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Editorial

Current Status and Future Directions of Research in Complex Signaling

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1 Introduction

The term ‘complex signaling’ reflects a recent scientific focus on the multiple elements frequently incorporated into animal signals (reviewed in Candolin, 2003; Hebets and Papaj, 2005; Partan and Marler, 2005; Bro-Jorgensen, 2010). It embodies a new appreciation that signals used in communication are regularly composed of numerous components and that each component may individually vary in a number of ways. For example, signal components may vary in their time or mechanism of production, in the efficacy of their transmission, and/or in their mechanism of reception, among others. Employing the term ‘complex signaling’ reminds us of the need to maintain a broad, inclusive view of the dynamic, interactive nature of communication when trying to understand its evolutionary history and current function.

1.1 Modality-specific terminology: Are the terms constraining the science?

Prior to delving into the current and future state of complex signaling research, I briefly discuss the modality-specific terminology prevalent in recent literature, acknowledging that I myself am responsible for promoting such terminology (e.g., “multimodal signal”, see Hebets and Papaj, 2005). Ultimately, I argue here that while modality-specific terminology certainly has a place, researchers need to be aware of the potential limitations the terminology places on our global understanding of the evolution and function of communication.

Initially, it makes intuitive sense to lump signals into categories based upon their physical properties. Sound, for example, is produced by a local concentration of molecules that moves through a medium and may consist of longitudinal waves or both transverse and longitudinal waves (Bradbury and Vehrencamp, 1998). We can measure specific properties of the waveforms (e.g., frequency or amplitude), and quantify the speed of

sound and the acoustic impedance associated with different media. Our knowledge of the science of sound is both comprehensive and detailed (Rossing, 1982), as it is for most other signal modalities (e.g., light, chemical, electric; Bradbury and Vehrencamp, 1998). These modalities, however, are defined solely upon the physical properties of the signal itself, irrespective of how the signal is produced and/or received or processed. Yet different animals have evolved distinct mechanisms for both producing and receiving signals in different sensory modalities. From a signaler or receiver’s point of view then, are signals that are produced and/or received by vastly different underlying mechanisms/structures, comparable? Is it still useful to lump signal components based solely upon their physical properties?

To elaborate, while both taste (gustation or contact chemoreception in arthropods) and smell (olfaction) involve stimulation by chemicals, smell typically refers to detection of chemical compounds in a gaseous state while taste typically refers to detection of chemical compounds in solution. In insects, olfactory sensilla (hairs) and contact chemosensory sensilla are structurally distinct (for details see Chapman, 1998), and their central nervous system processing is independent and dissimilar. Axons from olfactory receptors terminate in the brain antennal lobes, while axons from contact chemoreceptors terminate in the ganglion of the associated body segment (Chapman, 1998). From a receiver’s perspective, receiving and processing an olfactory and a contact chemosensory signal are quite separate, potentially as distinct as receiving and processing a visual and acoustic signal. As such, should we term complex signals composed of both gaseous chemicals and those in solution multimodal or unimodal? Certainly, failing to classify such a complex signal as multimodal could lead one to disregard potentially relevant hypotheses of complex signal function. For example, an olfactory/contact chemosensory signal could have evolved

through selection for ‘parallel processing’ or ‘sensory overload’ (see Hebets and Papaj, 2005). Furthermore, while we currently possess the knowledge to classify olfactory and gustatory components as separate in terms of their mechanisms of reception and processing, there could be cryptic receiver mechanisms in existence that have yet to be identified.

The potentially constraining nature of modality-specific terminology and categorization is highlighted here to reinforce the fact that to truly understand complex signaling, we must obtain detailed information on signal production and reception without being constrained by our categorization of signals into specific modalities. This is not to say that modality-specific terminology has no place, just that we must be aware of its potential limitations. Modality-specific categorization is relevant for understanding how selection for signal transmission, for example, has influenced complex signal form; it is arguably less useful, however, for understanding how sources of selection on signalers and/or receivers have influenced the evolution of complex signaling. Such a limited focus, as promoted by modality-specific terminology, could surely restrict, and even misdirect, our science.

2 Current Research in Complex Signaling

This special issue highlights a small sample of some of the pioneering work being conducted in the area of complex signal function and evolution. The contributions were chosen to highlight important approaches and/or conceptual frameworks for studying complex signaling. It is comprised of eleven manuscripts, including both reviews and empirical studies, encompassing a wide range of animal, and plant, taxa (e.g., arthropods, anurans, lizards, fish, and birds). The goal of this issue is to summarize the current state of the field, to highlight common techniques used to study complex signaling, to spark new research and ideas, and to explore fruitful future research directions. I begin my summary of the contributions with an overview of its organization.

