Abstract Non-human animals commonly perform mutual communication in which two individuals simultaneously exchange information in an interaction that can comprise multiple components and multimodal signals. The forms of mutual communication vary widely, ranging from simple greeting ceremonies to complex paired dances including multiple behavioural elements. Our understanding of mutual communication lags markedly because few systematic studies have examined this topic. In this review, we used the example of paired dances in red-crowned cranes (Grus japonensis) to examine two important aspects of mutual communication: structure and function. We reviewed the difficulty analysing the key characteristics of structure quantitatively (e.g. sequential pattern and complexity), and examined suitable analytic methods such as determining the four levels of its characteristics. We proposed that a combination of current methods and new methods, such as the Shannon entropy index and temporal associations among behavioural elements, is necessary to quantify the complexity of mutual communication. Regarding the function of paired dances, we critically discuss the pair bond hypothesis, which suggests that a paired dance strengthens pair bonds in monogamous, long-living birds. Testing this classical hypothesis remains a challenge due to the difficulty of performing quantitative analyses of paired dances and the ambiguous concept of pair bonds. We hope that the questions and predictions raised in this paper will encourage future research on mutual communication in non-human animals.

Key words: animal signals, paired dances, mutual communication, pair bonds, crane

1. Introduction

Communication is essential in all aspects of animal behaviour, such as mating, reproduction, parental care, and competition (Bradbury & Vehrencamp 2011). Many studies of animal communication have focused on one-way communication, in which information is sent from one individual to another [e.g. tail length of male long-tailed widowbirds, Euplectes progne (Andersson 1982); alarm calls of great tits, Parus minor (Suzuki 2011)]. Few studies have investigated mutual communication, in which information is sequentially or simultaneously exchanged between two individuals (Wachtmeister 2001). One example of mutual communication is a coordinated mutual display between long-term sexual or social partners (both heterosexual and same-sex relationships). The form of mutual display varies widely, ranging from a simple greeting ceremony to a complex paired dance including multiple behavioural elements. Mutual displays have been observed in many animals [messmate pipefish, Corythoichthys haematopterus e.g. (Sogabe & Yanagisawa 2008); wandering albatross, Diomedea exulans]
Compared with one-way communication, mutual communication is a complex process with multiple behavioural elements performed simultaneously by two individuals. For example, a paired dance by reproductive partners is composed of two behavioural sequences performed by the male and female at the same time. One individual could have sequential patterns of transition in response to its own behaviour and that of its partner. A long-term, familiar relationship is associated with the complexity of these mutual signals, although whether there is a cause-and-effect relationship remains unclear (see Chapter 3). For example, the red-crowned crane, *Grus japonensis*, performs many one-way aggressive displays to conspecific competitors; the duration of these interactions is brief (ca. < 1 hour), forming a fission-fusion system (Takeda et al. 2015). By contrast, pairs always coordinate their movement and their relationships can span many years (Masatmi & Kitagawa 1975).

Besides coordination with another individual, mutual displays can be complex for different reasons. Mutual displays can be comprised of multiple types of movement at the same time. For example, the red-crowned crane sometimes leaps while tossing small tufts of grass during paired dances (Masatmi & Kitagawa 1975). Mutual display can also be a multimodal signal, incorporating visual displays with kinematic components and acoustic components such as vocalisation. The Laysan albatross, *Diomedea immutabilis*, for example, vocalises during paired dances (Meseth 1975).

The behavioural forms of various mutual displays have been described since the earliest studies of animal behaviour (e.g. Huxley 1914; Morris 1958; van Tets 1965; Masatomi & Kitagawa 1975). These studies have contributed to the compilation of ethograms (lists of behavioural elements) used in mutual displays. To our knowledge, however, most studies have been at the level of description, and no quantitative studies have utilised all of the proxies that can be extracted from mutual displays (see Chapter 2). As a result, the comparison of different mutual displays tends to be based on only a few variables (e.g. number of behavioural elements, length of display), which grasps only part of the complexity and might miss a key hidden feature. Moreover, no systematic studies have tested functional hypotheses. This situation is partially due to the difficulty quantifying the pattern and complexity of mutual dance. No “silver bullet” exists for quantifying the complexity of mutual communication, because any single method is insufficient to describe all of the complex characteristics of mutual communication. Therefore, it is necessary to combine multiple methods to analyse the features of mutual communication.

