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ORIGINAL ARTICLE

Does multimodality *per se* improve receiver performance? An explicit comparison of multimodal versus unimodal complex signals in a learned signal following task

Tricia L. Rubi[1] · **David W. Stephens**[1]

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Abstract Multimodal signals are widespread in animal communication. Theoreticians have noted that, from an informational perspective, it is often not clear why multimodal signals should offer any benefit over unimodal complex signals. One possibility is that multimodal signals provide psychological benefits to receivers by virtue of the fact that they stimulate multiple sensory systems. Explicit comparisons of multimodal signals and unimodal complex signals are lacking, however. In this experiment, we examined the behavior of blue jays (*Cyanocitta cristata*) in a learned signal following task with two-component artificial signals that were either unimodal (visual-visual) or multimodal (visual-acoustic). We also manipulated the reliability of the components to verify that the subjects were able to follow each component type. We compared three measures of receiver performance—proportion of correct responses, learning rate, and reaction time. We found that while our subjects were able to follow both visual and acoustic signal components, performance did not differ in unimodal versus multimodal treatments.

Keywords Multimodal · Complex signals · Multimodal signals · Signaling · Communication · Receivers

Significance statement

Complex signals, and multimodal signals in particular, are prevalent in animal communication. It is not yet clear whether multimodal signals and unimodal complex signals are fundamentally different, and explicit comparisons of the two signal types are lacking. Our aim in this experiment was to test receiver performance when following multimodal and unimodal complex signals that differed only in the number of modalities tested. We found that our subjects performed equally well when following unimodal and multimodal signals, supporting informational, rather than psychological, predictions. In order to understand whether processing benefits can select for multimodal signaling, a broad, phylogenetic approach will be needed to determine how widespread multisensory processing pathways are, how they differ across taxa and sensory modalities, and whether such effects are seen outside of established signaling systems.

Introduction

Complex signals, defined as signals with multiple components, have become a popular topic in the field of animal communication. Increasingly, researchers are focusing on multimodal signals, defined as signals with components that occur across multiple sensory modalities—for example, a courtship signal that includes a dance and a vocalization, or a fertility signal that incorporates a color and an odor (see this journal's recent special issue (Higham and Hebets 2013) for an overview of multimodal signaling and the current state of research). Multimodal signals are widespread in animal communication, suggesting that multimodal signaling is a broadly beneficial strategy. It is not yet clear whether multimodal signals and unimodal complex signals, defined

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✉ Tricia L. Rubi
tricia.rubi@gmail.com

[1] University of Minnesota, 100 Ecology Bldg, 1987 Upper Buford Circle, St Paul, MN 55108, USA

as signals with multiple components in the same modality, should be treated as fundamentally different—indeed, this is the first of Partan's (2013) top ten unanswered questions in multimodal communication.

A major proposed benefit of multimodal signals is that they improve the performance of receivers (e.g., Partan et al. 2005; VanderSal and Hebets 2007; Kulahci et al. 2008; Siddall and Marples 2008; Rowe and Halpin 2013). From an informational perspective, there is no obvious reason why multimodal signals should offer any advantage over unimodal complex signals—as illustrated by Wilson et al. (2013), game theoretic models of multimodal signaling typically look very similar to unimodal models. Several authors have argued that multimodality itself can provide psychological benefits that improve signal perception or processing. In other words, multimodal signals may be beneficial simply by virtue of the fact that they stimulate multiple sensory systems. For example, Rowe (1999) cites evidence for perceptual effects such as intersensory facilitation (faster reaction time) and increased separability (enhanced ability to dissociate compounds into components), and argues that such phenomena should make bimodal signals broadly more effective than unimodal signals. Guilford and Dawkins (1991) argue that multimodal signals are more likely to cause potentiation, defined as an enhancing effect of one component on the learning of another. Siddall and Marples (2008) suggest that multimodal compounds may be learned faster and remembered longer. Hebets and Papaj (2005) hypothesize that multimodal signals might generate a stronger neural response due to sensory biases for multisensory stimuli. We still have much to learn about the potential mechanisms underlying such effects, and the mechanics of multisensory versus unisensory processing in general (see Alvarado et al. 2007; Gingras et al. 2009; Pluta et al. 2011 for work in this area).

