

# Crossmodal Comparisons of Signal Components Allow for Relative-Distance Assessment

Wouter Halfwerk,<sup>1,2,\*</sup> Rachel A. Page,<sup>1</sup> Ryan C. Taylor,<sup>3</sup> Preston S. Wilson,<sup>4</sup> and Michael J. Ryan<sup>1,5</sup>

<sup>1</sup>Smithsonian Tropical Research Institute, PO Box 0843-03092, Balboa, Ancón, Republic of Panama

<sup>2</sup>Institute of Biology, Leiden University, 2300 RA Leiden, the Netherlands

<sup>3</sup>Department of Biology, Salisbury University, Salisbury, MD 21801, USA

<sup>4</sup>Department of Mechanical Engineering, University of Texas at Austin, Austin, TX 78712, USA

<sup>5</sup>Department of Integrative Biology, University of Texas at Austin, Austin, TX 78712, USA

## Summary

Animals have multiple senses through which they detect their surroundings and often integrate sensory information across different modalities to generate perceptions [1, 2]. Animal communication, likewise, often consists of signals containing stimuli processed by different senses [3–6]. Stimuli with different physical forms (i.e., from different sensory modalities) travel at different speeds [7]. As a consequence, multimodal stimuli simultaneously emitted at a source can arrive at a receiver at different times. Such differences in arrival time can provide unique information about the distance to the source [8, 9]. Male túngara frogs (*Physalaemus pustulosus*) call from ponds to attract females and to repel males. Production of the sound incidentally creates ripples on the water surface, providing a multimodal cue [10]. We tested whether male frogs attend to distance-dependent cues created by a calling rival and whether their response depends on crossmodal comparisons. In a first experiment, we showed distance-dependent changes in vocal behavior: males responded more strongly with decreasing distance to a mimicked rival. In a second experiment, we showed that males can discriminate between relatively near and far rivals by using a combination of unimodal cues, specifically amplitude changes of sound and water waves, as well as crossmodal differences in arrival time. Our data reveal that animals can compare the arrival time of simultaneously emitted multimodal cues to obtain information on relative distance to a source. We speculate that communicative benefits from crossmodal comparison may have been an important driver of the evolution of elaborate multimodal displays [11, 12].

## Results

Males of the Neotropical túngara frog (*Physalaemus pustulosus*) aggregate at night in shallow seasonal ponds [13–15]. Males produce a single whine followed by up to seven chucks to attract females and defend their calling sites against other males. During aggressive interactions, males either increase their call rate (number of whines/s) and call complexity

(number of chucks per whine) or fight with intruders that approach within 5–10 cm [13, 16]. Calling creates an acoustic signal but simultaneously induces surface waves, or ripples, as a result of movements of the vocal sac and body wall associated with calling [10]. These water ripples are known to play a role in agonistic interactions between male frogs [17, 18] and can be integrated with sound into a multimodal signal [10]. Surface waves in shallow ponds propagate at a speed about 1,000-fold slower than airborne sound waves [7], thereby rapidly accumulating differences in arrival time with increasing distance and providing the basis for crossmodal distance cues (Figure 1).

We examined behavioral responses of male túngara frogs to sound- and call-induced water ripples of a mimicked rival. We constructed an experimental pool in which we placed a mesh enclosure, transparent to airborne and waterborne vibrations, which allowed us to situate focal males at different distances from the playback source.

