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RESEARCH ARTICLE

Integration of conflicting acoustic cues in sound localization in Cope's gray treefrog

Jain Pushpalatha Krishnan and Michael S. Reichert*

ABSTRACT

Sound localization is crucial for acoustically communicating organisms. However, many species must localize sounds in challenging conditions with high noise and signal degradation, which in some cases generate conflicting directional cues. Neural integration of repeated signal elements could improve the accuracy of sound localization, but little is known about how directional cues are integrated in natural animal acoustic communication. We studied how female Cope's gray treefrogs (*Hyla chrysoscelis*) integrate conflicting directional information in male acoustic advertisement calls. We performed two-speaker phonotaxis experiments in which two speakers broadcast overlapping synthetic advertisement calls, within which we systematically manipulated the timing relationships of pulses such that some pulses were leading in time on one speaker and the remaining pulses were leading on the other speaker. We tested alternative hypotheses of the mechanisms of integration by examining the effects of the percentage of leading pulses and their temporal order (at the beginning or end of the call) on female responses to a speaker and the latency to approach. Our results were consistent with integration across the entire call, and females moved towards whichever side broadcast the greater percentage of leading pulses, with no evidence for temporal order effects. We also found that females took longer to approach for stimuli with highly conflicting directional information. These findings give insights into the mechanisms of sound localization and information integration in challenging acoustic conditions.

KEY WORDS: Drift-diffusion model, Directional hearing, Phonotaxis, *Hyla chrysoscelis*, Sound localization

INTRODUCTION

The ability to localize sound sources is crucial for acoustically communicating organisms for social interactions, finding mates, tracking down prey and avoiding predators (Bee and Christensen-Dalsgaard, 2016; Moiseff et al., 1978; Müller and Robert, 2001; Payne, 1971). There are multiple sources of constraint on accurate sound localization. Sound localization relies on binaural hearing, i.e. comparisons between the properties of sounds arriving at each ear (Grothe et al., 2010; Litovsky and Goupell, 2021), but this raises fundamental challenges for small-bodied organisms because the short distance between the ears means that directional cues are minimal (Michelsen, 1992; Robert, 2005). Environmental effects on sound transmission add to the challenge of sound localization (Römer, 2015). Directional cues are prone to degradation due to reverberations, sound scattering and the attenuation of sound amplitude at increasing distances from the source (Michelsen and Rohrseitz, 1997; Wiley and Richards, 1978). Furthermore, noise interferes with sound localization by masking spatial cues in acoustic signals and reducing the signal-to-noise ratio (Caldwell and Bee, 2014; Reichert, 2015; Schwartz and Gerhardt, 1989). Even at the level of neural processing in receivers, neuronal noise can interfere with directional processing (Faisal et al., 2008; Neuhofer et al., 2011; Vogel et al., 2005). These obstacles to the effective reception of directional cues can reduce the receiver's ability to localize the source of sounds, and thus have acted as selection pressures on the evolution of both acoustic signal characteristics and receiver processing of sounds.

One strategy signalers use to improve the localizability of their acoustic signals is to produce signals with serially redundant elements (Luo et al., 2015; Ronacher and Hoffmann, 2003; Ronacher et al., 2000). When signals have elements such as repeating pulses or trills, receivers can take advantage of this repetition to increase the accuracy of their perception of the sound's location (Mowles and Ord, 2012; Payne and Pagel, 1997; Price, 2013). Serially redundant signals could improve receiver localization of sound by simply providing more opportunities to detect and process directional cues without necessarily involving any integration across multiple cues, which may be beneficial in environments with fluctuating noise levels (Vélez and Bee, 2011; Viemeister and Wakefield, 1991). Alternatively, serially redundant signals can allow receivers to integrate directional cues across multiple signal element repetitions, which can improve the accuracy of their directional perception by accumulating evidence and reducing the influence of noise (Heil and Neubauer, 2003). We focus on the latter mechanism because of evidence that it plays an important role in the processing of serially redundant signals (Alder and Rose, 1998). Such integration is a widespread strategy not only in directional hearing but also in decision-making processes more broadly (Bogacz et al., 2006; Gold and Shadlen, 2007; Wyart and Koechlin, 2016). However, there is much debate about the algorithm used for integration in different decision-making processes (Evans et al., 2017; Hyafil et al., 2023; Stine et al., 2020), and the understanding of the integration of information in decision making in wild animal systems is limited (Krakauer et al., 2017; Mobbs et al., 2018). Although integration across repeated signal elements could improve directional sound processing, some of the directional cues in a signal may be conflicting in natural acoustic environments because of background noise and acoustic clutter from fellow conspecific and heterospecific signalers and interference from obstacles in the environment (Kostarakos and Römer, 2015; Michelsen and Rohrseitz, 1997; Römer, 2015). Because of these effects, there can be situations in which one portion of a signal as

Department of Biology, Oklahoma State University, Stillwater, OK 74078, USA.

*Author for correspondence (michael.reichert@okstate.edu)

J.P.K., 0000-0002-3741-4317; M.S.R., 0000-0002-0159-4387

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perceived by the receiver will have directional cues indicating that the sound source is to the left side of the animal whereas the rest of the signal might direct the animal towards its right side (Kostarakos and Römer, 2010). The effects of conflicting information on animal decision making vary across tasks and there is still little consensus on the integration mechanisms involved (Ferrari and Chivers, 2013; Guiraud et al., 2025; Gür et al., 2021; Legge et al., 2016; Oberhauser et al., 2019). Investigating how information is integrated in naturalistic tasks is important to understand how animals communicate in challenging environments, and to reveal the underlying mechanisms of sensory processing.

The drift–diffusion model (DDM), although not the only proposed model of information integration in decision making (Carland et al., 2016; Ratcliff and Smith, 2004), is widely supported in different tasks and is a useful heuristic because it identifies relevant variables in the integration process that can be studied experimentally (Myers et al., 2022; Ratcliff and McKoon, 2008; Ratcliff et al., 2016). Alternative hypotheses for integration mechanisms under the DDM differ in the magnitude of the effect of different components of the integration process. In the case of sound localization of signals with repeated elements, the DDM models the integration process by assigning a sign to each signal element based on the direction it indicates (i.e. left or right), and a weight that corresponds to the strength of that information with respect to a decision-making threshold (Clemens et al., 2014, 2021). These values from each signal element are integrated and a decision is made when the integrated values reach one threshold or the other (corresponding to a decision to localize the signal to the left or to the right). Additional parameters can model the noisiness of the information provided by each element, the leakiness of integration (i.e. the degree to which earlier directional cues continue to contribute to the accumulated evidence relative to more recent cues) and urgency parameters that can weight signal elements based on their temporal order within the stimulus (Ratcliff et al., 2016).

