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COMMENTARY

Using cross-disciplinary knowledge to facilitate advancements in animal communication and science communication research

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ABSTRACT

Although humans may have more nuanced reasons for communicating – e.g. to teach or inform, to share or change opinions or attitudes – all animals engage in communication with members of their own as well as other species, and there are more similarities than differences between non-human and human communication. All communication systems are composed of the same basic elements and all face comparable challenges. In this Commentary, we explore the extent to which research investigating how non-human animals communicate with each other (animal communication) overlaps in questions and approaches with research focused on how humans communicate with each other. We place a special focus on human communication involving scientific content, i.e. science communication. We begin with a brief review of the fields of animal communication and science communication. We next synthesize literature from each field to examine the roles, impacts and potential interactions of communication system elements – signaling environments, signalers, signal form and receivers – on effective communication. We find that research examining animal and human communication, including science communication, often has different emphases. Animal communication research, for example, tends to focus more on the role of the signaling environment through quantification of receiver responses. In contrast, science communication research currently emphasizes relationship building between signalers and receivers, and quantifies aspects of the receiver's psychology. Informed by our cross-disciplinary assessment, we propose potentially productive avenues of future research in both animal communication and science communication.

KEY WORDS: Complex signaling, Environmental psychology, Receiver psychology, Relationship building, Signaling environment, Systems approach, Trust

Introduction

Communication involves the exchange of signals (see Glossary) – each composed of a particular physical form (e.g. acoustic, chemical) – that transmit through a given medium (e.g. water, air, print), are received by target (and sometimes non-target) receivers and are produced for a particular purpose (e.g. acquiring a mate). Communication can take place between members of the same species, or different species, and can even connect dramatically different life forms, e.g. flowers (plants) and insect pollinators (animals). Notably, commonalities exist across all communication systems, regardless of whether the signaling happens between spiders, humans, birds or frogs, and regardless of whether the communication display takes place in an educational setting, in a stadium or theater, in a predator–prey interaction, or during a reproductive attempt.

While communication between a human parent and her teenage daughter may initially seem distinct from communication between a male spider and a potentially cannibalistic female mate, upon closer inspection there are many similarities. All communication, for example, takes place in a particular environment (Fig. 1A, signaling environment) within which there is a signaler (Fig. 1B, signaler biology) that produces signals (Fig. 1C, signal form) aimed at eliciting a desired receiver response, and a receiver that perceives these signals and responds accordingly (Fig. 1D, receiver biology). Importantly, within any communication system there is also the potential for interactions and interdependence within and between all elements (Fig. 1, arrows). Such interactive, dynamic and potentially interdependent communication systems pose tremendous challenges for those who study them. Nonetheless, researchers across distinct disciplines have made important progress in understanding the evolution and function of both animal (non-human) and human communication. Each distinct field has a long and rich history with its own milestones and paradigm shifts along the way.

In this Commentary, we compare and contrast research in animal and human communication, with a specific focus on science communication. Our aim is to explore the potential for advancements in each field through increased cross-disciplinary knowledge. We begin with a brief overview of animal communication research, highlighting the types of questions and approaches scientists implement to increase their understanding of how and why animals communicate. Next, as a point of comparison, we relate our understanding of the current questions and approaches that are the focus of science communication research. Finally, we apply a communication system framework adapted from animal communication research to human communication research in an attempt to identify areas of similarity and difference between the fields. We conclude by identifying research approaches and questions that we perceive as currently unbalanced in their representation, i.e. topics that are under-represented/non-existent in one field (e.g. animal communication) but commonplace in the other (e.g. science communication). We acknowledge at the outset that our expertise is in animal communication and, thus, our reading of human/science communication research is not exhaustive.

A brief history of animal communication

Like human communication, animal communication (i.e. communication among non-human animals) has been the focus of scientific research for more than a century (Darwin, 1871). Animal communication research started predominantly with descriptive natural-history accounts of observable animal displays (Peckham and Peckham, 1889; Peckham and Peckham, 1890; Huxley, 1914; Tinbergen, 1953). It transitioned into correlational studies exploring

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Glossary

Infotainment
Media that combines information and entertainment; often referred to as 'soft news'.

Mate choice copying
A form of non-independent mate choice: when an individual's likelihood of mating with a 'target' individual is increased by observing a sexual interaction between the target and another.

Multimodal display
An animal display that incorporates signals in multiple sensory modalities (Hebets and McGinley, in press), e.g. visual + vibratory: dynamic movements of brightly colored legs detected by eyes plus the simultaneous production of song detected by ears.

Signal
A packet of energy or matter generated by a display or action of one organism (the signaler) that is selected for its effects in influencing the probable pattern of behavior of another organism (the receiver) via its sensory–nervous system in a fashion that is adaptive either to one or to both parties (Hebets and Papaj, 2005).

System 1 and system 2 thinking
Distinct modes of decision making; system 1 is fast, automatic and autonomous while system 2 is slow, controlled and effortful (Kahneman and Egan, 2011).