The objective of this paper was to review the key questions and challenges of mutual communication. As an example of mutual communication, we used paired dances in red-crowned cranes (Takeda 2016). We also discuss implications for human studies arising from studies of non-human animals (see Chapter 4).

2. Do mutual signals have a specific structure?

In mutual communication, animals often perform complex, elaborate displays. For example, throughout the breeding season, monogamous pairs of wandering albatrosses (*Diomedea exulans*) perform paired dances consisting of 22 behavioural elements, with a fixed transition pattern (Pickering & Berrow 2001). Pairs of red-crowned cranes perform mutual dances in all seasons, more frequently between the beginning of the reproductive season (late February) and the mating season (April) (Masatmi & Kitagawa 1975). Paired dances by the cranes consist of 14 types of behavioural elements (Figure 1; Mastomi & Kitagawa 1975; Ellis et al. 1998). Before copulation, a pair performs a fixed and mutual behavioural sequence, which is different from paired dances (Masatmi &
Kitagawa 1975). It is widely recognised that mutual signals have structural patterns; however, the statistical detection and demonstration of these patterns are not straightforward and necessitate a combination of multiple methods. Below, we briefly explain how to analyse mutual communication data, highlighting its multi-layered structure (see also Appendix 1 for the definition of the data unit).

We propose that the characteristics of paired dances can be classified into four levels. The first level describes the components of each element. Behavioural elements can be classified into two types according to length (Figure 2): event type, for short-duration, less variable elements; and state, for elements of variable duration, such that the start and end times are key characteristics. Multiple behavioural elements can be regarded as a single element when the sequence of these elements is fixed (Scholes 2006, 2008). Coding is an important initial step in analysing multi-layered data, such as

![Diagram of paired dances in red-crowned cranes](image-url)
Figure 2. An illustrative example of sequential mutual communication data including events and states. Each letter (A–H) indicates a different type of behavioural element. Circles and squares indicate events and state elements, respectively. Square width represents temporal duration. (a) Raw sequential data; (b) sequential data for a male and female analysed separately, ignoring duration; (c) sequential data based on changes in behavioural elements; (d) sequential data based on time (using a 1 second interval; note that this interval is not suitable because it neglects the occurrence of some behavioural elements). Different sampling results in a different dataset. Note that the current methods are not perfect as some types of sequential data are difficult to analyze (e).

paired dances, because different codings of the primary data result in different data sets and consequently different proxies of mutual communication.

The second level concerns within-individual patterns, such as behavioural diversity and behavioural transitions according to temporal patterns (i.e. the sequence of elements). Such analyses are not unique to studies of mutual communication, and can be used for the analysis of signals emitted by a single individual. The third level concerns between-individual patterns such as behavioural synchrony, behavioural dependency, and temporal association (Figure 3). Finally, the fourth level concerns relationships between male and female performances at the level of the dance bout, such as behavioural symmetry (i.e. correlation of performance between partners; Takeda 2016) and similarities between bouts (i.e. consistency of performance among different bouts).

Although previous studies have focused on individual levels (first, second, and part of the third levels: Pickering & Berrow 2001; first, second, and third levels: Vanderbilt et al. 2015; fourth level: Sogabe & Yanagisawa 2008), no single study has considered all
levels simultaneously. This is unfortunate, as consideration of all levels is necessary to answer biological questions on mutual communication (Takeda 2016).

Below, we review three key sub-questions for investigating the structure of mutual communication focusing on these four levels. Note that we focus on these standard questions in studies of animal communication (Bradbury & Vehrencamp 2011) because of space limitations, although other questions are worth addressing.

(A) Does mutual communication have sequential patterns?

Understanding sequential patterns is essential for understanding the structure of animal signals (Bradbury & Vehrencamp 2011). Various methods used in birdsong analysis can be used to detect sequential patterns (Kershenbaum et al. 2016); however, only simple analyses have been used to study mutual communication (e.g. Pickering & Berrow 2001; Kraaijeveld & Mulder 2001).

Analysis of residuals and chi-square sub-tests (Haberman 1973) has been used to analyze element types, sequential order, and behavioural synchrony within a pair in paired dances. Based on the total number of occurrences of each element, an expected frequency can be calculated under the assumption of random occurrence. If the observed frequency of a given transition is statistically higher than the expected frequency, a null hypothesis (mutual communication has no specific structure or patterns) can be rejected, and the transition can be regarded as a series of characteristic transitions or synchrony.