## Experiment I: Distance-Dependent Impact of Ripples on Receiver Response

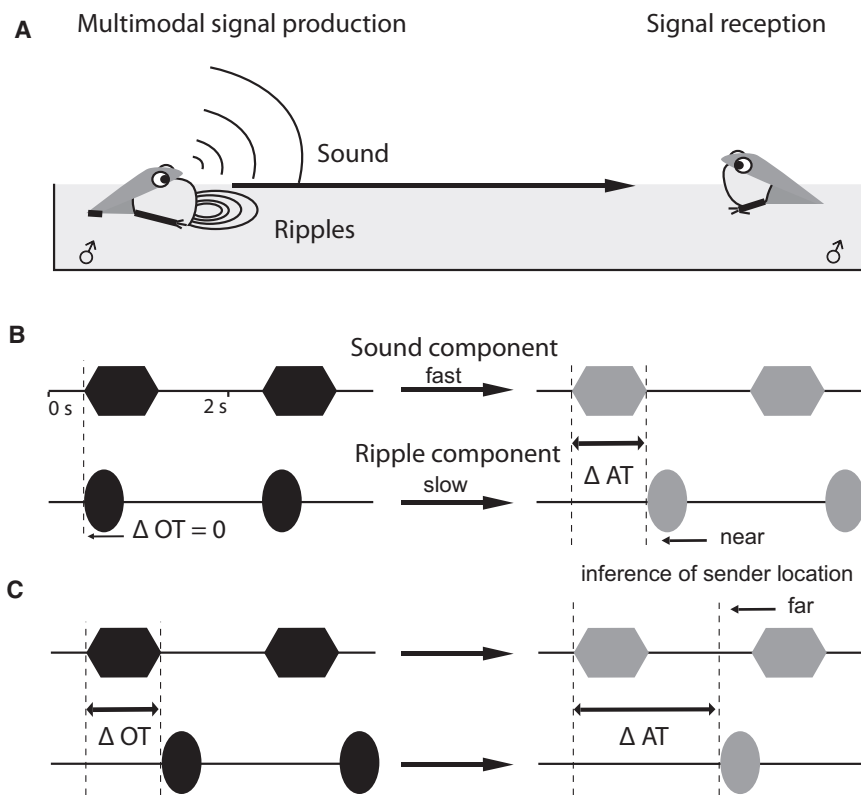
We first tested male vocal responses to the call of a mimicked rival male, broadcast with and without water ripples, at varying distances. Males had a higher overall call rate during sound with added ripples than during sound alone (generalized linear mixed model [GLMM], effect of ripples:  $n = 17$ , degrees of freedom [df] = 1,  $t$ -value = 6.02,  $p < 0.001$ ; Figure 2A). Vocal response to a simulated rival decreased with increasing distance when ripples were added (effect of distance<sup>2</sup>:  $t$ -value = 2.36,  $p = 0.02$ ), but not when calls were presented in isolation (Figure 2A). Importantly, there was also an interaction effect between distance and ripple treatment (ripples | distance<sup>2</sup>:  $t$ -value = 2.07,  $p = 0.041$ ), suggesting that males attend to distance-dependent cues associated with ripple propagation.

Adding ripples to the sound playback also increased overall call complexity of the male's vocal response (effect of ripples:  $\chi^2 = 10.48$ ,  $p = 0.001$ ; Figure 2B). Furthermore, males showed a decrease in call complexity with increasing rival distances (GLMM, effect of distance:  $df = 1$ ,  $\chi^2 = 16.02$ ,  $p < 0.001$ ), but we did not find an interaction effect between ripple treatment and rival distance ( $\chi^2 = 0.63$ ,  $p = 0.43$ ).

## Experiment II: Decoupling of Unimodal and Multimodal Cues

Call rate of the male was highest in response to the playback of ripples plus sound at a distance of 15 cm and lowest in response to the playback at 60 cm (Figure 2A). Given these differences, we then positioned receiver males 15 cm from our playback source and varied three cues that males could have used in the first experiment to respond to a rival that was relatively far away: (1) sound amplitude, (2) ripple height, and (3) difference in arrival time between ripples and sound (hereafter referred to as  $\Delta$ AT; see also Figure 1C and Table 1). The three cue treatments (all with a control and experimental condition) were independently manipulated and presented to focal males by a full factorial design. Only  $\Delta$ AT requires crossmodal

\*Correspondence: [wouter.halfwerk@gmail.com](mailto:wouter.halfwerk@gmail.com)



**Figure 1. Crossmodal Comparison of Differences in Time of Arrival Provides Distance Information**

(A) Communication displays often involve synchronized production of multimodal cues, such as frogs producing sounds and water ripples while calling. Inter- and intrasexual receivers can rely on unique properties of these multimodal displays by assessing the differences in time of arrival of the bimodal cue components. (B) Schematic representation of two signal components (e.g., sound and ripples) that propagate through different mediums (e.g., air and water surface, respectively). Sound and ripples are simultaneously produced (difference in onset time, or  $\Delta OT = 0$ ) at an average rate of 2 Hz but arrive with time differences at the receiver (difference in arrival time, or  $\Delta AT$ ) as a result of different propagation speeds. Reception of the  $\Delta AT$  accumulates with distance and could potentially be used by receivers for the assessment of distance to the sender.