Systems approach
An approach that evaluates the interactive nature and interdependence of system elements and how they relate to system purpose. In animal communication, it might explore how display components interact to alter function, and how function varies in different states of the system.

the relationship between an animal's signaling traits and other attributes, often in an attempt to determine signal content or message (Doucet and Montgomerie, 2003; Ryan, 1980; Chaine and Lyon, 2009; Galeotti et al., 1997; Zuk et al., 1995) (Fig. 2A).

A major paradigm shift happened in the early 1990s with the recognition that signal form is influenced not only by the need to convey a particular message but also by the way that signals travel through the environment and are detected, discriminated and remembered by a receiver, i.e. by 'receiver psychology' (Guilford and Dawkins, 1991). New lines of research began to explore the role that the environment and the psychology of the receiver play in the evolution of signal form (reviewed in Rowe, 2013) (Fig. 2A). Scientists began, for example, to quantify the transmission efficacy of signals across varying environments (Elias et al., 2010, 2004; Hebets et al., 2008; Joyce et al., 2014). There was also increased interest in understanding how receiver responses might be influenced by the way in which an animal's nervous system processes and compares multiple bits of information, by the neural circuitry underlying sensory processing and by the perceptual variability inherent across multiple receivers (Guilford and Dawkins, 1991; Guilford and Dawkins, 1993; Miller and Bee, 2012; Rowe, 1999, 2013; Cummings, 2015; Hebets and Papaj, 2005; Bateson and Healy, 2005; Hoke et al., 2017).

Most recently, animal communication research has begun to tackle the complexity inherent in communication systems. In the mid 2000s, a framework for studying complex signaling was introduced: a framework that integrated across content-based (i.e. focusing on messaging), efficacy-based (i.e. focusing on the signaling environment and/or the receiver's psychology) and inter-signal interaction hypotheses of complex signal function (Hebets and Papaj, 2005). Indeed, the increasing recognition of interactions within communication systems led to a call for incorporating a systems approach (see Glossary) into communication studies – an approach that, among other things, considers the overall architecture of a display, including how components might interact to alter their function and how signal function might vary in different states of the system (Hebets et al., 2016).

Current research in science communication

Science communication is a subset of human communication (Adler et al., 2016; Littlejohn and Foss, 2010) that is distinguished by its content, which by definition is science related. Similar to any communication system, it can take place in a variety of signaling environments, can have a number of different signalers, can employ signals with varying physical form and message content, and can target a number of distinct receivers (Fig. 1).

The science of science communication is a rapidly expanding cross-disciplinary field that incorporates studies from psychological, social, behavioral and decision scientists (NAS, 2017, 2018). The predominant areas of research foci in science communication include: communicating about politically charged topics, creating a collaborative community, incentivizing scientists to engage in science communication, communicating with policy makers, enhancing trust in scientists, evaluating science communication, and communicating uncertainty (among others) (NAS, 2018). In reviewing this list, it is apparent that research focuses on both the capacity for (e.g. increasing incentives among scientists) and the efficacy of (e.g. communicating about politically charged topics) science communication. From a research perspective, the goals and challenges of studying animal and science communication are quite distinct.

Science communicators identify specific goals *a priori*; with each goal associated with desired receiver responses (Hebets, 2018) (Table 1). The challenge then for both practitioners and researchers is to determine a strategy that most effectively elicits these responses. In science communication, we can choose (a) the signaling environment, (b) the signaler and (c) the communication message. We can also (d) assess the receiver's psychology (e.g. through self-reflective surveys) (Figs 1 and 2B). In contrast, in non-human animal communication, evolutionary history has already established (b) animal signalers and (c) signal form. Scientists are thus challenged with determining (c) the communication message and (d) the receiver's psychology by observing receiver responses (Fig. 2A). With these fundamental differences in mind, we review what is known about communication system elements and their role in effective communication across animal and human/science communication.

Communication system elements (Fig. 1)

A: Signaling environment

Animal communication

All animals exist and interact in a space that can be defined by both physical and social attributes. In animal communication, it is well established that the environment can exert a strong influence on the detectability or discriminability of signals, especially environmental noise (Andersson and McGregor, 1999; Brumm and Slabbekoorn, 2005). Scientists often distinguish the abiotic (e.g. temperature, wind, etc.) from the biotic (e.g. predator density, social environment, etc.) components of the environment (see fig. 1 in Patricelli and Hebets, 2016) and explore how each might impact animal signaling. Temperature, for example, is an abiotic attribute of the environment that can influence both the form of a signal as well as the receiver's response. Temperature influences signaling in crickets (Martin et al., 2000), fireflies (Michaelidis et al., 2006), fish (Ladich and Schleinzer, 2015; Vicente et al., 2015) and bats (Camaclang et al., 2006), among others.

