Advanced Review

Animal communication

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Animal communication is first and foremost about signal transmission and aims to understand how communication occurs. It is a field that has contributed to and been inspired by other fields, from information technology to neuroscience, in finding ever better methods to eavesdrop on the actual 'message' that forms the basis of communication. Much of this review deals with vocal communication as an example of the questions that research on communication has tried to answer and it provides an historical overview of the theoretical arguments proposed. Topics covered include signal transmission in different environments and different species, referential signaling, and intentionality. The contention is that animal communication may reveal significant thought processes that enable some individuals in a small number of species so far investigated to anticipate what conspecifics might do, although some researchers think of such behavior as adaptive or worth dismissing as anthropomorphizing. The review further points out that some species are more likely than others to develop more complex communication patterns. It is a matter of asking how animals categorize their world and which concepts require cognitive processes and which are adaptive. The review concludes with questions of life history, social learning, and decision making, all criteria that have remained relatively unexplored in communication research. Long-lived, cooperative social animals have so far offered especially exciting prospects for investigation. There are ample opportunities and now very advanced technologies as well to tap further into expressions of memory of signals, be they vocal or expressed in other modalities. © 2014 John Wiley & Sons, Ltd.

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INTRODUCTION

Of all the many research fields and disciplines involved in the life sciences, communication has probably received the most attention in decades involving innovative research in ethology, physiology, psychology, and relevant technological inventions. Indeed, for human society the last three decades have represented a communication revolution. In the inventive grid that has been generated, from space satellites to computers in the home, from e-mail to internet, and to social media, a new social and political virtual reality has been created. The ramifications are profound. Human communication is practised in such different ways than was conceivable a few decades ago that our definitions and ideas about the abilities of animals to communicate have been changed too. For instance, we now know that vast memory storage can fit into minute structures, and thus can imagine more easily that small brains may not mean small cognitive capacity. We now have good records of vision,[1–3] auditory ability,[4,5] and olfaction,[6,7] as well as research results for electrical[8] and chemical[9] perception and communication in animals.

ANIMAL PERCEPTIONS UNDER THE MICROSCOPE

Nevertheless, the road to a very active and highly successful research field of animal communication was not at all smooth. The Descartian view of animals was anything but conducive for any significant probing into animal communication since animals

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were considered to be no more than automatons, responding to the world in preset ways. Strangely, it was probably the discovery of echolocation that heralded in some change. Initiated in 1938 by Donald Griffin and involving the physicist G.W. Pierce, who developed piezoelectric crystals, ultrasound was transformed into frequencies audible to humans and this was a significant event for researchers in so far as the discovery clearly indicated that humans cannot hear or see, hear, feel, or touch everything other species might be able to perceive. In the 1950s, it was discovered that dolphins also use echolocation.[10] Then, in 1953, and of significant scholarly repercussions, came a substantial critique by the American ethologist Daniel D. Lehrmann of Konrad Lorenz's insistence on innate behavior. The paper 'A Critique of Konrad Lorenz's Theory of Instinctive Behavior' was highly important because, as an alternative, he stressed the role of experience and learning. While highly theoretical, the productive debates that ensued underlie much of the writing on communication to this day even though arguments and perspectives have changed significantly.

We now know that learning is indeed a crucial precondition for much in communication. Living organisms as small as bees can form memories, are capable of learning, and can effectively communicate on the basis of such memory.[11] Moreover, communication spans a vast range of activities from the simplest inherent actions and responses to the most sophisticated processes that presume knowledge of a state of mind of another in order to be made.

In view of the wide span of capabilities by which animals communicate, the field is constantly subject to revision and keeps producing large and often fascinating volumes on the subject. In the last 50 years or so, there have been at least as many books published on animal communication as there are years. Books have been published on specialized means of communication, such as vibrational,[12] ultrasonic,[13] vocal,[14] and concerning taste and smell,[15] visual,[16] nonverbal,[17] and gestural[18] communication, as well as focusing on specific classes of animals, such as communication by anurans or fishes[19,20] and many on communication by primates and birds. For obvious reasons, they cannot all be mentioned. The number of published papers on animal communication is also staggering.

What this review can do is allude to main lines of argument and development and provide insights about alarm calls as just one, albeit pertinent, example of animal communication, note the present currents and influences on the field, and provide a few pointers for future directions based on our own research[21–24] and on rereading the literature in preparation for this review.

This review is largely a testimony to the extraordinary scientific achievements in the field of animal communication in the last 10 years, providing also an historical perspective of how the science of animal communication has progressed in concert with substantial technological and neuroscientific advances.

The review is subdivided into nearly equal parts, moving from definitional problems to vocal behavior generally and alarm calls specifically, and devoting a separate section to referential signals, including intentionality. Presenting specific highlights in the field (out of many possible ones) lends itself to illustrating effectively some of the theoretical tensions and disagreements on one hand while revealing the multifarious and dynamic nature of the field on the other hand. Theoretical antecedents in light of cognition in communication are discussed and a final section addresses some very recent findings in neuroscience and the way in which cognitive processes are being revealed under strict experimental conditions. Concluding remarks argue that the field has moved into a new and exciting phase to address cognition and communication and can do so with confidence because methods have been found that provide a biological basis for cognitive complexity in communication.

DEFINITIONAL PROBLEMS

A simple definition of what communication in animals actually means is almost immediately difficult. Researchers of different theoretical persuasions have tried to reflect the emphasis of their position in the definition they have given for communication.

Any definition of communication is a little uncertain because of the variables involved. It sounds very simple: one needs at least two players (A and B), A sending a signal and B receiving it and changing its behavior as a consequence. However, an utterance that we observe and designate as a signal may not be intended as a signal at all. The individual from whom a sound may have emanated may have produced the call for any number of purposes; e.g., a self-directed call to map out location as echolocation was presumed to do, a call uttered involuntarily when encountering something frightening or unexpected. This makes the original issuer of the call not a signaler while it could still be a signal to a receiver. Even if it is, in fact, a communicative signal (more of that below), points A and B may be divided by time and place (Figure 1).