(C) Example of experimental manipulation to mimic a sender that is farther away. A signal that is produced nearby can mimic the  $\Delta AT$  of a sender farther away by manipulation of the  $\Delta OT$ .

comparison and is therefore referred to as multimodal cue, whereas the other two cues (sound amplitude and ripple height) are referred to as unimodal cues.

#### Use of Unimodal and Multimodal Cues during Rival Contests

Males decreased call rate when  $\Delta AT$  increased, suggesting that they perceived the rival male as relatively far away (GLMM, effect of  $\Delta AT$ :  $n = 16$ ,  $df = 8$ ,  $\chi = 8.09$ ,  $p = 0.004$ ; **Figure 3A**). Males also decreased call rate in response to decreased ripple heights (effect of ripple height:  $\chi = 10.5$ ,  $p = 0.001$ ), but not to decreased sound amplitude (effect of sound amplitude:  $\chi = 0.18$ ,  $p = 0.67$ ). Male call complexity was significantly reduced in response to decreased sound amplitude ( $\chi = 3.88$ ,  $p = 0.049$ ; **Figure 3B**), showed a trend in response to decreased ripple height ( $\chi = 3.66$ ,  $p = 0.056$ ), and was not significantly affected by  $\Delta AT$  ( $\chi = 1.06$ ,  $p = 0.30$ ). These latter results show that males do not adjust call complexity in response to differences in arrival time between calls and ripples, which is consistent with the lack of a significant interaction in the first experiment (**Figure 2B**). We did not find any significant interactions between the three treatments, which were subsequently removed from final models.

#### Comparing Effect Sizes of Experiments I and II

We compared male call rates by using effect sizes from experiments I and II and assessed whether vocal responses matched on the basis of different cues. The response to a relatively faraway rival (at 60 cm) was reduced by 9.5 calls/min in comparison to the response to a relatively nearby rival (15 cm). Males independently reduced call rate by 4.4 calls/min when we mimicked  $\Delta AT$  of a relatively near versus far

rival and by 4.6 calls/min when ripple height was manipulated. When  $\Delta AT$  and ripple height were simultaneously manipulated, call rate was reduced by 9.0 calls/min, suggesting that vocal response is based on both cues.

#### Discussion

Multimodal signal components travel at speeds dictated by the physics of their respective modalities. As a consequence, differences in time of arrival between the multimodal components accumulate with distance. We have shown that male frogs can assess differences in time of arrival between ripple and sound cues produced by calling rivals, a capacity that requires crossmodal comparison. Furthermore, we have shown that males use crossmodal comparisons to discriminate between near and far rivals and to respond appropriately. Call rate is presumed to function as an aggressive response in túngara frogs [16], and the reduction in call rate (associated with increased rival distance) suggests that crossmodal comparisons aid assessment of relative threat levels posed by rivals at varying distances.

Most social animals have been shown to rely on environmental cues to assess distance to competitors, a process known as ranging [19–21]. However, many cue properties used for ranging, e.g., signal intensity or frequency-dependent signal attenuation [20–22], also change in response to environmental variation, such as temperature, turbulence, and the amount and size of clutter along the transmission line [23–25]. Furthermore, cues such as signal intensity can vary with physical properties or the motivational state of the signaler [22, 26] and may therefore not provide reliable information on distance. Speed of transmission is more predictable but is mostly useful when simultaneously produced cues are compared across modalities. Because ripple onset is synchronized with sound onset through production constraints,