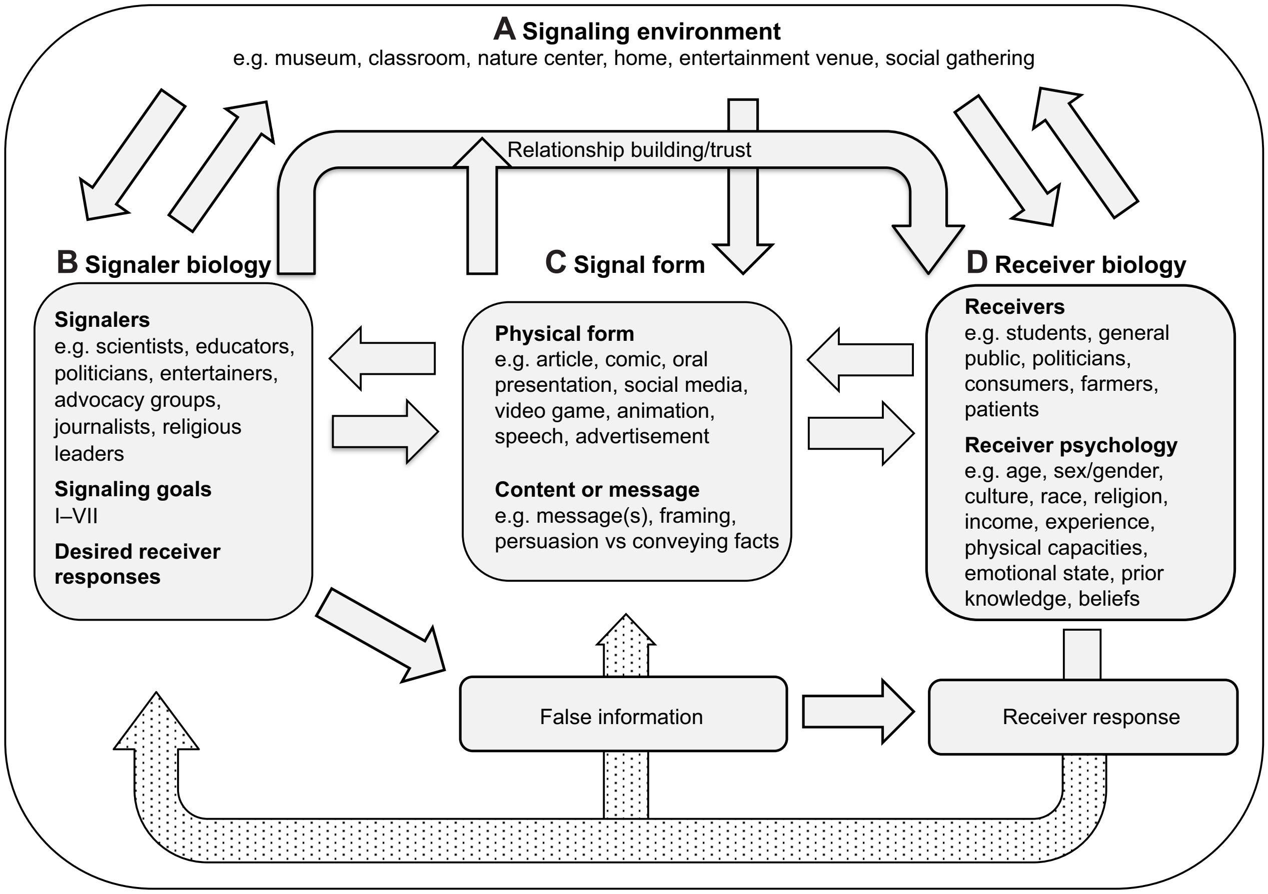

Fig. 1. Communication can be viewed as a system with interacting elements. All communication takes place within a signaling environment (A) and involves a signaler. Signaler biology (B) encompasses the signaler's identity, goals and desired receiver responses (see Table 1 for science communication goals and desired responses). Signalers produce signals of a particular form. Signal form (C) includes the physical form as well the signal's content or messaging, which is received by receivers. Receiver biology (D) encompasses the identity and psychology of target receivers, including their perceptual capacity. The receiver response provides feedback to the signaler, in real time and/or following communication, and may also be influenced directly by the signaler's biology (not shown for simplicity). False information may be present in the system and can directly influence receiver responses. Arrows represent the potential for interactions among system elements. Dotted arrows represent opportunities for assessment and iterative signaling revisions.

Biotic factors can also influence animal signaling. Displaying male sage grouse, gladiator frogs and wolf spiders all increase signaling in response to the presence and/or feedback of target receivers (i.e. receptive females) (Taff et al., 2014; Sullivan-Beckers and Hebets, 2011; Höbel, 2015). Signaling birds adjust the directionality of their calls depending on the location of their intended receiver (Yorzinski and Patricelli, 2010); and animals ranging from spiders (Kotiaho et al., 2004) to fiddler crabs (Kahn et al., 2014) to katydids (Symes et al., 2016) to multiple insects and frogs (reviewed in Gerhardt and Huber, 2002) adjust the timing of their calls based on conspecifics in their social environment. The presumption in all of these instances is that the observed adjustments in signal form, signaling location and signaler behavior increase the likelihood of achieving the desired receiver response.

Receivers, in addition to signalers, can also be influenced by their social environment. Evidence of mate choice copying (see Glossary; Brooks, 1998; Dugatkin, 1998; Galef and White, 1998; Godin et al., 2005), for example, or learning based on social experiences (reviewed in Hebets and Sullivan-Beckers, 2010; Hebets and Sullivan-Beckers, in press) is widespread across diverse animal taxa. Indeed, sociality in non-human animals has been suggested to drive the evolution of complexity in communication systems (Hauser, 1996; Blumstein and Armitage, 1997; Pollard and Blumstein, 2012; Freeberg et al., 2012; but see Ord and Garcia-Porta, 2012).

