

Asymmetrical integration of sensory information during mating decisions in grasshoppers

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Decision-making processes, like all traits of an organism, are shaped by evolution; they thus carry a signature of the selection pressures associated with choice behaviors. The way sexual communication signals are integrated during courtship likely reflects the costs and benefits associated with mate choice. Here, we study the evaluation of male song by females during acoustic courtship in grasshoppers. Using playback experiments and computational modeling we find that information of different valence (attractive vs. non-attractive) is weighted asymmetrically: while information associated with nonattractive features has large weight, attractive features add little to the decision to mate. Accordingly, nonattractive features effectively veto female responses. Because attractive features have so little weight, the model suggests that female responses are frequently driven by integration noise. Asymmetrical weighting of negative and positive information may reflect the fitness costs associated with mating with a nonattractive over an attractive singer, which are also highly asymmetrical. In addition, nonattractive cues tend to be more salient and therefore more reliable. Hence, information provided by them should be weighted more heavily. Our findings suggest that characterizing the integration of sensory information during a natural behavior has the potential to provide valuable insights into the selective pressures shaping decision-making during evolution.

acoustic communication | insects | decision-making | courtship | drift-diffusion model

One crucial decision in the lifetime of an animal is the decision with whom to mate. The males of many animals have evolved elaborate traits to attract females (1). These traits often involve the production of calling or courtship songs (2–4). Females base their decision to engage in courtship and to mate on the properties of these signals. Though many different factors drive and constrain the evolution of behavioral decisions in general (5, 6), the way information is integrated in the context of mate selection may reflect the fitness costs and benefits associated with mate choice. These costs depend on the mating system, e.g., the abundance of potential mating partners, the likelihood and costs of multiple matings, direct benefits of mating, and the costs of assessing a potential mate (7–10).

Here, we investigate the implementation of a decision-making strategy by studying the integration of song features during courtship in grasshoppers. Acoustic courtship in the species *Chorthippus biguttulus* involves bidirectional communication. Males produce calling songs consisting of a sequence of simple stereotyped subunits—30–50 syllable-pause pairs. The female waits until the end of this song and indicates her readiness to further engage in a courtship ritual by producing a response song that allows the male to localize and approach the female (11) (Fig. 1A). This phase of courtship constitutes a first, important preselection step before females make their final assessment of an approaching mating partner. Not responding or responding to a male calling from a distance is the first step in this sequence, which likely reduces the female's costs of assessing potential mates (10).

Though many of the stimulus features influencing a female's decision during the preselection phase have been identified (12–

14), little is known about how this information is dynamically integrated over the course of the song. In the mating system of *C. biguttulus*, direct mating benefits do not exist and multiple mating is rare, hence much is at stake with the decision for a mate (15). Females should thus be selective and exploit all information provided by the song—i.e., they should not be impulsive decision-makers, which respond after hearing a few attractive song subunits. In addition, because mating with a male of a different species greatly reduces female fitness (9), nonattractive song features associated with other species should be weighted heavily to avoid such mistakes.

We used playback experiments with mixed sequences of two types of song subunits to determine the dynamics of integration: subunits that exhibit attractive, species-specific features and nonattractive subunits with negative features as found in songs of other species. Attractor networks and drift-diffusion models are successful in uncovering the dynamics of information integration during decision-making (16). Here, we chose drift-diffusion models, because this model class allows a direct mapping between model parameters and the phenomenology of decision-making in terms of weights for sensory information, integration noise, and decision thresholds (17).

Fitting such a model to our behavioral data reveals that attractive and nonattractive subunits are integrated in a strongly asymmetrical manner. The model suggests that the weight of attractive subunits in the decision is negligible relative to that of nonattractive subunits; this leads to nonattractive subunits effectively vetoing female responses. Actual female responses are

Significance

Decision-making involves integrating different pieces of sensory information over time. Looking at how sensory information is weighted and integrated during a natural behavior can yield insight into the evolutionary forces shaping that behavior. Here, we investigated how female grasshoppers of the species *Chorthippus biguttulus* integrate information provided by male calling songs. Fitting a drift-diffusion model to behavioral data, we find that integration is highly asymmetrical: an unattractive song subunit far outweighs an attractive subunit. This asymmetrical integration is consistent with theories of sexual selection because it helps females avoid potentially costly interactions with unsuitable mating partners if the song belongs to another species or indicates a low-quality male; moreover, it suggests that song-based decision-making in grasshoppers is optimized by evolution.

