

Interaction between visual and chemical cues in a *Liolaemus* lizard: a multimodal approach

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ABSTRACT

Multimodal communication involves the use of signals and cues across two or more sensory modalities. The genus *Liolaemus* (Iguania: Liolaemidae) offers a great potential for studies on the ecology and evolution of multimodal communication, including visual and chemical signals. In this study, we analyzed the response of male and female *Liolaemus pacha* to chemical, visual and combined (multimodal) stimuli. Using cue-isolation tests, we registered the number of tongue flicks and headbob displays from exposure to signals in each modality. Number of tongue flicks was greater when a chemical stimulus was presented alone than in the presence of visual or multimodal stimuli. In contrast, headbob displays were fewer in number with visual and chemical stimuli alone, but significantly higher in number when combined. Female signallers triggered significantly more tongue flicks than male signallers, suggesting that chemical cues are involved in sexual recognition. We did not find an inhibition between chemical and visual cues. On the contrary, we observed a dominance of the chemical modality, because when presented with visual stimuli, lizards also responded with more tongue flicks than headbob displays. The total response produced by multimodal stimuli was similar to that of the chemical stimuli alone, possibly suggesting non-redundancy. We discuss whether the visual component of a multimodal signal could attract attention at a distance, increasing the effectiveness of transmission and reception of the information in chemical cues.

1. Introduction

Complex animal interactions typically engage several sensory modalities simultaneously or in sequence (Candolin, 2003; Otovic and Partan, 2009; Smith and Evans, 2013). When animals communicate with each other by using signals from different sensory modalities, this interaction is referred to as multimodal communication (Hebets and Papaj, 2005; Partan and Marler, 2005). According to Smith and Evans (2013), the term “modality” is used to describe the sensory system with which a signal is produced by a signaller and perceived by a receiver. Multimodal communication can broadly involve the use of cues which have not been under selective pressures in their communicative function but evolve into signals by a process of ritualization (Bradbury and Vehrencamp, 2011; Ruxton and Schaefer, 2013).

Multimodal signals have been classified as redundant and non-redundant depending on whether they convey similar information (i.e., back-up signal) or different information (i.e., multiple-messages signal), respectively (Partan and Marler, 2005; Bro-Jørgensen, 2009). Components of a redundant signal provide the same information and produce

the same qualitative response in the receiver (e.g., Partan and Marler, 2005). When combined, the components might elicit an equivalent response, or an enhanced response, in terms of frequency (see Partan, 2013). However, components of non-redundant signals carry different information and generate different responses in the receiver when combined (Partan and Marler, 2005). Non-redundant signals can provoke the same responses when combined (independence), one signal can overshadow (dominance) or modify (modulation) the effect of the other, or a new response can emerge (emergence, more information in Partan and Marler, 2005). For example, male wolf spiders (*Schizocosa* sp.) court females using seismic and visual signals (Uetz and Roberts, 2002). Female *Schizocosa uetzi* were more receptive to seismic signals than to visual signals (non-redundant: dominance; Hebets, 2008), whereas *Schizocosa stridulans* females responded equally to signals of both modalities (redundant; Hebets and Uetz, 2000; Hebets, 2005).

Besides the information content of multimodal signals, Hebets and Papaj (2005) have proposed several testable predictions about why and how complex signals evolved. They also proposed the efficacy-driven hypothesis, which addresses how signals travel through the

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environment and are received by the receiver, and the inter-signal interaction hypothesis, suggesting that the presence of one signal or signal element alters the perception of a second signal or signal element. For example, the visual and acoustic aggressive signals of dart-poison frogs elicit a response only when there is considerable overlap in both time and space between the triggers of both sensory modalities (Narins et al., 2003). Moreover, one signal can increase the probability of detection and/or discrimination of a second signal, making it more conspicuous by acting as an amplifier. Movement can increase the detectability of visual traits (Fleishman, 2000) and ornamental colours can amplify other colours (Candolin, 2003).