Under the averaging hypothesis, all signal elements are weighted equally, and evidence is combined across the entire signal to make a decision in favor of whichever side has the greater total amount of evidence (Bogacz et al., 2006). In the context of the DDM, this would occur if each signal element receives a small weight relative to the response threshold such that a threshold is not reached before the end of the signal. For sound localization with conflicting directional cues, this hypothesis predicts that when there is equal evidence for both sides, decisions will be random (i.e. an equal probability of localizing to either side), and when there is more evidence indicating one side, then decisions will almost exclusively favor that side, regardless of the difference in the amount of evidence between the two sides (Fig. 1).

We examined two alternative hypotheses that could result in different patterns of response. First, the graded evidence hypothesis proposes that the likelihood of decisions in favor of one stimulus varies continuously with the evidence in its favor. Under this hypothesis, all signal elements are again weighted equally, but whereas the averaging hypothesis predicts a step function, the graded evidence hypothesis predicts a continuous approximately linear function (Fig. 1). Second, in the temporal order hypothesis, acoustic elements are weighted differently depending on when they occur within the signal. Such temporal order effects are common; for instance, many species are known to weight earlier signal elements more heavily than later signal elements (Clemens et al., 2021; Reichert and de la Hera, 2022; Reichert and Ronacher, 2019; Reichert et al., 2017; Seeba et al., 2010). In this scenario, responses will be biased towards the side indicated by directional cues in the first part of the signal and conflicting cues later in the signal are less influential, although the opposite pattern is also possible. For example, responses to a signal in which the first half indicates that the sound is coming from the left and the second half indicates that it is coming from the right could be biased towards the left even though the absolute amount of directional information in the signal is equal for each side. Distinguishing among these hypotheses gives insights into both the mechanisms and the function of animal decision-making processes. For instance, bias towards earlier or later signal elements could indicate a role of processes such as attention, sensory adaptation or leaky integration in signal processing (Bronfman et al., 2016; Levi and Huk, 2020; Yashiro and Motoyoshi, 2020). Strategies that integrate and weight evidence equally over the entire signal could reflect the importance of accurate decision making by incorporating all of the available evidence, rather than a speedy but potentially less accurate decision (Bogacz et al., 2010; Chittka et al., 2009; Heitz, 2014). When information processing is noisy, the relationship between the weight of the evidence and the response may more closely resemble a linear than a step function (Benjamin et al., 2009).

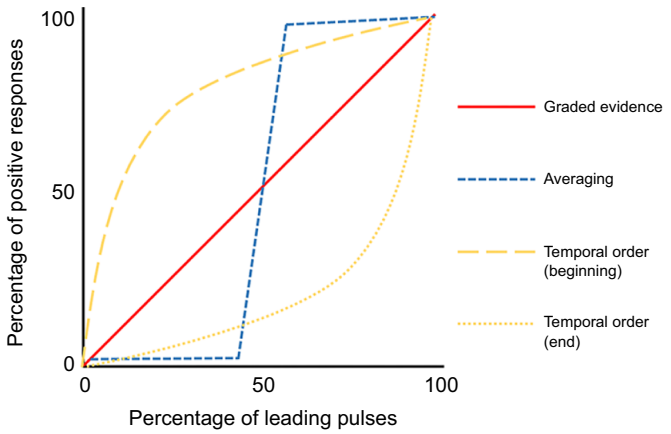


Fig. 1. Illustration of alternative hypotheses for integration. Each line depicts a hypothesized relationship between the percentage of leading pulses broadcast from the reference speaker and the percentage of trials in which females approach that speaker. The stimuli contain conflicting directional information in which some percentage of the pulses are leading on one speaker and the remaining pulses are leading on the other speaker. Here, the reference speaker is defined as the speaker that broadcasts leading pulses in the first part of the call. In the 'graded evidence' hypothesis (solid red line), the likelihood of decisions in favor of one stimulus varies continuously with the evidence in its favor, and each pulse is weighted equally, resulting in an approximately linear relationship with a slope of one. In the 'averaging' hypothesis (blue dashed line), each pulse is again weighted equally but now the decision is biased towards whichever side has the greater total evidence, and thus females are expected to rarely respond to the speaker with less than 50% of the directional cues favoring it, but to almost always respond to the speaker with greater than 50% of the directional cues favoring it, leading to a step function. In the 'temporal order' hypothesis, the weighting of directional cues depends on where they are in the signal. Directional cues at the beginning of the signal could be most influential (dashed yellow line; here the reference speaker is highly favored because it, by definition, broadcasts leading pulses at the beginning of the signal), or directional cues at the end of the signal could be most influential (dotted yellow line; likewise, here the individuals rarely move towards the reference speaker because by definition it has lagging pulses at the end of the signal). All of these hypotheses assume that information is integrated across the entire signal; they differ in how information from different signal elements is weighted when making the decision. Note that these are generalized curves that are not based on specific quantitative values (e.g. the exact slope of the step function) and are meant to illustrate the differences in general shape expected under each mechanism.

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We tested the effects of conflicting directional cues on sound localization in the context of stimuli varying in the temporal delay between signal elements. Humans and many other species use such temporal delays to localize sounds. Specifically many species experience the precedence effect, in which when acoustic stimuli arrive at the receiver from multiple locations separated by short amounts of time, the earlier-arriving (i.e. leading) source is more influential than the later-arriving (i.e. lagging) source in determining the perception of the origin of the sound (Brown et al., 2015; Dent and Dooling, 2004; Lee et al., 2009; Litovsky et al., 1999; Wyttenbach and Hoy, 1993). Integration of repeated stimulus elements affects the expression of the precedence effect. In humans, the strength of the precedence effect builds up across repeated presentations of lead–lag stimulus pairs (Clifton and Freyman, 1989; Freyman et al., 1991). In the phenomenon of onset dominance, elements at the beginning of the stimulus are weighted more heavily than those later in the stimulus, even if these provide conflicting directional information (Freyman et al., 1997; Saberi, 1996; Saberi and Perrott, 1995; Stecker and Hafter, 2002), although in some cases elements at the end of the stimulus can be heavily weighted (Stecker and Hafter, 2009). There is some debate about whether the common observation of a non-human animal preferential response to leading sound stimuli is due to the precedence effect (Brown et al., 2015; Greenfield, 2005). Regardless, natural sound localization tasks often involve overlapping sounds from different sources (e.g. reverberation or two spatially separated overlapping signalers), and leading signal preferences allow for tests of integration mechanisms in these scenarios, for which there is still a limited understanding.