At the behavioral level, a number of empirical studies have found that receivers exhibit enhanced responses to multimodal signals relative to isolated components (e.g., Hughes 1996; Narins and Grabul 2005; VanderSal and Hebets 2007; Siddall and Marples 2008; Uetz et al. 2009; Stynoski and Noble 2011). While such studies seem to support the idea that multimodality improves signal processing, few of them are able to make inferences about the effect of multimodality *per se.* First, few studies have directly compared multimodal signals to unimodal complex signals (though see Hauglund et al. 2006; Taylor and Ryan 2013 for relevant work). Comparing whole multimodal signals to isolated components confounds the effect of multiple modalities with the effect of multiple components, which is problematic because complex signals themselves have been hypothesized to improve receiver performance (e.g., Hebets and Papaj 2005). To truly test for modality effects, the signals being compared should have the same number of components. Second, most studies test responses to natural signals toward which receivers already have innate or learned responses. In such situations, reduced responses to isolated components may simply be a result of testing "partial signals" rather than a result of modality effects. Importantly, such studies also do not address whether enhanced processing of multisensory stimuli selects for multimodal signals, or vice versa—it is also plausible that selective pressures arising from communication select for perceptual or cognitive mechanisms that facilitate processing of multisensory stimuli. In the former case, we should expect to see enhanced receiver performance when following any multisensory stimuli, provided that receivers can perceive and follow cues in all tested modalities.

The aim of this study was to compare receiver performance on a learned signal following task, focusing on two-component signals that differed only in whether they were cross-modal. Captive blue jays (*Cyanocitta cristata*) served as our experimental subjects. We used novel, artificial signals with components in two modalities—visual (color components varying in hue) and acoustic (sound components varying in frequency). As part of our design, we confirmed that our subjects were able to perceive and follow both color and sound cues. We hypothesized that, if broad psychological benefits promote multimodal signaling, receivers should perform better when following multimodal signals than when following unimodal complex signals (assuming that they are able to perceive and follow cues from both modalities). Alternatively, if multimodality is not inherently beneficial for receiver processing, we expect to see similar performance when following multimodal and unimodal signals (in agreement with game theoretic predictions—see Wilson et al. 2013).

Methods

All housing and experimental procedures were approved by the University of Minnesota Institutional Animal Care and Use Committee (protocol #1109A04421).

Overview

Blue jays (*Cyanocitta cristata*) served as our experimental subjects. Inspired by aposematic signaling, our experimental signals were computer-generated butterfly images. Each signal had two components that were independently informative about the true state of our virtual butterfly ("good" or "bad"). Subjects were rewarded for accepting butterflies in the good state and rejecting butterflies in the bad state. The first component was a visual component (color) in unimodal and multimodal treatments—we refer to this component as the fixed component. The second component was a visual component (color) in unimodal treatments, and an acoustic component (a pure tone) in multimodal treatments—we refer to this component as the varied component (see Fig. 1 for example stimuli). Each component could be in one of two states—it could either

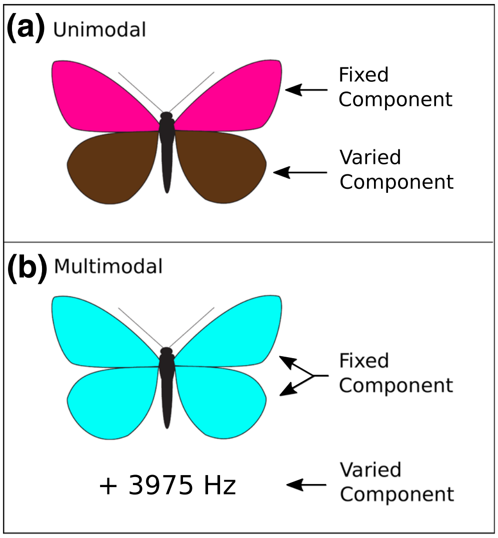


Fig. 1 Example stimuli. We refer to component 1 as the fixed component, since it is a color in both unimodal and multimodal treatments. We refer to component 2 as the varied component, since it is a color in unimodal treatments and a tone in multimodal treatments. **a** A unimodal stimulus: component 1 is the forewing color and component 2 is the hindwing color. **b** A multimodal stimulus: component 1 is the color of the wings and component 2 is a pure tone

indicate that the true state was good or that the true state was bad. If the component was color, the hue of the color (e.g., red versus green) was the informative difference; if the component was sound, the frequency of the tone (e.g., 1000 Hz versus 2000 Hz) was the informative difference.

We also experimentally varied the reliability of signal components. Signal reliability is the degree to which the signal state (or component state) accurately reflects the true state. We quantified reliability with the variable q, which we defined as the conditional probability: $q = \mathrm{P}(\text{true state is good} \mid \text{component state indicates "good"}) = \mathrm{P}(\text{true state is bad} \mid \text{component state indicates "bad"})$. We tested two levels of reliability ($q = 0.7$ and $q = 0.95$) in a full factorial design, resulting in four reliability pairings. At each reliability pairing we completed two treatments, a unimodal treatment and a multimodal treatment, resulting in a grand total of eight treatments. Testing behavior across a range of reliabilities allowed us to confirm that receivers were able to perceive and follow both color and sound cues.