Science communication

Similar to animal communication, science communication takes place in extraordinarily different environments ranging from school classrooms to zoos, museums and science centers, to public rallies, home living rooms and more. Just as in animal communication, abiotic and biotic components can differ dramatically across these environments and, as such, the signaler behavior, signal form and precise signaling location might need to be adjusted in accordance with environmental conditions.

Driven by the recognition that the physical environment can influence human behavior, the 1960s gave birth to a sub-discipline of psychology called 'environmental psychology' (reviewed in Bechtel, 2002). A framework now exists in which psychologists identify and measure abiotic variables, e.g. color, heat, light, sound, etc., and their impact on human behavior (Mehrabian and Russell, 1974). Abiotic factors are now known to alter emotional responses such as arousal, pleasure or dominance (Mehrabian and Russell, 1974), and their impact can vary across receivers. The color of a room, for example, can influence one's emotional and physiological state (Küller et al., 2006), affecting introverts more than extroverts (Küller et al., 2009). In fact, it is human–environmental interactions that psychologists posit as being responsible for some observed irrational and/or illogical human behavior (Mehrabian and Russell, 1974). Sensory-based psychological phenomena such as attention

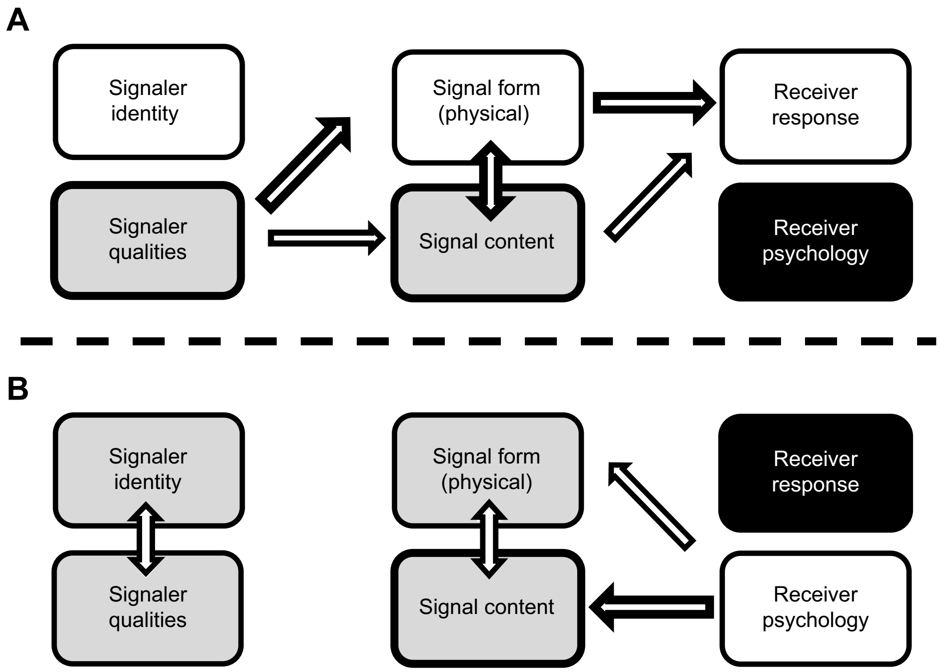

Fig. 2. Different perceived research foci of animal communication and science communication research (excluding the role of the signaling environment). (A) Animal communication; (B) science communication**.** White boxes indicate communication elements that are known *a priori* or are typically observed and quantified by researchers. Gray boxes indicate communication elements that researchers are often trying to infer or identify. Black boxes indicate elements that are little known, challenging to study and/or rarely of focus for researchers. Arrows indicate relationships that researchers commonly quantify and/or attempt to understand. Thickened outlines indicate the elements that appear to receive the most research attention. In comparing animal and science communication, it is evident that each field starts off with different knowns and unknowns; each has its own predominant research foci; and there are notable differences in the directionality of interest with respect to relationships between system elements. [Note: while there is research in each field that is not represented in this figure (e.g. how receiver psychology might have influenced signal form over evolutionary time), our intention was to represent our perception of the most common research areas.]

can also be influenced by the physical environment, e.g. color might influence human affiliation or attraction (Elliot and Maier, 2014). Despite their presence in psychology, the extent to which these ideas are incorporated into science communication research or practice is unclear.

The social environment, unsurprisingly, also influences human behavior. With respect to science communication, comments from other receivers influence one's perception of the validity of scientific findings (Hinnant et al., 2016). In a study that explored the effects of blog comments, for example, researchers found that uncivil comments led to polarization of the perception of risk – an effect that interacted with a receiver's level of religiosity (Anderson et al., 2014). Also relevant to science communication is the knowledge that humans consistently monitor their social environment and adjust their individual opinions and decisions to match that of the perceived majority (Matthew and John, 2009). Given the demonstrated impact of the social environment on science communication, we propose that an increased emphasis on the abiotic environment and its potential interactions with other system elements could lead to new strategies for effective science communication (Table 2).