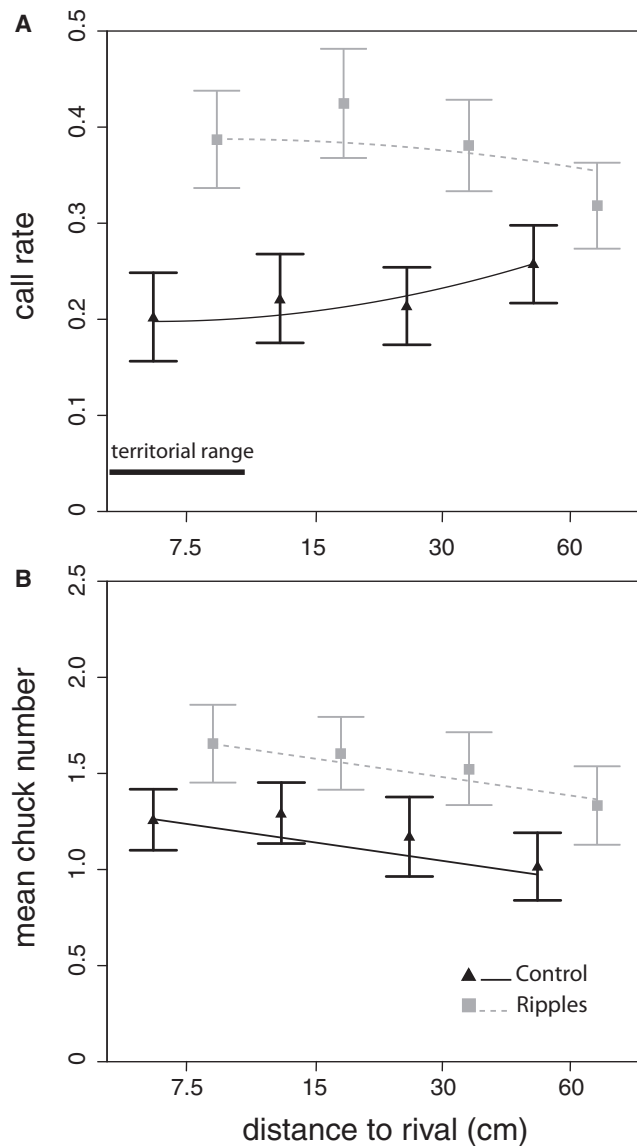


Figure 2. Experiment I: Vocal Responses of Male Frogs to Different Rival Distances

(A) Male frogs showed an overall increase in call rate in response to a rival when ripples were added to the playback of sound. Call rate decreased with distance to the mimicked rival for the playback of ripple plus sound, but not for the control playback of sound only. Males responded the most to ripple playback at 15 cm and the least to playback at 60 cm. Males placed inside the territorial range, which is defended in the field by chasing and grabbing intruding males, showed lowered call rates and occasionally stopped calling and released the air necessary for calling in response to ripples. Error bars indicate the 95% confidence interval.

(B) Frogs showed decreased call complexity in response to increasing distance between the focal male and mimicked rival. Playback of water ripples increased call complexity but did not show a distance-dependent effect. Error bars indicate SE. Response curves were created with effect sizes and intercepts from significant model estimates. All data points are arbitrarily shifted to the left or right for clarification.

crossmodal comparison of their difference in time of arrival can thus provide additional information on rival distance.

Our data do not provide insights on the accuracy with which male frogs assess rival distances or whether frogs use categorical or continuous distance perception.

Table 1. Distance-Dependent Cue Estimates and Manipulations

Cue Type	Value at 7.5 cm	Value at 15 cm	Value at 30 cm	Value at 60 cm	Change between 15 and 60 cm
Sound amplitude	89	86	82	80	-6 dB
Ripple height	200 $\mu\text{m}$	100 $\mu\text{m}$	50 $\mu\text{m}$	25 $\mu\text{m}$	-75 $\mu\text{m}$
$\Delta\text{AT}$	0.25 s	0.5 s	1.0 s	2.0 s	+1.5 s

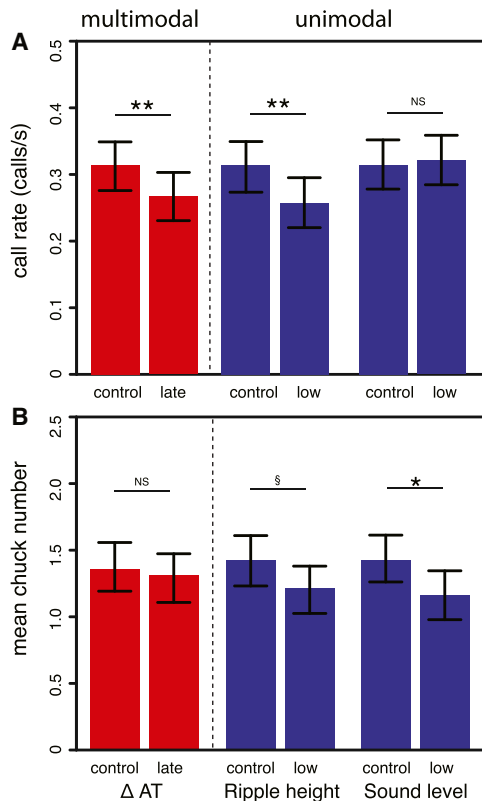
Examining the type and level of accuracy of the distance perception in túngara frogs would require experimental presentation of a large range of ripple-sound time intervals. We have shown, however, that túngara frogs discriminate between rivals that are relatively near or far away. Such relative-distance assessment is likely to be useful because vocal competition in lek-breeding frogs is often intense, and males risk losing calling territories to rivals [13]. A critical task for males, therefore, is to discriminate among rivals that are relatively far away or encroaching upon their territory.