Subjects

Our test subjects were eight adult blue jays of unknown sex, randomly selected from a captive colony. We housed subjects in the testing chambers for 23 h per day. They were removed for an hour for health checks, cleaning, and maintenance. The experimental day began each morning at 07:00 and ran until 15:00. Subjects received all of their food from the apparatus except when weight dropped dangerously low. We provided *ad libitum* water and maintained subjects on a 12 hour light/dark cycle.

Testing apparatus

We built each testing apparatus into a separate sound attenuation chamber (Fig. 2). We presented visual stimuli on an LCD screen at the front of the apparatus and acoustic stimuli from a speaker attached to the chamber lid. The food cup was located directly under the screen, and the two response keys (MED Associates ENV-123AM) were located on either side. "Reject" keys were marked with an X and "Accept" keys were unmarked, and the positions of the two keys were randomized across subjects. A response perch and indicator light were located at the rear of the box. A MED-PC computer program (MED Associates, Burlington, VT, USA) controlled inputs and outputs and recorded data.

Stimuli and treatment design

We generated the visual stimuli using Adobe Illustrator (Adobe Systems, San Jose, CA) and the acoustic stimuli using Audacity (Audacity Team). In unimodal treatments, the stimuli were butterfly stencils with two colors corresponding to the forewing and the hindwing (Fig. 1a). We designed the stencils such that the areas taken up by the two colors were equal in size. In both unimodal and multimodal treatments, all colors used within a single treatment were spaced at least 80° apart on the Adobe Illustrator color wheel. In multimodal treatments, the butterfly stimuli had a single color on both wings and were always accompanied by a pure tone (Fig. 1b). The eight tones used for multimodal treatments were evenly spaced from 1000 to 3975 Hz, within the range of peak sound sensitivity for blue jays (Cohen et al. 1978). The tones paired together in a treatment differed by at least 850 Hz. Tone amplitude at the rear perch during playback was at least 60 dB.

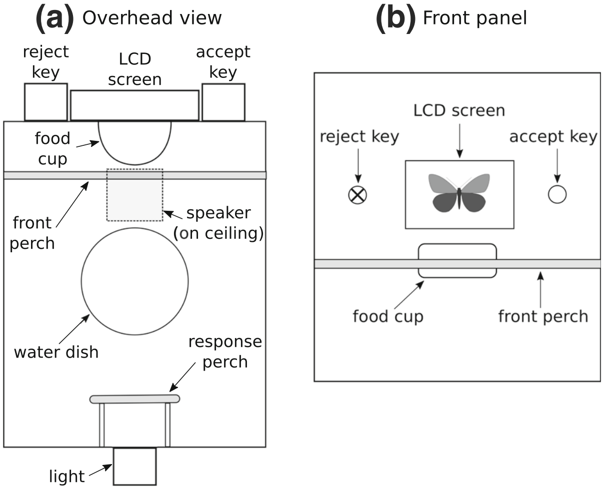


Fig. 2 An example configuration of the testing apparatus (the left-right positions of the accept and reject keys were randomized across subjects). **a** Overhead view. **b** Front panel view

Each subject completed all eight treatments in a different order, and we analyzed the results using a within-subjects design. We constructed eight stimulus sets by pseudo-randomly combining 24 colors (two in each multimodal set and four in each unimodal set) and eight tones (two in each multimodal set) following the restrictions just described. These eight stimulus sets were used for all subjects. Each subject saw each stimulus set in only one treatment. We pseudo-randomly assigned stimulus sets to treatments such that two subjects saw each stimulus set in a given treatment. For each subject, we randomly assigned the colors and tones as the positive and negative components (that is, indicating "good" and "bad," respectively). This randomization scheme controlled for effects of treatment order, stimulus set, and individual colors and tones.

Trial walkthrough

Trials were separated by an intertrial interval (ITI) of 110 s. At the start of each trial, the computer determined the trial type (free or forced) and the true state (good or bad) based on the treatment parameters. The computer then independently assigned the states of the signal components probabilistically based on the component reliabilities. To begin the trial, a flashing light at the rear perch indicated that the trial was ready to begin. The subject initiated the trial by hopping to the rear perch, which caused the butterfly stimulus to appear on the screen and, if applicable, the acoustic playback to begin. The two response keys were also illuminated. The signal was presented continuously until the subject responded; that is, the visual stimulus remained displayed on the screen and acoustic components played continuously. Subjects pecked the accept key or the reject key to respond, which immediately extinguished the response keys and ended the signal playback. Correct responses were rewarded with two food pellets, accompanied by a flashing magazine light. When subjects responded incorrectly, the signal and keys extinguished and no food was delivered. If a subject had not responded within 15 minutes, the trial aborted, the ITI restarted, and the trial was repeated.