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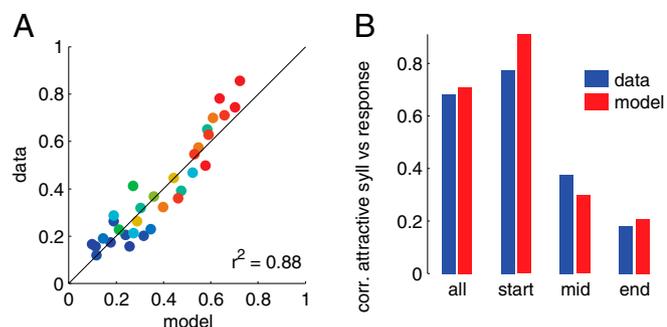


Fig. 3. A drift-diffusion model predicts behavioral choices. (A) Predictions of a drift-diffusion model and actual behavior. The color code corresponds to fraction of attractive syllables in the full song ranging from 1.0 (red) to 0.0 (blue). (B) Correlation (r^2) between measured/predicted responses and the fraction of attractive syllables in different parts of the song [data, blue (Fig. 2); model, red].

features or the lack of attractive features (Fig. S2). Along with sensory information, decision noise with SD σ is added at each time step. The forgetfulness of the integrator is set by the integration time constant τ . When the decision variable crosses a positive or negative threshold (θ_+ and θ_- , respectively), the female commits to a decision and stops integrating further. If neither threshold is crossed after the song ends, the decision is based on the sign of the information accumulated thus far. A positive value leads to the female producing a response song that stimulates the male's approach. A negative value is associated with a rejection of the male; in this case, no response song is produced. Without loss of generality, we set the weight for positive information w_+ to 1. The other five parameters (w_- , τ , σ , θ_+ , and θ_-) were free to vary and were fitted to the behavioral data using a genetic algorithm (Fig. S3).

The model predicts behavioral responses very well ($r^2 = 0.88$; Fig. 3A); moreover, it reproduces the relation between the fraction of attractive syllables in different parts of the song and the response, e.g., the beginning of the song correlates most strongly with predicted behavior (Fig. 3B, compare blue and red bars).

Model Parameters Reveal Strongly Asymmetrical Integration. The data reliably constrained the model parameters (Fig. S3 and Table 1, Upper), which in turn allowed inference about how female grasshoppers integrate song quality information during courtship. The model parameters are easily interpreted as to their contribution to the decision dynamics: The time constant corresponds to the number of syllables that potentially influence the decision. The weight for each type of information and the decision thresholds determine the susceptibility of each type of decision to sensory information and noise. In this modeling framework, the strong influence of a song's beginning on the female grasshopper's response probability could indicate a large weight for positive information and a low threshold for positive decisions (10).

Perfect integration of information. The time constant of integration found by the genetic algorithm is much longer than the duration

of the songs ($\tau = 213 \pm 29$ syllables vs. a song duration of 33 syllables), which means that the decision variable barely drops over the course of the song. Given that natural songs rarely contain more than 50 syllables, the model indicates that females can potentially assess the full male song for making a decision (Fig. 4A and B). Indeed, a model with perfect integration exhibits virtually identical performance and similar parameter values (Table 1, Lower), which is well in accord with theories of optimal decision-making, since it allows utilization of all information provided by the sensory input (20).

Positive and negative information is weighted asymmetrically. The model's weight of negative information was much higher than that of positive information ($w_- = -46.5 \pm 4.3$ vs. $w_+ = 1.0$). Thus, the impact of each syllable type on the integrated information is highly asymmetrical—a single nonattractive syllable strongly reduces the decision variable, whereas attractive syllables have comparatively small effects (Fig. 4A and B).

Positive information only negligibly impacts the decision. The small weight of positive information seems inconsistent with the interpretation of an impulsive decision provided above. Nonetheless, impulsive decisions could occur if the low weight of positive information were compensated by a decision threshold that was equally low. However, the asymmetry in decision thresholds is much weaker than that in weights, differing only 4.5-fold instead of 47-fold for the weights ($\theta_+ = 175.7 \pm 5.8$, $\theta_- = -795.7 \pm 98.7$; Fig. 4A and B and Table 1).

Indeed, attractive syllables have only a negligible impact on the modeled female decision; this is revealed by quantifying the sensitivity of each type of decision to the amount of sensory information. Sensitivity is given by the ratio between the threshold and weight and measures the amount of information needed for a perfect, noiseless integrator to cross threshold. For negative decisions, 18 nonattractive syllables drive a noiseless perfect integrator to the decision threshold ($\theta_-/w_- = 17.1$). In contrast, for a positive decision, 176 attractive syllables are needed to reach threshold ($\theta_+/w_+ = 175.7$). For naturally occurring songs, whose duration rarely exceeds 50 syllables, the positive threshold will thus never be reached by positive information alone.