### A Multimodal Cocktail Party

Effective communication requires receivers to assign signal components to the same or different sources, a process known as perceptual binding [27, 28]. Our data show that such processes can span multiple sensory modalities and thus require crossmodal comparison of components that differ in spatial and temporal cues [29, 30]. The perception of multimodal signal components with different times of arrival may be especially challenging when many signalers display at the same time and place, such as frogs calling from choruses or birds singing at dawn [31]. The number of male túngara frogs that call in the same puddle can vary greatly, ranging from just one to several hundred, according to time and place [13]. For crossmodal comparison to be possible, males would thus often have to be able to discriminate between males. To do so, males could rely on other spatial cues, such as directionality, to perceptually group different signal components or synchrony in arrival times between ripples and sound. Other important factors involve the delay at which ripples arrive at the receiver. At large distances, ripples of a first call may arrive after the sound produced during a second call. Under these conditions, discrimination of very near or very far rivals would most likely require additional cues, such as intensity- or distance-dependent modulation of the ripple form [32]. Finally, males have to carry out such complex perceptual tasks among a myriad of other sensory cues, such as ripples produced by approaching females, rain, or wind [18, 32, 33].

### Conclusion

Animals have to track the location of their social competitors to allow for effective defense of resources, such as food, shelter, or mates [1, 26]. We have shown that frogs are able to assess the differences in transmission speeds between modalities and that they can use the obtained information to assess relative rival distance and presumed competitive threat. Emergent properties that only arise when signal components are combined across sensory modalities may provide communicative benefits. Such benefits may help explain why communication in the animal kingdom has evolved elaborate and complex multimodal displays [11], despite the intrinsic costs of having to process information in multiple perceptual systems [34] and risks associated with increased eavesdropping by predators and parasites [10, 35].



**Figure 3. Experiment II: Vocal Responses of Male Frogs to Different Cue Components of a Nearby and Faraway Rival**

(A) Male túngara frogs adjusted call rate in response to manipulation of onset times between sound and ripples produced by a mimicked rival ( $\Delta$ AT, late = ripple playback was delayed in comparison to sound onset). Comparison of time of arrival required processing of cues in multiple modalities (multimodal cue). Males also adjusted call rate in response to altered ripple height (low = lowered ripple height at playback site), but not in response to changes in sound amplitude. Error bars indicate the 95% confidence interval.

(B) Male frogs adjusted call complexity in response to changes in unimodal cues, namely altered sound amplitude (low = lowered sound level at playback site) and possibly ripple height. Error bars indicate SE.  $^{\circ}$ p < 0.10,  $^*$ p < 0.05, and  $^{**}$ p < 0.01.

### Experimental Procedures

We conducted the experiments in November 2012 at the Smithsonian Tropical Research Institute (STRI) laboratory in Gamboa. We collected calling male túngara frogs 1–3 hr after sunset, toe clipped them for individual recognition after the experiment, and released them back to the field. Additionally, we recorded calling frogs between March and April 2014 in a laboratory at The University of Texas at Austin (UTA). All research reported here complied with IACUC protocols from the STRI and UTA. We obtained all required permits from the Government of Panama.

At STRI, we tested frogs in a pool (80 × 34 × 4 cm) filled with 4.5 liters of rainwater in a hemianechoic chamber. We placed a loudspeaker (Nanosat 5.0 connected to a NAD C316BEE amplifier) at the short side of the pool and attached a small metal tube to the pool's side to create ripples by blowing air on the water surface. We positioned the metal tube in front of the speaker 11 mm from the surface and 10 mm from the side of the pool. The tube was connected to a motor-driven pumping system that pushed 20 ml of air back and forth (this pump system was previously used to drive vocal sac inflation of a robotic frog; see Taylor et al. [36] for the design). Both the loudspeaker and the pumping system were driven by a desktop computer outside the test chamber.