In the last few years, studies of complex signaling across different taxa (e.g. arthropods, anurans, lizards, fish, and birds) have increased (see Hebets, 2011). The *Liolaemus* genus, with more than 250 Neotropical lizard species (Iguania: Liolaemidae; Abdala and Quinteros, 2014), offers great potential to study multimodal communication. *Liolaemus* lizards show a great diversity of forms in size, reproduction, diet, behavioural displays and colour patterns, which could be influenced by their habitat or their phylogenetic history. Most studies on *Liolaemus* communication have focused on visual displays (Halloy, 1996, 2012; Halloy and Castillo, 2006; Labra et al., 2007; Vicente and Halloy, 2015) or chemical exploration (Labra, 2008, 2011). Just a few, however, have explored the interaction between modalities (e.g., Fox and Shipman, 2003; Martins et al., 2004). This is the first study that evaluates a *Liolaemus* lizards response to multimodal stimuli. Here we report the responses of *Liolaemus pacha* lizards exposed to chemical, visual and multimodal (combined) stimuli.

Fox and Shipman (2003) found that several *Liolaemus* species with a less aggressive display rely more on chemical cues, whereas those with more active aggressive behaviour (e.g., chase, bite, push-up, lick, lateral displays) are more visually oriented. In *Sceloporus* lizards, an inhibition between chemical and visual signals (Ossip-Klein et al., 2013), between aggressive displays (postures and colour patches) and chemical behaviour (e.g. Hews and Benard, 2001; Hews et al., 2011), and between colour patches and headbob displays (Baastians et al. 2013; Martins et al., 2015) has been suggested. This trade-off implies that when a signal is reduced or lost, or a modality absent, lizards may rely on another signal or modality. Considering that *Liolaemus* and *Sceloporus* lizards are morphologically and ecologically similar and have been regarded as examples of evolutionary convergence, we may expect to find an inhibition between both sensory modalities (e.g., Martins et al., 2004; Thompson et al., 2008; Ossip-Klein et al., 2013). Thus, our first hypothesis is that chemical cues inhibit a visual response and vice versa. This means that when the chemical modality is not being used, the visual response (e.g., number of headbob displays) increases. On the other hand, when the visual modality is not being used, the chemical response increases. We also proposed a second hypothesis for the response with a combined stimulus: chemical and visual signals combined trigger the same qualitative response (i.e., headbob displays and tongue flicks), being redundant. Our results would help to understand the role of different kinds of signals used by *Liolaemus* lizards, as well as by other lizard species, in different contexts such as courtship, reproduction, sexual selection, territoriality, etc.

2. Materials and methods

Liolaemus pacha is an oviparous and insectivorous lizard with sexual dichromatism. Males are more colourful, showing a dorsolateral pattern of yellow, reddish and light-blue spots, whereas females are brownish and cryptic (see Juárez Heredia et al., 2013). Both males and females have a white ventral coloration. During the reproductive season occurring during the austral spring (October to December; Ramírez Pinilla, 1992), males establish their territories (Halloy and Robles, 2002), patrolling the surroundings, actively defending these by displaying, chasing and even attacking other males (Halloy, 2012; Vicente and Halloy, 2015). *L. pacha* is found at Los Cardones, northwestern

Argentina, located 20 km east of the town of Amaicha del Valle (26°40'1.5" S, 65°49'5.1" W; 2725 m), in the province of Tucumán (Juárez Heredia et al., 2013). The site is located on the western slope of the Sierras Calchaquías and corresponds to the phytogeographic region of Prepuna (Cabrera and Willink, 1980). It is characterized by a semi-arid climate and by the presence of tall cacti (*Trichocereus terscheckii*), scattered shrubs and large rocks.

We captured 10 female and 10 male adults by noose (16–20 October 2013). Upon capture, the lizards were kept in individual cloth bags and taken to the Animal Behaviour Institute (Fundación Miguel Lillo, Tucumán, three hours by car), where they were exposed to ambient temperatures (20–35 °C) and the natural photoperiod (13L:11D). Lizards were housed individually in plastic terraria (Exo-Terra Faunarium, 37 cm × 22 cm × 25 cm), covered with a plastic mesh and with a synthetic leather fabric as a substrate. Each terrarium had a rock for basking and shelter. The terraria were located on shelves and visually isolated from one another with cardboard. Because sun rays did not reach the terraria directly, UV fluorescent linear light bulbs (i.e. “daylight” tubes; Sylvania Reptistar T8) were placed over the enclosures for three hours each day. There was a bowl of water permanently available in each terrarium and mealworms (*Tenebrio molitor*) were given every couple of days. Lizards were held in their enclosures for at least five days, without being disturbed, before testing started. The experiments lasted less than a month, and once they were over, all lizards were returned and released where they had been captured.