Operationally, communication can be thought of as the culmination of a series of modular events: (i) a signaler produces a signal that is (ii) transmitted through the environment and finally (iii) received and processed by the receiver, ultimately affecting the receiver’s behavior. Given the modularity inherent in such a simple signaler-receiver paradigm, approaches to understanding complex signaling often reflect this modularity, with

studies focused upon (i) signal production and form, (ii) signal transmission and the signaling environment, and (iii) signal reception and receiver psychology (sensu Rowe, 1999). In summarizing the content of this special issue, I will use this modular approach.

2.1 Signal production and form

Research focused on signal production and form typically reflects an interest in the potential content of signal components – in the message(s) conveyed. Such research seeks to understand how selection for signal content has influenced signal form and function. In exploring hypotheses of signal content, numerous approaches have been employed. For example, content-based hypotheses of complex signal function (e.g., multiple messages versus redundant signals; Møller and Pomiankowski, 1993; Johnstone, 1996) make specific predictions about the patterns of co-variation among signal components. These patterns can be tested by quantifying individual components and analyzing their degree of covariance (Hebets and Papaj, 2005). Such an approach was taken by Gumm and Mendelson (2011) in their comprehensive analysis of nuptial color variation across 17 species of darters in the genus *Etheostoma*. The authors find that darter coloration is evolutionarily labile and their observed patterns of color evolution across body segments support the hypothesis that different signal components have been subject to different evolutionary pressures (Gumm and Mendelson, 2011).

Another approach used to gain insight into potential signal content involves manipulating signals and/or signalers and assessing receiver response and/or signal form. For example, robotic animals, or artificial flowers, can be invaluable tools for exploring the putative information content of signal components. Multiple contributions in this Special Issue employ the use of animal robots and other artificial devices to examine complex signal function (artificial flowers (‘flobots’ sensu Papaj, personal communication): Leonard et al., 2011; robotic lizards: Partan et al., 2011; robotic frogs: Taylor et al., 2011; flobots: Vergara et al., 2011). Additionally, researchers often directly manipulate signaler quality and assess the corresponding variation in signal form. Wilgers and Hebets (2011) use this technique to test the condition-dependence of the visual and seismic courtship components of a wolf spider. They find both components to be condition-dependent and suggest that these two signals may convey redundant information (Møller and Pomiankowski, 1993; Johnstone, 1996; Partan and Marler, 1999). Interestingly, in the contribu-

tion by Taylor et al. (2011), the authors engage in a thought-provoking discussion of the potential shortcomings of the frequently employed classification system of redundant versus non-redundant information (e.g., Partan and Marler, 1999; Partan and Marler, 2005).

A final approach employed by Clark (2011) in his study of the Calliope hummingbird *Stellula calliope* involves exploring the mechanism(s) of signal component production. Through a series of manipulations, the author demonstrates that male courtship displays consist of three acoustic components, each with an independent production mechanism (Clark, 2011). While female responses to individual or combined components are not assessed in this study, knowledge of signal production mechanisms enables one to form hypotheses regarding signal function. For example, due to their independent production mechanisms, Clark (2011) suggests that each component may convey different information (e.g., multiple messages; Møller and Pomiankowski, 1993; Johnstone, 1996).

2.2 Signal transmission and the signaling environment

As discussed previously, modality-specific distinctions are important with respect to the efficacy of signal transmission, as signals with different physical properties display distinct transmission characteristics. As such, one approach taken by researchers to explore the influence of the signaling environment on complex signal evolution and function is to examine the attenuation of complex signals and their components in different signaling environments (e.g., acoustical signals: Romer and Lewald, 1992; plant-borne vibrations: McNett and Cocroft, 2008; substrate-borne vibrations: Hebets et al., 2008; Elias et al., 2010). As technology increases and the portability of field equipment improves, research on modality-specific component transmission and reception across signaling environments will likely be a rich area of future study, especially as it relates to a changing environment.

Directly manipulating the signaling environment is a useful way to gauge the relative importance of different signal components in eliciting appropriate receiver responses. In this issue, Wilgers and Hebets (2011) manipulate the signaling environment such that they can independently ablate the seismic and visual courtship signal components of the wolf spider *Rabidosa rabida* and subsequently ask whether each component is necessary and/or sufficient to enable mating. Their finding that pairs were able to mate, albeit at low levels, in environments which successfully transmitted only visual

components or only seismic components suggests that the each is sufficient, and potentially redundant, in its information content (redundant/backup signals; Møller and Pomiankowski, 1993; Johnstone, 1996). Similarly, Vergara et al. (2011) experimentally decouple visual and olfactory cues of the plant *Oenothera acaulis*, in order to examine the responses of the facultative floral larcenist cockroach *Blatta orientalis*. Their results suggest that olfactory cues act as long range attractants, while visual cues only marginally increased attraction at short range (Vergara et al., 2011).