There are four types of transition in the data in which two individuals perform two elements respectively: (i) from male to female, (ii) from female to male, (iii) from a previous element to the next by a male, and (iv) from a previous element to the next by a female. Synchrony between the male and female can also be tested by comparing the observed and expected frequencies of the co-occurrence of a given behavioural element between two individuals.

Wandering albatrosses perform paired dances, which mainly consist of sequences of rapid head movements, snapping, and preening, during the mating season. Pickering & Berrow (2001) identified significant transitions within a pair of wandering albatrosses using residual analysis (see also Takeda 2016 for red-crowned cranes) of four behavioural sequences: male to male, female to female, male to female, and female to male. Their study showed that 115 of 632 observed transitions were statistically significant, and that there were sex differences in partner responses, with 43% of transitions from female to male being different from those from male to female.

One note of caution regarding this approach is that it is impossible to separate two possibilities. One possibility is that the performance of one behavioural element is a result of within-individual transition and not the result of the preceding behavioural element of the partner. The other one is that...
the performance is a result of a between-individual transition irrespective of its own preceding behavioural element. In order to separate these possibilities, a more complicated method (e.g. transfer entropy; Schreiber 2000) is necessary. In addition, this analysis lacks the power to detect rare transition patterns. This approach also requires researchers to pool data to ensure sufficient sample sizes, but this has two problems. First, pooling data masks inter-bout variation, although dances typically vary among seasons or pairs. Second, the results are subject to the pooling fallacy, i.e. they are likely to be affected by a few exceptional bouts (Martin & Bateson 2007).

(B) To what degree is a mutual signal complex?

Animal signals display various degrees of complexity, which have arisen through adaptive evolution (Bradbury & Vehrencamp 2011). Shannon entropy (information theory) is a suitable approach for measuring the complexity of signals (Appendix 2). These indices can consider information beyond simple measures such as the number of elements in a signal. However, only a handful of studies have used entropy to examine complex displays (Dalziell et al. 2013; Vanderbilt et al. 2015).

The lance-tailed manakin (Chiroxiphia lanceolata) is a lekking species in which two males cooperate to perform complex acrobatic mutual displays such as leaping in turn to attract females visiting an arena (DuVal 2007). Using Shannon’s entropy (see Appendix 2), Vanderbilt et al. (2015) showed that the complexity of this mutual display was affected by the presence of a female. That is, dance performances by two males were better predicted (joint entropy was significantly lower) and coordinated (mutual information was significantly higher) in the presence of a female than in the absence of a female. Conversely, individual dance performances (individual entropy) were unrelated to the presence of a female. Thus, the study found that the presence of a signal recipient was an important factor affecting the complexity of their dual performances.

(C) Which properties are biologically important in communication?

Animals often use sequences to convey meaning to the receiver (e.g. species identity: Gerhardt & Huber 2002; individual traits: Root-Gutteridge et al. 2014; resource availability: Slocombe & Zuberbühler, 2006; predator risk: Suzuki et al. 2016). Which signal components play important roles in mutual communication and what information the signal contains remain largely unknown. This question is particularly puzzling with respect to paired dances because it is typically composed of behavioural elements that are used for different purposes in different contexts. For example, some monogamous animals perform similar displays in affiliative and competitive situations (e.g. butterflyfish, Chaetodon lunulatus (Yabuta 2002); herring gull, Larus argentatus (Tinbergen 1959)). In red-crowned cranes, an arch display is used in paired dances and also signals a threat in competitive situations such as joining a flock (Takeda et al. 2015). It is not rare for behavioural elements used during aggressive and affiliative contexts to co-occur in a single bout of paired dances (Masatmi & Kitagawa 1975). Interpreting such behavioural “recycling” is difficult; two explanations are possible. The first is that information contained in each component (e.g. affiliative or aggressive intention) is preserved in mutual signals, and information indicated by an entire paired dance is the sum of information contained in each component (Takeda 2016). The other possibility is known as the meta-communication hypothesis (Bateson 1955), which suggests that components become meta-communicative signals and have different meanings depending on the presence of other components within the signal. In red-crowned crane paired dances, the original meaning of a given behavioural element (e.g. aggressive intention) might be changed to a different one (e.g. “this is a dance”) by its association with other components. In this way, a recipient may be able to avoid the
misinterpretation of signals, such as the fact that a sender’s aggression-like element is not “real aggression”. The meta-communication hypothesis was supported by a study of play behaviour in Hanuman langurs, *Semnopithecus entellus* (Śpinaka et al. 2016); however, it has been neglected in studies of mutual communication. Although this hypothesis does not explain what information paired dancing conveys, it provides a method for considering how multiple components combine to convey a single meaning. Testing the meta-communication hypothesis in mutual communication scenarios would be an appropriate avenue for future research.