The signal may be marred by distortions and interferences. It may be instantaneous or slow depending on environment and modality. Warning calls tend

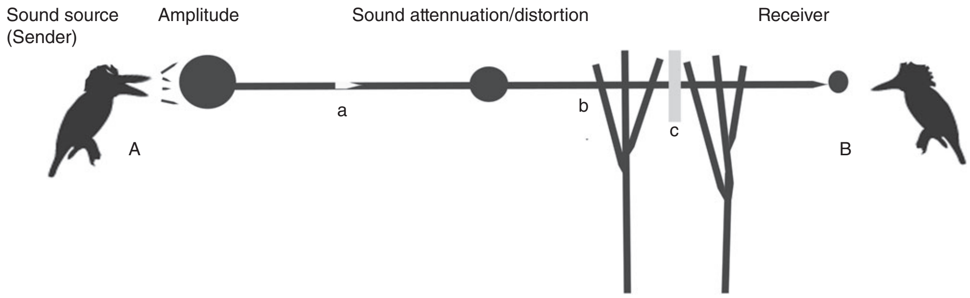

FIGURE 1 | A simple model of vocal communication. Sender (A) on the left, vocalizes and the sounds are heard by the receiver (B). Typically, however, the signal will not arrive in the same state in which it was at the point of departure. Distance alone makes the amplitude of the sound diminish (called attenuation). Other factors can cause a decrease or even a distortion: 'a' signifies another sound source of a similar frequency which makes it more difficult to perceive the signal sent from A past point a; 'b' represents a typical range of possible obstructions, such as trees and shrubs, refracting the sound; 'c' is an often invisible obstruction, such as sounds created by wind, updrafts, and fog, able to distort sounds. At the very least, B will receive a signal of lower amplitude than at which the signal was sent. In other words, noise and distortions can become a real problem for communication.

to be swift, while an odiferous message may take a long time to discover. Such variations in delay time from sending the signal to changing the behavior of the receiver and the intensity of the signal (from obvious to very subtle) mean that any definition of communication has to be quite broad. Animal communication may have evolved specifically to benefit a conspecific receiver and, it can be a very efficient way of avoiding serious conflict. It may also be possible to argue that animal communication has become more complex and cognitively demanding in those instances in which innovations, sociality, and longer life spans fostered the evolution of larger brains and the need for more complex communication (Figure 2).

So far the passage of a signal from A to B would be regarded as successful communication if B changed its behavior in response to the signal. The word 'communication' is and remains thorny and even controversial at some juncture because implied in it may be an assumption that communication means conveying information, when 'information' is understood in the sense of 'meaning'. Others argue instead that such presumption of implied meaning is merely speculative and we should concentrate on measurable signals. Thus, the term 'communication' itself has roused scholars to controversies, also very recently.[25] Although there are many disparate fields that have influenced or shaped animal communication including mathematics, philosophy, and linguistics,[26–29] the real controversy and oppositional stance is between those who followed Dawkins and Krebs and, later, Maynard Smith's notion of animal signals[30–33] and those who insist that information (as content with meaning) is central to animal communication studies.[34,35] Dawkins and Krebs offered a succinct definition, namely, that animal signals are actions or structures that change another organism's behavior and thereby benefit the sender. The problem was that this did not lead to clarity because not all signals benefit the sender and not even all signals require a change in the recipient's behavior. Maynard Smith and Harper added in 1995 that a signal increases the fitness of an individual by altering the behavior of other organisms detecting it, and that the signal has characteristics that have evolved because they have such an effect.[30–33]

While this is a useful and widely accepted definition it is not one that is interested in communication *per se* but specifically in signals. Information and communication do not feature in their accounts. If we turn to the father of modern information theory, we are, in a way, no wiser. Shannon devised a number of theorems now used in modern radio engineering. His most famous theorem $C = B \log_2(1 + S/N)$ addresses problems of communication. Notably, however, 'communication' in the mathematical, engineering sense for sound transmission is not concerned with meaning and contents but with the ultimate carrying capacity of band-limited communication channels, thus far removed from cognitive science. Indeed, psychology relegated the theory to the realm of statistics and mathematical probabilities.[36]

Information as it is used in the context of evolutionary biology, ethology, neurobiology, and philosophy carries first and foremost meaning. Meaning in communication has been extensively explored in human language. Whether we go with Millikan's notion of biologically cooperating mechanisms or use the original linguistic concepts developed by Grice[37–39] about human communication it does not carry us far in animal communication because the bar is set too high in the sense that humans are said to derive meaning from an awareness of each other's state of mind and they can express such an awareness in language (Box 1).