We used a synthetic call consisting of a whine plus one chuck played at 0.5 calls/s and 82 dB sound pressure level (SPL; 20  $\mu$ Pa at 50 cm, measured with Extech SPL meter type 407764, set to C-weighted, fast, and max). The

pumping system produced 5–30 Hz water waves that traveled at a maximum speed of 30 cm/s (as measured from video). We set ripple height at the source to 2 mm and estimated the height at different distances by using attenuation levels (at 20 Hz) provided by Lang [37]. We checked ripple height close to the source by holding fine-grain sand paper (which has low capillary action) perpendicular to the water surface and by measuring the water line with a digital caliper before and after ripple playback. Properties of ripple stimuli were based on data from a similarly sized frog species [17]. At UTA, we recorded water waves of two male túngara frogs in a 1 × 1 m tank filled with 20 liters of water at a distance of 15 cm. Ripples were recorded with a laser Doppler vibrometer (LDV; Polytec OFV-534) and a controller (Polytec OFV-500, set to 5 mm/s/volts). The two males produced waves with peak heights between 50 and 120  $\mu$ m. Additionally, we measured our setup with the LDV. Our pumping system generated waves with peak heights of 60–150  $\mu$ m at a distance of 15 cm. Both the male frogs and the machine produced waves with a peak amplitude of 6 Hz.

We conducted two experiments to test whether the response of male túngara frogs to a mimicked rival changes with distance and whether this change depends on unimodal and/or multimodal cues derived from ripples and sound. In the first experiment, males were exposed for 1 min to a unimodal treatment (sound playback accompanied by blowing air outside the pool) or a multimodal treatment (simultaneous sound plus ripple playback within the pool). Males were placed in the pool and constrained by a mesh wire cage (20 × 13 cm; mesh 6 × 6 mm) with a transparent plastic top, and stimuli were broadcast to them from varying distances (7.5, 15, 30, or 60 cm between the speaker and center of the cage). Prior to each experiment, males were stimulated to call with a low-amplitude 5 min playback of a natural frog chorus. Males were stimulated with chorus playback in between the 1 min trials until they started calling. The order of the trials was randomized. Trials with no acoustic response of the vocal male were repeated once.

We calculated changes between different distances in three different cues accessible to males: sound amplitude, ripple height, and  $\Delta$ AT (see Table 1). We used these measurements to design a second experiment in which we broadcast stimuli from a distance of 15 cm to a focal male and altered sound amplitude, ripple height, and  $\Delta$ AT as if a rival were 60 cm away. We thus delayed ripple onset times by 1.5 s to mimic  $\Delta$ AT at 60 cm distance (see also Figure 1C). We altered ripple height by positioning the tube 18 mm from the water surface (as opposed to the original 11 mm), decreasing wave height by 300  $\mu$ m at the source, which corresponded to a similar estimated change of ~75  $\mu$ m between 15 and 60 cm. Sound amplitude was lowered by 6 dB, the change in amplitude measured with the SPL meter. Trials lasted 1 min with a 30 s silent period in between, and the order of trials was randomized.

We recorded males with an infrared-sensitive camera (Everfocus, model EHD500) attached to a desktop computer and an omnidirectional microphone (Sennheiser ME62) attached to a Marantz recorder (PMD660, sample rate 44.1 kHz). We quantified the number of calls and the mean number of chucks produced throughout the 1 min trials to calculate call rate and call complexity (both of which are known to reflect the level of motivation and aggressive response [16]).

Response measures were analyzed with GLMMs in R [38]. Call-complexity models were analyzed with an identity link function with normal error distribution (in the package lme4) and with call rate as a fixed effect to control for any covariance between the two response variables. Likewise, call-rate models included call complexity as a fixed factor and were analyzed with an identity link function with a Gamma error distribution (with Penalized Quasi-Likelihood in the package MASS) or a normal error distribution depending on model fit. Model fit was assessed with Akaike information criterion scores and quantile-quantile plots. For experiment I, fixed effects included ripple playback (yes or no) and distance or distance squared depending on model fit. For experiment II, fixed effects included sound level (control versus low), ripple height (control versus low), and ripple timing (control versus delayed). Interactions among fixed effects were added to all models and removed from final models when not significant. We used likelihood-ratio tests or Wald statistics to test for the significance of fixed effects. All models included male ID and playback order as random effects. We discarded all trials in which males did not call back, and we only analyzed males that reliably called in at least five out of eight trials of an experiment. The 95% confidence intervals shown in the graphs were calculated with Markov chain Monte Carlo simulations (n = 10,000) in the package LanguageR.

