Animal signals: always influence, sometimes information

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Because signals evolve to influence the behaviour of receivers, we believe the term ‘influence’ provides the basis for a general definition of animal signals. We will argue that the reason a receiver’s behaviour is influenced by signals is often, but by no means always, because the receiver gains information as a result of attending to the signals. We suggest that definitions of information that focus on what the receiver gains by assessing signals are the most useful, allowing an organism’s response to signals to be discussed in the same framework as its responses to other important aspects of its environment, rather than setting communication apart from the rest of behavioural and evolutionary ecology. Our view of signals, then, is that they evolve to influence the behaviour of receivers, and that the information gained by receivers is one possible means by which signallers exert their influence. We make our case by discussing four examples, some of which are new to this literature.

10.1 Introduction

Owren, Rendall and Ryan have challenged definitions of animal signalling in terms of information. For example, they reject definitions of animal signalling “as a process in which evolutionarily specialised morphology or behaviour in a signaller is used to encode and convey information to a perceiver, who in turn relies on evolved neural and perceptual processes to decode and recover the information” (Owren et al., 2010, p. 758). They prefer to define
animal signalling as “the use of specialized, species-typical morphology or behaviour to influence the current or future behaviour of another individual” (p. 771). We agree that a definition of signalling that is based on ‘influence’ should extend to all examples of animal communication. If signals do not influence the behaviour of receivers in a way that benefits the signaller, on average, it will not pay animals to signal, and communication would not be maintained by selection. We also agree that there are animal signals that influence without providing information; we give an example of this below. However, we believe that animals can be influenced by signals because of the information they gain from them; again, we give an example below. Although we believe that animals can gain information from signals, like Owren et al. we are uncomfortable with the idea that when animal signals are informative, there must be a signaller encoding the information and a receiver decoding that same information; a third example, described below, makes this point. We think that receivers can gain information even if senders do not intend to provide information, and we discuss below a fourth example, of human language users who cannot fully identify other people’s informational needs.

We adopt the position that receivers sometimes gain information from signals, in the same sense that they gain information about other aspects of the environment by sampling the environment with their sensory systems (Dall et al., 2005; Wagner & Danchin, 2010). Given that signals evolve to influence the decisions of other individuals, one useful definition of information based on statistical decision theory is “the change in a receiver’s estimated probabilities that a given condition is currently true” (Bradbury & Vehrencamp, 2011). Some of those arguing against the ‘information perspective’ are in agreement that receivers at least sometimes gain information by attending to signals. For example, Morton and Coss (this volume) state that “information or content is just whatever the signal is correlated with and what perceivers infer or ‘make’ of the signal given their own private information, context, age, sex etc”. Information in this sense is not the ‘phlogiston’ invoked by Rendall and Owren (Ch. 6 of this volume), or the ‘transmitted information’ that Morton and Coss (Ch. 8 of this volume) do not find in signals; as noted by Bradbury and Vehrencamp (2011), it does not ‘flow’ between signaller and receiver. In Bradbury and Vehrencamp’s sense, animal decisions are based on information about relevant aspects of the environment, which sometimes include signals. For example, a butterfly gains information about host plants from the shape of their leaves (Parmesan, Singer & Harmis, 1995). But animals can also gain information from signals, as when a honeybee learns the location of a foraging site from the dances of a nestmate (Seeley, 1995).
10.2 Signals that reduce information

In this section, we describe an example of communication during mate localisation by insects. We focus on a signal produced by competing males, which influences receivers not because it allows them to gain information, but because it interferes with their perception of other signals. We think the utility of this example for the information-versus-influence debate is that both sides can agree that the signal does not provide information. Instead, the question is whether it should be considered a signal at all. We will argue that a common function of signalling is to reduce the information a receiver can obtain from other signalers, and that excluding this function from the definition of ‘signal’ would be counterproductive.

In many insects, mate choice involves an ongoing back-and-forth alternation of signals, or ‘duet’ between male and female (Bailey, 2003). Duetting occurs in some fireflies, katydids, grasshoppers and cicadas, and is especially common in insects such as leafhoppers that communicate with substrate-borne vibrations (Bailey, 2003). In most cases, it is the female who remains stationary while the male searches. During the duet, the female signals immediately after the male’s advertisement signals, and the male finds the female by attending to directional cues provided by her signal.

Duetting systems are vulnerable to eavesdropping by competing males, and a variety of specialised signals have evolved in this competitive context (Bailey, 2003). In general, signals produced by the duetting male reduce the benefit of eavesdropping (e.g. by preventing a listening male from detecting the female’s response; Hammond & Bailey, 2003), and signals produced by the eavesdropping male either disrupt the ongoing duet (Cooley & Marshall, 2001; Mazzoni et al., 2009a, 2009b) or cause the female to respond preferentially to the eavesdropper (Bailey & Field, 2000). Here we focus on an example from the research of one of the authors, which involves signal masking that occurs during mate-searching when more than one male is present.

