156 10). Stimuli were repeated at a variable rate because each time the male moved, we had to re-
157 position the speakers to center the male once he was again stationary. 44 stimuli contained 12
158 syllables to mimic a typical female song, but we also tested shortened stimuli with 8 (3 stimuli),
159 5 (33 stimuli) or 3 (1 stimulus) syllables to better characterize the dynamics of integration. We
160 include data for male responses from a total of 81 stimuli (Fig. S1). Data for 38/81 stimuli were
161 previously published in [23].

162 Male lateralization behavior was quantified as follows. First, the response for each male was
163 quantified as the proportion of turns directed towards the stimulus channel designated as the
164 reference out of the total number of turns towards either stimulus ("0" if the male turned away
165 from the reference speaker, "1" when the male turned towards the reference speaker). For
166 some stimuli, males responded to the stimulus but turned forward instead of towards one of the
167 speakers and we scored these responses as "0.5", equivalent to a decision probability of 0.5
168 towards (score 1.0) and 0.5 away (score 0.0) from the reference speaker. We then averaged the

169 responses across all males tested with that stimulus (N=15-23 males tested per stimulus,
170 median 20 males). The experimental setup did not allow us to score turning latencies and those
171 data were therefore not available for model fitting. However, our stimulus design, with conflicting
172 cues placed in different positions within the song, allows us to reliably infer the dynamics of cue
173 integration from the response scores (see below).

Stimulus design

175 The dynamics of sensory integration in males were inferred using artificial female songs that
176 varied in duration and in the sequence of directional cues (see Fig. S1 for all stimulus patterns).
177 Each syllable provided one of three types of directional cue: 1) Level cues: we generated stimuli
178 with level differences by silencing some syllables on one speaker channel. This effectively
179 results in an 8 dB interaural level difference [39,40], 2) Timing cues, in which the syllable from
180 one speaker led the other by 4 ms, or 3) no directional cues ("neutral"), in which syllables were
181 presented simultaneously at equal amplitude from both channels. Both timing and level cues
182 elicit orientation responses in male grasshoppers, but are expected to provide directional cues
183 of different strength depending on the magnitude of each cue. We did not attempt to equalize
184 the strength of the timing and level cues used for our stimuli, and instead estimated these
185 parameters from the models. We systematically varied the number and location within the song
186 of these directional cues to generate stimuli with different amounts of directional information,
187 and in some cases with conflicting directional information. This stimulus design with serially
188 conflicting directional cues was critical for calibrating the model parameters [41]. For instance,
189 responses to songs in which syllables at the beginning of the song indicated a female in the
190 direction of one speaker and those at the end of the song indicated a female in the opposite
191 direction reveal over how many syllables males integrate and when decisions are fixed.
192 Combining this stimulus design with a neural model of decision making (see below) allowed us
193 to infer the sensory weights and thresholds, and estimate decision times, even in the absence of
194 reaction time data. A control stimulus with neutral directional cues elicited turning responses
195 with random directions (score 0.53, random turning would produce 0.5). Another control
196 stimulus that was broadcast from only one speaker, reliably elicited turns in males (90% of
197 trials) and all of those turns were correctly directed towards the broadcasting speaker. See Fig.
198 S1 for a list of all stimulus patterns used in this study.

Comparison of correlations between the stimulus and the behavior

200 We assessed the strength of the relationship (squared Pearson's r) between the males' turning
201 responses and different parts of the 12 syllable stimuli, by dividing each stimulus in thirds
202 (syllables 1-4, 5-8, 9-12), calculating the average directional cue for each third, and correlating
203 that average with the males' turning responses (Fig. S2B). To account for stimulus-intrinsic
204 correlations, arising from regularity in the stimulus sequences (Fig. S1), we also correlated the
205 average cue for each third with the average cue over the full song (Fig. S2A). This revealed that
206 the middle of the song was most strongly correlated with the cues from the full song, which is a
207 result of our stimulus design because the cue direction often changed halfway through the song
208 (Fig. S1). The difference of the correlation obtained from the behavior and from the full stimulus
209 indicates stimulus thirds that are more or less influential on the behavior than expected from the
210 stimulus statistics (Fig. S2C, 1C).