## Acknowledgments

We are grateful to Jennifer Finley and Amanda Lea for valuable help during the experiments. Justin Touchon and Stuart Dennis provided statistical advice. We thank Barrett Klein and Paul Clements for fabricating the pneumatic robotic frog system. Comments from four reviewers greatly improved the paper. We thank the Smithsonian Tropical Research Institute for the infrastructure critical to conducting this work, as well as logistical and permitting support. The research was funded through an NWO grant (825.11.026) to W.H., an KNAW grant (UPS/297 /Eco/1411J) to W.H., and an NSF grant (IBN 0517328) to R.C.T., M.J.R., and R.A.P.

Received: March 9, 2014

Revised: April 29, 2014

Accepted: May 28, 2014

Published: July 17, 2014

## References

1. Bradbury, J.W., and Vehrencamp, S.L. (2011). *Principles of Animal Communication*, Second Edition (Sunderland: Sinauer Associates).
2. Calvert, G.A., Spence, C., and Stein, B.E., eds. *The Handbook of Multisensory Processes* (Cambridge: MIT Press).
3. Hebets, E.A., and Papaj, D.R. (2005). Complex signal function: developing a framework of testable hypotheses. *Behav. Ecol. Sociobiol.* *57*, 197–214.
4. Partan, S., and Marler, P. (1999). Communication goes multimodal. *Science* *283*, 1272–1273.
5. Rowe, C., and Guilford, T. (1996). Hidden colour aversions in domestic chicks triggered by pyrazine odours of insect warning displays. *Nature* *383*, 520–522.
6. McGurk, H., and MacDonald, J. (1976). Hearing lips and seeing voices. *Nature* *264*, 746–748.
7. Markl, H. (1983). Vibrational communication. In *Neuroethology and Behavioral Physiology: Roots and Growing Points*, F. Huber and H. Markl, eds. (New York: Springer-Verlag), pp. 333–353.
8. Holldobler, B. (1999). Multimodal signals in ant communication. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* *184*, 129–141.
9. Todt, D., and Fiebelkorn, A. (1980). Display, timing and function of wing movements accompanying antiphonal duets of *cichladasa-guttata*. *Behaviour* *72*, 82–106.
10. Halfwerk, W., Jones, P.L., Taylor, R.C., Ryan, M.J., and Page, R.A. (2014). Risky ripples allow bats and frogs to eavesdrop on a multisensory sexual display. *Science* *343*, 413–416.
11. Higham, J., and Hebets, E. (2013). An introduction to multimodal communication. *Behav. Ecol. Sociobiol.* *67*, 1381–1388.
12. Taylor, R.C., and Ryan, M.J. (2013). Interactions of multisensory components perceptually rescue túngara frog mating signals. *Science* *341*, 273–274.
13. Ryan, M.J. (1985). *The Túngara Frog: A Study in Sexual Selection and Communication* (Chicago: University Of Chicago Press).
14. Rand, A.S., and Ryan, M.J. (1981). The adaptive significance of a complex vocal repertoire in a neotropical frog. *Z. Tierpsychol.* *57*, 209–214.
15. Ryan, M.J. (1980). Female mate choice in a neotropical frog. *Science* *209*, 523–525.
16. Bernal, X.E., Akre, K.L., Baugh, A.T., Rand, A.S., and Ryan, M.J. (2009). Female and male behavioral response to advertisement calls of graded complexity in túngara frogs, *Physalaemus pustulosus*. *Behav. Ecol. Sociobiol.* *63*, 1269–1279.
17. Walkowiak, W., and Munz, H. (1985). The significance of water surface-waves in the communication of fire-bellied toads. *Naturwissenschaften* *72*, 49–51.
18. Hobel, G., and Kolodziej, R.C. (2013). Wood frogs (*Lithobates sylvaticus*) use water surface waves in their reproductive behaviour. *Behaviour* *150*, 471–483.