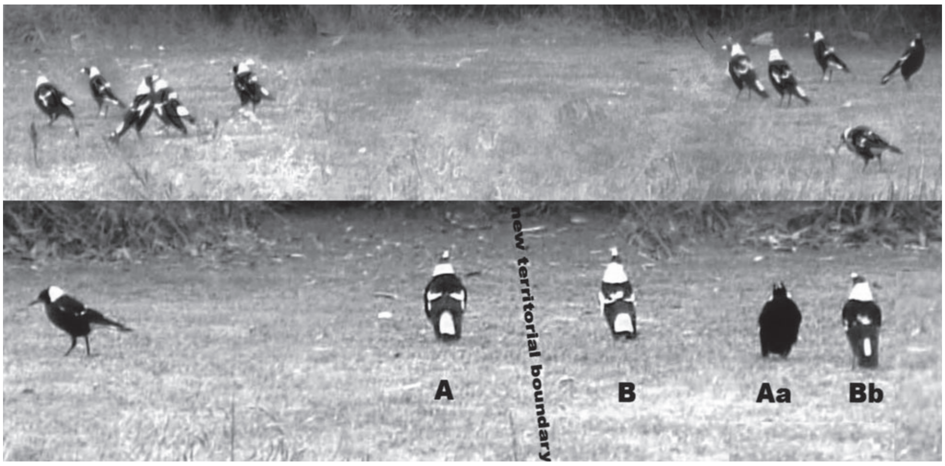

FIGURE 2 | Settling of boarder dispute by negotiation and vocal signal. Australian magpies, *Gymnorhina tibicen*, are territorial birds and use a ritualized caroling call, sometimes in duet with their lifelong partner, to indicate permanent occupancy. At close range, ritualized signals and vocalizations can be a very energy-efficient way of solving a conflict without anyone getting hurt. The territorial boarder is clearly marked on the image. In the upper image two neighbouring magpie groups meet on the ground. Instead of fighting, the two magpie males (A and B), lower image, approached each other from either side of the boarder. Both then paraded in a slow and deliberate way up and down that stretch of boarder. Then they stopped and aligned with each other, both caroling. The female of group A (Aa) then crossed the boarder, thought to be an appeasement gesture, and aligned herself in opposite direction with the other female (Bb). These two are adult females of the respective group and long established breeding pairs. Once the two females had lined up, they too began caroling with each other. In a second round of caroling, A started, followed by Aa, then B, followed by Bb. In other words, the second bout of caroling was a caroling duet of the breeding partners rather than of the ones facing each other off. After a third bout in the same formation, the caroling birds dispersed and walked back to where they had come from (to left of the boarder for A and Aa, and right for B and Bb). Later observations showed that the group on the right did not move past that line, nor did the group on the left. Group B had infringed the boarders but did not do so again. The neighbors had reached a genuine and lasting peace for the season. (Adapted from Kaplan, see Ref 24.)

BOX 1

WHAT IS INFORMATION?

Information theory is the quantitative study of signal transmission and is largely applied to information technology and communications engineering. However, the term ‘information’ is a widely used term in everyday language and generally denotes the acquisition of knowledge from others or from the environment (i.e., nongenetic knowledge) that, as Dachin et al.[40] argue, includes everything that reduces uncertainty.

Information falls into several different categories and it may be important for studies in animal communication to distinguish between the various categories. (1) Personal information only known to the individual or its group, usually about physical habitat and resources. (2) Social information (personal information can become public through various means of communication or vicarious acquisition either via (a) inadvertent cues (e.g., locational) or (b) via some measure of public performance. (3) Overt signals intentionally communicated in any relevant modality, abbreviated as ISI (inadvertent social information) and PI (public information). Inadvertent private information can turn into PI and both ISI and PI can turn into cultural (widespread) practice. In animal communication, most studies are conducted in the first category while we have relatively few examples (but increasing) of the third (intentional signaling). It is this second category that has been largely neglected. Yet cooperative species in particular may derive their information from the group specific social context for which most of the signals are meant.

However, new methodologies and changed attitudes to animals have made it possible to ask new and different questions and research designs have similarly changed (in innovative ways) to address the problem of ‘meaning’ and cognition in animal communication. Research has found that there are ravens that console a distressed mate, and South African babblers in a cooperative framework, negotiate their future contributions to the raising of offspring well before this is put in practice.[41,42] In those cases, there is no doubt that awareness of the state of mind of the other has to precede the actual behavior. While this is cognitively complex, and it may be specific to a group and a lifetime, other much simpler changes occur that are adaptive and stable and may require rather little individual cognitive ability. Those theoreticians who prefer to study animal communication as signals are skeptical of overinterpretations and inferring too much from animal signals. The risk for cognitive ethology on the other hand is to underestimate the simple process and the importance of associative learning, be this from cues in the environment or from conspecifics. It remains the most important dictum in science to be as parsimonious as possible, perhaps especially so in the interpretation of behavior.[43]

It is thus also important to be methodologically aware that signal characteristics may be learnt or not, or intentional (as is implied by the notion of 'sending a signal'). Indeed, deciphering signaling between parties (knowing or not) is part of the fascination in many of today's research efforts. It also depends where the emphasis is placed: (1) on the signaler, (2) on the means of achieving specific signals, (3) on the nature and type of signal, or (4) on the receiver. The possible juxtapositions are numerous.

VOCAL BEHAVIOR

Among the many forms of vocal behavior (from single elements to syllables to ornate song), almost all of which have been studied extensively, alarm calls have proven to be particularly useful to study precisely because alarm calls/mobbing calls or warning calls are typically short, can be easily measured in terms of origin, use, and response, and because they may also be fueled by either the motivational or intentional systems. Tinbergen[44] recognized four motivational states: hunger, aggression, sex, and fear. Alarm calls may fall into at least one or two of these motivational states (fear and aggression). They may be intentional (more of this below) in the sense at least that they are implicitly a mechanism for providing a warning of a specific risk as perceived by the caller to others, hence *ab ovo* involving at least a dyad if not more (signalers or receivers).

Research has also identified how interaction with the environment or certain physiological events can alter signals or outcomes. For instance, there is substantial variation in an individual's vocal performance, and many of these variables have been well researched in avian species. Photoperiod,[45] change of season,[46] overall health, genetic endowment, sex, and age are just some of the variables that affect performance and expression of vocal repertoire, and, more importantly, may also reveal certain qualities and traits to the receiver. It has been shown that manipulation of hormone levels can induce singing and even alter the song control regions in the brain.[47–51]

Alarm calls, and also mobbing calls, have presented researchers with a puzzle though (which may also explain the long-standing research in this area) since they may not just indicate the presence of a predator but signify a multitude of other things, such as an attempt by an individual to muster support from conspecifics or even from heterospecifics.[52,53] They may be issued to not only alert others to the presence of a predator but also draw the predator's attention to the signaler, i.e., the calling may be interpreted as a behavior that is at once life preserving, selfish, altruistic,[54] or seemingly suicidal by drawing attention to itself and increasing the risk of capture.