Trial types

We arranged trials in blocks of 40, beginning with eight forced trials followed by 32 free trials. Forced trials (also known as "no choice" trials) are similar to free trials, except that they require subjects to respond in a predetermined way and experience the associated reward. This ensures that subjects experience all possible choices and outcomes in a treatment. For example, in a forced correct accept trial, the computer assigned the component states and the apparatus illuminated the signal and accept/reject keys, exactly as in free trials. However, the trial only ended when the subject pecked the accept key (that is, the reject key was not responsive). The subject received a reward in forced correct trials, but not forced incorrect trials. Subjects responded freely in free trials.

Stability assessment

Subjects continued in a treatment until signal following behavior had stabilized, and responses from the period of stable responding were used in the analysis. The first 600 trials of each treatment constituted the learning period. Trials from the learning period were not used to assess stability. After the learning period had ended, the treatment continued until the subject completed three consecutive days of stable signal following. Specifically, the treatment continued until (1) the overall accept rate for all pooled stimuli was greater than 0.1 and less than 0.9, and (2) the accept rates for each stimulus differed by less than 17 % across the 3 days. These criteria ensured that subjects were following the signal (that is, they were not simply accepting or rejecting every stimulus) and that responses to each stimulus had stabilized. If these criteria were not met by the time subjects had completed 3500 trials, the treatment ended and the final 3 days were used in the analysis.

Data analysis

Each subject completed all eight treatments in a different order, and we analyzed the data using a within-subjects design. For all measures except learning rate, we focused on data from the 3-day period of stable responding (or, if responses never stabilized, the final three days of the treatment). All free trials from the 3-day period were included in the analysis—typically around 550 trials per subject per treatment.

We assessed performance based on three measures: the proportion of correct responses (P(Correct)), the reaction time, and the learning rate. The reaction time was measured as the time elapsed between the presentation of the signal on the screen and the moment the subject registered a response. Learning rate was defined as the total number of trials completed in a treatment (i.e., the number of trials completed before the stability criterion was met). If behavior had not stabilized by the end of the treatment, the total number of trials was set to 3500 (the maximum treatment length). In addition to performance, we assessed which component influenced decisions more strongly. To do this, we examined responses to the subset of signals in which the components disagreed—that is, one component indicated that the true state was good and the other indicated that the true state was bad. We focused on these cases because responses to the signals in which the components agreed did not provide information about preference. We then determined the proportion of "follow responses" for the varied component (P(Follow Varied Component)). We define a follow response as accepting a component signaling "good" or rejecting a component signaling "bad." Recall that in unimodal treatments the varied component was a color, and in multimodal treatments it was a sound—thus, this measure allowed us to test for biases toward sound or color cues. The following rate for the fixed component was necessarily the inverse of P(Follow Varied Component) because following the fixed component and following the varied component were mutually exclusive strategies for disagreeing signals. Therefore, we report the statistics for following the varied component only.

To summarize, we calculated four dependent measures: (1) P(Correct), (2) reaction time, (3) learning rate, and (4) P(Follow Varied Component). We analyzed each of these dependent measures with a $2 \times 2 \times 2$ repeated measures analysis of variance with factors of modality (unimodal or multimodal), reliability of the fixed component (0.7 or 0.95), and reliability of the varied component (0.7 or 0.95). We performed statistical analyses using R 3.2.1 (R Core Team 2015). To estimate our power to detect differences due to modality effects, we performed a post hoc power analysis using the program G*Power (Faul et al. 2007). Following Cohen's (1988) framework, we determined that our design had sufficient power (0.87) to detect moderate (0.3) effects at alpha 0.05.