6

Modelling

211 The stimulus is defined as a sequence s(t) with t=[1, … , T], T being the number of syllables in
212
213 the stimulus, and a sign indicating the side of the cue relative to the reference speaker ("-1"
214 away from the reference, "+1" towards the reference, "0" neutral).

Averaging model

216 As a baseline, the averaging model simply averages the directional information over the full
217 song and the predicted response ρ is then a function of that average: ρ=f(x(T+1)), with x(t+1) =
218 x(t) + Z(s(t)), x(0)=0. The sign function Z(s(t)) returns -1 if s(t)<0 and +1 otherwise. To account
219 for saturation effects, we set f to be a sigmoidal, which was fitted to minimize the mean squared
220 error over all stimuli between the prediction ρ of the averaging model and the males' turning
221 response r. However, this only marginally increased the performance of the simple averaging
222 models (r^2 linear: 0.72, r^2 sigmoidal: 0.75).

Drift-diffusion model

224 In a drift-diffusion model, the cues from each syllable are weighted and assigned a sign based
225 on the direction they indicate. The weighted cues are then integrated with an integration
226 timescale τ, which determines the "leakiness" of integration, with a value of infinity
227 corresponding to perfect integration with no forgotten information, and smaller values
228 corresponding to forgetting of information that came before that time interval. Noise σ is added
229 to the integrated sensory information from each syllable, and the decision is fixed when a
230 decision threshold of either +θ or -θ is crossed, indicating the decision to turn towards or away
231 from the reference speaker, respectively. If the threshold is not crossed before the end of the
232 song, the decision is made based on the sign of the integrated information at the end of the
233 song. An urgency gain parameter was included to account for the possibility that sensory
234 weights increase or decrease over time [6,42]; increased urgency may be expected for males
235 that need to localize receptive females quickly upon receipt of evidence that one is present.
236 More precisely, the integrated information x after syllable t is given by

$$x(t+1) = \begin{cases} -\theta, \text{if } x(t) < -\theta \\ \theta, \text{if } x(t) > \theta \\ x(t)/\tau + w(t)s(t) + \eta(t)\sigma, \text{otherwise} \end{cases}$$

238 with x(0)=0, an integration time constant τ, and a decision threshold θ. Noise η(t) was drawn at
239 each time step from a normal distribution with zero mean and unit variance. For timing cues, w
240 was fixed to 1.0 for all models. For level cues, w was fixed to 1.0 for models that did not
241 differentially weight timing and level cues ("single cue" in Table S1) and optimized during fitting
242 for models that did ("two cues"). For models with urgency gain, the sensory weight changed
243 over time and was defined as w(t)=w*(1+(t-1)γ), with γ being the urgency gain [42]. Experiments
244 with alternative implementations in which the urgency gain reduced the threshold over time [6]
245 yielded similar results of negligible gain. The decision threshold θ was sticky – once it was
246 crossed, integration ceased and x(t) was fixed to ±θ. The predicted response, ρ, was
247 determined by the sign of the integrated information after the last syllable, Z(x(T+1)) averaged
248 over 1000 different instantiations of the noise η. The simple averaging model can be considered
249 a special case of a drift-diffusion model with w=1 for level and timing cues, σ=0, τ=∞, and θ=∞.

250   *Model fitting and evaluation*

251   The parameters of the drift-diffusion models were optimized by minimizing the mean-squared

252   error between the predicted and the males' responses using a Genetic Algorithm ([43], see [44]

253   for details). To speed up convergence, upper and lower bounds were defined for all parameters:

254    $0<w_L<10$, $1<\tau<40$, $0<\sigma<5$, $0<\theta<10$, $0<\gamma<10$. We ensured that these bounds did not affect the

255   final parameter estimates. Fits were evaluated using leave-one-out cross-validation. That is, the

256   model parameters were fitted on all but one stimulus (and its mirror version) and a prediction

257   was then generated for the left-out stimuli. Doing this for all stimuli resulted in 81 parameter

258   estimates and 157 predictions. The squared Pearson's coefficient of correlation, r^2, between the

259   predictions and the males' responses was used to quantify model performance. Different

260   models were compared using Akaike's Information Criterion (AIC), which penalizes models with

261   many parameters. The AIC score is given by $AIC = 2k + n\ln(e)$, where k is the number of

262   parameters of the model, n is the number of samples used for fitting the model, and e is the sum

263   of squared residuals between the predicted and the male's responses: $e = \sum(r-\rho)^2$. Smaller AIC

264   scores are better.