There have been many explanations that may hold in specific situations, one being the 'pursuit deterrent' hypothesis that argues that the calls may deter predators from further pursuit because they signal the fitness of the prey.[55,56] In such cases, the calls are thought to be directed not toward conspecifics but to the predator. In some visual displays, usually toward ambush predators (such as felines and some birds of prey), open presence, sometimes accompanied by displays of physical prowess in some ungulates, called 'stotting', is now a well-recognized method by some prey species to let a predator know that their surprise attack has been foiled by discovery and that the fitness and alertness of the intended target would make capture unlikely.[57,58] A further function identified as beneficial for the prey is alarm calling for the purpose of changing the behavior of offspring; silencing nestlings, or making juvenile ungulates freeze and hide until the mother indicates by calling that the danger is gone, can save lives.[59]

Many contextually specific uses of alarm calls have been identified (see also recent review[60]). They may be used for brood training and protection, as has been described in the moustached warbler showing that survival rates increased when a strong positive correlation existed between a parent issuing antipredator alarm calls and a chick's ability to perform appropriate antipredator responses.[61] Alarm calls have been described as an investment in mates[62] and as anticipation in future reciprocity.[63] The hypothesis proposed by Ridley et al.[64] is reciprocal altruism, suggesting that mutual protection of the group, while appearing altruistic at the time, will ultimately benefit the survival of group members. Krams et al.[65] drew similar conclusions in pied flycatchers.

That song in songbirds is learned in an overwhelming number of species is no longer a matter for debate, after nearly 100 years of research in this field.

It is extremely well documented in zebra finches,[66] in white-crowned sparrows,[67] and in nightingales[68] and in several other songbirds. In the psittacine group (parrots, cockatoos),[69] corvids (ravens), and the cracticidae (including Australian magpies), studies have shown that against predictions many of the short vocalizations, i.e., utterances other than song, are learnt behaviors[70] and that alarm calls are referential and stable signals.[71] Many birds that are capable of lifelong learning (i.e., having a plastic brain) and can acquire new vocalizations tend to live in cooperative family groups and may need such versatility for complex social interactions. Such abilities may derive from a high-capacity memory system documented largely in songbirds and primates.[72]

Yet most documented examples of teaching and skill acquisition in animals, and these are surprisingly scant as a recent review found,[73] are not related to communication but to the business of living in general. For instance, teaching offspring has been found in relation to hunting skills (ranging from otters to lions and eagles), then, in much smaller measure, to foraging skills, motor skills, food, and/or predator identification. Only a very small number of publications on active teaching of offspring are related to skills specifically related to communication.[73] We cannot tell at this point whether this distribution of skill attainment by active teaching reflects actual practice or is the result of researcher bias. Teaching itself requires some form of communication and performance by the recipient. It is fair to say that the rush to identify signals in all its possible variations has led to a certain neglect of developmental aspects. It also seems that there is a tendency to assume that learning largely occurs as observational and associative learning rather than via active teaching. Yet some avian species and some primates have an exceptional long period of development and spend considerable time growing up in their natal or family group, surrounded by group members or at least accompanied by one parent. In the latter scenario, it is not far-fetched to postulate that acquisition of communicative skills is favored in social species.

REFERENTIAL SIGNALS

The idea of motivational versus intentional signals has been raised repeatedly. The former refers to an internal event, the latter to an actual external event. Connected with it is the need for an individual to indicate clearly what it is that is to be imparted to a conspecific. A referential signal is a stable and universally understood signal (at least by conspecifics in a regional context if not further afield) that has a semantic content rather than being generalist. For instance, in case of this being an alarm call instead of warning that there is a predator about, the call would specify which species type (snake, bird of prey, or feline). It is or can be intentional, in that it is other-directed and refers to very specific things that the signaler has observed and passes in the signal.[74] Following the work by Cheney and Seyfarth in the 1980s,[75] studies of ground-dwelling mammals—including squirrels, meerkats, marmots, and Diana monkeys[76–79]—have shown animals to have a demonstrated ability to discriminate between different dangerous species and produce alarm calls that can even identify the type of predator in the call itself.

There is probably not a single extant avian species without some means of issuing an alarm call. To do so referentially, however, could not be assumed because it could simply derive from affect (i.e., reflect a motivational state). To ascertain this, such calls had to be tested experimentally. In quite a few cases of disparate avian species, for instance, as in chickens, in bobwhite quail *Colinus virginianus*, ravens *Corvus corax*, yellow warblers *Dendroica petechima*, black-capped chickadees *Poecile atricapilla*,[80–84] and Australian magpies *Gymnorhina tibicen*[64] referential alarm calls were found. That is, it was clearly shown that the species in question referred to an identifiable external stimulus (as compared to its own motivational state). Referential signals so far discovered and studied include both alarm calls and food calls, be this in primates or in birds.

In 2007, Evans and Evans[85] made an important distinction between referential and representational calls. In a controlled set of experiments the researchers established that referential and representational calls may not have the same visible impact on the receivers of the call. In referential signals, particularly in alarm calls, there is an immediate response by the receiver. In representational calls responses may not always be forthcoming. Representational calls, such as a food call, may relay the correct message of food availability[86,87] and even be specific as to quality and amount[88] but, as Evans and Evans[85] found, the recipients responded when they had not fed but did not respond if they had recently fed. Hence, the signal may well have been heard and understood but not always acted upon. This means that the recipient's understanding of that signal may well remain unobservable. In terms of definitions of animal communication as signals that require a change of behavior in the receiver, the discovery undermined one of these key definitional pillars. Moreover, not acting may also involve active decision making.

In summary then, there are multiple possibilities of what recipients will and can take from signals.

Hence, the basic definitional condition that a message needs to show a change of behavior in the recipient simply does not and cannot describe all forms of interaction when, arguably, communication has occurred.