Table 1. Goals of science communication and associated responses desired from audiences (modified from Hebets, 2018)

Communication goal		Desired receiver response
IA. Share research findings IB. Share excitement of science	→	ia. Gain a general understanding of scientific findings ib. Increase excitement about science
II. Increase appreciation for science as a way of understanding and navigating the world	→	ii. Recognize importance of and use scientific knowledge in decisions regarding health, nutrition, the environment, etc.
III. Increase knowledge and understanding of science of a specific issue	→	iii. Issue-specific knowledge gain (e.g. importance and safety of immunizations)
IV. Influence people's opinions, behavior and policy preferences	→	iv. Change in opinion, behavior or voting patterns
V. Seek solutions to societal problems by engaging with diverse audiences	→	v. Share concerns and perspectives on issues raised by the communicator
VI. Engage youth as future scientists	→	vi. Increase in positive science identity
VII. Maintain or improve public trust in scientists	→	vii. Belief of scientist's findings

B: Signaler biology

Animal communication

Animal signalers encompass foragers aiming to share information about a potential food source (e.g. honeybee waggle dance; Dyer, 2002; Gruter and Farina, 2009; Menzel et al., 2011), prey warning off predators (Rowe and Guilford, 1999; Rowe and Halpin, 2013) and males (or females) attempting to attract and acquire a mate (Andersson, 1994), among others. Given that the identity of the signaler is seemingly inflexible in many evolved animal communication systems (e.g. it is all members of one sex that engage in courtship signaling), instead of focusing on signaler identity, scientists tend to focus on signaler traits and their relationship with receiver responses in an attempt to determine signaler 'quality', e.g. foraging history, immune response, etc. (Fig. 2A).

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Table 2. Example research questions identified from the cross-disciplinary comparison of animal communication and science communication research

A. Animal communication

Does the individual identity of the signaler (particularly in social groups) impact the efficacy of communication?
- Are there particular individuals that are more effective at eliciting receiver responses? If so, why?
- Can social network analysis be combined with communication theory to explore the role of signaler identity in animal communication?

To what extent does animal communication facilitate relationship building/trust?
- Does the prolonged courtship observed across many animal taxa function to build trust between signalers and receivers?

Can/does non-human animal communication facilitate system 2 decision making (e.g. slow, conscious, effortful)?
- Under what circumstances, if any, do non-human animal receivers engage in slow, conscious, effortful, complex decisions following communicative interactions? Does this relate to signal form?

Does viewing false information (e.g. animal mimicry) through the lens of communication open new avenues of research or new interpretations of old research?
- Are validated strategies for overcoming false information in science communication (e.g. early warnings of misinformation, repetition of retractions, compelling alternatives) equally effective in animal systems with false information?
- How do animals learn about false information and can such knowledge inform the challenge of misinformation in science communication?

Under what circumstances are there long-term consequences of communication between two individuals?
- Are there currently observable behavioral outcomes in receivers that are the result of earlier communicative interactions?
- Are there short-term versus long-term effects of communication between signalers and receivers?

Do animals use cognitive short cuts/heuristics in decision making associated with communication?

B. Science communication

To what extent can practitioners strategically use the signaling environment (physical and social) to increase the impact of science communication?
- Does the abiotic signaling environment interact with signal form and might this influence signal design?
- Does the biotic signaling environment interact with the receiver's biology?

To what extent do the physical form of signals and the receiver's biology interact?
- Are particular signaling modalities more/less effective with particular receivers?

Is eliciting system 2 thinking in receivers necessary to achieve all science communication goals?
- Which goals of science communication might be more effectively achieved with system 1 versus system thinking in receivers?

Can practitioners of science communication purposefully build degeneracy and/or redundancy into their system?
- To what extent does redundancy (same structure/same function, e.g. using the same signal for the same message over and over) versus degeneracy (different structure/same function, e.g. using different signals for overlapping messages) increase the robustness of science communication across signaling environments and across receivers?

Are there short-term responses of receivers that could be observed and quantified?
- How might researchers design experiments such that receiver behavior can be observed immediately following the perception of science communication?

To what extent can knowledge of the detectability, discriminability and memorability of signals inform signal design given the noisy, heterogeneous communication platforms of the 21st century?
- Can science communicators leverage attention-altering signal design to increase detectability and discriminability in a noisy online platform?

Science communication

Traditionally, we think of science communicators as educators, scientists or journalists. With the proliferation of online communication venues and the ease with which individuals can gain access to communication platforms, however, more science communicators are taking the stage: politicians, entertainers, religious leaders, etc.