265

Results

Noisy integration to threshold explains turning behavior.

Based on the correlation of the cues in different parts of the song with behavior, we find that the beginning of the song influences behavior more than expected (Fig. 1C, S2). This suggests an integration process in males that does not always consider information from the full female song but instead fixes decisions rapidly and dynamically with the available sensory evidence [23]. To account for this finding, we fitted different models of cue integration and decision making. Model comparison (Akaike Information Criterion) revealed that the simplest model that explained our data is a drift-diffusion model with an infinite integration time in which timing and level cues had different weights, but their weights did not change over time (i.e., an urgency gain of zero) (Table S1, Fig. 2A-C, Fig. S3). We consider this as the best fit model in discussions below. A threshold-less model that simply averaged directional cues with identical weights for both cue types across the entire song performed worse (Fig. 2C) as did a drift-diffusion model variant with identical weights for both cue types (Table S1). These simpler models performed well on average (Table S1) because for many stimuli in our dataset, the average cue still predicted the behavior well. However, the performance gap between these models and our best fit model was much higher for stimuli with conflicting or mixed cues, for which correct weighting and stopping of integration after threshold-crossing were crucial model parameters for predicting males' behavior (Fig. 2C). Adding even more complexity to the model with the addition of leaky integration or an urgency parameter did not improve performance (Table S1). Model parameters were similar for all of the fitted variants of the drift-diffusion model, indicating that our results are robust to changes in model complexity.
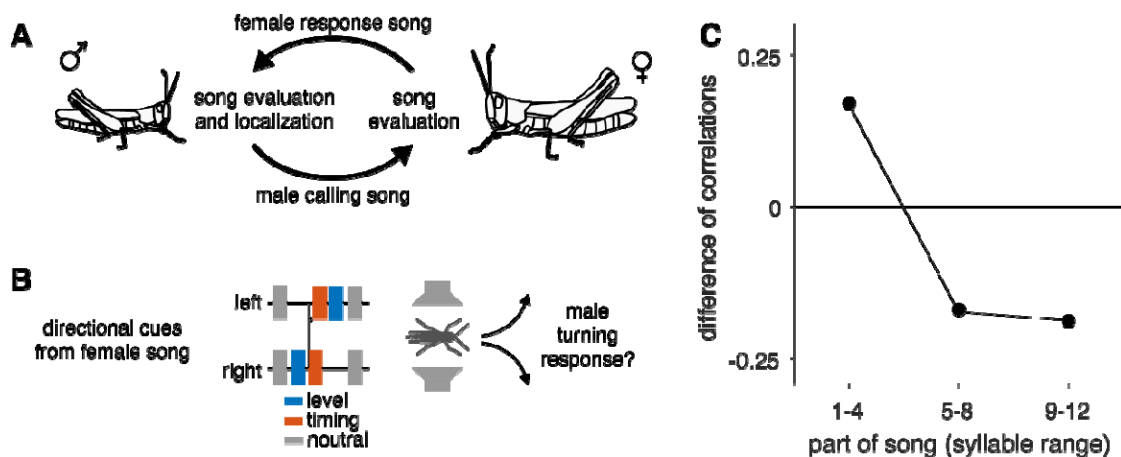
**Figure 1 – Performance of a simple averaging model compared to male behavior**
A Bidirectional acoustic communication during mate search in the grasshopper *C. biguttulus*.
B Schematic of the paradigm – two speakers were placed on either side of the male, artificial female song is played, and the direction of the male turning response is scored. Directional cues are provided by each syllable and arise from level differences (sound on one speaker only, blue) or timing differences (sound on one speaker delayed by 4ms, red). Both cue types are known to elicit turning responses in males.
C Difference in the correlation of different thirds of the 12 syllable songs observed in behavior and estimated from the stimulus statistics. The beginning tends to be more, the middle and end less influential on behavior than expected from the stimulus statistics. See Fig. S2 for details and number of stimuli.
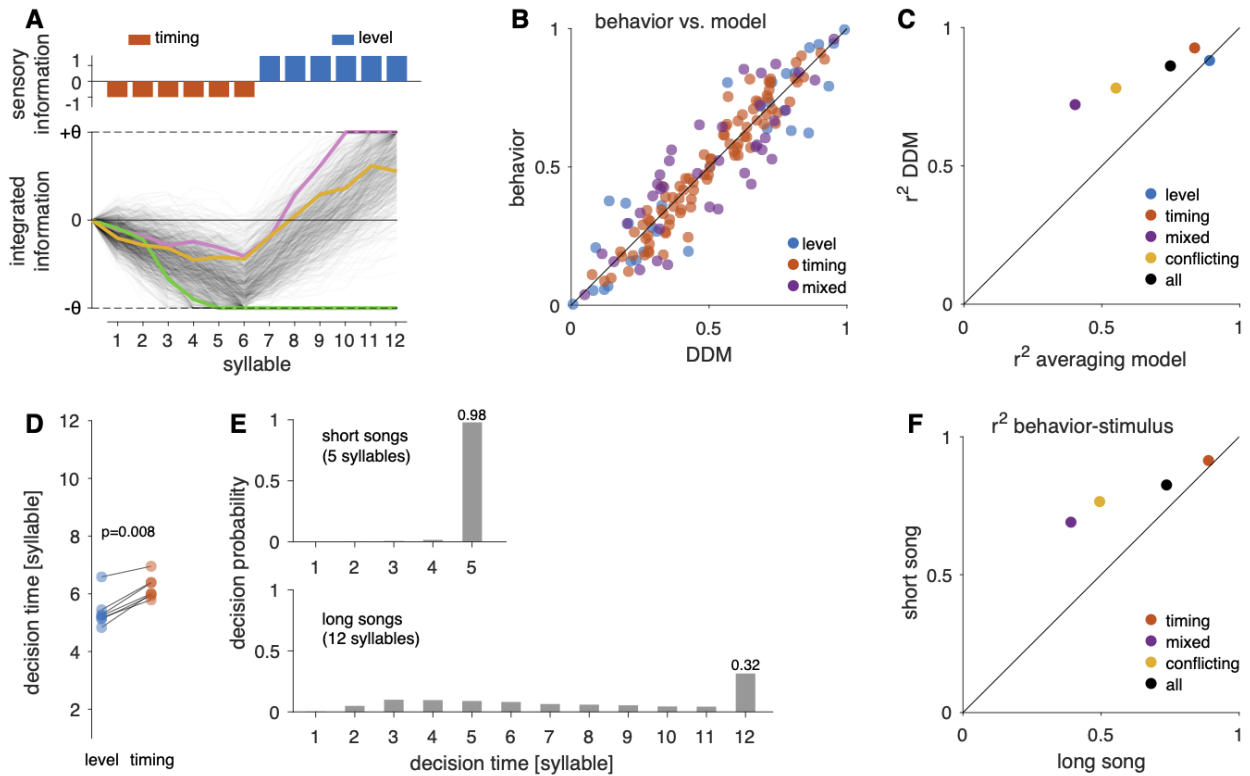
Figure 2 – A drift-diffusion model (DDM) reproduces the behavior well and reveals dynamics of temporal integration.