Cope's gray treefrogs, *Hyla chrysoscelis*, are an ideal system for investigating the integration of directional cues in natural sound localization tasks. Males of this species produce calls containing serially redundant pulses to attract females during the breeding season (Gerhardt, 2001). Females perform phonotaxis, in which they localize advertisement calls produced by males and approach them to initiate mating (Gerhardt, 1994). Mate localization is highly accurate despite taking place in low-light conditions and in dense and noisy choruses (Bee, 2008a; Caldwell and Bee, 2014; Caldwell et al., 2014; Vélez et al., 2013). Female phonotaxis is readily elicited in the lab, and their localization abilities can be studied based on patterns of movement towards sound sources (Bee and Christensen-Dalsgaard, 2016; Caldwell and Bee, 2014; Gerhardt and Bee, 2007). When presented with two overlapping advertisement calls in which the call from one speaker is leading and the other is lagging, females of the closely related species *Hyla versicolor* generally move towards the leading call, and this pattern of response appears to be consistent with the precedence effect in which the leading call is perceived as a single percept rather than a preference for leading over lagging calls perceived separately (Marshall and Gerhardt, 2010; Reichert et al., 2016; Schwartz and Marshall, 2006). Here, we tested the effects of conflicting directional cues on sound localization in female *H. chrysoscelis*. Specifically, we manipulated the number of leading pulses broadcast from a given speaker and the temporal order of directional cues favoring each speaker. We hypothesized that females would orient towards the speaker that broadcast the highest number of leading pulses, and used the specific pattern of response across variation in the number of leading pulses on one side to test alternative hypotheses about how directional information is integrated. Based on prior work in other taxa (Clemens et al., 2021; Reichert and Ronacher, 2019), we also predicted that leading pulses at the beginning of the call would be weighted more in localization than leading pulses at the end of the call.

MATERIALS AND METHODS

Field collection

Female *Hyla chrysoscelis* (Cope 1880) were collected as amplexed pairs from several ponds in Payne County, OK, USA between 20:00 h and 24:00 h from 15 May to 20 June 2023. We transferred them to the laboratory inside a plastic container with a small quantity of water to prevent dehydration. To prolong females' motivation to respond to experimental stimuli, we placed the containers on ice in a cooler (Gall et al., 2019). All experiments were conducted after allowing the frogs to warm up to the testing temperature of 25°C, following removal from the cooler. Once each female was tested, it was returned to its pond of origin. All procedures were carried out with the approval of the Institutional Animal Care and Use Committee at Oklahoma State University (protocol number AS-19-4 and IACUC-22-22) and with permits from the Oklahoma Department of Wildlife Conservation (permit number W2308).

Acoustic stimuli

We performed phonotaxis trials to examine how females make localization decisions by integrating conflicting directional cues. Each speaker broadcast a standard synthetic *H. chrysoscelis* advertisement call with characteristics based on average call traits in our study population. Synthetic call stimuli were generated with a custom script using the seewave version 2.1.6 and tuneR version 1.4.2 packages in R version 4.1.0 software (Sueur et al., 2008; https://CRAN.R-project.org/package=tuneR; https://www.r-project.org/). Each call consisted of 30 pulses with a pulse rate of 50 pulses s^{-1} and two frequency peaks at 1.3 and 2.6 kHz, with the former having a relative amplitude to the latter of −6 dB. Each pulse had a duration of 10 ms, with a 10 ms interval between consecutive pulses (except when the leading speaker switched, see below), and had a typical pulse shape for *H. chrysoscelis*, with a concave-down rise and concave-up fall. The call had a linear rise of 50 ms. The call period, the time between the onset of one call and the next, was 5.58 s.

We then assembled call files into a stereo recording and manipulated the timing of call pulses on one track relative to those on the other to generate stimuli with varying directional cues. For the standard leading–lagging stimulus, we delayed the entire playback on one track by 4 ms. This meant that the call broadcast from one speaker would be leading by 4 ms relative to the otherwise identical call broadcast from the other speaker. In this scenario, females typically move toward the leading speaker (Marshall and Gerhardt, 2010). We then generated a series of additional stimuli that varied in the number of pulses that were leading on each speaker. To do so, we introduced an additional delay of 8 ms between two pulses at a specific point in the originally leading track such that any subsequent pulses would now be lagging by 4 ms. For instance, if the first three pulses were leading on the left channel, then the subsequent 27 pulses on that channel would be lagging (and as a consequence the last 27 pulses would be leading on the right channel; Fig. 2). We systematically generated these conflicting stimuli in steps of three pulses, for a total of nine conflicting stimuli (Table S1). We randomly chose which track was broadcast from which speaker to control for side biases. We tested a total of 21 females with these stimuli. Of these, 18 responded in all 10 trials (nine conflicting stimuli plus the standard stimulus; one female each responded in four, six and seven trials). Waveforms of all stimuli are shown in Fig. S1.

Biases in phonotaxis towards leading stimuli have been shown to be robust to the duration of the delay between leading and lagging

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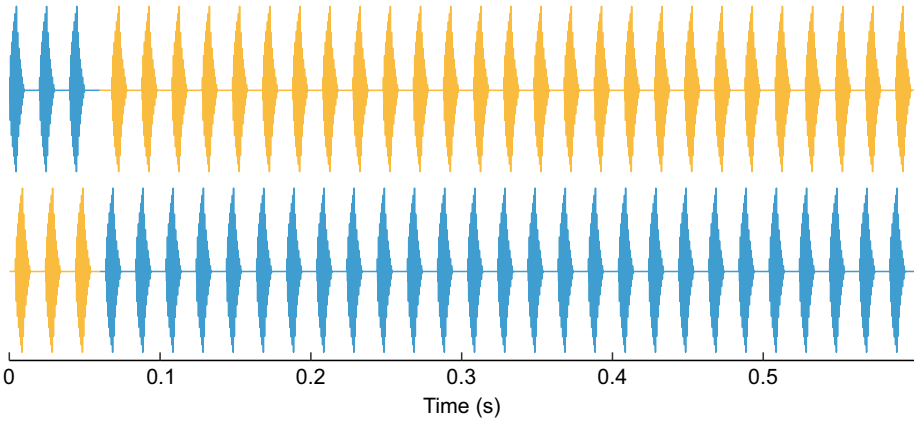


Fig. 2. Example waveform of one of the stereo playback stimuli. For this stimulus, the top (left) channel has the first three pulses leading (blue) and the last 27 pulses lagging (yellow) with respect to the bottom (right) channel. In this example, the left channel would be the reference speaker because it is the first channel to have leading pulses. Note that the silent period after the call to allow for a call period of 5.58 s is not shown.

speakers in *H. versicolor* (Marshall and Gerhardt, 2010). We tested whether this was also the case in *H. chrysoscelis* by measuring female responses to an additional set of stimuli in which all pulses were leading on one speaker but with different delays between leading and lagging stimuli (0.5, 1, 2, 3, or 5 ms, in addition to the standard 4 ms described above). We tested a total of 22 females with these stimuli, including all 21 tested with the conflicting stimuli above, and one not tested with any of those stimuli, but tested with one of the varying delay stimuli (Table S1). Of these, 19 responded in all six trials (one female responded in one trial and two females responded in three trials).