Communication research in the mid to late 1900s demonstrated a strong influence of the 'communicator' on receivers. Audience members were found to agree with a communicator's position if they saw the communicator as similar to themselves (Mills and Jellison, 1967; Feldman, 1984). The attractiveness and identity of a communicator was shown to impact their persuasiveness (Eagly and Chaiken, 1975), e.g. newscasters were found to be more trustworthy than political candidates (Worchel et al., 1975; Andreoli and Worchel, 1978). Signaler identity was also shown to interact with signal form (Fig. 1). In one study, for example, 'likable' and 'unlikable' communicators delivered the same message in different forms, i.e. writing, audiotape or videotape. The likable communicator was more persuasive in the video and audiotape while the unlikable communicator was more effective in writing (Chaiken and Eagly, 1983). Similarly, television was found to be an effective medium for newscasters but an ineffective medium for political candidates (Andreoli and Worchel, 1978). Importantly, communicators can make strategic choices that influence how they are perceived – an area of research ripe with possibilities.

Science communication research has also focused on the importance of the signaler. Local 'opinion leaders' (i.e. trusted community members), for example, are increasingly recruited to engage in science communication because of their proven communication efficacy (reviewed in Nisbet and Markowitz, 2016). People are more likely to consider news trustworthy and credible if it is recommended by a friend perceived to be knowledgeable (Turcotte et al., 2015). Different science communicators are also known to convey the same information in different ways. Co-authors of the same scientific study, for example, differ in the way they summarize their research, leading to discrepancies in the 'sharability' and ratings of the work (Milkman and Berger, 2014). Notably, while the importance of the signaler's identity and their social role in the community is an active area of research in science communication (Fig. 2B), it has been relatively unexplored in animal communication research (Fig. 2A, Table 2).

C: Signal form

Animal communication

Signal form encompasses both (a) the physical form(s) of communication displays and (b) the message or content (Fig. 1). The physical form is expected to be influenced by how a signal transmits through the environment and is perceived and processed by target receivers. Animal signals are commonly categorized into distinct physical forms associated with sensory modalities (e.g. visual, acoustic, chemical) that mirror the sensory systems used to receive them (e.g. vision, hearing, smell) (Hebets, 2011). In terms of content, signal form in animal communication is hypothesized to vary with signaler attributes as a means of conveying information such as immune function (Ahtiainen et al., 2004; Navara and Hill, 2003), age (de Kort et al., 2009; McDonald, 1989; Kiefer et al., 2006), mating history (Kokko et al., 1999; Harris and Moore, 2005), paternal care abilities (Grunst and Grunst, 2015), etc.

Recent research in animal communication focuses on understanding the evolution and function of communication displays that incorporate numerous signals within and between sensory modalities – multimodal signaling (Higham and Hebets, 1999; Hölldobler, 1999; Partan and Marler, 1999; Partan and Marler, 2005; Rowe and Guilford, 1999) (Fig. 2A). Scientists ask why some species have complex, multimodal displays (see Glossary; e.g. visual pigmentation, dynamic visual movements and vibratory song) while closely related taxa do not (e.g. only vibratory song) (Hebets et al., 2013). Explanations for complex animal displays include the following: distinct signals contain different messages (e.g. species identity plus parasite load) (Candolin, 2003; Johnstone, 1996; Møller and Pomiankowski, 1993); signals with distinct physical form travel through the environment differently, thereby increasing the likelihood of transmission across a heterogeneous environment (Hebets and Papaj, 2005; Candolin, 2003); and/or different display components target different receivers (Hebets and Papaj, 2005), among others (reviewed in Hebets and McGinley, in press). Display components are also known to have non-additive, or interactive, effects on receivers (Hebets, 2005; Taylor et al., 2011; Leonard et al., 2011), potentially providing additional signaling benefits. The vibratory song of a courting male wolf spider, for example, appears to focus a female's visual attention on his ornamentation (Hebets, 2005).

Science communication

While signal form has been predetermined by evolutionary history in non-human animals, science communication practitioners are challenged with determining how to (a) best physically convey their information to target audiences, (b) frame their message(s) in a way that increases the likelihood of achieving their goal and (c) build a trusting relationship with their receiver(s) (Fig. 1).

Science communication arguably transcends animal communication in its opportunities for diverse signal form. Physically, science communication can embody a variety of print options (e.g. newspapers, books, poems, comics, short stories, blogs, website, 3D printing, etc.), visual or performing arts, podcasts, theater, computer games, etc. For each physical form, some, but not enough, research exists regarding its efficacy. Visual and performing arts, for example, are suggested to be effective owing to their ability to impact people's emotions (Curtis et al., 2012), which are, in turn, known to impact science learning (Sinatra et al., 2014). Podcasts (Birch and Weitkamp, 2010) and cartoons (Shurkin, 2015) have also been championed as important forms of science communication. Humor has been touted as particularly effective, but the evidence for this is mixed at best (Pinto et al., 2015; Fisher, 1997; Rule and Auge, 2005; Wanzer et al., 2010). Interestingly, physical form in science communication may help overcome specific communication challenges. Humor, for example, might be particularly useful for decreasing the likelihood of counter-arguments while performing arts may work best with receivers that respond to strong characters with a positive mission. In science communication, each signal form offers different affordances in terms of the ability to help a communicator shape/reshape potential beliefs. This is distinct from the more common mechanistic – sensory stimulus/receiver response – approach to understanding physical signal form in non-human animals, which in turn appears underexplored in science communication studies (Table 2).