Results

Performance measures

We found no significant difference in the proportion of correct responses during stable signal following in multimodal versus unimodal treatments (Fig. 3). A repeated measures ANOVA indicated a significant interaction between the reliability of the fixed component (rel. fixed) and the reliability of the varied component (rel. varied) (repeated measures ANOVA: $F_{1,7} = 52.008$, $p < 0.001$); however, there were no significant interactions involving modality (rel. fixed × modality: $F_{1,7} = 0.547$, $p = 0.484$; rel. varied × modality: $F_{1,7} = 0.520$, $p = 0.494$; rel. fixed × rel. varied × modality $= 1.276$, $p = 0.296$), nor a significant main effect of modality ($F_{1,7} = 0.227$, $p = 0.649$). We next assessed the response time during stable responding. The average response time was 30.39 ± 0.8 tenths of a second (mean ± SE). The response time data violated the sphericity assumption, so we applied a square root transformation. We found no significant differences in response time (square root transformed) due to reliability, modality, or any interactions (rel. fixed: $F_{1,7} = 3.405$, $p = 0.108$; rel. varied: $F_{1,7} = 0.025$, $p = 0.878$; modality: $F_{1,7} = 0.874$, $p = 0.381$; rel. fixed × rel. varied: $F_{1,7} = 0.437$, $p = 0.530$; rel. fixed × modality: $F_{1,7} = 1.921$, $p = 0.208$; rel. varied × modality: $F_{1,7} = 0.751$, $p = 0.415$; rel. fixed × rel. varied × modality: $F_{1,7} = 1.439$, $p = 0.269$). Finally, we assessed the learning rate. We found no significant difference in the learning rate in multimodal versus unimodal treatments (Fig. 4). A repeated measures ANOVA indicated a significant effect of the reliability of the varied component only ($F_{1,7} = 7.066$, $p = 0.033$). There were no significant interactions (rel. fixed × rel. varied: $F_{1,7} = 1.117$, $p = 0.326$; rel. fixed × modality: $F_{1,7} = 3.130$, $p = 0.120$; rel. varied × modality: $F_{1,7} = 0.950$, $p = 0.362$; rel. fixed × rel. varied × modality: $F_{1,7} = 0.359$, $p = 0.568$), nor significant main effects of modality ($F_{1,7} = 2.087$, $p = 0.192$) or the fixed component ($F_{1,7} = 1.179$, $p = 0.313$).

Component preference

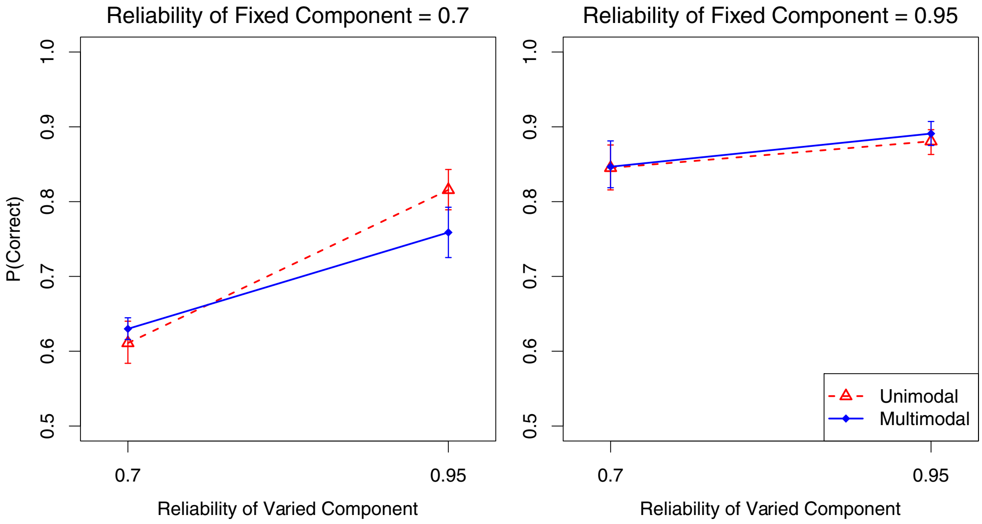
Most subjects followed sound at a higher rate than color in at least one treatment; however, subjects had a tendency to prioritize color cues. A repeated measures ANOVA revealed that P(Follow Varied Component) was significantly influenced by modality ($F_{1,7} = 13.387$, $p = 0.008$), as well as the reliabilities of the fixed component ($F_{1,7} = 31.827$, $p < 0.001$) and the varied component ($F_{1,7} = 14.851$, $p = 0.006$). The interaction between modality and the reliability of the varied component bordered on significance ($F_{1,7} = 3.995$, $p = 0.086$) (Fig. 5).

Discussion

As expected, receivers were sensitive to component reliability—the reliabilities of both components significantly influenced the proportion of correct responses during stable responding, as well as the number of trials completed before stability was reached. Though most receivers readily followed both color and sound components, we found no evidence that our experimental receivers processed multimodal signals any differently than they processed complex unimodal signals. None of the three performance measures we examined (proportion of correct responses, learning rate, and response time) differed significantly between unimodal and multimodal treatments. In other words, we found no evidence that multimodality *per se* was beneficial for receivers in this study.