We note that our study is focused on the integration of directional information within a single call presentation, and our stimuli varied at that level. However, because our playback design involved repeated playbacks of these stimuli until females approached one of the speakers, it is possible that integration at longer time scales (i.e. across multiple calls) also occurred. Gray treefrogs show auditory grouping in which pulses are perceived as a call only when they are in close temporal proximity to one another, and these percepts determine the directional response, so we expected that directional decisions would be made largely at the level of individual calls, although we cannot rule out longer integration time constants (Schwartz and Hossain, 2017; Schwartz et al., 2010a). We return to this issue in the Discussion.

Phonotaxis test procedure

We tested female phonotaxis in a semi-anechoic chamber (described in Reichert and de la Hera, 2022). Females were placed under an acoustically transparent wire-mesh cage in the center of a 2 m diameter circular arena. The playback speakers were separated from one another by 90 deg and placed along the edge of the arena such that each was 1 m from the female starting point. This angle was chosen because previous work presenting leading and lagging stimuli with this angular separation between speakers found evidence for precedence effects in which the sound was perceived as a single source originating from the leading speaker, allowing us to assess the integration of directional information (Marshall and Gerhardt, 2010). Similarly, previous work using speaker separations of 90 deg or greater found evidence for sequential integration in which stimuli from the two speakers were integrated into a single percept (Bee and Riemersma, 2008; Farris et al., 2002; Schwartz and Gerhardt, 1995). Playbacks were performed at 85 dB SPL (fast, C-weighted) at 1 m, calibrated using a Larson Davis 831c (Depew, NY, USA) sound-level meter. The stereo stimulus was played from a PC using Adobe Audition software and broadcast through Orb Mod1 speakers (Orb Audio, New York, NY, USA) via an external sound card (Motu 16A; Motu Inc., Cambridge, MA, USA), an attenuator (Tucker-Davis PA5; Tucker Davis Technologies, Alachua, FL, USA) and an amplifier (Crown XLS 2002; Crown Audio, Inc., Elkhart, IN, USA). The chosen stimulus was first broadcast for 30 s before the female was released. We then released the female into the arena by pulling on a rope attached to the cage. The female's movements were monitored by an experimenter outside the chamber using an infrared camera connected to a video monitor. Females were given 5 min to make a response, defined as exhibiting positive phonotaxis and approaching within 10 cm of one of the playback speakers.

The first trial for each frog was a choice between standard calls of *H. chrysoscelis* and *H. versicolor*. This served to confirm that the female was in fact *H. chrysoscelis* as our populations include small numbers of the morphologically indistinguishable *H. versicolor*. After this first trial, the experimental stimuli were presented in a randomized order to control for any influence of the order of stimulus presentation. When females responded, we recorded which speaker they approached and the response latency (the amount of time between when the female was released and when it entered the response zone). Failure to respond within 5 min was recorded as a non-response. When a non-response occurred, we exposed the female to a single-speaker playback of a standard *H. chrysoscelis* call to ensure that it was still motivated to respond. If it did not respond to this stimulus, it was excluded from further trials, and the previous non-response was excluded from analyses. Each individual was provided with a minimum of 1 min of rest between trials before it was tested again. As long as females remained responsive, we tested their response to each of the 15 stimuli.

Statistical analysis

All statistical analyses were run in R version 4.5.0 software (https://www.r-project.org/). We performed statistical tests to evaluate the effects of specific stimulus characteristics on our response variables. Our evaluation of support for the different hypotheses of integration (Fig. 1) was based on both these analyses, which can address whether integration takes place at all and whether there are temporal order effects, and on a qualitative evaluation of the pattern of response to distinguish between the averaging and graded evidence hypotheses. We analyzed effects of conflicting stimuli on two measures of female sound localization: the speaker they approached and the latency to approach. Because conflicting stimuli had both leading and lagging elements broadcast from each speaker, we quantified responses with respect to a 'reference' speaker, which was designated as the speaker that played the track

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with leading pulses at the beginning of the call, or in the case of the stimuli with no conflicting directional information, the track with leading pulses. We analyzed the influence of the percentage of leading pulses on female responses (i.e. which speaker was approached) with a generalized linear mixed model (GLMM), using the glmer function of the lme4 version 1.1-37 package (Bates et al., 2015). Each individual trial was entered as a data point for this analysis, with the dependent variable being whether the female approached the reference speaker in that trial (binomial response family) with a fixed effect of the percentage of leading pulses on the reference speaker. We included individual ID as a random effect as multiple trials were performed using the same female.

We tested the influence of the temporal order of the leading pulses on female responses by comparing responses to sets of stimuli with the same percentage of leading pulses, but in which those pulses were at either the beginning or at the end of the stimulus. Here, we quantified responses to the speaker broadcasting the lower percentage of leading pulses (or, for the 50% leading, 50% lagging stimulus to the speaker that broadcast the leading pulses at the beginning of the call). Our reasoning was that, if there were temporal order effects, for a given percentage of leading pulses we would see a difference in responses to the speaker broadcasting that proportion of leading pulses depending on whether they were at the beginning or end of the call. We tested this in a GLMM with the speaker approached as the dependent variable (binomial), the percentage of leading pulses (10%, 20%, 30%, 40% or 50%), the temporal order of those leading pulses (beginning or end) and the interaction between those two variables as factors, and individual ID as a random effect. We also performed separate tests for temporal order effects for each percentage of leading pulses using a binomial test for the stimulus with 50% leading pulses on each channel and chi-squared tests for the rest of the stimuli. We note that the latter tests do not account for repeated measures of the same individual and therefore do not meet the assumption of statistical independence, but we used these rather than GLMMs because the latter were singular or unidentifiable because of the low variation in the response variable.