19. Richards, D.G. (1981). Estimation of distance of singing conspecifics by the Carolina wren. *Auk* *98*, 127–133.
20. Mercado, E., 3rd, Schneider, J.N., Green, S.R., Wang, C., Rubin, R.D., and Banks, P.N. (2007). Acoustic cues available for ranging by hump-back whales. *J. Acoust. Soc. Am.* *121*, 2499–2502.
21. Wagner, W.E. (1989). Graded aggressive signals in Blanchard's cricket frog: vocal responses to opponent proximity and size. *Anim. Behav.* *38*, 1025–1038.
22. Owen, P.C., and Gordon, N.M. (2005). The effect of perceived intruder proximity and resident body size on the aggressive responses of male green frogs, *Rana clamitans* (Anura: Ranidae). *Behav. Ecol. Sociobiol.* *58*, 446–455.
23. Richards, D.G., and Wiley, R.H. (1980). Reverberations and amplitude fluctuations in the propagation of sound in a forest - Implications for animal communication. *Am. Nat.* *115*, 381–399.
24. Wiley, R.H., and Richards, D.G. (1978). Physical constraints on acoustic communication in atmosphere - implications for evolution of animal vocalizations. *Behav. Ecol. Sociobiol.* *3*, 69–94.
25. Dingle, C., Halfwerk, W., and Slabbekoorn, H. (2008). Habitat-dependent song divergence at subspecies level in the grey-breasted wood-wren. *J. Evol. Biol.* *27*, 1079–1089.
26. Stevens, M. (2013). *Sensory Ecology, Behaviour, and Evolution* (Oxford: Oxford University Press).
27. Klemen, J., and Chambers, C.D. (2012). Current perspectives and methods in studying neural mechanisms of multisensory interactions. *Neurosci. Biobehav. Rev.* *36*, 111–133.
28. Farris, H.E., and Ryan, M.J. (2011). Relative comparisons of call parameters enable auditory grouping in frogs. *Nat. Commun.* *2*, 410.
29. Taylor, R.C., Klein, B.A., Stein, J., and Ryan, M.J. (2011). Multimodal signal variation in space and time: how important is matching a signal with its signaler? *J. Exp. Biol.* *274*, 815–820.
30. Narins, P.M., Grabul, D.S., Soma, K.K., Gaucher, P., and Hödl, W. (2005). Cross-modal integration in a dart-poison frog. *Proc. Natl. Acad. Sci. USA* *102*, 2425–2429.
31. Bee, M.A., and Micheyl, C. (2008). The cocktail party problem: what is it? How can it be solved? And why should animal behaviorists study it? *J. Comp. Psychol.* *122*, 235–251.
32. Bleckmann, H. (1985). Perception of water surface waves: how surface waves are used for prey identification, prey localization, and intraspecific communication. In *Progress in Sensory Physiology 5*, H. Autrum, D. Ottoson, E.R. Perl, R.F. Schmidt, H. Shimazu, and W.D. Willis, eds. (New York: Springer-Verlag), pp. 147–166.
33. Akre, K.L., and Ryan, M.J. (2011). Female túngara frogs elicit more complex mating signals from males. *Behav. Ecol.* *22*, 846–853.
34. Gomez, D., Thery, M., Gauthier, A.L., and Lengagne, T. (2011). Costly help of audiovisual bimodality for female mate choice in a nocturnal anuran (*Hyla arborea*). *Behav. Ecol.* *22*, 889–898.
35. Zuk, M., and Kolluru, G.R. (1998). Exploitation of sexual signals by predators and parasitoids. *Q. Rev. Biol.* *73*, 415–438.
36. Taylor, R.C., Klein, B.A., Stein, J., and Ryan, M.J. (2008). Faux frogs: multimodal signalling and the value of robotics in animal behaviour. *Anim. Behav.* *76*, 1089–1097.
37. Lang, H.H. (1980). Surface-wave discrimination between prey and nonprey by the back swimmer *Notonecta glauca* L (hemiptera, heteroptera). *Behav. Ecol. Sociobiol.* *6*, 233–246.
38. Team, R.C. (2012). *R: A Language and Environment for Statistical Computing* (Vienna: R Foundation for Statistical Computing).