We also observed a notable sensory bias in our subjects—subjects tended to prioritize color cues over sound cues. This trend was most apparent in the two treatments where sound and color were equally reliable - in these treatments, seven out of eight subjects followed color (the fixed component) at a higher rate than sound (the varied component). In the analogous unimodal treatments, preferences for following the forewing color (the fixed component) or hindwing color (the varied component) were much more evenly split. Two subjects did not follow sound at a higher rate than color in any treatment. The observed color preference in our subjects makes sense given avian sensory ecology. Birds have excellent color vision, and likely use visual cues more than acoustic cues when foraging and assessing aposematic signals (though acoustic aposematism is seen in several insect groups with avian predators—e.g., Masters 1979; Brown et al. 2007;

Fig. 3 Mean P(Correct) across subjects in each treatment. Error bars indicate standard error. This measure refers to the proportion of correct responses during stable signal following. A repeated measures ANOVA revealed a significant interaction between the reliability of the fixed component and the reliability of the varied component. There were no significant effects of modality or interactions involving modality

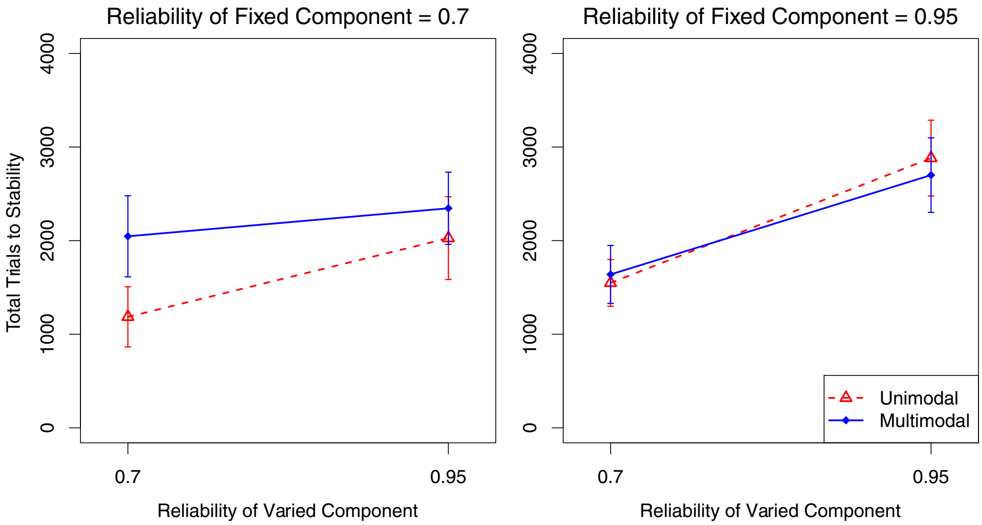


Bura et al. 2009). While an interesting side note, we do not believe that this bias affects our core results. Most birds followed sound at a higher rate than color in the treatment in which sound was the more reliable component. Importantly, we did not see decrements in performance in that treatment—if we had, we would have observed significant interactions between modality and the component reliabilities when analyzing the performance measures. This illustrates that while our subjects had a tendency to prioritize color cues, this bias was easily overcome. Furthermore, such minor biases are common across taxa and should not preclude the use of multimodal signals by receivers.

These results certainly do not rule out the hypothesis that multimodality can improve receiver processing; however, they call into question the generality of such an effect. If multimodality itself is broadly and inherently beneficial for receiver processing, we expect receivers to perform better when following multimodal stimuli, provided that receivers are able to perceive and follow cues in the tested modalities. We found no evidence for such an effect in this study. Of course, this experiment has tested only one species and two modalities—more work is needed testing a range of taxa on modalities appropriate to their sensory systems. It seems likely that some species will possess special adaptations to process certain categories of multimodal signals. A broad, phylogenetic approach is needed to determine how widespread such effects are and how they differ across taxa and sensory modalities. In addition, in order to test the hypothesis that enhanced multisensory processing selects for multimodal signals, we must verify that processing benefits (where they exist) precede multimodal signaling. Selection pressures arising from communication can shape sensory systems and cognitive pathways as well—a phylogenetic approach may also help distinguish between these alternatives.