The model thus challenges our initial interpretation of impulsivity in female choice behavior. Given the inability of positive information alone to drive decisions, we then asked (i) What drives positive responses? and (ii) Why do decisions depend largely on the beginning of songs (Figs. 2 and 3B)?

Integration noise often drives female responses. In addition to quantifying the sensitivity of a decision to sensory information, we examined the impact of decision noise on each decision. The integration noise level σ found by the genetic algorithm was 97.6 ± 8.8 . Noise sensitivity corresponds to the number of noise steps of size σ to reach the decision threshold and shows that positive responses are highly susceptible to integration noise: two noise steps are sufficient to drive a positive response ($\theta_+/\sigma = 1.8$). In contrast, negative information is much less sensitive to noise: nine noise steps are needed for a purely noise-driven negative response ($\theta_-/\sigma = -8.2$). This high noise sensitivity in combination with the negligible impact of positive sensory information suggests that it frequently is integration noise that induces positive threshold crossings (Fig. 4A and C).

Table 1. Parameter values for leaky and nonleaky drift-diffusion models

Model	r^2	w_+	w_-	τ	σ	θ_+	θ_-
Leaky	0.88 ± 0.02	1	-46.5 ± 4.3	213 ± 29	97.6 ± 8.8	175.7 ± 5.8	-795.7 ± 98.7
Perfect	0.88 ± 0.02	1	-46.5 ± 1.9	∞	102.7 ± 3.8	187.4 ± 7.0	-880.4 ± 78.6

r^2 , cross-validated correlation coefficient between model prediction and behavior. w_+ , w_- , weight for positive and negative evidence. τ , integration time constant in units of syllables; perfect integration corresponds to $\tau = \infty$. σ , SD of the noise added at each integration step. θ_+ , θ_- , threshold for positive and negative decisions.

so-called “ascending neurons”—are sensitive to the number of offsets in a syllable and thereby exhibit differential responses to positive and negative information; this is achieved through the interaction of differently timed excitatory and inhibitory inputs (25).

By contrast, very little is known about the circuits that further process and integrate this sensory information. The results in this study provide a starting point for future electrophysiological studies in the grasshopper brain to identify the neural circuits involved in decision-making. The parameters of the drift-diffusion model can be easily mapped to properties of neural circuits: weights for positive and negative information could correspond to the efficacy of synapses feeding positive and negative information to the integrator. Alternatively, the vetoing of female response could be implemented by proper placement of inhibitory inputs in a dendritic tree (26). The near-perfect integration of information (Table 1) could be implemented as a recurrent network or through synaptic plasticity (27, 28). Otherwise, the slow accumulation of intracellular calcium or of extracellular signaling molecules has also been implied in information integration (29–31).

Note that we have used only two syllable types in this study; however, there likely exists a diversity of different syllable types, ranging from strongly repellent to neutral (weight close to zero) to highly attractive. It will be interesting to see whether the weight of a syllable depends on the values of other syllables recently heard by the animal, i.e., whether the value of a syllable is absolute or context dependent (32); the latter could adapt the weighting of syllables to maintain mating preferences in varying acoustic environments and social contexts.

Noise in the model is implemented as internal noise and could be located either in the feature detector neurons or in the integrator neurons themselves. In natural conditions, external noise is another source of variability that can either distort attractive stimulus features or mask unattractive ones (18, 33, 34)—future studies will explore how both noise sources interact during feature detection and integration.

Asymmetrical Integration as a Consequence of Sexual Selection. The parameters determining song integration during courtship likely reflect the costs and benefits associated with mate choice, and this is true even though the evolutionary optimization of decision-making during courtship is likely constrained in several ways. For instance, song evaluation in grasshoppers is shaped by selective pressures exerted on the auditory system by demands not directly associated with mate selection, such as the detection of predators (35). Also, traits that have evolved in contexts other than mate choice can induce perceptual biases that affect female decisions (5, 6, 36). Still, the highly asymmetrical integration is consistent with predictions made by theories of optimal decision-making and of sexual selection.