A DDM responses for a 12-syllable stimulus (top) with the first 6 syllables containing timing cues (red) away from the reference speaker (-), and 6 syllables with level cues (blue) towards the reference speaker (+). Each cue type is assigned a weight (height of bars, top). Stimulus information is integrated noisily and a decision towards the reference (+) or opposite (-) speaker is fixed when the decision threshold θ is crossed. Thin black lines indicate 1000 runs with independent noise realizations. Colored lines highlight example runs that cross the negative threshold (green), the positive threshold (purple), or no threshold (orange), in which case the decision is determined by the sign of the evidence at song end (+).

B Proportion of turns towards the reference speaker in model and behavior. Color indicates cue composition of the songs. Diagonal line corresponds to perfect match between model and behavior. All points are close to that line (r^2=0.86).

C R^2 between model predictions and behavioral data for the best fitting model (DDM) compared to that of a simple averaging model for different data subsets (see legend). The best fitting model outperforms the simple averaging model in particular for stimuli with mixed (purple, stimuli containing timing and level cues) and conflicting cues (yellow, stimuli with cues from both sides).

D Mean decision time (syllable at which threshold is crossed) for seven stimuli with matching patterns (lines) but level (blue) or timing (red) cues. Consistent with their higher weight in the model, level cues drive decisions by about 1 syllable earlier (p=0.008, left-sided sign test). See Fig. S4 for the decision time distributions for each of the stimuli depicted here.