Three types of experiments were carried out in which we compared lizard responses (20 lizards, 120 trials) when exposed first to chemical stimuli, then to visual stimuli and finally to multimodal stimuli. Initially, we tested the chemical modality, using the enclosure of another conspecific lizard as a source for chemical stimuli. Each lizard was removed from its own enclosure and was placed at random in a terrarium previously occupied by a different male or female lizard. Subsequently, we tested individual responses to visual stimuli, also presented in random order with respect to stimulus sex. In this experiment, each lizard was kept in its home enclosure. Lizards could see but not smell each other because we switched the plastic mesh for a hermetic cover. Finally, to evaluate responses to multimodal stimuli, we introduced at random two lizards in a neutral (i.e., clean and stimulus-free) glass arena (70 cm × 35 cm × 35 cm). Here, lizards were free to move around, see, approach and contact the other lizard, as well as detect chemical scents. After each trial in the enclosure and the neutral arena, we cleaned walls and floor by wiping these with alcohol (70%).

All individuals ($N = 20$) were used as scent donors or signallers, but also as receivers. Thus, all lizards were tested six times each (three trials with male stimuli and three trials with female stimuli) and used six times as a stimulus. However, each individual was used only once a day to minimize stress. All trials took place between 10:00 and 17:00 h, during the lizards' usual activity period and when ambient temperature ranged from 28 to 33 °C. All tests were recorded with a digital camcorder (Sony HDR Cx-290) placed at 50 cm from the terraria, for 30 min. Based on preliminary testing, we observed that lizards generally started tongue-flicking within the first 15 min. We filmed lizards for 30 min so that we had 10 min of behaviour following the initial tongue-flick. Recordings were viewed post-trial to avoid disturbing the lizards. Ten trials that did not reach the 10-min-recording criterion were excluded from the analyses. Prior to all trials, lizards were placed under a dark cover for one minute to minimize stress produced by handling, after which the observer slowly removed the cover and started recording. When finished, the lizard was returned to its own enclosure and kept undisturbed until the next trial on the following day.

We recorded the same variables in all three types of experiments: number of tongue flicks, as a measure of chemical exploration, and the number of headbob displays, as a measure of visual response. All frequencies were recorded as behaviour counts beginning after the first behavioural display and over the next 10 min. We compared the variables between the sensory modalities (chemical, visual and combined),

the sex of the signaller (male or female) and the sex of the receiver (male or female). We performed generalized linear mixed models (GLMMs) with the free software R (v. 3.2.0; R Core Team, 2015), because of the repeated measures design. The sensory modality, the sex of the receiver and the sex of the signaller were fixed effects, whereas the individual identity of the lizard subject was considered a random effect. Repeated measures taken from the same focal individual are a common source of pseudoreplication. It is necessary to take this into account to avoid violating one of the fundamental assumptions of statistical models, which is the independence of errors. Because our data, using a Poisson distribution, were overdispersed (i.e., variance larger than the mean; Zuur et al., 2009) and our variables were counts, we changed our models to a binomial negative distribution with log-link function, using the glmmADMB package (Fournier et al., 2012; Skaug et al., 2014). All variables and the interactions among them were initially included in the models. We then fitted our models, dropping the non-significant variables ($P > 0.05$), until the final models contained only significant terms (Zuur et al., 2009). Significant variables were considered to be those explaining the variation in the response variable (Zuur et al., 2009). We applied Bonferroni's correction for multiple comparisons between treatment levels, using the R package multcomp. All tests were two-tailed and differences were considered significant at $P \leq 0.05$. Values are reported as $\bar{X} \pm SE$.