We tested the influence of the percentage of leading pulses on the latency to approach with a linear mixed effects model (LMM) using the lmer function in lme4. The dependent variable was the latency to approach with both linear and quadratic effects of the percentage of leading pulses on the reference speaker as fixed effects, and frog ID as a random effect. We included the quadratic effect to test whether decisions were slower when the directional information was most conflicting (i.e. when there was a similar percentage of leading pulses on each channel). All response latencies were included, regardless of the speaker that was approached.

We tested the influence of varying delays between leading and lagging pulses on stimuli without conflicting directional information (0.5 to 5 ms) on response to the reference speaker using a GLMM with delay as the independent variable and individual ID as a random effect. We tested the influence of delay on latency to approach using an LMM, again with delay as the independent variable and individual ID as a random effect.

RESULTS

Effects of the percentage of leading pulses and their temporal position

Females were more likely to approach the speaker broadcasting calls with a greater percentage of leading pulses (P<0.001; Table 1, Fig. 3). When the reference speaker had less than 50% leading pulses, females almost always approached the other speaker and there was no clear increase in responses to the reference as the percentage of leading pulses increased (Fig. 3). Likewise, when the reference speaker had more than 50% leading pulses, females almost always approached it, and again there was no clear change in the proportion approaching the reference speaker as the percentage of leading pulses increased (Fig. 3). For a given percentage of leading pulses, we found no statistically significant effect of whether those pulses were at the beginning or end of the call on female responses, both for the model including all stimuli (Table 2, Fig. 4; Fig. S2) and for tests for each specific percentage of leading pulses (Table 3).

We found both a significant linear (P=0.014) and quadratic (P=0.001) relationship between the percentage of leading pulses in the call and the response time. Response times were on average longest for stimuli with an intermediate percentage of leading and lagging pulses (Table 4, Fig. 5A).

Table 1. Effect of percentage of leading pulses on approach to the reference speaker

Factor	Estimate	s.e.m.	z	P
Intercept	−5.469	0.928	−5.892	
Percentage leading pulses	0.116	0.019	6.196	<0.001

Results are from a generalized linear mixed model (GLMM) with a binary variable of whether the female approached the reference speaker or the other speaker, with female ID as a random effect.

Effects of varying delays

We tested the influence on female responses of varying delays between the leading and lagging pulses in stimuli with 100% of the pulses leading on one channel. Females almost always approached the speaker broadcasting leading pulses, regardless of the delay

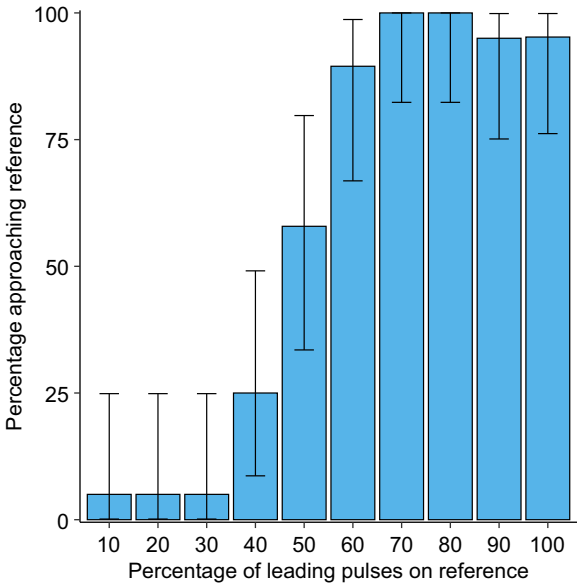


Fig. 3. The effect of the percentage of leading pulses in the stimulus broadcast from the reference speaker on the percentage of responses to that speaker. Note that the *x*-axis depicts the percentage of leading pulses from the speaker where the leading pulses were broadcast first (i.e. the reference speaker). Thus, the *y*-axis shows the percentage of trials in which females approached the reference speaker when the reference speaker had a given percentage of leading pulses at the beginning of the call (the remaining pulses were lagging on the reference speaker). Whiskers represent the 95% confidence interval of the proportion.

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Table 2. Effects of temporal order on responses

Factor	Estimate	s.e.m.	*z*	*P*
Intercept	−5.224	1.156	−4.519	
Temporal order	0.790	2.125	0.372	0.71
Percentage leading pulses	0.107	0.028	3.816	<0.001
Percentage leading pulses×Temporal order	−0.061	0.063	−0.978	0.33

For each percentage of leading pulses, we measured the proportion of responses that were to the speaker broadcasting that percentage of leading pulses in trials where those pulses were at the beginning or end of the stimulus (designated by the temporal order variable; reference level is the trial where that percentage of leading pulses was at the beginning of the stimulus). For the 50% leading pulses, stimulus response data were input as approach to the speaker with the leading pulses at the beginning, and the temporal order was coded as beginning. Results are from a GLMM with female ID as a random effect.

duration (0.5 ms, 17/20; 1 ms, 20/20; 2 ms, 20/20; 3 ms, 20/20; 4 ms, 19/20; 5 ms, 20/20). There was no significant effect of the duration of the delay between leading and lagging pulses on the latency to approach (P=0.30; Table 5, Fig. 5B).

DISCUSSION

We investigated the influence of conflicting directional cues on sound localization in female *H. chrysoscelis* by conducting two-speaker phonotaxis trials using varying numbers of leading pulses favoring each side. We found that females preferred stimuli with more leading pulses and that the conflicting stimuli were challenging for female decision making; specifically, frogs took the longest time to respond to stimuli in which the directional evidence was equal or approximately equal on the two sides. However, there was no evidence that the temporal order of leading and lagging pulses affected their response. Together, our results give insights into the mechanisms of integration of signal elements in sound localization in challenging acoustic conditions, which we discuss below.

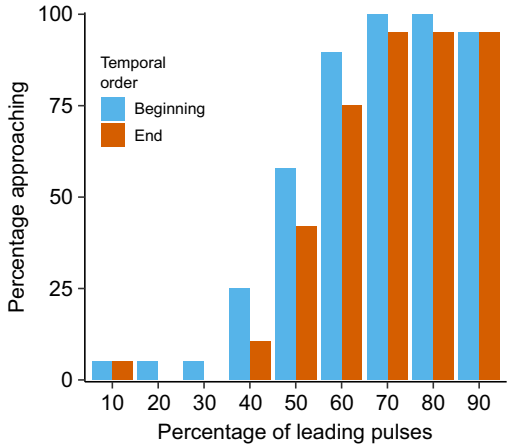


Fig. 4. The effect of the percentage of leading pulses and the temporal order of the leading pulses in the stimulus on the percentage of positive responses to the speaker broadcasting that stimulus. Blue bars represent the response to the speaker with leading pulses at the beginning of the call. Orange bars represent the response to the speaker with leading pulses at the end of the call. Note that this graph indirectly presents some of the data twice; for instance, the percentage of individuals that approached the stimulus with 40% leading pulses at the beginning is the same as those that did not approach the stimulus with 60% leading pulses at the end, because these are two different ways of depicting the same outcome of the same stimulus presentation.