3. What is the function of mutual signals?

From a behavioural ecology perspective, the most intriguing questions concern the function of complex mutual signals. Mutual communication plays an important role in forming familiar and long-term relationships between two performers (Takeda 2016). Particularly, paired dances by monogamous, long-lived birds have been classically speculated to strengthen long-term pair relationships (Huxley 1923; Armstrong 1942; Wachtmeister 2001). The “pair-bond hypothesis” is based on characteristics commonly found in bird species that perform paired dances [e.g. red-crowned crane (Masatomi & Kitagawa 1975); blue-footed booby, *Sula nebouxii* (Torres & Velando 2003); wandering albatross (Pickering & Berrow 2001)]. In these species, both males and females care for chicks and form long-term relationships, with the pair continuing to perform the dance after pair formation. However, rigorous and quantitative tests of this hypothesis have not been conducted, perhaps because a paired dance is difficult to quantify, as mentioned. A more serious problem is that the pair-bond concept is ambiguous. In general, the term pair-bond implies a pair with mutual contribution to reproduction and cooperative parental care (Armstrong 1942; Black 1996). However, it is not easy to devise testable predictions from this concept; efforts made to establish and maintain pair bonds may be qualitatively different. Individuals may need to assess the characteristics of their partner, such as their compatibility, and strengthen their relationship during the establishment of a pair bond. If the pair-bond hypothesis is related to the period of pair formation, it is predicted that paired dance performance will be positively associated with the quality and consequences of the pair bond, measurable in terms such as reproductive success. Conversely, a pair may not need to strengthen, but merely maintain their relationship if the pair has been stable for a sufficient period. The fact that a pair of red-crowned cranes dances after pair formation suggests that mate choice and pair formation are not the only factors explaining paired dances. It is predicted that paired dance performance is positively associated with the length of the pair bond. Thus, an interpretation of pair bonds could produce the opposite predictions. To avoid confusion, it is important to update the concept of the pair bond by developing a measurable proxy. One possible proxy is physiological synchrony. Sexual hormones, such as testosterone, regulate the physiology of reproduction and control sexual behaviours (Adkins-Regan 2005). A previous study in greylag geese (*Anser anser*) showed that within-pair testosterone synchrony was positively related with long-term reproductive success (reviewed in Hirschenhauser 2012). If the synchrony of sexual hormones within a pair is an important factor for boosting reproductive success, pairs may use dance performances as signals representing their physiological states and encouraging reproductive preparation in each other. It would be interesting to investigate a relationship between dance performance and covariation of sexual hormone levels within a pair, as well as how inter-pair variation in dance and hormonal (non)synchrony result in inter-pair variation in reproductive output.

A theoretical study proposed an alternative explanation: that paired dances function to manipulate the sexual partner into providing a greater reproductive effort than usual during the reproductive season (Wacht-
meister & Enquist 2000; Wachtmeister 2001). If members of a pair attempt to manipulate each other, paired dances would become increasingly elaborate and complex as the consequence of an evolutionary arms race within the pair. This notion assumes an evolutionary conflict within a pair during pair maintenance, for example, in the amount of parental care provided by each member. No empirical studies have tested this hypothesis, and its assumptions should be critically examined. When pairs continue their relationships for life (i.e. divorce is rare) and extra-pair paternity (EPP) is low, pairs share an interest in equal reproductive success. In such cases, evolutionary conflicts would not logically be expected within a pair. Although our understanding of the degree of fidelity (divorce rate and EPP) is limited, particularly in socially monogamous birds (Black 1996), this hypothesis may not be applied in such species.

In summary, the function of paired dance remains unknown, partly because it is difficult to manipulate and produce signals used in its performance. Such an experiment may be made possible using robots or video stimuli; however, there are logistical difficulties in instantly matching or changing the movement of a partner in species with complex paired dance behaviours.