E Decision times for short songs with 5 syllables (top, N=66 stimuli) and long songs with 12 syllables (bottom, N=83 stimuli). For most long songs, integration reaches threshold before song end. For nearly all short songs, integration fails to cross threshold. Short song mostly contained timing cues (Fig. S1). Numbers in the last bar indicate the probability of not reaching the threshold for the two stimulus sets.

F Correlation of behavior with the average directional cue over the full song for short and long songs. The failure of threshold crossing before song end for short songs (E, top) leads to integration over the full song and a higher correlation with the average directional cue. There is no "level" stimulus set for this analysis since our data set did not contain such stimuli for short songs (cf. C, Fig. S1).

**Males integrate directional cues with long memory, cue-specific weights, low thresholds, and high noise**

333   The best fit model indicated that males can integrate directional cues over the whole song, and
334   even in models with a leaky integration, the time constant was estimated at 24 syllables (Table
335   S1), which is twice as long as both the longest song in our dataset (12 syllables; 1.19 s) and a
336   typical female song (12-15 syllables, mean±SD = 1.18±0.23 s; [45]). Thus, sensory information
337   from the whole song has the potential to influence the localization response. The decision
338   threshold θ of the best fit model had a value of 7.14. Level and timing cues were weighted
339   differently, with the level cue outweighing the timing cue by a factor of 1.65. The minimum
340   number of syllables required to cross the threshold (θ/w) was therefore 8 for timing and 5 for
341   level cues, meaning that the stronger level cues drove faster decisions (Figs. 2D, S4). The low
342   threshold resulted in decisions usually being fixed before the end of long 12-syllable songs (Fig.
343   2E), consistent with our finding that the beginning of the song is more and the end of the song is
344   less influential than expected for observed male turning responses (Figs. 1C, S2). This means
345   that males trade accuracy in favor of speed, since responding before the end of song can result
346   in localization errors if sensory information early in the song is unreliable. For the short songs,
347   which largely consisted of the weaker timing cues, sensory information was insufficient to drive
348   decisions by crossing the threshold in our model, and the turning direction was determined by
349   the value of the integrated information at the song end (Fig. 2E). This is consistent with the
350   observation that the average directional cue over the full song is more predictive of behavior for
351   the short songs, than for the long songs (Fig. 2F). The noise level σ of the best fit model was
352   2.25; thus, the signal-to-noise ratios (w/σ) were 0.44 for timing cues and 0.73 for level cues.
353   Localization cues provided by single syllables are therefore relatively noisy, and integration is
354   indeed necessary to infer sound direction reliably.
355