Table 3. Statistical tests of the effects of temporal order of leading pulses on responses for each percentage of leading pulses

Percentage leading pulses	Test	Test statistic	d.f.	*P*
50%	Binomial			0.65
40%	chi squared	0.577	1	0.45
30%	chi squared	<0.001	1	1
20%	chi squared	<0.001	1	1
10%	chi squared	<0.001	1	1

For each percentage of leading pulses, we compared the proportion of responses to the speaker broadcasting that percentage of leading pulses in the trial where those pulses were at the beginning of the call versus the trial where those pulses were at the end of the call. For the level of 50% leading pulses, there was a single stimulus and so we used a binomial test to determine whether there was a significant bias towards one speaker (i.e. the one with leading pulses at the beginning) or the other (i.e. the one with leading pulses at the end). For other percentages of leading pulses, we used a chi squared test.

Models of integration

Our data best support the averaging model, in which the speaker that females approached was the one that played the larger number of leading pulses. In some formulations of the DDM of information integration, if the available evidence does not reach a threshold by the end of the stimulus, then individuals may make a decision based on the direction of the accumulated evidence up to that point (Bogacz et al., 2006). Such a mechanism would lead to a sigmoid-shaped curve in which localization decisions are biased heavily against the speaker with less directional evidence in its favor and therefore biased heavily towards the speaker with more directional evidence in its favor, regardless of the absolute amount of evidence. Our data largely conform to this pattern and only for the 40/60% stimuli was there any substantive variation among females in which speaker they approached, except for apparently random responses to the 50/50% stimulus in which an equal number of directional cues favored each side. Our data are inconsistent with the temporal order hypothesis because there was no evidence that, for any given amount of directional information, the information at the beginning or end of the stimulus was more influential. Likewise, there is little support for the evidence accumulation hypothesis because the percentage of females approaching a speaker did not clearly increase continuously with the amount of directional evidence favoring that stimulus. We note that these conclusions are based on a qualitative evaluation of the pattern of responses. We used the DDM as a conceptual framework and our data could discriminate among alternative predictions from different model types, but because our primary outcome variable was a binary response and our sample sizes were modest, there is not sufficient resolution to reliably estimate or quantitatively compare alternative DDM parameterizations (Lerche et al., 2017).

Our results give insights into the specific parameters underlying the integration of directional information. First, it appears that evidence is accumulated from the entire signal, indicating that

Table 4. Effect of the percentage of leading pulses on the latency to approach

Factor	Estimate	s.e.m.	*t*	*P*
Intercept	58.79	9.808	5.993	
Percentage of leading pulses (linear)	0.64	0.256	2.492	0.014
Percentage of leading pulses (quadratic)	−0.007	0.002	−3.268	0.001

Results are from a linear mixed model with female ID as a random effect.

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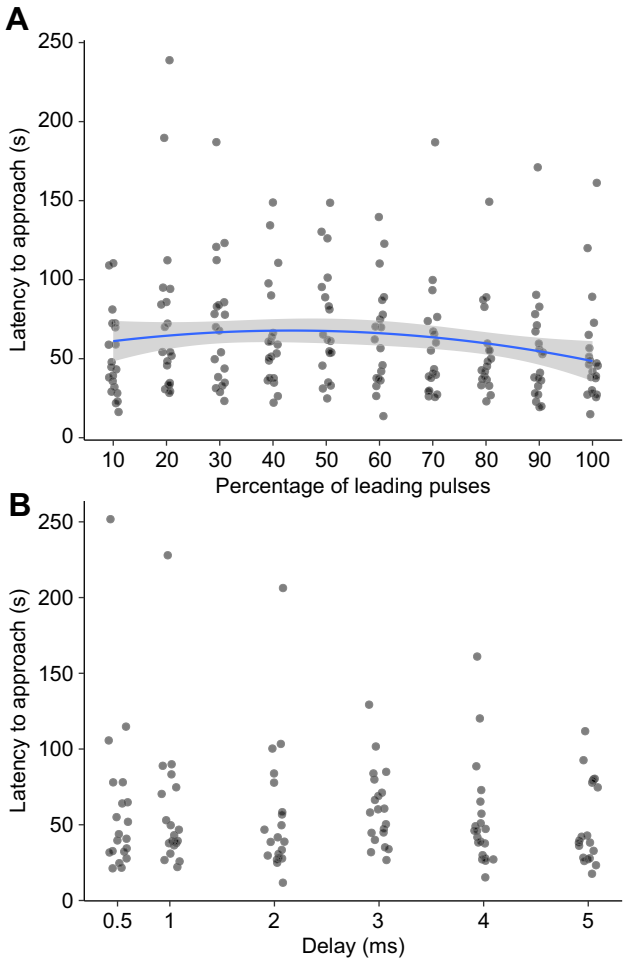


Fig. 5. Response times to the different stimuli. (A) Effect of the percentage of leading pulses on the latency to approach (i.e. how long it took the female to reach the speaker from the start of the trial). Note that the *x*-axis depicts the percentage of leading pulses from the speaker where the leading pulses were broadcast first (i.e. the reference speaker). The latencies are plotted for responses to both the reference and non-reference speakers. The blue line represents a quadratic effect of the percentage of leading pulses on the response time, with the shading representing the 95% confidence interval. Horizontal jitter and slight transparency are added to the points for better visualization. (B) Latency to approach for stimuli varying in the duration of the delay between leading and lagging pulses. Points are slightly jittered horizontally for better visualization.

information from each individual pulse has a low weight relative to threshold. This finding corresponds with behavioral observations, in which female gray treefrogs usually do not initiate phonotactic movements until after the end of a call (Beckers and Schul, 2004; Gupta et al., 2020). Female *Chorthippus biguttulus* grasshoppers also integrated information across the entire song (Clemens et al., 2014). In contrast, male *C. biguttulus* tested for localization to conflicting directional cues using a similar paradigm to the current study weighted individual elements in female response songs much more heavily such that they often reached threshold and initiated directional movements before the song was complete (Clemens et al., 2021; Reichert and Ronacher, 2019). That female *H. chrysoscelis* integrate directional information across the entire signal is not surprising, given that they also evaluate signal components such as the number of pulses, which necessarily involves attending to the entire signal (Bee, 2008b). Attending to the entire signal should also improve the accuracy of the directional perception, which is important given the challenges for sound localization in the noisy chorus and the potentially considerable costs of locomotion in the complex three-dimensional environment that must be navigated to reach a calling male (Bee, 2015).