4. Conclusion and future directions

Here, we reviewed the key questions pertaining to mutual communication. Our discussion was designed to raise new questions and biologically feasible predictions rather than to answer existing questions. Few studies have been conducted on this topic, and we hope to encourage future research on mutual communication in non-human animals. Below we list three challenges that deserve further attention.

(i) Structure: comparison with birdsong

Current methods are not sufficient to fully grasp the complex characteristics of mutual signals. In studies of animal signals, birdsong has been a popular subject, for which researchers have been developing sophisticated analyses (Kershenbaum et al. 2016). We believe that birdsong analysis methods can be used to analyse paired dances because birdsong and mutual communication share many characteristics (e.g. sequential data containing multiple elements).

However, we should remember critical differences in structure between birdsong and paired dances. It is often difficult to annotate dance sequences due to the difficulty of classifying their components, whereas birdsong annotation can be conducted using a sonogram. It is also impossible to measure the intensity of each dance display using annotation. In contrast to birdsong analysis, where acoustic properties such as amplitude and frequency can be measured, it is difficult to measure the degree to which individuals dance for mutual (physical) communication.

As mentioned, previous studies of mutual communication did not analyse all of the components included in sequential data (see Chapter 1) and, in particular, ignored temporal associations between behavioural elements. Temporal responsiveness is important in judging whether communication actually occurs between signalers and receivers (Bradbury & Vehrencamp 2011). For example, canebrake wrens (*Thryothorus modestus*) perform duets, in which the temporal interval depends on the speed of duet playbacks as stimuli (Marshall-Ball et al. 2006). In red-crowned cranes, each member of a pair successively reacts to the other’s behaviour; e.g. one crane leaps immediately after the other does the same (Takeda 2016). These temporal patterns are thought to be common in mutual communication; however, we lack appropriate methods to quantify this behaviour. It is necessary to develop new methods for analysing temporal association, among performers of mutual communication (Takeda 2016). The development of methodologies will help to quantify paired dances, as well as other behaviours, like play (Palagi et al. 2016) or group displays of three or more individuals (Perrot et al. 2016), that involve similar structures.
(ii) Tinbergen’s four whys

It is also important to consider mutual communication in the context of Tinbergen’s four whys (Tinbergen 1963). We briefly consider three of the whys (mechanism, development, and phylogeny) below, excluding function, although little is known regarding these questions.

Mechanism: To accomplish complex mutual communication, various proximate mechanisms should be involved and selected for. To coordinate movement and perform joint rhythmic behaviour between two individuals, each individual must react to visual and acoustic stimuli by the other individual and its own movement by the sensor-motor pathway. These neural systems have not been studied (but see a case for solo dances: Fuxjager & Schlinger 2015).

Development: The degree to which mutual signals are genetically determined is completely unknown; however, it appears that learning plays a role in their acquisition. In golden-collared manakins (Manacus vitellinus), males learn the precise location of a sapling for jumping during elaborated courtship dances (Coccon et al. 2012). In red-crowned cranes, solo dances by young individuals are simpler than dances by adults (unpublished data).

Phylogeny: A comprehensive survey of the occurrence of mutual communication across species has not been conducted. Although a hypothesis explaining the evolution of paired dance needs to be elaborated, this is not straightforward, due to our lack of understanding of the function of paired dance. It is predicted that both social and ecological factors are associated with the distribution of mutual communication. The pair bond hypothesis predicts that pair cooperation is critical for the evolution of paired dance. For example, pairs may need to cooperate against conspecifics when intraspecific parasitism is high. Soma & Garamszegi (2015) tested this idea for paired dances in Estrildid finches and found that the effect was likely but did not reach statistical significance. A stable environment such as on or around water (e.g. water birds) might be one of important factors, because stable environments can prevent the separation of a pair and help to maintain long-term relationships (Black 1996). A phylogenetic study of New World blackbirds suggested that biogeography, not mating system, affected the complexity of gestural displays (Miles et al. 2017). As in these studies, it would be fruitful to use phylogenetic comparative analyses to test how well species-specific ecological, social, and reproductive factors predict the occurrence and form of mutual communication in other clades.