2.3 Signal reception and receiver psychology

Understanding the mechanisms of signal reception and processing and their respective influence on various aspects of receiver psychology, such as learning and memory, are critical for understanding receivers as a source of selection on complex signal evolution (Rowe, 1999). Multiple papers in this special issue address the broad topic of receiver psychology in complex signaling (Leonard et al., 2011; Siddall and Marples, 2011 a, b; Taylor et al., 2011; Vergara et al., 2011), and the relatively large number of such contributed manuscripts reflects a growing interest in this topic.

Taylor et al. (2011) use robotic frogs to examine the responses of females of two different species (squirrel treefrogs *Hyla squirella* and the túngara frog *Physalaemus pustulosus*) to various combinations of visual and acoustic male courtship signals. Interestingly, the pattern of response differs between the species, suggesting underlying differences in their 'receiver psychology' (sensu Rowe, 1999). Similarly, in separate studies on two different avian taxa (domestic chick *Gallus gallus domesticus* and wild robin *Erithacus rubecula*), Siddall and Marples (2011a, b) explore the influence of combinations of stimuli from different sensory modalities on receiver learning and memory. All three studies nicely highlight the effects of the complexity of such interactions on receiver responses, as they all find variation in the influence of stimulus combinations.

Despite the recent increase in studies focusing on aspects of receiver psychology, there are numerous basic sensory and psychological factors that continue to be overlooked (e.g., receiver habituation, signal localizability, etc.; Owren et al., 2010). This is certainly an area worthy of future study and one in which the basic challenges faced by receivers in terms of foraging, locomotion, habitat choice, and predator avoidance could shed light on perceptual biases that may influence complex signal evolution (e.g., Endler and Basolo, 1998; Boughman, 2002).

3 Future Research in Complex Signaling

3.1 Complex signaling beyond animals

Understanding the principles guiding the evolution of complex signaling in animal systems, such as various aspects of the receiver's psychology discussed above, can inform us about more than just animal signals. For example, a receiver psychology approach is currently being used in studies exploring the evolution of floral phenotypes (Leonard et al., 2011; Vergara et al., 2011). Leonard et al. (2011) provide an engaging, accessible, and compelling synthesis of functional hypotheses relating to the evolution of complex floral displays. This contribution highlights one of the most promising avenues for future research – applying concepts and knowledge of receiver psychology to our understanding of the evolution of complex traits beyond animal signals. For example, in addition to contributing important progress to areas such as the evolution of floral form and function, a complex signaling framework (sensu Hebets and Papaj, 2005; Leonard et al., 2011) could provide significant advances to topics such as the evolution of plant defensive strategies and compounds, the evolution of parasitic plant form and function, pest management as influenced by pest foraging decisions, and even disease transmission as it relates to host choice (which could be influenced by vector psychology). Whenever two organisms routinely interact, aspects of their sensory and processing systems, as well as their more general psychology, are sure to influence the evolution of their interaction.

It is worth noting that studying plant-pollinator interactions in a context developed for animal communication, as advocated by Leonard et al. (2011), can enrich *both* areas of research (plant-insect interactions and animal communication). The wealth of theory and data, including detailed fitness considerations for both parties, that exists for plant versus pollinator perspectives on signaling can surely inform students of animal communication. Additionally, such plant-animal systems are frequently more experimentally tractable than animal signaling systems and may prove useful for testing certain hypotheses of complex signal function that may be otherwise difficult to test.

3.2 Incorporating increasing complexity

Research in animal signaling has progressed from a focus on signals in isolation, to one in which we routinely acknowledge and address the complexity of individual animal displays (reviewed in Partan and Marler, 1999; Candolin, 2003; Hebets and Papaj, 2005; Partan

and Marler, 2005; Bro-Jorgensen, 2010). We are now ready to add the next level(s) of complexity – the plasticity inherent in many signalers (Van Staaden and Smith, 2011; Wilgers and Hebets, 2011), the dynamic nature of organism interactions (Patricelli et al., 2011), and the dynamic nature of both ecological and social environments, which can lead to variation in selection pressures (Bro-Jorgensen, 2010).

Researchers are beginning to focus on behavioral plasticity and its relationship with complex signal evolution and function. Van Staaden and Smith (2011) nicely demonstrate the plasticity of individual fishes' signal repertoires as they compare intra- and interspecific signal variation across six species of Malawian cichlids. They discuss the sources of variability in cichlid signaling and provide suggestions for future research. Similarly, Wilgers and Hebets (2011) find plasticity in the courtship signaling of the wolf spider *R. rabida*, as males adjust their composite courtship display based upon the signaling environment. Future studies focusing on signaler plasticity are certain to provide more insight into complex signal evolution and function.

Patricelli et al. (2011) wrap up this Special Issue with an ambitious, thought-provoking manuscript calling for the incorporation of economic models of negotiation in a market into studies of complex communication. They discuss the utility, as well as potential pitfalls, of studying the complexity of dynamic courtship in terms of negotiations. While their manuscript focuses on lekking animals, the ideas are certainly more broadly applicable and their manuscript nicely illustrates the complexities of communication.

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