



# Inhibitory interactions between multimodal behavioural responses may influence the evolution of complex signals

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(Received 28 July 2007; initial acceptance 26 September 2007;  
final acceptance 27 December 2007; published online 1 May 2008; MS. number: A10825R)

Most animal displays make use of multiple sensory modalities (visual, acoustic and chemical signals) to convey similar information. Although multimodal displays may allow producers to use displays in a wider variety of social and physical contexts, it is difficult to explain their evolution because of the likely increased costs to senders and receivers. In this study, playback experiments in two contexts were used to study the behavioural responses to visual (headbob displays) and chemical (femoral pore secretions) signals in sagebrush lizards, *Sceloporus graciosus*. Lizards in the field tended to headbob in response to headbob displays and to engage in chemical exploratory behaviour when presented with chemical secretions. Territorial residents produced fewer headbob displays and head-turns in response to a combined signal produced by a robotic lizard than they did to either signal presented alone. This inhibition was confirmed in the laboratory, where presentation of a visual stimulus alone decreased chemical exploratory behaviour and presentation of a chemical stimulus alone decreased the number of headbob displays produced. The absolute cost of this interaction between sensory modalities may be low because the two behavioural responses are redundant, both allowing the receiver to acquire additional information, either by engaging a second lizard in a bout of interactive visual displays or by absorbing more of their scent. Thus, in sagebrush lizards, multiple signals may be evolutionarily maintained because behavioural responses to different sensory modalities are redundant and, hence, the cost of negative interactions between those responses is low.

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**Keywords:** behaviour; behavioural evolution; chemical communication; multimodal signal communication; pheromone; sagebrush lizard; *Sceloporus graciosus*; visual communication

Many animals use multiple structurally distinct signals, often involving multiple sensory modalities, to convey similar information. Evolutionary theoreticians have outlined conditions under which multiple communicative signals are likely to evolve. First, multiple signals conveying similar information (i.e. redundant signals) are most likely to persist over evolutionary time when they convey slightly different information (e.g. different aspects of male quality; Johnstone 1996; van Doorn & Weissing

2004) between sender and receiver. Thus, multiple signals may be found when the same display is used by senders in multiple behavioural contexts (e.g. aggression and courtship; Andersson et al. 2002; Martins et al. 2005). Multiple signals may also be evolutionarily designed to trigger receivers with different sensory preferences (Kodric-Brown & Nicoletto 2001; Patricelli et al. 2003) or to function well in multiple physical contexts (Hebets 2005; Taylor et al. 2005). Second, multiple signals are evolutionarily stable when the costs of producing or perceiving multiple signals are low (Iwasa & Pomiankowski 1995). For example, multiple signals may be the result of different males pursuing different strategies, with each creating only one type of signal (Johnstone 1996; Cummings et al. 2006). Elias et al. (2006) found that constraints on the production of multiple signal components also depend on whether the components are produced by the same

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physical structures at the same time. Similar constraints are possible in the physical structures used to perceive animal signals. Here, we used playback experiments with sagebrush lizards, *Sceloporus graciosus*, to test for interactions between the specific behavioural responses elicited by signal components in different sensory modalities that may also influence the cost of multimodal display perception.

Partan & Marler (2005) emphasized the information content of multimodal signals, and the distinction between redundant versus nonredundant signals. Males of many species use multiple signal components to convey information about different aspects of their physiological and genetic quality. For example, different elements of cricket song (Scheuber et al. 2003), cardinal plumage colour (Jawor & Breitwisch 2004), house finch plumage colour (Badyaev et al. 2001) and peacock displays (Loyau et al. 2005) contain information about different aspects of male quality. Other species use some signal components to attract receiver attention and other signal components to convey their message (McLennan 2003; Diaz & Thiel 2004; Hebets 2005). Many insect groups combine aposematic coloration (visual) with odours (chemical), rattles and clicks (acoustic) in signals to attract the attention of potential predators (Rowe & Guilford 1996; Lindström et al. 2001), and snapping shrimp (Hughes 1996) convey more complex information on body size and sex by combining visual and chemical cues. Thus, Hebets & Papaj (2005) encouraged researchers to consider proximate reasons for multiple displays, including 'efficacy-driven' (i.e. multiple receiver sensory systems or physical habitats).