Asymmetrical weights reflect reliability of sensory cues. In Bayes-optimal integration of information, cues are weighted by their reliability (37). In our case, nonattractive syllables exhibit salient features that reliably indicate “wrong male”—a large weight should therefore be assigned to negative information. In contrast, the differences between the attractive syllables of conspecifics of different quality rely on more subtle features of the song that are prone to be distorted by environmental noise (33, 38, 39). Hence, positive information tends to be less reliable and should therefore be weighted less. The distribution of weights found in the model is thus consistent with optimal cue integration (37).

Asymmetrical weights reflect fitness costs of misdecisions. Differential weighting leads to a consistent rejection of bad singers—be they heterospecifics or conspecifics of inferior quality—at the cost of enabling only poor discrimination between different grades of good singers. The weights thus reflect the differential costs associated with a (mis)decision: it is much more costly to engage in courtship and to mate with a poor singer than to miss a good one. A poor singer is likely to be a heterospecific mating with whom

produces hybrid offspring with developmental defects and high mortality rates (21). In addition, hybrid males are often behaviorally sterile, because their hybrid song is not attractive to females of either parental species, thus further increasing the fitness costs for the female (9); to a lesser extent, this also applies to mating with a conspecific low-quality singer. Songs with interrupted syllables are often produced by males that have crippled wings or have lost a hindleg. These song deficits thus point to problems during molt, which are likely transmitted to the offspring, thereby reducing the female’s fitness. In contrast, mating with a conspecific good singer will normally produce healthy and fertile offspring. The additional fitness gained by a long search for a better singer is relatively small compared with the severe costs of mating with a poor singer that may belong to a different species or provides inferior genetic material. Hence to reliably avoid the high hybridization costs in the presence of noisy information integration, nonattractive syllables should be assigned a large weight (8).

More generally, our results suggest that the dynamics of decision-making may influence how a behavioral pattern is interpreted. Usually a mate choice behavior is interpreted as “females prefer attractive traits.” However, different weightings can underlie the same mate choice pattern and these weightings can reflect the costs and benefits of the choice behavior as well the reliability of the traits involved (10): (i) attractive traits could be weighted strongly positively in the case of sensory biases or “honest” traits (1, 6, 7); (ii) attractive traits could be weighted less than nonattractive ones if mating occurs rarely and errors are costly (9); and (iii) attractive traits could be ignored altogether if mating is costly to the female as in the case of sexual conflict (40). In our experiments, nonattractive syllables dominated mate choice (case ii above)—it might thus be more appropriate to label the nonattractive syllables repellent and to interpret the choice behavior as “females are repelled by nonattractive syllables.”

Conclusion

Our behavioral data in combination with the drift-diffusion model suggest that the dynamics of decision-making reflect the selective pressures that have shaped choice behavior. In the model system used here—song evaluation in the grasshopper *C. biguttulus*—asymmetrical integration of information is consistent with optimal cue integration and with predictions from theories of sexual selection and sexual conflict. Mating systems influenced by different selective pressures are expected to exhibit other modes of information integration. For example, in species where females directly benefit from copulation through nuptial gifts (41, 42), females should weight information more symmetrically. In addition, the relative costs and benefits are expected to change with the status of the female, e.g., sensory experience or age (43, 44). Hence, the dynamics of integration processes are expected to change in an adaptive manner over the lifetime of an animal. Our approach thus provides a rich framework to study the adaptation of decision-making processes on evolutionary and individual time scales.

Methods

Thirty-two sequences consisting of an attractive and a nonattractive syllable (Fig. 1 *B* and *C*) were presented in pseudorandom order to virgin female *C. biguttulus*. Female response songs were detected and song attractiveness was quantified as the average female response probability over 18 trials per animal and 27 animals. We then fitted a drift-diffusion model to these responses using a genetic algorithm. See *S1 Methods* for details.

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Supporting Information

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SI Methods

Stimulus Design. Attractive and nonattractive syllables were created as follows: The attractive syllable consisted of a 72-ms-long noise pulse (5–40 kHz) of constant amplitude followed by 12 ms of silence (Fig. 1B). This type of song subunit exhibits a syllable-to-pause ratio that elicits female responses with high probability (1). The nonattractive syllable was generated by modulating the amplitude of the attractive pulse with Gaussian low-pass noise (0–200 Hz) using a signal-to-noise ratio $\log_{10}(\sigma_{\text{signal}}^2/\sigma_{\text{noise}}^2)$ of ~ 0.5 . This noise modulation of the amplitude introduced gaps in the syllables known to reduce female response probability (2, 3).