Table 5. Effect of varying delays between leading and lagging stimuli on the latency to approach

Factor	Estimate	s.e.m.	*t*	*P*
Intercept	62.5	8.789	7.111	
Delay	−1.383	1.329	−1.040	0.301

Results are from a linear mixed model examining the latency to respond to stimuli in which 100% of the pulses were leading on one speaker, but in which the amount of delay between the leading and lagging speaker varied (0.5, 1, 2, 3, 4 or 5 ms), with female ID as a random effect.

Second, our finding that the temporal order of directional information does not affect decision making indicates both that integration is not 'leaky', at least over the time scale of an individual call, because otherwise the pulses at the end of the call would have had a stronger influence on sound localization, and that the weighting of directional information is constant across the call. In some previous studies in other species, earlier arriving cues were more heavily weighted in decision making, even in cases with high decision-making thresholds (Clemens et al., 2014; Huk and Shadlen, 2005; Pinto et al., 2018). The apparent equal weighting of directional information across the call found in our study again points towards an integration mechanism that evaluates the entire call. Furthermore, unlike another aspect of integration of signal elements in *H. chrysoscelis* in which the recognition of species-specific pulse rates is mediated by interval-counting neurons that can be reset by aberrant inter-pulse intervals, the lack of bias towards directional information at the end of the call indicates no such resetting process in sound localization (Gupta et al., 2021; Kamath et al., 2026; Rose et al., 2015).

Third, the strong bias towards choosing the speaker with the greater percentage of leading pulses regardless of the absolute number of leading pulses suggests that the noisiness of evidence processing is relatively low (Benjamin et al., 2009). If the signal to noise ratio for the information from each pulse was low, then we would have expected to see more variation in which speaker was approached in response to conflicting stimuli, but for most stimuli, responses were nearly unanimous to one side or the other. This finding is not surprising given our experimental design in which we tested females in optimal acoustic conditions in a semi-anechoic chamber with no background noise, and the highly effective directional hearing mechanism in this species (Bee and Christensen-Dalsgaard, 2016). The acoustic environment in natural choruses is much noisier and raises challenges for sound localization even when there is no conflicting directional information (Bee and Schwartz, 2009; Caldwell and Bee, 2014; Gerhardt and Klump, 1988), so an important next step to understanding the integration process would be to measure female responses to conflicting stimuli in more naturalistic environments. We speculate that in these circumstances, there would be a more linear relationship between the amount of directional information and the likelihood of a response because noise would lead to an increased likelihood of choosing the side with less evidence as the evidence favoring that side increases. This raises an important general caveat, which is that our interpretation of hypotheses of the mechanisms of integration is based on behavioral responses, but these patterns can be generated by multiple underlying mechanisms. For instance, a linear relationship between the amount of directional information and the likelihood of a

response could be generated by a truly linear underlying decision criterion, or a step function subject to heavy processing noise (Benjamin et al., 2009). This is a general challenge in studies of decision making, where multiple mechanisms can generate similar outcomes, and extensive testing is needed to distinguish among them (Stine et al., 2020).

Design considerations and future directions

An important aspect of the experimental design for interpreting our results is that these were closed-loop experiments in which the female was able to move freely in the arena, and our main measurement of localization was approach to one of the speakers. One consequence of this is that the directional cues perceived by the female necessarily varied as it moved closer to one speaker or the other, which would have both altered the perception of the manipulated timing differences between the speakers and generated intensity differences, which can also be used for sound localization (Caldwell and Bee, 2014). It is difficult to predict the effects of these factors on patterns of female responses, particularly as they vary continuously with female position in the arena, but most likely this would be an additional source of noise that would contribute to a more linear response function. Our results indicate that responses were strongly biased towards the speaker broadcasting more leading pulses; that this pattern held up across stimuli suggests that these factors had minimal effects on female responses.

Our design also raises questions about how our conflicting stimuli were perceived. One possibility is that females perceived the stimulus as a single sound source, but with conflicting information about its location. Females in the closely related *H. versicolor* also show phonotaxis towards sound sources broadcasting leading pulses, and there is evidence that they experience the precedence effect, in which the perception of sound direction is dominated by the leading stimulus and perceived as a single sound (Brown et al., 2015; Litovsky et al., 1999; Marshall and Gerhardt, 2010; Reichert et al., 2016). Studies of humans have used similarly conflicting stimuli and observed build-up phenomena, in which the precedence effect is strengthened with additional playback of sounds with lead–lag relationships (Clifton and Freyman, 1989; Freyman et al., 1991). In some cases, sounds continue to be perceived from the location of the originally leading stimulus even when the timing relationship is switched and the sound from that location is now lagging (Freyman et al., 1997; Saberi and Perrott, 1995). Thus, female *H. chrysoscelis* likely perceived our stimuli as a single sound source, with the integration of directional information favoring whichever side had more leading pulses. Alternatively, the stimuli could have been perceived as two separate calls, one corresponding to the speaker broadcasting the initially leading pulses, and the other being perceived as starting when the timing relationship was switched and coming from the other speaker. If this were the case, then the patterns of response we found could partly reflect preferences for longer calls (Bee, 2008b). We consider this unlikely because in *H. chrysoscelis*, sequential integration of other call characteristics into an apparent percept of a single call occurs even for spatial separations between speakers greater than the 90 deg used in our study (Bee and Riemersma, 2008). There is similar evidence for integration of signals from separated speakers in other species (Farris et al., 2002, 2005; Gerhardt et al., 2000; Schwartz and Gerhardt, 1995; Schwartz and Serratto Del Monte, 2019). Finally, as discussed above, there is evidence for precedence effects based on spatially separated call elements in *H. versicolor*, and this is likely also to be the case in the closely related *H. chrysoscelis* (Marshall and Gerhardt, 2010).

Another consequence of the closed-loop design is that stimuli were repeated multiple times before females completed their approach to a speaker. Thus, integration may also have been occurring at longer time scales than that of a single call. We found some evidence that females took longer to approach when the directional information in the stimuli was more conflicting, suggesting that this more challenging situation required them to take longer and evaluate more calls before responding. However, we did not measure specific movements during phonotaxis, so it is unknown whether the variation in response latencies stems from variation in the time to initiate phonotaxis from the release point, or in variation in movement towards the speaker once phonotaxis began. Longer-term integration seems to be involved in other aspects of signal evaluation in gray treefrogs, such as choosing an attractive mate based on the rate and duration of its calls (Schwartz et al., 2004). Longer integration times increase the accuracy of decision making (Abbott and Sherratt, 2013; Brunton et al., 2013), and decisions often take longer when options are more similar (Abraham et al., 2004; Dyer and Chittka, 2004; Rinberg et al., 2006; Roitman and Shadlen, 2002). However, even if this longer-term integration was taking place, because within a trial the stimuli did not vary, our inferences about the effects of the proportion of leading stimuli on response remain valid, and longer integration times would only mean that more total pulses contributed to the decision.