By contrast, the 'message' in the alarm call may not just contain a general warning that a predator has been spotted but the recipient may also decode from it the predator's size,[88] the urgency or nearness of danger,[89] or even something about kinship, status, age, status, and sex of the caller.[90] Recipients may vary their responses accordingly. For instance, in Californian ground squirrels at least, information about age of caller prompts a different response in listeners.[91] Alarm calls by juvenile vervet monkeys tend to get ignored because they are unreliable and at times incorrect but the same vervet monkey juveniles may learn to recognize the alarm calls issued by starlings.[92]

The fact that animals may recognize signals of heterospecifics and act on them is intriguing because, in those cases in which alarm calls are clearly not part of a species' genetic makeup, their recognition has to include some form of learning. Recognition, in this case, has to include its specific representational value of a real event or a potential danger (warning of a predator). There has often been a nagging question whether certain similarities of a heterospecific signal may not be enough to trigger the same response as the one used by a specific species.[93] However, when a starling utters a referential alarm call, the characteristics of the bird calls are substantially different from the sound characteristics of any vervet monkey vocalizations. If they have rather little in common why should a starling's alarm call trigger an appropriate response in a vervet monkey? Sound properties are an unlikely source of such a response. Hence, acquisition of knowledge by experience and based on a set of specific and reliable cues may teach a monkey to heed the bird's call each time. The starling's call has thus meaning.[94]

Referentiality is not confined to auditory expression although they are the only ones capable of being expressed across substantial distances. Visual signals tend to be at close range, within sight of the receiver. Claims that they may be semantic or functionally referential have usually not been made. Indeed, visual signals, apart from those associated with mating, have all too often tended to be ignored and yet they often play a significant role in the communication of animals. Gestures in apes and other primates, however, are a very important exception[18,95,96] because gestures are processed in the equivalent area of the brain as speech in humans and hence these visual signals have been seen as putative precursors to language development.[97] Not surprisingly, gestures have been studied extensively in primates.

Until very recently, there was no expectation that referential gestures would be possible in species other than primates, because it was thought that hands and arms were needed to engage in pointing and gestures. Recent research by Kaplan[98] has found, however, that the Australian magpie *G. tibicen* is able to point referentially, as shown in a series of controlled experiments in the field using a taxidermic model of a wedge-tailed eagle *Aquila audax*, one of their predators.[98] The first magpie, on discovering the eagle, vocalized and used its beak to point at this half hidden eagle placed under a small tree. The subsequently arriving magpies then watched the pointing of the first bird, followed its direction, and then also pointed until the entire group was present. The pointing gesture was not carried out so that the magpies could get something for themselves (as in gestures used in begging for food), but to let the remainder of the group know of the presence of the eagle. The posture was exaggerated and differed markedly from other postures.[97] Referential pointing has now also been shown in ravens.[99] Australian magpies are a social species, as are common ravens and primates, and their survival hinges on cooperation which may foster the evolution of complex signals. Cooperation and group living may thus be important variables to consider in the study of communication. Indeed, Bouchet et al.[100] found, when comparing some primate species, that social complexity parallels vocal complexity.

THEORETICAL DEVELOPMENTS

Researchers in the 1950s and 1960s were obviously fully aware of the risks of overtheorizing the behavior of animals and instead opted to simply record and document what they saw and heard. They tended to categorize calls and visual displays and placed the emphasis on the sender and on specific functions, most of which had to do with basic survival tasks, such as actions concerned with reproduction, food, predators, territory, or offspring. Signals were not labeled as such, instead authors described behavior as display behavior or vocal behavior and thus avoided many of the pitfalls of communication theories while providing a wealth of knowledge. They did so in such engaging ways of writing and provided meticulous details that the accounts of displays and other behaviors are still important and a pleasure to read today.[17,101,102] Specifically, they left behind a detailed record of ritualized behavior, such as greeting and courtship displays offering invaluable and never repeated insights into the daily lives of birds and other animals.

Ritualized behavior, no matter how complex, may consist of one simple and unambiguous message. Males may advertise themselves as outstanding breeding candidates or the display may say 'stay away' when territorial boundaries need defending. Courtship rituals, by contrast, rely on careful mutual attention of two players who need to coordinate their activities rather precisely if an agreement for a union is to be forged. One of the best known and most dramatic courtship rituals that seals a lifelong bond and largely relies on motion and body posture is performed by grebes (Podiceps ssp.) as a dance on water. In horned grebes *Podiceps auritus*, the male 'bounces' forward, dives several times, then both male and female rise to full height by treading water, facing each other in what is sometimes referred to as a 'penguin' display; they continue to dance in that posture until finally swimming apart. Lyrebird males (Menuridae sp.) are famous for their dancing as well as for their vocal displays in courtship dances.[103,104] The most exceptional and unique display is one performed by the Albert lyrebird and was first described by Curtis[103,104] but went largely unnoticed by the world. The male displays on a mound in the depth of forests of Eastern Australia and dances, revealing a specialized set of feathers (the lyre) that is shimmered during the dance. While he dances he also sings in the loudest and most melodious pure tones of any bird known. Most of the sequences of song are mimicked snippets from other birds, cleverly choreographed (with transitional segments, lead-ins, and fade outs of an accomplished musician), and delivered forcefully. However, the piece of the display that is most astounding is the male's ability to add yet another dimension to the performance, namely percussion. With his left foot, he holds on to a vine that typically grows to full height of trees particularly in wet rain forests. Then he pulls on the vine and does so rhythmically, fitting with his song and dance, a movement that generates a clearly audible rustling and swishing and becomes a percussionist addition to the performance. Why this is remarkable is that animals have been consistently thought of as being incapable of producing rhythm, a trait thought to be unique to humans.[105]

Most of the papers on displays remained descriptive and, while fascinating, were not designed for formulations of theories of communication. In the 1980s, however, a major shift in thinking about and researching into animal behavior is usually attributed to a paper reporting the very specific meaning of alarm calls of vervet monkeys showing that adults had different calls for various predators call.[106] Male vervet monkeys, *Cercopithecus aethiops*, make a deep barking call for a leopard and females make short, high-pitched chirps in the same circumstance. A chutter-like call is made for a snake and a single cough-like call for an eagle. Seyfarth and Cheney[106] found that, when the call they had identified as indicating the presence of a leopard was played back, the monkeys would dash to the nearest tree and climb it. On hearing the snake call, they would stand up on their hind limbs and peer into the grass. When the eagle call was played, they would look up and take cover. Some years later, as already mentioned, it was found that chickens make different calls for aerial predators than they do for predators on the ground.[74] The researchers played back to hens the recorded calls made by the cockerel in response to seeing a ground and an aerial predator in a controlled setting, i.e., a cage in the laboratory. Here the hens could not see any predators and were not exposed to any other stimuli that might cause them to vocalize. They tested each female chicken individually playing the two kinds of alarm signals through a loudspeaker. When the aerial alarm call was played, a chicken hearing it crouched and looked up as if trying to catch sight of the predator in the air. When the ground-predator alarm call was played, the chicken hearing it ran for cover or strutted while calling in a way that might drive the predator away. Thus, the two alarm calls have specificity and signal to the receiver to take the appropriate measures to avoid being caught. In both cases, be it vervet monkey or domestic chicken, it was shown that two species, far removed phylogenetically from each other, had developed signals that were functionally referential. They further tested and were able to show that these calls were produced intentionally.