3. Results

The best model explaining the variation in the number of tongue flicks included the sensory modality and the sex of the signaller as explanatory variables ($P \leq 0.05$; Table 1). Neither the sex of the receiver nor the interactions among variables were significant ($P > 0.05$). Tongue flicks decreased when lizards were exposed to signals in both modalities (15.17 ± 2.22 ; Figs. 1 and 2) instead of only the visual (19.61 ± 2.17) or chemical modality (25.39 ± 3.05). These differences were only significant between multimodal and chemical modalities (Tukey test: $z = -3.61$, $P < 0.001$). The visual modality did not differ from the chemical modality (Tukey test: $z = -1.30$, $P > 0.05$) nor from both signals combined (Tukey test: -1.63 , $P > 0.05$). Overall, the male signaller triggered significantly fewer tongue flicks (17.85 ± 1.93) than the female signaller (22.38 ± 2.27 ; $P \leq 0.01$; Fig. 3).

The best model explaining the variation of headbob displays was determined by modality and the sex of the receiver ($P \leq 0.05$; Table 1). The sex of the receiver showed a trend to influence the number of headbob displays, although it did not quite achieve significance

Table 1

Parameter estimates ($\pm SE$), 95% confidence interval limits (CL) and P value for explanatory variables describing variation in the number of tongue flicks and headbob displays of *Liolaemus pacha* in fitted models. All parameter estimates represent expected differences among modality, sex of signaller and sex of receiver, with respect to reference values: chemical modality, female signaller and female receiver. See the text (Section 1) for details.

Response variable	Explanatory variable	Estimates $\pm SE$	CL		P value
			Lower	Upper	
Tongue flicks	Intercept	3.27 ± 0.14	2.98	3.55	***
	Modality (visual)	-0.19 ± 0.14	-0.47	0.09	NS
	Modality (both)	-0.53 ± 0.15	-0.81	-0.24	***
	Signaller (male)	-0.27 ± 0.12	-0.50	-0.04	*
Headbob displays	Intercept	0.85 ± 0.56	-0.25	1.96	NS
	Modality (visual)	-0.63 ± 0.52	-1.66	0.40	NS
	Modality (both)	1.58 ± 0.57	0.45	2.70	**
	Receiver (male)	1.12 ± 0.61	-0.07	2.31	NS

NS, $P > 0.05$.

* $P \leq 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

($P = 0.06$; Table 1; Fig. 3). Neither the sex of the signaller nor the interactions among variables were significant ($P > 0.05$). Headbob displays showed a significant increase when multimodal stimuli were present (19.94 ± 4.69 ; Figs. 1 and 2), compared to chemical cues (8.66 ± 3.30 , Tukey test: $z = 2.76$, $P = 0.02$) or visual signals (4.33 ± 1.88 , Tukey test: $z = 3.03$, $P = 0.007$). There were no differences between chemical and visual modalities (Tukey test: $z = -1.20$, $P > 0.05$). Male signallers performed more visual displays than female signallers, though the difference did not quite achieve significance (males: 16.02 ± 3.99 ; females: 6.40 ± 1.50 ; $P = 0.06$).