Our conflicting stimulus design necessarily required us to introduce a longer gap than normal between one pair of pulses to cause a formerly leading channel to now be lagging within the same call (Fig. 1). *Hyla chrysoscelis* has been shown to be less responsive to calls with a single 40 ms inter-pulse interval compared with calls with only the normal inter-pulse interval of 20 ms, reflecting the activity of interval-counting neurons (Kamath et al., 2026). In our stimuli, the altered inter-pulse interval was 28 ms and it is unknown whether this shorter abnormal interval affects female responses. In *H. versicolor*, a similar increase in magnitude of the inter-pulse interval (60 ms instead of the normal 50 ms) had no effect on call attractiveness, although an interval of 75 ms was less attractive (Schwartz et al., 2010b). Because females still responded strongly to the reference speaker, which contained the altered inter-pulse interval, for any of the stimuli with greater than 50% leading pulses, we consider it unlikely that the manipulated inter-pulse interval can explain the patterns in our results, although this should be addressed in future studies.

Finally, it is important to note that our design measured lateralization (i.e. a binary sound localization as coming from the left or the right, irrespective of the angle between the head and the sound source) because our primary response variable was female approach to spatially separated speakers. However, there is evidence that female *H. chrysoscelis* can extract more detailed location information from sounds that affects their approach angle to a speaker (Caldwell and Bee, 2014). It remains an open question whether conflicting directional information affects the perception of sound location at a finer scale than lateralization. Our latency to approach data can indirectly address that question because presumably better fine-scale localization would lead to a faster approach to a speaker, and we found evidence that the quality of directional information did affect how quickly females approached, although the effect size was not large and there was much variation in response latencies.

We found that varying the delay between the pulses from the two speakers from 0.5 ms to 5 ms did not influence the response rate or the latency of response. Females were highly responsive and preferred the leading pulses across this wide range of delays,

indicating that the results in our other experiments were not specific to the delay that we used (4 ms). Our finding of a response bias towards the stimulus with leading pulses across a broad range of delays is similar to results from a previous study of *H. versicolor* (Marshall and Gerhardt, 2010). However, we cannot rule out the possibility that the magnitude of delay affects female localization behavior when they are exposed to conflicting stimuli as all the stimuli in these control trials were non-conflicting (i.e. all the pulses were leading on one speaker). Furthermore, a previous study on a grasshopper species reported improved localization in noisy conditions when the lag between signal elements was increased (Reichert, 2015), and similar effects could apply in *H. chrysoscelis* tested in more natural noisy conditions. In *H. chrysoscelis*, characteristics of the binaural interaction component of the auditory brainstem response, an index of directional sound processing, varied across a similar range of binaural delays to those tested here, which suggests that although lateralization is robust to delay duration, finer-scale aspects of sound localization may not be (Pushpalatha Krishnan et al., 2026).

The natural consequences of phonotaxis towards leading pulses and the integration of conflicting stimuli require further study in *H. chrysoscelis*. The phenomenon we observed in which females usually approached the stimulus with more leading pulses may reflect directional hearing mechanisms for localizing a single sound source. Inter-aural differences in the arrival time of a sound are a major cue used in sound localization in frogs and other species (Gerhardt and Bee, 2007). Although physical arrival time differences are very small (Caldwell et al., 2014), these are magnified in neural processing (Christensen-Dalsgaard, 2005). Furthermore, in natural acoustic environments, reverberation and echoes can cause sound from the same source to arrive with much larger delays. This, combined with neuronal noise, can lead to both large delays in sound arrival at the two ears and conflicting directional information (Kostarakos and Römer, 2010). The delays we used are all well within the range of natural reverberations (Richards and Wiley, 1980), and thus we argue that our results are relevant to the challenge faced by female receivers to localize a calling male in complex acoustic environments, which may involve both processing of inter-aural time differences and the precedence effect. If, however, females perceived our stimuli as two separate calls, our findings could still be relevant to the challenge of discriminating among two different callers whose calls temporally overlap. Many frog species show preferences for leading calls (Bosch and Marquez, 2002; Grafe, 1996; Höbel, 2024; Larter and Ryan, 2024), and although gray treefrogs do not actively overlap one another's signals under most circumstances, they may sometimes overlap by chance (Reichert and Gerhardt, 2013). In this case, small variations in pulse rate may lead to conflicting sounds of the type we tested, in which some pulses from the same individual's call are leading and others are lagging with respect to those in the call of another individual.

Regardless of the specific function of bias in responding to stimuli with leading pulses, our results give important insights into the process by which this information is integrated. Important next steps will be to determine how integration takes place across signal characteristics and time scales. For instance, interval-counting neurons are involved in pulse rate recognition in *H. chrysoscelis* and the physiological integration process is well described (Gupta et al., 2021; Kamath et al., 2026; Rose et al., 2015), which raises the question of how these neurons function under conflicting directional information that could affect pulse rate perception. Directional processing must also interact with longer-term processing of other temporal features such as call effort that determine female attraction to calls (Krueger et al., 2026), but little is known about longer-term integration of call information. Finally, neural investigations of binaural processing of conflicting cues could potentially clarify the role of the precedence effect and other phenomena in information integration, as in a study in humans where the buildup phenomenon in the precedence effect affected the binaural interaction component of the auditory brainstem response (Dean and Grose, 2020). It would be of particular interest to measure how neural responses are modulated as conflicting cues are introduced, which has been done in humans (Appelbaum et al., 2011). Future studies should aim to test these mechanisms to expand our understanding of the strategies used by receivers in evaluating and responding to signals in complex environments.

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Competing interests
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Author contributions
Conceptualization: J.P.K., M.S.R.; Data curation: J.P.K., M.S.R.; Formal analysis: J.P.K., M.S.R.; Investigation: J.P.K., M.S.R.; Methodology: J.P.K., M.S.R.; Project administration: M.S.R.; Supervision: M.S.R.; Visualization: J.P.K., M.S.R.; Writing – original draft: J.P.K., M.S.R.; Writing – review & editing: J.P.K., M.S.R.

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