Hebets & Papaj (2005) also emphasized the potential importance of explanations involving 'intersignal interaction', in which the presence of one signal or signal element alters the perception of a second. For example, the visual and acoustic aggressive signals of dart-poison frogs (Narins et al. 2003, 2005) elicit a response only when there is considerable overlap in both time and space between the triggers of both sensory modalities. In guppies, static and dynamic aspects of a visual signal interact such that female guppies prefer brightly coloured males when male display rate is low, but they show no preference for orange when males display at a high rate (Kodric-Brown & Nicoletto 2001). Similarly, the presence of sound can improve visual discrimination learning in chickens (Rowe 2002). Visual and chemical signals are combined by hawkmoths, which can learn to distinguish two odours when they are presented on yellow flowers, but not on blue flowers (Balkenius & Kelber 2006). Similarly, chicken predators show a bias against conspicuous food items, but only when those items are presented with pyrazine odour (Lindström et al. 2001). Such interactions between signals may change the costs and benefits of signal perception in complex ways, potentially facilitating the long-term persistence of multiple signals. Behavioural responses may also interfere with each other, with the response to one signal precluding, constraining or facilitating the response to a second. For example, an animal may not be able to sing and produce a visual display in response to a call.

Although most research on lizard communication has focused on the use of visual headbob displays

(Carpenter & Ferguson 1977; Ord & Martins 2006), many lizards from a variety of genera in the well-studied Iguania group also use chemical signals, secreting substances from femoral or cloacal pores (Alberts et al. 1993; Labra et al. 2003; Martins et al. 2006). Lizard visual and chemical signals are likely to interact on behavioural, ecological and evolutionary scales because they serve similar functions and are produced in similar contexts. In general, Iguanian lizards move about their territorial boundaries, producing headbob displays and/or depositing chemical secretions at preferred perches (Carpenter & Ferguson 1977). Although headbob displays are thought to function in territorial defence, courtship (Martins 1993; Decourcy & Jenssen 1994) and sometimes antipredator behaviour (Leal 1999), the details of headbob display structure are extremely variable (Martins 1991, 1994) and seem to have evolved primarily in response to selective pressure for increasing diversification to allow for individual, sex, population and species recognition (Jenssen 1977; Carpenter 1978; Ord et al. 2001; Kelso 2006). Iguanian chemical signals are similarly diverse (Alberts 1991; Escobar et al. 2001), and preliminary studies show that they are used in territorial behaviour and in a variety of recognition contexts (e.g. sex, mate, kin and species recognition; Alberts & Werner 1993; Labra et al. 2001, 2003).

Although there are no obvious temporal relationships between production of visual and chemical signals (Martins et al. 2006), the frequency of visual displays and the quantity of chemical secretions are both associated with steroid hormone levels (Alberts et al. 1994; Moore et al. 1998); therefore, a common endocrine mechanism may affect both types of communicative signals. Lizards are likely to perceive the headbob displays and chemical deposits of near neighbours repeatedly throughout the day, both separately (the receiver sees a broadcast display from a distance or tongue-flicks a chemical deposit laid earlier in the day) and together (when the two animals engage in a close interaction). When sagebrush lizards direct headbob displays towards particular conspecifics, the display is produced at relatively short distances (<10 cm; Martins 1994), a distance at which chemical cues are also likely to be transferred. Moreover, because signal perception is often not a passive behaviour, but instead requires that the receiver move closer to a stimulus, alter body posture, or engage in other behaviour that permits continued reception of the signal; these behavioural responses may alter the receiver's response to subsequent signals.

In this paper, we describe two experiments testing the behavioural response of sagebrush lizards to visual and chemical signals, alone and in combination. First, we measured the response of territory holders in their natural environment to signals produced by a robotic playback system. We then confirmed our results in a very different laboratory context, placing subjects in a novel arena and testing their response to visual and chemical stimuli created using a mirror image. In each experiment, we compared differences in the behavioural responses produced when communicative stimuli were presented alone and/or in combination.

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