Songs consisted of mixed sequences of 33 attractive and nonattractive syllables in which the proportion of attractive syllables varied from 1 to 0 in various parts of the song (Fig. 1C and Fig. S1). The duration of the song models was 2.8 s.

Playback Experiments. Female responses to these songs were quantified in playback experiments. After the first copulation, females of the species *Chorthippus biguttulus* resist multiple matings for a long time, and do not respond to male calling songs. Therefore, we used only virgin females that were placed in a soundproof chamber. Stimulus playback and recording of female responses was controlled by custom-written software (Labview 7; National Instruments) (Matthias Hennig, Humboldt Universität zu Berlin, Berlin, Germany). Each song was presented 18 times in a randomized sequence (for details, see ref. 4).

Female response probability was taken as the fraction of trials that elicited at least one female response song. To account for different motivation levels, probabilities were normalized by the response probability of the stimulus that was most frequently responded to by that female. Females that responded more than three times to 3 s of continuous noise were discarded as non-selective (4/31). For all further analyses, we took the average response probabilities from 27 individual females.

Drift-Diffusion Model. Integration of song was modeled using a drift-diffusion model with sticky bounds:

$$x_{t+1} = \begin{cases} \theta_-, & \text{if } x \leq \theta_- \\ \theta_+, & \text{if } x \geq \theta_+ \\ \frac{x_t}{\tau} + w_+ + \sigma \zeta_t, & \text{if } s_t = 1 \\ \frac{x_t}{\tau} + w_- + \sigma \zeta_t, & \text{if } s_t = -1 \end{cases}$$

The subscript t marks the syllable number—integration is discrete with each syllable corresponding to one time step. x_t is the integrated evidence up to the current syllable (initial value $x_0 = 0$). τ is the integration time constant of the leaky integrator (in units of syllables). s_t is the syllable type and is 1 for attractive and -1 for nonattractive syllables. w_+ and w_- are the weights for each syllable type. ζ_t is zero mean, unit variance Gaussian noise added at each time step, σ sets the SD of that noise. θ_+ and θ_- are the sticky bounds: if the accumulated evidence x_t reaches either threshold, it will stay there and the animal commits to a decision. If no threshold crossing occurs, the animal's decision is based on the sign of the integrated evidence at stimulus end.

We explored alternative formulations of the drift-diffusion model, which lack a noise term or which include a bias term or a time-dependent gain for the sensory evidence (5). Excluding the noise term reduced model performance and led to un-

realistic, binary prediction values. Adding additional parameters (bias term, time-dependent gain) did not improve performance and strongly reduced the reproducibility of the parameter values obtained over individual cross-validations. We therefore used the standard model formulation for all analyses.

In drift-diffusion models, sensory information is provided by dedicated feature detectors for positive and for negative evidence; this is a sensible assumption in situations where an animal is trained to discriminate between two alternatives, e.g., two sound frequencies (6) or the left- or rightward object motion (7). Though there may exist detectors for specific nonattractive features in grasshopper song evaluation (8), explicit recognition of all negative evidence in general is unrealistic. In communication systems in which the majority of signals fail to elicit any response, detecting such a large class of signals would require unfeasibly many feature detectors. Because the integration of evidence in the model is linear, a simple extension can solve this problem: the output of neurons detecting attractive features is combined into a single syllable score. This score is high for attractive syllables and low (i.e., zero) for all nonattractive stimuli. This score can then be mapped onto positive and negative evidence using a negative bias term (Fig. S2).

For this study, we focus on how different types of sensory information—differentiated by the temporal pattern of a song subunit—are integrated to yield the female decision and not on how this integration is initiated. We therefore assume that integration starts at zero and is triggered by the occurrence of a signal that is sufficiently loud against the background noise level and has the adequate, broadband carrier spectrum (1). Focusing on the temporal pattern and not on the carrier spectrum is well justified, because the songs of different grasshopper species in the *Chorthippus* group do not differ much in their carrier spectrum, but in the pattern of amplitude modulations (9, 10).

The model was fitted using a genetic algorithm (11, 12). Because the noisy integration is linear, parameters are determined up to an offset and/or a common scaling factor. We therefore fixed the positive weight to $w_+ = 1$. Our conclusion of asymmetrical integration of evidence is independent of this linear transformation of the parameters. For fitting, the other parameter values were constrained to $[-50, 0]$ for w_- , $[0, 250]$ for τ , $[0, 200]$ for θ_+ , $[-1, 000, 0]$ for θ_- . These constraints were found using exploratory trial runs and served to speed up the fitting procedure. We ensured that none of the bounds affected the fitting results.