4. Discussion

We found that when *L. pacha* lizards were exposed to either chemical or visual stimuli alone, the number of tongue flicks was greater than the number of headbob displays, whereas lizards responded to combined stimuli with more headbob displays (Fig. 1). Our results reject our hypothesis of an inhibition between chemical and visual cues because we did not find a greater number of headbob displays with the visual stimulus alone. Thompson et al. (2008) found an inhibitory effect in the lizard *Sceloporus graciosus*, showing that exposure to a chemical stimulus decreased the number of headbob displays and exposure to a visual stimulus decreased chemical exploratory behaviour. In contrast, we observed a dominance of the chemical modality, because, with the visual modality alone, lizards also responded with more tongue flicks than with visual displays. Our results suggest that visual and chemical signals in *L. pacha* might be non-redundant. Multiple messages provide the benefit of transferring different types of information, for example, different aspects of the signaller's quality, species identity and dynamic and fixed information (Hebets and Papaj, 2005). The dominance of the chemical modality would influence the behavioural ecology of *Liolaemus* lizards in different ways. Chemical cues are not only cheaper to produce than visual signals (Wyatt, 2003) but may also be more informative (e.g., López and Martín, 2001, 2012). The use of the chemical channel would reduce the risk of detection by eavesdroppers, such as visual predators, and thus it would increase survivorship (Partan and Marler, 2005). Therefore, *L. pacha* lizards might take advantage of using chemical cues to communicate. The presence of chemical cues alone or in combination with a visual stimulus triggered the same qualitative response (i.e., tongue flicks and headbob displays) of almost the same frequency, whereas with only a visual stimulus the total response decreased (see Fig. 2). Moreover, the response elicited by multimodal stimuli was mainly visual, showing an increase of headbob displays. These results indicate that visual stimuli alone may be less informative than chemical stimuli because the overall response decreased in comparison to the response to the chemical signal alone. Also, lizards flicked their tongues more often when given a visual stimulus only than when given a visual and chemical stimulus combined, suggesting that lizards are making an attempt to gather more information. When visual and chemical stimuli are combined, it might take less time, and probably less energy, to get an idea of the other individual's intentions.

The dominance of one sensory modality has been found in other animal groups as well. For example, in the spider *Schizocosa stridulans*, seismic signals dominate over visual signals in the courting male (Hebets, 2008). In the hermit crab, individual recognition is regulated by chemical more than by visual signals (Gherardi and Tiedemann, 2004). Finally, in the dart frog, *Epipedobates femoralis*, aggression between males responds more to the visual signal of the vocal sac than to the acoustic signal (Narins et al., 2003).

The sex of the signaller had a significant effect on the number of tongue flicks, with female stimuli being more explored than male stimuli (Table 1; Fig. 3). Lizards may gather information on the sex of the conspecific, showing a preference for certain chemical scents, in this case, female scents. Our results agree with previous studies on other *Liolaemus* lizards (e.g., Labra, 2008) and on this species (Vicente and

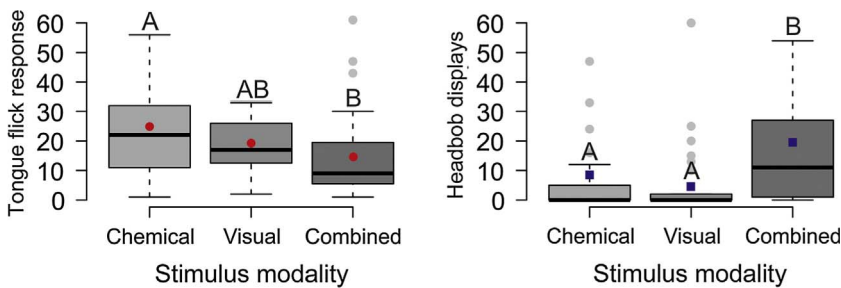


Fig. 1. Variation in the receiver response of male ($N = 10$) and female ($N = 10$) *L. pacha* lizards to chemical, visual and combined stimuli. Left: number of tongue flicks, right: number of headbob displays, with medians, means (left: circles; right: squares), quartiles, and grey dots representing outliers. Means with the same letter are not significantly different ($P > 0.05$).

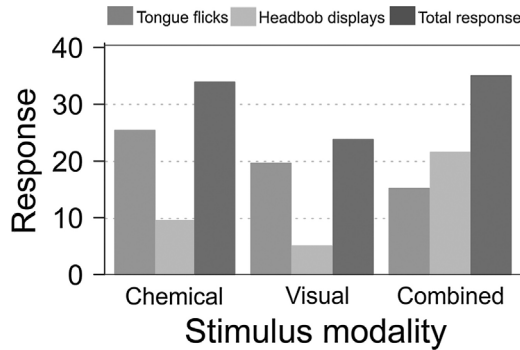


Fig. 2. Mean number of behavioural responses (tongue flicks, headbob displays and sum of tongue flicks and headbob displays) of male ($N = 10$) and female ($N = 10$) *L. pacha* lizards to chemical, visual and combined stimuli.