356
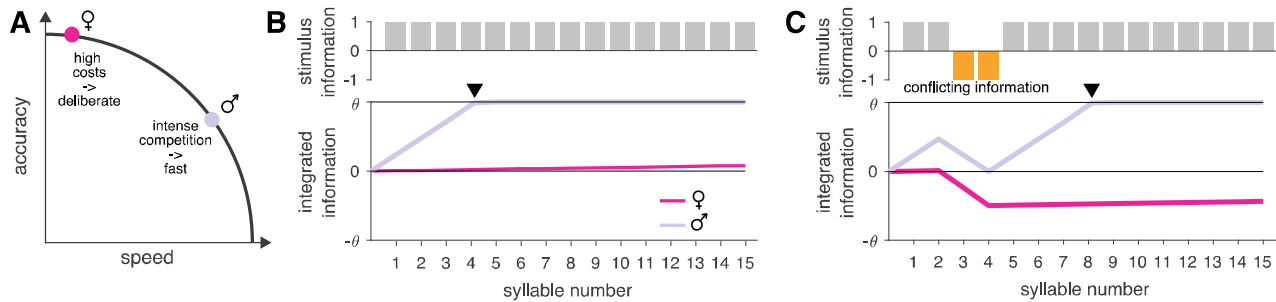
357

358 **Figure 3 – Sex-specific speed-accuracy trade-offs arise from differential integration dynamics.**
359 **A** Males and females differentially resolve speed-accuracy trade-offs when responding to acoustic communication
360 signals. Females (magenta) pay high costs from errors and therefore maximize their accuracy by deliberation at the
361 cost of speed. Males (gray) face intense competition with other males and trade accuracy in favor of speed.
362 **B, C** Integration dynamics tune decision making to the sex-specific speed-accuracy trade-offs. Shown is the
363 integrated information (bottom) for females (magenta) and males (gray) for stimuli (top) with unequivocal (B) and
364 conflicting (C) information. Integrated information is scaled relative to the decision thresholds θ to facilitate the
365 comparison between sexes. For females, individual stimulus elements correspond to species-typical (gray) and
366 untypical (orange) patterns. Species-typical cues have low weight and are not sufficient to fix decisions before song
367 end (B). Conflicting (negative) cues have a strong weight and practically veto positive responses (C). For males, the
368 stimuli correspond to directional cues. Individual cues have high weight, which accelerates decisions (black
369 arrowhead) for unequivocal information (B). Long integration times improve accuracy when cues are conflicting (C).
370 See also Table S2. Female data from [29].

371

372

373

Discussion

374

375 Our drift-diffusion model of temporal integration applied to male behavior demonstrates that
376 sexual selection has shaped the neural processing of acoustic stimuli to favor speedy decisions
377 in males, in contrast to the slower, but more accurate decisions in females (Fig. 3A). The model
378 accurately reproduced the males' localization behavior (Fig. 2B, C) and the model parameters
379 describe an integration process that is consistent with the pressures facing males to rapidly
380 localize a stationary, singing female in a noisy environment (Fig. 2D-F, Table S1). The same
381 modeling technique was previously used on females of the same species evaluating songs of
382 potential mates [29], and the differences in model parameters correspond with expectations of
383 sexual selection theory that females should have a higher threshold for response and strongly
384 avoid unattractive signal characteristics (Table S2). This is a rare demonstration of variation in
385 temporal integration strategies associated with ecologically relevant and natural behaviors.

386 **Decisions in males are fast for strong cues and accurate for weak cues**
387 We found that males had a low threshold for response: the average time to decision inferred
388 from the model was much less than the duration of the standard female song stimulus used in
389 this study (Fig. 2D, E). Thus, when the evidence is strong, males can decide quickly. This
390 corresponds with the behavior of males in localization experiments, in which they frequently turn
391 towards a song before it ends [40]. The best fit model had higher weights for level cues than for
392 timing cues (Table S2, Fig. S3B), and decisions were therefore faster with level cues than with
393 timing cues (Fig. 2D). This does not imply that level cues always predominate over timing cues;
394 instead the difference likely arose because of the specific values chosen for each cue: the

395 unilateral level cues (resulting in an approximately 8 dB ILD) were expected to provide stronger
396 directional information than the bilateral timing cues (4 ms ITD) [40]. Importantly, this finding
397 implies that cues are weighted by their strength, such that decision making is accelerated when
398 evidence is strong.
399
400 Although we expected males' decisions to be biased towards speed, accuracy is also important
401 because mistakes in localization could cause males to move out of hearing range of the female
402 and prevent them from finding one another [35,46]. The signal-to-noise ratio for a single syllable
403 was low (0.44 and 0.73, respectively), and males therefore did integrate over multiple syllables,
404 although they usually reached threshold and made a decision before they heard all of the
405 syllables in the full song (Fig. 2D, E). This also means that males would be less accurate in
406 case directional cues early in the song indicate the wrong direction. Nevertheless, the model
407 indicated that males had the capacity to integrate over a much longer time period if directional
408 cues were weak and the threshold was not reached (Table S1). Thus, when directional cues
409 were too weak for a speedy decision, males could integrate additional sensory information,
410 which should improve signal-to-noise ratios and ultimately lateralization accuracy [32]. This
411 explains the high accuracy of male directional responses in the presence of noise [35]. Long
412 integration times are maladaptive when the information being integrated changes more rapidly
413 than the integration time constant, leading to erroneous decisions [10,47]. However, in this
414 system long integration may have few costs because the information evaluated by males in the
415 female song, her position, is constant prior to the turning decision because females remain
416 stationary while singing. The integration dynamics in males therefore resolve the speed-
417 accuracy tradeoff by allowing for flexibility in decision making: Sensory information is able to
418 drive fast responses when it is strong, but long integration times allow accurate localization of
419 the female in case of weak cues.
420
421 While our experiments were designed to assess the decision-making strategies of males on a
422 population level, some variation in decision-making strategies could depend on male state or
423 consistent differences between individuals. In other species, competitively inferior males use so-
424 called satellite or sneaker strategies to avoid direct competition with dominant males [48].
425 However, in *C. biguttulus* direct agonistic interactions between males are rare and the primary
426 means of competition is the ability to rapidly localize females. Slow decision making, similar to
427 females', is therefore unlikely to be an advantageous alternative strategy for males in this
428 species. Given that our model explains the behavior measured from different sets of males so
429 well (r^2=0.86, Fig. 2 B, C), variation among individuals is likely low, and our main conclusion –
430 that males trade accuracy in favor of speed – is likely to be robust to these factors.
431
432 **Integration of courtship signals is tuned to sex-specific costs**
433 Our finding that male *C. biguttulus* have a low threshold for response contrasts with the results
434 from previous studies using a similar behavioral and modeling paradigm to characterize
435 temporal integration in females of the same species [29,30]. Females were tested with songs
436 consisting of a mixture of attractive and unattractive syllables. There was a large difference
437 between males and females in how they weighted sensory information. In females, positive
438 cues had a weak influence and on their own could not reach the threshold by the end of the