The manner in which receivers perceive signals, e.g. listening with headphones versus speakers, can also influence their physiology (e.g. pulse transit time, respiratory sinus arrhythmia, etc.) (Kallinen and Ravaja, 2007), which can in turn influence their response. Similarly, the simultaneous perception of signals in distinct sensory modalities (e.g. vision and sound) can influence human attention (Spence et al., 2000; Spence et al., 1998; McGurk and MacDonald, 1976). A greater understanding of such perceptual influences and cross-modal interactions could be particularly helpful for designing science communication displays. In one study of online science communication, for example, the authors suggested that 'science communication has turned into infotainment' (see Glossary; Molek-Kozakowska, 2017). The authors interpret this as a negative, but we wonder whether 'infotainment' might simply reflect a necessary signaling design for increasing the detectability, discriminability and memorability of information in a noisy online platform (Table 2).

In terms of content, the framing of scientific information has received a great deal of attention (reviewed in Nisbet and Markowitz, 2016). Researchers have compared the effectiveness of conveying the same message as gains versus losses, e.g. positive outcomes from responding (living longer by quitting smoking) verses negative outcomes from failing to respond (dying sooner by continuing to smoke) (Toll et al., 2007), and as episodic (i.e. personal stories) versus thematic approaches (reviewed in NAS, 2017). Studies have found that affirming, rather than threatening, people's values is a more effective strategy for controversial science topics (Kahan, 2010), and messaging strategies that employ a 'leveraging, involving, visualizing and analogizing' (LIVA) strategy are recommended (Jamieson and Hardy, 2014; Hardy and Jamieson, 2017). Science communication content, however, goes well beyond framing, as it includes message risks, benefits, honesty, openness, etc. Indeed, framing provides the context for the content. It is unclear whether there is a parallel in animal communication.

Understanding how to build meaningful, trusting relationships between signalers and receivers is a major focus of current science communication studies (NAS, 2017, 2018). Certain strategies are known to be important in connecting with target receivers, e.g. making the information personally relevant to receivers (Jucan and Jucan, 2014) or using metaphors and/or pop-culture icons (e.g. the science of superheroes) to provide a familiar frame of reference (Pramling and Säljö, 2007; Zehr, 2011, 2014, 2016). Storytelling and personal narratives are also commonly employed, effective methods for science communication (Dahlstrom, 2014). However, researchers are also exploring strategic choices communicators make to more effectively listen, to treat people with respect and fairness, and to demonstrate listening skills. Related to this is the core idea of system 1 (peripheral) versus system 2 (central route processing) thinking (see Glossary). System 1 thinking is described as automatic, fast and typically unconscious while system 2 is effortful, slow, controlled and conscious (Kahneman and Egan, 2011). Eliciting system 2 thinking is hypothesized to be more effective for achieving particular science communication goals, e.g. increasing appreciation for science as a way of understanding and navigating the world, influencing people's opinions, behavior and policy preferences (Hebets, 2018; NAS, 2017). A similar distinction and/or focus on relationship building and system 1 versus 2 thinking is not commonplace in animal communication studies, yet may be relevant to understanding particular signaling systems (Table 2).

False information can be a major barrier to effective science communication as it can lead to undesired receiver responses (Fig. 1). Climate change/global warming, for example, is a topic for which there is much false information circulating, creating challenges for efforts to help secure our planet's future (van der

Linden, 2015). Unfortunately, it is difficult to correct or counter false information (Lewandowsky et al., 2012; NAS, 2018). To date, three factors have showed promise: (i) early warnings of misinformation, (ii) repetition of retractions and (3) simple, coherent, compelling alternatives (Lewandowsky et al., 2012). This remains an active research focus (NAS, 2018).

Similarly, the honesty versus dishonesty of information has been, and continues to be, a major component of animal communication research (Biernaskie et al., 2014; Gil and Gahr, 2002; Krakauer and Johnstone, 1995; Schluter and Price, 1993; Searcy and Nowicki, 2005). Typically, however, the 'honesty' of animal communication studies relates solely to traits that are proposed to reflect a signaler's quality. Other types of false information in signaling, e.g. mimicry, traditionally fall outside of communication studies, except in rare cases such as aggressive mimicry, e.g. female fireflies falsely signaling heterospecific identity so as to attract a heterospecific male as a meal (Lloyd, 1965). It would be interesting to apply our understanding of overcoming false information from science communication to animal communication and vice versa (Table 2).

D: receiver biology

Animal communication

Following the previously discussed paradigm shift that expanded animal communication studies to include a role of the receiver, scientists now acknowledge and appreciate that signal evolution and function are influenced by an animal's nervous system, including the neural circuitry underlying sensory processing, and by the perceptual variability inherent across multiple receivers (Guilford and Dawkins, 1991; Guilford and Dawkins, 1993; Miller and Bee, 2012; Rowe, 1999, 2013; Cummings, 2015; Hebets and Papaj, 2005; Bateson and Healy, 2005; Hoke et al., 2017). Unfortunately, these aspects of receivers remain difficult to study in most non-human animals and are thus poorly understood (Fig. 2A). Instead of directly assessing aspects of the receiver's biology (Fig. 1), most studies attempt to understand receiver psychology by correlating variability in receivers (e.g. age, hunger state, prior experiences, etc.) with their responses to signaling. Similarly, researchers explore variability in signaler behavior related to aspects of the receiver such as a female's receptivity display (Sullivan-Beckers and Hebets, 2011, 2014) or the receiver's sex (Gavassa et al., 2013).