The operational definition for intentionality was rather simple and ingenious. To be regarded as an intentional signal, the caller needed to make the call only when it had an audience. That is, even when seeing the predators, no calls should be issued if there was no audience. Indeed, this was the case.[80–84] Hence, the interpretation that animals just act in affect and cannot help themselves but utter emotive calls was disproven.

By having shown the various segments that make for unmistakable acts of communication, the groundwork was laid for claiming and investigating communication in animals in which both the signaler and the receiver (or reactor) understand the context and can act accordingly.

Intentionality has been a topic of great interest in philosophy for centuries partly because it seems to attest to freedom of choice and thought. In science, by contrast, preference was at first given to thinking of such acts, even if intentional, as adaptive, i.e., as part of a template and genetically fixed. Seyfarth and Cheney,[107] however, also dispelled this notion by showing that juvenile vervet monkeys made mistakes when practising their own version of issuing warning calls. In other words, it became clear that this behavior had to be learned, involved recognition of the animals that are dangerous (despite similar silhouettes, neither a vulture nor a stork but only an eagle is dangerous), and clearly involved memory of predators, attributing the correct call to each and making a call only when others were present to be warned. Learning and cognition were involved and this set the scene for an entirely different and new line of investigations about animal behavior in general and animal communication in particular. It also became clear that such investigations would benefit greatly from some degree of interdisciplinarity and indeed the field of animal communication has interacted with and mutually benefited from neuroscience, specifically neurophysiology, and neuroethology, comparative psychology, ethology, ecology, even musicology, and developmental biology and acoustics.

However, at the same time as these discoveries were made, the theory proposed by Wilson[108] in 1975 was powerful enough to almost halt progress in the cognitive line of investigations (except in primatology) for another two decades. Wilson said that communication is an action by one organism that alters the behavior pattern of another organism in a fashion that is adaptive to either one or both of the participants. The word 'adaptive' is important here. Wilson said that by 'adaptive' he meant that the signaling, or the response, or both, have been genetically programmed by natural selection.[108] Hence, this definition confines communication to events (for signaler and receiver) that have become part of the genetic characteristics of the species. Means of communication that are learnt during the individual's lifetime, and may be passed on from one generation to the next by cultural transmission, are not included in Wilson's definition of communication. Of course, genes always play some role in behavior—for example, genes determine whether we have hands or wings and such factors influence what kinds of signals can be sent. But that is not what Wilson meant by adaptive signaling; he meant that the behavior of signaling, or the behavior of the response itself, is to a large extent controlled by genes. The book by Dawkins[109] followed just a year after Wilson's but while following closely in Wilson's footsteps it radicalized the theoretical perspective of the drivers for behavior. For Dawkins, behavior was only a by-product of the actions of the genes. Accordingly, all that needed to be established was whether an action had benefits or costs. The advantage of this perspective was that all life was interconnected by playing a preinstalled game. Actor and reactor were playing out the same game of self-preservation. The model was built on conflict and competition and sported a vocabulary and considered scenarios deeply indebted to capitalism. The vocabulary is the same and the goals are the same. Everyone is in it to win and will fight for dominance, driven by a basic instinct, or rather by genes programmed to reproduce themselves. In this concept, altruism was logically impossible and cooperation was seen as a means to a selfish end at best.[110,111] Dawkins produced the logically most coherent, if not brilliant, communication theory ever considered but it was deeply pessimistic if not cynical and ultimately also flawed. Indeed, it seemed that cognition had disappeared entirely and was almost superfluous and itself suspect of human overinterpretation. Decision making as an act representing choices had all but disappeared and developmental studies were out of favor.

What followed was the application of game theory to animal interactions which, as has recently been argued, has played a major role in reshaping our view of animal communication, transforming it from a mutualistic sharing of information into a self-serving contest between 'mind readers' and 'manipulators'.[112] However, true to the characteristics of selfishness, human imagination soon discovered that selfishness, as manifested in signals, can include deception, manipulation, and coercion to name a few key features, qualities that can be adaptive, as in plants and some animals, but they can also be based on cognitive processes, decision making, and experience.[113,114]

In so doing, cognition came back in by the backdoor into various theories, such as theory of mind applied to great ape research projects and finding its most fascinating expression in a book by Whiten and Byrne[115] called *Machiavellian Intelligence*. Indeed, deception has been documented in species other than primates. Møller, for instance, showed deception in status signaling in house sparrows, *Passer domesticus*,[116] and false alarm calls for the purpose of resource usurpation in domestic chicken,[117] in great tits, *Parus major*,[118,119] and similarly in drongos, *Dicrurus paradiseus* that managed to trick mixed-species bird flocks for resource usurpation.[118,119] These observations about false signaling have sneaked into accounts in such a way that the cognitive complexity cannot be denied. However, even in deception it is not always achieved by false alarms or calls. For instance, something I observed in South America, a capuchin male discovered a rich food source in fallen fruit. He was alone. He saw it, turned around, and when no-one was looking he gorged himself on the fruit, making no sound whatsoever. Then he took fruit in his hands, as many as he could carry, hid under a tree, and continued feeding rapidly. He then dropped the last bit of fruit, walked on and away from the scene, waited, then turned around, and gave a food signal. Others joined him soon after and the group was feeding together. In other words, the food signal was 'honest' but he had simply delayed it to ensure that he had his fill first. While coercion and aggression may not demand any cognitive capacity, deception and manipulation do. The more intelligent an organism is, the more devious it can also become. There may be punishments and corrections if found out[120,121] but such signaling is clearly rule-breaking and designed to deceive. It must be based on a decision that the individual made.