439 song; in other words, females rarely commit to a positive decision before the end of the song.
440 However, negative cues (i.e., unattractive song syllables) had a much stronger weight and even
441 a few unattractive syllables could reach the threshold for not responding. In contrast, in males,
442 we found that clear directional information had a strong weight and was capable of driving
443 responses before the end of a typical female song. Both sexes had integration times that were
444 longer than the duration of typical songs, but in females this likely serves less to enhance the
445 signal-to-noise ratio (as we argue is the case for males), but rather to ensure the detection of
446 unattractive elements at any point in the song, preventing them from initiating courtship with a
447 low-quality or heterospecific male.

449 There are some differences in the behavioral paradigms because females were tested for a
450 response to songs with both positive and negative information on male attractiveness, while
451 males were tested using only attractive syllables but with varied directional cues. Pattern and
452 directional information are extracted from the song in parallel pathways and the pattern decision
453 then gates turning [36]. Thus, turning in males in this study reflects both the attractiveness of the
454 song syllable and the quality of directional cues. Despite these differences, both the female
455 decision to respond and the male decision to turn signal readiness of each sex to further
456 escalate the courtship interaction. Therefore, the integration differences between males and
457 females reflect differences in the costs and benefits of decision-making strategies affecting each
458 sex. Future studies examining integration of stimuli with unattractive pattern information in
459 males would further elucidate sex differences in temporal processing in this species.

461 The neural circuits that integrate directional cues over time to control male turning behavior are
462 unknown. Peripheral circuits extract directional cues from afferent inputs but do not integrate
463 this information across multiple syllables [49-51]. The evaluation of the song pattern and
464 integration of directional cues is likely to happen in the brain and its results are relayed to the
465 motor centers via descending interneurons [52], but this has not been assessed systematically.
466 In the female brain, auditory activity has been recorded in the lateral protocerebrum, the
467 superior medial protocerebrum and the central complex (CX) [53,54] and electrical stimulation of
468 the CX can elicit the behavioral responses to song in females [55]. In the insect brain, the CX is
469 a central circuit for orientation behavior with integrator properties [56,57]. It may therefore drive
470 responses also in males and CX neurons themselves or their presynaptic partners may have
471 sex-specific properties that reflect the sex-specific speed-accuracy trade-offs evident from
472 behavior.

474 Although the specific neural circuits have not been identified, our drift-diffusion model is realistic
475 because it replicates identified neural processes. All model parameters map to biophysical
476 properties of decision making neurons and circuits [58,59]: Sensory weights could correspond to
477 the number and strength of synapses to an integrating neuron. The integration time constant
478 could correspond for instance to the kinetics of intracellular calcium, or to factors that determine
479 the dynamics of a recurrent network [60,61]. The decision threshold could correspond to a
480 spiking threshold determined by the density of sodium channels at the spike initiation zone or
481 controlled by neuromodulators [60,62,63]. Sexual selection could act on these parameters to
482 produce the sex-specific integration of sensory information seen in grasshoppers. Our results

483   therefore point the way towards a study of the evolution of sensory processing mechanisms in
484   realistic ecological contexts and natural behaviors.
485

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