As mentioned previously, our results are in agreement with economic predictions of stable signal use. For example, in a

Fig. 4 Mean number of trials to stability across subjects in each treatment. *Error bars* indicate standard error. A repeated measures ANOVA revealed a significant main effect of the reliability of the varied component. There were no significant effects of modality or interactions involving modality



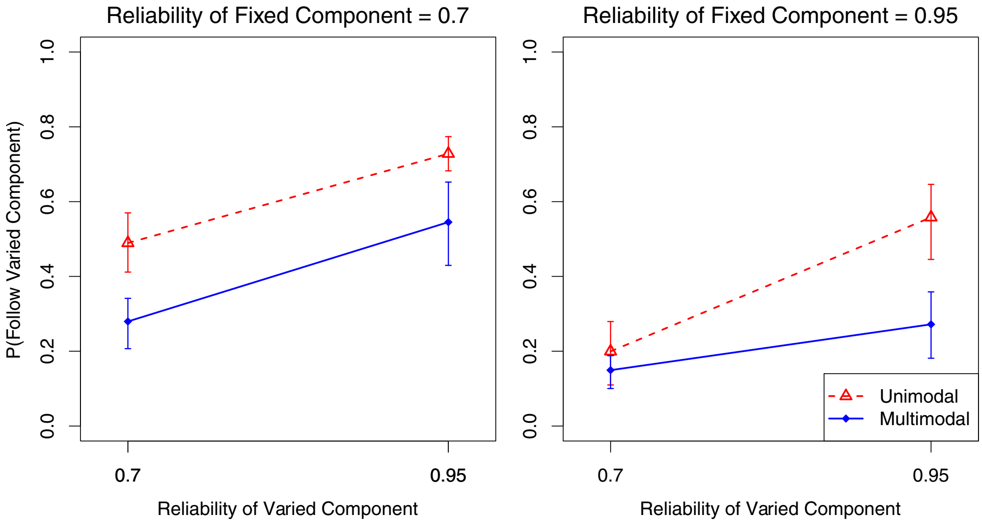


Fig. 5 Mean P(Follow Varied Component) across subjects. *Error bars* indicate standard error. This measure refers to the proportion of "Follow Varied Component" responses when the two stimuli disagree. Data are taken from a period of stable signal following. A repeated measures ANOVA revealed significant main effects of modality, the reliability of the fixed component, and the reliability of the varied component

recent paper Wilson et al. (2013) comprehensively demonstrated that, in the absence of further assumptions, it is not clear that a basic multimodal signal offers any advantage over a unimodal signal. This experiment supports this assertion (relatedly, Wilson et al. (2013) also find that, in many cases, multicomponent models (multimodal or unimodal) seem to offer no benefit over single component models, a conclusion supported by Rubi and Stephens (2015)). If multimodal signals offer no basic informational benefits over unimodal signals, why then are they so widespread in nature? Wilson et al. (2013) also outline a number of constraints on signaling systems that can make following multimodal signals a beneficial receiver strategy. We argue that these additional constraints may explain why multimodality is beneficial in many (and perhaps most) signaling systems.

A particularly compelling argument is that multimodal signals are better able to overcome environmental noise (Candolin 2003; Hebets and Papaj 2005; Wilson et al. 2013). For example, a vocalization is relatively unhindered by dense foliage, while bright plumage is unaffected by acoustic background noise. There is some empirical evidence for this hypothesis; for example, both humans (Ross et al. 2007) and macaques (Chandrasekaran et al. 2011) integrate mouth movements and vocalizations to improve performance on vocal communication tasks in noisy environments. Environmental noise is a ubiquitous problem in natural signaling systems—it is conceivable that this benefit alone could explain the prevalence of multimodal signals in nature. Another possibility is that the individual components of multimodal signals target different types of receivers. This argument is most compelling for aposematic signals with multiple receiver species that vary in sensory abilities (Andersson et al. 2002; Ratcliffe and Nydam 2008; Wilson et al. 2013). A comprehensive overview of the constraints that could favor multimodal signaling is outside the scope of this paper; however, for more information, we refer readers to the review in Wilson et al. (2013).

Concluding summary

In this experiment, we compared the performance of blue jays on a learned signal following task using two-component signals that were either unimodal (visual-visual) or multimodal (visual-acoustic). We found that, though receivers were able to follow signals in both the visual and acoustic modalities, they performed no differently when following unimodal versus multimodal signals. In other words, we found no evidence for the hypothesis that multimodality is inherently beneficial to receiver processing. Nevertheless, it is likely that some species will possess special adaptations for processing multisensory stimuli. Moving forward, a broad, phylogenetic approach is needed to determine how common such effects are, how they differ across taxa and sensory modalities, and whether such effects give rise to, or result from, multimodal communication.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval All housing and experimental procedures were approved by the University of Minnesota Institutional Animal Care and Use Committee (protocol #1109A04421).