NEW EVIDENCE: NEW DIRECTIONS?

The most recent theoretical development that has had, and no doubt will continue to have, a crucial impact on many fields but especially on cognition and communication comes from the astounding findings in neuroscience. In 2009, Rendall et al.[122] were still able to argue that animals may only appear as if they understand (for instance a semantic contents of vocalizations) but that it was virtually impossible to prove this (for review, see also Ref 123) and hence, by implication, it was beyond scientific inquiry. That impasse is increasingly broken via the progress that is being made in neuroscience, following behavior while simultaneously tracking brain activity, eye movement, or vocal tract activities. First, the mapping of the song control system in birds,[124,125] followed by the identification of a speech-related center (used for gestures) in monkeys and apes,[126,127] told us precisely about the relationship between specific signals and brain activity. In the case of birds, this research has identified where, how, and what learning occurs in the acquisition of song and the capacity for long-term memory of vocal signals.

Indeed, between 2004 and 2008 the cognitive field of avian and primate studies advanced in such fundamental ways that it is almost impossible to conceive of how we thought before these discoveries were made. First, mirror neurons in macaques were discovered and described in a series of papers by a team in Parma, Italy, showing that movement can be learned by encoding movement of others in the observer's brain and then imitated against this representation.[128] In 2008, Prather et al.[129] discovered that there are mirror neurons for vocalizations in birds, used for learning and learned vocal communication. They showed convincingly that a bird listening to a conspecific's vocalization activates neurons that would also fire had the bird sung the same passages itself. It also explained why birds can mimic sounds not part of their own species repertoire (and thus not part of its own genetic template).

In addition, technology concerned with communication and with acoustics has moved so far ahead that we can measure accurately just about any sound from infrasound to ultrasound and anything in the visual spectrum. Acoustic specialists have pushed the science of sound to new heights and neuroscience now has sophisticated neuroimaging. Here methods have become very important. Researchers, such as Suthers, have perfected techniques to test vocal production in living birds[130] and Marzluff was perhaps the first to show how a supposedly esoteric topic like face recognition in corvids and concomitant brain activity could be demonstrated in a living bird using neuroimaging.[128,131] Moreover, mirror neurons have implications not just for imitation, learning, and memory formation but also for intentionality. Iacoboni et al. went so far as to entitle one of their papers 'Grasping the intentions of others with one's own mirror neuron system'.[128]

Also new are research designs that investigate the ability in human actors to select communicative actions, i.e., actions directly designed to modify the mental state of another agent without using language or traditional communicative channels. Studies by Galantucci[132] or Noordzij et al.[133] demonstrate that neural correlates of intentional communication can be shown to exist by using a simple movement of geometric shapes that the sender knows but the receiver does not, forcing the sender to find ways of communicating without words. By using an event-related functional magnetic resonance imaging design, they were able to isolate cerebral activity evoked when planning a communicative action and when interpreting the meaning of that action. As Noordzij et al. show, and I quote: 'These cerebral responses, in both sender and receiver, were localized in the right posterior superior temporal sulcus (pSTS), a region previously associated with attribution of intention and they were independent from sensory inputs and motor outputs'.[132,133]

It has been legitimate to remain skeptical when assumed cognitive processes could only be inferred and the results at risk of being overinterpreted. However, neuroscience has become instrumental in putting the arguments about the absence or presence of cognitive processes from inference of observed behavior squarely back into biology by producing evidence of highly specific forebrain activity. Such methods seem to offer great potential for future research in animal communication. Brumm[134] argues that many specializations have come together or overlap to have produced the achievements so far.

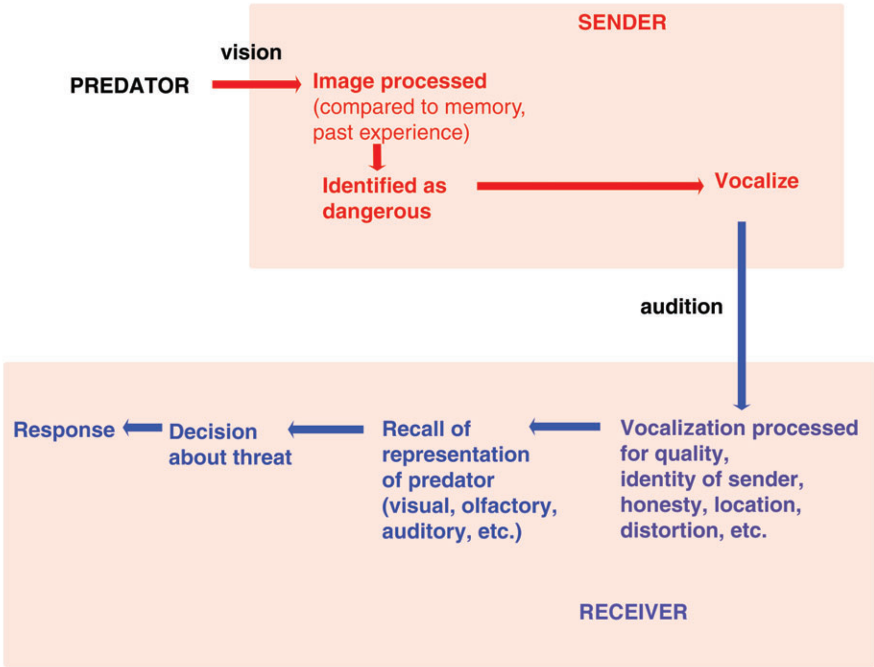

FIGURE 3 | Diagram describing the process of signal transfer. A sender may see a predator (visual experience), the image is processed in the brain (representational integration or dissociation). The image is recognized (memory) and identified as representing danger—then this bundled information, consisting of the visual image just seen plus the interpretation of it drawn from memory (be it acquired by experience or learning), is followed by a translation into a different modality, as a vocal signal—heard by receiver—and in this case there are even more processes involved because it may involve assessment of quality of signal, origin of caller, seriousness of event, location, and urgency plus judging the auditory signal across space taking into account attenuation and possible distortion; then the receiver translates the auditory signal received into a representational/visual concept and on this basis makes a decision on whether or how to act in response.