(iii) Implications for human studies

Researchers will derive two benefits from comparing mutual communication in non-human animals and humans. First, the comparison will elucidate cognitive and psychological components promoting the evolution of human mutual communication. A recent study proposed that rhythmic dances must be unique to humans because dances should require highly cognitive abilities such as the imitation of other behaviours with musical beats (Laland et al. 2016). This idea is controversial (Ravignani et al. 2016), because animals with less sophisticated cognitive abilities can perform elaborate and coordinated dances. For example, although the red-crowned crane has a relatively small brain among avian groups (Lefebvre et al. 2004), they perform complex mutual dances (Takeda 2016). Rather than linking dance and cognitive abilities directly, it is feasible that dance was an evolutionary precursor for components of dance such as musical rhythmic synchronisation (Patel et al. 2009; Hasegawa et al. 2011; Patel 2014). Note that these discussions need not always accompany phylogenetic closeness. When humans and close relatives (e.g. great apes) exhibit a similar trait, it is likely that a common ancestor of those species acquired that trait. Conversely, similarities found in distant phylogenetic groups (e.g. humans and birds) lead us to seek a common characteristic between these species because that
characteristic may explain the evolution of the target trait. Such a scenario can often provide a parsimonious explanation for the evolution of a seemingly complex trait because distant species sometimes exhibit similarities in other traits such as large brain size and sophisticated cognitive abilities. We encourage further research on both similarities and dissimilarities in dances between human and non-human animals.

The second benefit is that researchers of non-human animals can exploit frameworks and methods used in human studies. Studies of mutual communication in humans range widely, including those of humans alone (Tomasello 2010), those comparing humans and domestic animals (Nagasawa et al. 2015), and those comparing humans and robots.

Appendix 1. Definition of data unit

Defining the data unit is an important first step in the analysis of mutual communication. The simplest method is to consider all behavioural elements as “events” and ignore their duration (Figure 2b, c). It is possible to define the time frame with respect to changes to the combination of behavioural elements by either individual (Figure 2c). This definition can incorporate the duration of elements to some extent, but overestimates the length of a given element if a partner changes its behaviour frequently during that element. Alternatively, a behavioural chain can be constructed based on a time frame defined by the researcher (e.g. 0.1 sec), such that a given behavioural event that lasts 5 sec occupies 50 timeframes. This method can incorporate the duration of elements into the analysis to quantify associations between multiple sequences (Figure 2d); however, it will overestimate the transition probability within long-duration elements if autotransitions (transition from one event to an identical element) are not excluded. As such, each method of defining the data unit represents a trade-off. The most suitable method for a study of mutual communication will depend on the study species and the objectives of the study.

Appendix 2. The use of Shannon entropy in analysing mutual communication

Here, we explain the calculation and biological meaning of three types of indices (Shannon, 1948). We denote two dance bouts as $X$ and $Y$, each of which consist of behavioural elements $x$ and $y$.

(1) Entropy: $H(X)$

$$H(X) = -\sum_{x \in X} p(x) \log p(x)$$

$P(x)$ is a proportion of time spent on element $x$. That is, the total number of data units during which an individual performs a behavioural element $(x)$, divided by the total number of data units. $H(X)$ reflects the behavioural diversity of the dance content. A high entropy value indicates that a dance bout exhibits a high diversity of behavioural elements.

(2) Joint entropy: $H(X; Y)$

$$H(X; Y) = -\sum_{x \in X, y \in Y} p(x, y) \log p(x, y)$$

$P(X, Y)$ is the proportion of data units containing two particular elements by two individuals, i.e. the total number of data units in which one individual performs a behavioural element $(x)$ while the other simultaneously performs a different behavioural element $(y)$, divided by the total number of data units. $H(X; Y)$ reflects the behavioural predictability of the dance content. A low joint entropy value indicates that the dance bout exhibits high behavioural predictability within each pair.

(3) Mutual information: $I(X; Y)$

$$I(X; Y) = H(X) + H(Y) - H(X; Y) = \sum_{x \in X} \sum_{y \in Y} p(x, y) \log \frac{p(x, y)}{p(x)p(y)}$$

Mutual information $(I(X; Y))$ reflects the independence of the dance content. A high mutual information value indicates high dependency within the dance.
Signals in these communications commonly multiple modalities and components, and frameworks and methods are well developed relative to studies of non-human animals (e.g., Knapp et al. 2013). Unfortunately, studies of non-human animals have lagged behind in terms of research effort and methods. It would be fruitful for researchers of non-human animals to collaborate with researchers of humans to discover new perspectives.

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