References

Alvarado JC, Vaughan JW, Stanford TR, Stein BE (2007) Multisensory versus unisensory integration: contrasting modes in the superior colliculus. J Neurophysiol 97:3193–3205

Andersson S, Pryke SR, Ornborg J, Lawes MJ, Andersson M (2002) Multiple receivers, multiple ornaments, and a trade-off between agonistic and epigamic signaling in a widowbird. Am Nat 160:683–691

Brown SG, Boettner GH, Yack JE (2007) Clicking caterpillars: acoustic aposematism in Antheraea polyphemus and other Bombycoidea. J Exp Biol 210:993–1005

Bura VL, Fleming AJ, Yack JE (2009) What's the buzz? Ultrasonic and sonic warning signals in caterpillars of the great peacock moth (Saturnia pyri). Naturwissenschaften 96:713–718

Candolin U (2003) The use of multiple cues in mate choice. Biol Rev Camb Philos 78:575–595

Chandrasekaran C, Lemus L, Trubanova A, Gondan M, Ghazanfar AA (2011) Monkeys and humans share a common computation for face/voice integration. PLoS Comput Biol 7:e1002165

Cohen J (1988) Statistical power analysis for the behavioral sciences, 2nd edn. Erlbaum, Hillsdale, NJ

Cohen S, Stebbins W, Moody D (1978) Audibility thresholds of the Blue Jay. Auk 95:563–568

Faul F, Erdfelder E, Lang A-G, Buchner A (2007) G*Power 3: a flexible statistical power analysis program for the social, behavioral, and biomedical sciences. Behav Res Methods 39:175–191

Gingras G, Rowland BA, Stein BE (2009) The differing impact of multisensory and unisensory integration on behavior. J Neurosci 29: 4897–4902

Guilford T, Dawkins MS (1991) Receiver psychology and the evolution of animal signals. Anim Behav 42:1–14

Hauglund K, Hagen S, Lampe H (2006) Responses of domestic chicks (*Gallus gallus domesticus*) to multimodal aposematic signals. Behav Ecol 17:392–398

Hebets EA, Papaj DR (2005) Complex signal function: developing a framework of testable hypotheses. Behav Ecol Sociobiol 57:197–214

Higham JP, Hebets EA (2013) Multimodal communication [special issue]. Behav Ecol Sociobiol 67:1381–1539

Hughes M (1996) The function of concurrent signals: visual and chemical communication in snapping shrimp. Anim Behav 52:247–257

Kulahci IG, Dornhaus A, Papaj DR (2008) Multimodal signals enhance decision making in foraging bumble-bees. Proc R Soc London B 275:797–802

Masters WM (1979) Insect disturbance stridulation: its defensive role. Behav Ecol Sociobiol 5:187–200

Narins P, Grabul D (2005) Cross-modal integration in a dart-poison frog. P Natl Acad Sci USA 102:2425–2429

Partan SR (2013) Ten unanswered questions in multimodal communication. Behav Ecol Sociobiol 67:1523–1539

Partan S, Yelda S, Price V, Shimizu T (2005) Female pigeons, *Columba livia*, respond to multisensory audio/video playbacks of male courtship behaviour. Anim Behav 70:957–966

Pluta SR, Rowland BA, Stanford TR, Stein BE (2011) Alterations to multisensory and unisensory integration by stimulus competition. J Neurophysiol 106:3091–3101

Ratcliffe JM, Nydam ML (2008) Multimodal warning signals for a multiple predator world. Nature 455:96–99

R Core Team (2015) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, http://www.R-project.org/

Ross LA, Saint-Amour D, Leavitt VM, Javitt DC, Foxe JJ (2007) Do you see what I am saying? Exploring visual enhancement of speech comprehension in noisy environments. Cereb Cortex 17:1147–1153

Rowe C (1999) Receiver psychology and the evolution of multicomponent signals. Anim Behav 58:921–931

Rowe C, Halpin C (2013) Why are warning displays multimodal? Behav Ecol Sociobiol 67:1425–1439

Rubi TL, Stephens DW (2015) Should receivers follow multiple signal components? An economic perspective. Behav Ecol (published online, doi: 10.1093/beheco/arv121)

Siddall EC, Marples NM (2008) Better to be bimodal: the interaction of color and odor on learning and memory. Behav Ecol 19:425–432

Stynoski JL, Noble VR (2011) To beg or to freeze: multimodal sensory integration directs behavior in a tadpole. Behav Ecol Sociobiol 66: 191–199

Taylor RC, Ryan MJ (2013) Interactions of multisensory components perceptually rescue túngara frog mating signals. Science 341:273–274

Uetz GW, Roberts JA, Taylor PW (2009) Multimodal communication and mate choice in wolf spiders: female response to multimodal versus unimodal signals. Anim Behav 78:299–305

VanderSal ND, Hebets EA (2007) Cross-modal effects on learning: a seismic stimulus improves color discrimination learning in a jumping spider. J Exp Biol 210:3689–3695

Wilson AJ, Dean M, Higham JP (2013) A game theoretic approach to multimodal communication. Behav Ecol Sociobiol 67:1399–1415