THE FUTURE: CONCLUDING REMARKS

Neuroethologist and ornithologist have been hand in glove for decades of research on song and primatologists have worked on cognition of apes together with neuroscientists and psychologists to identify precise areas of the brain involved in gestures used to communicate. How differentiated are the visual and vocal/auditory pathways used in communication and what kind of processing takes place and in which hemisphere of the brain? In human infants, for instance, sensory pathways are relatively undifferentiated and lead to cross-modal influences in infants' perception.[132,133]

Signals in the environment are rarely monomodal but multimodal. Important to add here is that even a signal in one modality (say a visual signal) usually cross-cuts modalities in a single organism in the sense that objects perceived visually are translated into auditory signals (Figure 3). How do these translations from visual to auditory and back to visual work? Are there specialized mechanisms or is this reliant on general cognitive capacity that involves the integration at many levels in the brain including the hippocampus, the Wulst, and the amygdala? How does cross-modal integration work in animals,[135] is there a hierarchy in which stimuli are processed? Does an organism respond faster if it is in one modality or another? How does the initial assessment by the animal come about? And in which region(s) of the brain is it processed? For instance, we discovered in free-living Australian magpies (only the second avian species tested in the natural environment) that assessment as opposed to attack of a predator is processed in different hemispheres.[136] Magpies used the left eye/right hemisphere (LE/RH) prior to withdrawal and the right eye/left hemisphere (RE/LH) prior to an approach. Viewing prior to approach was low arousal (alert posture not adopted) and withdrawal of high arousal. Withdrawal is therefore a behavior that results from processing visual information in the RH (receiving inputs from the LE), whereas approach follows processing by the LH (inputs from RE). The RH appears to control most aspects of predator–prey interactions, suggesting that a suite of antipredator strategies may have been organized within the RH.[137] But we do not know whether signals about predator–prey interaction are therefore also largely processed by the RH.

Cognitive scientists distinguish between several core knowledge systems, such as those related to physics, mathematics, geometry, and psychology. The debate is very well summarized in a recent review by Vallortigara et al.[138] It also suggests that signals could be investigated in terms of the knowledge systems we already know are well developed in birds and primates and even in some invertebrates so far tested.

That the research in the field of animal communication has entered a new phase is obvious in the many recent and vigorous debates. They are not all going in the same direction. Sociobiologists continue to assert, although at a very sophisticated level (and having left the backdoor open for cultural transmission via 'memes'), that genes determine everything and at the other end of the spectrum are those who think animals are capable of free thought. Others argue that there is too much anthropocentric interpretation. By using the words 'information' and 'meaning' when describing signals, we have borrowed terminology from linguistics that may be misleading and a disservice to science.[122] Animals are said to respond to underlying acoustic structures and that, so signal research argues, are what we should look at.[123] In a recent review of referential communication in mammals, it was admitted that we do not know enough (actually: next to nothing) on how animals categorize their environment.[139] Such categorizations are perceptual and suggest that varying sensory dimensions are continuously transformed into symbolic equivalence classes for producing reliable behavior.[64,140] How varying acoustic structures are perceived and categorized might therefore provide crucial insight into the cognitive domains of animals and there is no reason to presume that they are the same categories that humans have made for themselves.

Importantly, there are also questions about a relationship between sociality and signal complexity, and between long periods of maturation and cognitive ability. The point has recently been made that long-lived species are more likely to be social, or rather, from an evolutionary point, that group living fosters longer term survival.[64,140]

Group living with horizontal and vertical hierarchies have been said to constitute the preconditions for complex communication and higher cognition. These capabilities have been associated with and explored in communication among great apes, dogs, wolves, and dolphins.[141–143] Only in recent years has a link been made between these social variables and the expression of complex cognitive abilities in the vocal behavior of mammals and avian species.[25]

There is an international society for the study of attention and performance.[144] While their interest is in the human species, every single part of their work would be important to investigate in animals and be very interesting in the study of animal communication. First of all, a very basic concept that seems to get lost at times is that communication is dynamic and it is a process. It derives from one living organism with a certain age, ability, life experience, and individual confidence to identify something in the environment worth telling others about or even advertising or getting frightened by—be this triggered by a food discovery, territorial incursion, a predator, an irregularity, or a novel object and it may require translation from one modality into another (Figure 3). We know far too little of the brain mechanisms underlying cognitive processes in making and receiving signals and should be emphasizing questions of why, what, and when information from the environment is processed; also whether there are substantial species differences and what these are.

For example, a recent review of functionally referent signals[145] reminded us that signals may be intrinsic (internal events of caller) or extrinsic (concerning something in the environment) and that we have evidence of referential signaling of far too few species. That is true but how will the next ones be chosen and for what good theoretical reason? It would appear to be very fruitful to test species known to be cooperative group living animals and long-lived. It is noticeable that avian species that have been chosen tend to be natives of the Northern Hemisphere. However, most of the cooperative and long-lived avian species are natives of the Tropics and the Southern Hemisphere and the underrepresentation of such species in any debate (even when there are research publications of such species already available) has limited the opportunities to test hypotheses of signal characteristics against parameters of life history (and high brain to body weight ratios). To date, we have no evidence as to whether signal characteristics alter or multiply in number or get more into the multimodal range or become even more subtle with sociality. It is not just affect but reliable and possibly even more precise signaling that may be important, as diversification of signals might imply.

The field is wide open and it would appear to be premature to pit effect of signals against 'information' or to suggest that the framework for functionally referential signals has been either so undermined or exploded[146] that we can drop it as a useful term. In fact, a new chapter has just started and it is largely unexplored.

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