Halloy, 2016), where the authors found sexual recognition based on chemical cues. Based on chemical cues, lizards can explore, among other traits, the sex of a conspecific (López and Martín, 2001; Cooper and Pérez-Mellado 2002), the species (Labra, 2011), as well as fighting capabilities (Carazo et al., 2007) and reproductive quality (López and Martín, 2005).

Our results offer a line of future investigations dealing with the inter-signal interaction hypotheses suggested by Hebets and Papaj (2005) according to which a signal alters either the production of a second signal or a receiver’s response to a second signal. We may speculate that visual signals in *L. pacha*, such as headbob displays, attract the attention of a potential receiver and show the signaller’s location (i.e. “alerting” sensu Hebets and Papaj, 2005). Once detected, the receiver could reinforce the information about the signaller with chemical cues (e.g., Carazo et al., 2008). Candolin (2003) suggested that some cues may increase detection at a distance whereas others may reflect quality at closer range. López and Martín (2001) found males of Iberian wall lizards, *Podarcis hispanica*, to pay attention to female coloration at long range, whereas chemical cues seemed to be more

important at close range. Moreover, we cannot disregard the role that colour signals and other visual signals, such as forelimb waves, lateral compression, and tail waves, could have in lizard communication. For this reason, future studies should include the full spectrum of visual signals, in order to allow for a better interpretation of the whole process.

The present study represents an important step in understanding the relative roles of two different types of sensory cues in an evolving exchange of information between both sexes. Males might assess females as potential mates and perhaps evaluate their reproductive condition and, since females show aggression to other females in their own home range (Halloy and Robles, 2002), chemical cues are probably involved in recognition. More studies are needed to evaluate the information content of each signal, assessing how different contexts (courtship, mate choice, male–male competition) may influence the interaction between these signals.

5. Conclusions

To conclude, we did not find an inhibition between chemical and visual signals in *Liolaemus pacha* lizards. With unimodal stimuli (i.e., chemical or visual alone) the response was dominated by tongue flicks, whereas with multimodal stimuli (i.e., chemical and visual combined), headbob displays increased significantly. Our results show a dominance of the chemical modality, suggesting that in *L. pacha* visual and chemical signals might be non-redundant. This is the first study assessing a *Liolaemus* lizard’s response to multimodal stimuli, so future studies should deal with a full spectrum of visual signals, such as colouration and other behaviours (e.g., forelimb wave displays, tail waves, lateral compression).

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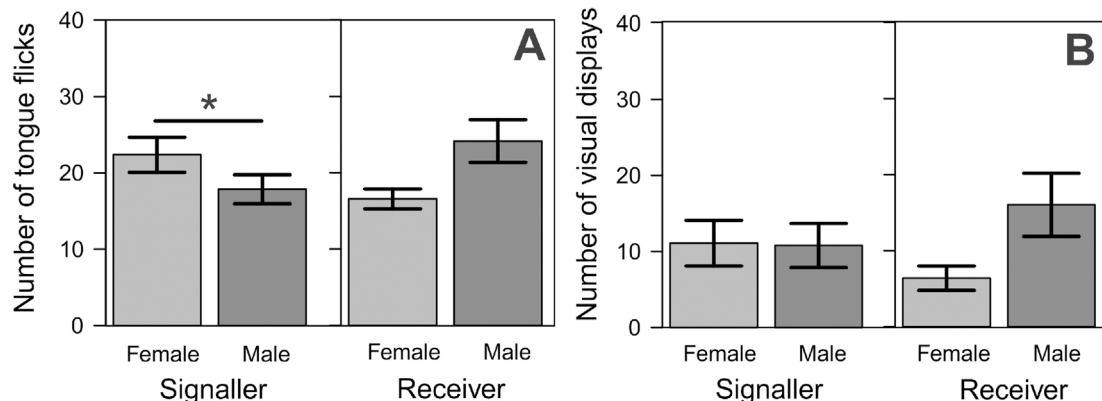


Fig. 3. Variation (means \pm SE) in the number of (A) tongue flicks and (B) headbob displays between signallers and receivers of *L. pacha* lizards. Asterisk indicates a significant difference ($P \leq 0.05$).

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