Model performance was evaluated by leave-one-out cross-validation; i.e., the model was fit using 31 of the 32 stimuli to find the optimal parameter values. Then, a prediction was made for the left-out stimulus. Repeating this procedure such that each stimulus is left out once yields a set of 32 models and one prediction for the left-out stimulus. Model performance was taken as Pearson's coefficient of correlation r^2 between the predicted and measured responses.

Most model parameters were reproducible across the 32 cross-validated models (see SDs in Table 1). Fits starting with different initial parameter sets always converged to similar solutions, indicating that a globally optimal solution was well defined and was always found by the fitting algorithm.

To ensure that model parameters were well constrained by the data, we quantified model performance for parameter values around the optimal one found by the genetic algorithm—if the found optimum lies in an error minimum, then the parameter is well constrained (Fig. S3). All parameters except τ and θ_- lay in

a clearly defined minimum. The integration time constant τ and the negative threshold θ_- were defined only up to a minimal value; as for τ , this was because integration was effectively perfect—hence, as long as τ was much longer than the stimulus duration, model performance was optimal. A model with perfect integration exhibited identical performance and highly similar parameter values (Table 1). As for θ_- , the strongly asymmetrical integration made this parameter only semidetermined—as long as θ_- exceeded a value so that very early noise-induced threshold crossings were improbable, the strong bias induced by the large weight for negative evidence ensured that the model output remained virtually identical. Thus, the fact that two parameters were semidetermined does not reflect a lack of data but the idiosyncrasies of the decision process being modeled.

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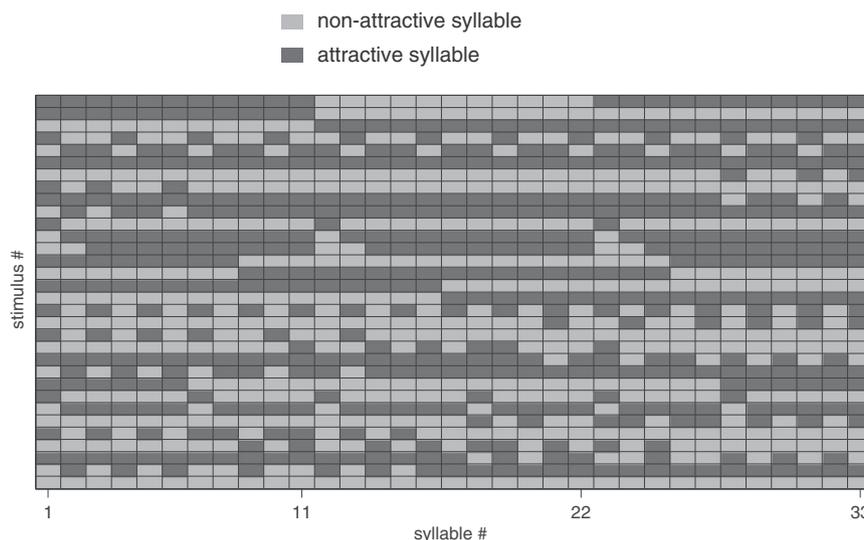


Fig. S1. Stimulus set. Syllable sequences of all 32 songs. Each song consisted of 33 syllables that were either attractive (black) or nonattractive (gray) as shown in (Fig. 1B). Song duration was ~ 2.8 s.

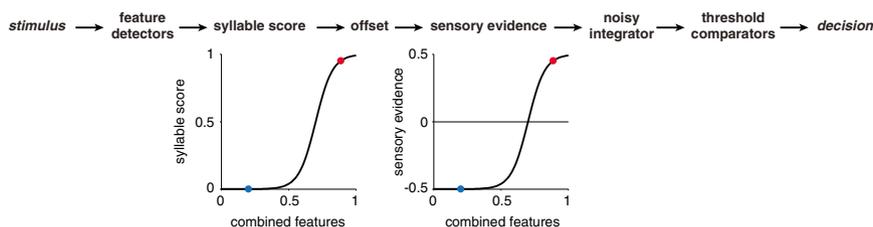


Fig. S2. General model schematic. The pattern of amplitude modulations of a syllable is processed by a bank of feature detectors, the combined output of which yields a score that ranges between 0 (unattractive syllable) and 1 (very attractive syllable). A simple transformation (e.g., a negative offset) turns this score into information with positive and negative values. The information is then accumulated using a noisy integrator and compared with a threshold for a positive or negative response. The blue dot corresponds to a putative nonattractive, the red dot to an attractive syllable.