Unlike in science communication, animal communication researchers do not have direct access to the thoughts and motivations of receivers (Fig. 2B). The receiver's biology is an area of research that has the potential to expand rapidly in animal communication and one that might benefit from insights and approaches of science communication (e.g. differentiating system 1 and system 2 thinking).

Science communication

Similar to the appreciation of receiver psychology in animal communication was the realization among human communicators that people are cognitive misers, frequently relying on fast, automatic, autonomous thinking (system 1) rather than slow, controlled, effortful thinking (system 2) (Kahneman and Egan, 2011). Humans also tend to process information in a way that helps maintain their existing attitudes or self-identity (i.e. motivated processing) (Kahan, 2016). The focus on 'engagement' in science communication is, in fact, predominantly aimed at trying to encourage audiences to use deeper-level processing, as such processing increases the likelihood of fostering new beliefs or changes to existing beliefs (NAS, 2017, 2018).

In addition to a focus on eliciting effortful, deeper processing in receivers, the importance of identifying a target audience and modifying signal form accordingly is prevalent in science communication literature and training (e.g. Campbell, 2011; Manzini, 2003; Walters et al., 1997; NAS, 2017, 2018; AIBS Communications Boot Camp for Scientists www.aibs.org/). Similar to other animals, human receivers vary in a number of ways. They vary in their exposure to media of different forms, in their perception of risk, in their political and religious views, in their gender, race, etc., and this variation impacts their reactions to science communication (NAS, 2017). Pre-existing ideas can influence one's acceptance of scientific information, especially as it relates to evolution (Lawson and Worsnop, 1992; Sinatra et al., 2003, 2008); and political views influence the way in which identical information on climate change is viewed (Hart and Nisbet, 2012). Understanding one's target audience, however, requires preliminary data collection and errors in assessing an audience's ability to receive a message could restrict one's ability to convey a message effectively.

Although attempting to account for differences in receiver psychology has been at the forefront of science communication strategies, it is worth noting that receivers also vary in their perceptual capacities (e.g. vision impaired or low in hearing). Some communicators are developing learning activities that are effective with a range of receivers – e.g. visually impaired as well as sighted individuals (Stender et al., 2016) – but this appears to be the exception rather than the rule. Science communication appears to focus more on signal processing as compared with signal reception (Table 2).

Conclusions

As scientists deeply committed to engaging with the public towards the goals of increasing science learning and understanding (Hebets et al., 2018; Hebets, 2018), we began this project with a curiosity about what the field of animal communication might have to offer the research and practice of science communication. In the end, however, we found (perhaps unsurprisingly in hindsight) that human/science communication research also has many things to offer animal communication research. For each field, we share some of the research questions that emerged for us following our cross-disciplinary comparison (Table 2) – questions that could lead to fruitful new research avenues and understanding.

Although all communication systems share fundamental elements, the fields of animal and science communication each have different starting points in terms of knowns and unknowns. In animal communication, signalers and signal form already exist and researchers are forced to observe receiver responses in an attempt to determine signal content and receiver psychology. In contrast, in science communication, signal content and receiver responses are identified *a priori* and researchers (and practitioners) are able to modify signaler identity, signal form and signaling environments in order to elicit desired receiver responses. Receiver responses, however, appear to be rarely observed directly in science communication, as assessments of receiver psychology tend to be used as proxies for future behavior.

Animal communication and science communication researchers also tend to focus on different system elements, interactions and directionalities of cause and effect. In animal communication studies there is a strong focus on the signaling environment, on the transmission/reception efficacy of signals with distinct physical form, and on complexity per se; similar ideas appear relatively unexplored in science communication (e.g. to what extent can/should science communication encompass multicomponent/

multimodal signaling). Meanwhile, science communication focuses on eliciting deeper thinking and processing and on relationship building and trust. Again, these foci appear relatively unexplored in animal communication. We suggest that all these areas of focus are relevant to both fields.

Finally, a recent call for incorporating a systems approach into animal communication research encourages the testing of systems-level hypotheses for system design, e.g. increased redundancy (shared structure/shared function) and degeneracy (different structure/overlapping function) provides robustness across changing conditions (Hebets et al., 2016). These same hypotheses are relevant for science communication. Repetition of messages, i.e. redundancy, in fact is known to increase the efficacy of communication. The more frequently information is encountered, the more likely it is perceived as true (Fazio et al., 2015). The use of multiple signalers to convey the same message similarly represents system degeneracy (different structures/overlapping function), and its effect on the efficacy of communication should be investigated. As animal communication research explores the extent to which a systems approach can advance the field, we urge a similar approach for science communication. Importantly, the insights gained from this cross-disciplinary investigation should similarly apply to non-scientific communication (e.g. literature or history) as well.

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