The treehopper *Tylopelta gibbera* is a small, sap-feeding insect whose signals are transmitted as substrate-borne vibrations through the stems and leaves of its herbaceous host plants (Legendre, Marting & Cocroft, 2012). Males search for females by producing two-part advertisement signals (Figure 10.1A): the first part is a whistle-like downsweep (the ‘whine’), and the second is a higher-pitched series of pulses. If an unmated female finds the signal sufficiently attractive, she produces a vibrational signal of her own, a low-pitched drone rich in harmonics (Figure 10.1A). The male then engages in a localised search, walking along the stem and up side branches, stopping every few centimetres to produce a bout of one to five advertisement signals, each of which usually elicits a female reply.
If a second male is on the same plant with a duetting pair, he immediately begins producing advertisement signals. The female replies to both males, producing her signal immediately after the signals of first one male, then the other. She mates with the first male to arrive. Tellingly, mate localisation takes longer when more than one male is present (Legendre et al., 2012). Each male produces not only advertisement signals, but also a new kind of signal, carefully timed to overlap with the pulses of the other male’s advertisement signal (Figure 10.1B, 10.1C). The masking signal impedes localisation by suppressing female responses: masked advertisement signals are only about one-third as likely to evoke a female reply. Masking benefits the signaller because when the female does not respond to a rival, the rival fails to gain information on whether the female’s signals are arriving from ahead or behind, and from what distance. Duetting between a female and each of two males results in a series of complex, fast-paced acoustic interactions as each male alternately

\[ \text{Figure 10.1 Spectrograms of the vibrational signals of duetting } Tylopelta \ gibbera \text{ treehoppers. A, Male advertisement signal and female response. B, Masking signal overlapping the pulses of a competitor’s advertisement signal. C, Playback to a male } T. \ gibbera \text{ of four computer-generated duets, with three masks produced by the focal male; the first and third masks overlap with the virtual male’s pulses, while the second follows closely after the virtual female response.} \]
produces advertisement signals (which may be masked by its rival), masks any advertisement signals of the rival male and moves to a new signalling location.

Our working hypothesis is that the psychophysical basis of the reduction in female responses lies in signal masking (Legendre et al., 2012). That is, the overlapping signal masks the pulses produced by the first male, where ‘masking’ is defined as an increase in the threshold for detecting one stimulus, caused by the presence of a second stimulus (Gelfand, 2010). Consistent with the interpretation that masking signals interfere with the female’s perception of the pulses, females seldom reply to playback of signals lacking any pulses after the whine (P. R. Marting & R. B. Cocroft, unpublished data). We do not argue that no receiver can gain any information from the presence of masking signals (e.g. that there is more than one male present), but that the reduction in female responses to masked advertisement signals results directly from decreased audibility of the pulses. It is not simply a consequence of the female’s perception that there is a second male present, because during experimental playbacks of unmasked signals from more than one male, females typically reply to almost every signal (Marting & Cocroft, unpublished data). In our view, masking signals are an example of signalling that is best understood on the influence, rather than the information, definition.

Our argument in favour of an influence definition of communication in T. gibbera rests on the claim that the masking vibrations produced by competing males are signals. However, someone committed to an information account could simply counter that if the masking vibrations do not provide information, they are by definition not signals.¹ We argue below that this solution has undesirable consequences. The main issue is that reducing the information that receivers can obtain from rivals is a common function of signals, sometimes involving specialised signals, and sometimes involving the timing of an individual’s mating signals relative to those of neighbours. Excluding from consideration as signals all cases in which information is decreased, rather than increased, would require arbitrary distinctions, and separate out phenomena that are best considered under the same theoretical umbrella.

The masking vibration of T. gibbera is only one of many examples of signals whose function is to interfere with communication. Masking signals have been found, for example, in some species of katydids (Bailey, MacLeay & Gordon, 2006; Bailey & Field, 2000), periodical cicadas (Cooley & Marshall, 2001) and

¹ We thank Ruth Millikan, Ulrich Stegmann and an anonymous reviewer for pressing this point.
leafhoppers (Mazzoni et al., 2009b). Because duetting is widespread in vibrational communication systems, an under-studied modality (Cocroft & Rodriguez, 2005), there are probably many more examples of vibrational ‘interference’ signals remaining to be described (e.g. Miranda, 2006).

In addition to the use of specialised masking sounds or vibrations, individuals in many species use their advertisement signals to mask those of competitors. In choruses of acoustic frogs and insects, the timing of a male’s signals relative to those of its neighbours can have a profound effect on attractiveness. For example, when one advertisement signal follows closely after another, females in many species prefer the leading signal (Greenfield, 2005). This ‘leader preference’ can result from a number of mechanisms including the precedence effect, which is thought to be an adaptation for enhanced signal detection in the presence of echoes: when the same sound arrives from two directions, separated by a short time delay, the listener will detect both but only localise the first (Gelfand, 2010). Although males cannot lead all other signallers in a chorus, they can attend to the signal timing of their closest neighbours, and adjust their own timing accordingly (Snedden, Greenfield & Jang, 1998); males likewise attempt to initiate their signals at times outside the ‘forbidden interval’ after the start of a rival’s signal (Höbel, 2011). A male that signals just before a rival reduces the information a listener can obtain from the rival’s signal. There is a clear parallel with the masking vibrations of T. gibbera, which likewise reduce the female’s information about the rival’s signal, albeit through a different psychoacoustic mechanism. In the case of chorusing species there has been no specialisation of functions into one signal that provides information and another that reduces information; instead, the advertisement signal has both functions, with the interference function depending entirely on signal timing.

Because communication often occurs in a competitive context, it is not surprising that a common function of signals is to interfere with the signals of

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2 In some Australian katydids, competing males have a complex repertoire of signals used during competitive mate localisation. Duetting males may produce loud series of clicks immediately after a female reply, preventing eavesdroppers from detecting the female (Bailey et al., 2006); eavesdropping males may ‘over-sing’ a rival’s advertisement signal, preventing a female reply (Bailey et al., 2006), or they may produce a short series of clicks during the rival’s signal, causing some females (which approach the signalling male in that species) to localise the eavesdropper instead of the duetting male (Bailey & Field, 2000). When a duetting periodical cicada male detects the arrival of a second male, it produces a ‘buzz’ during a key portion of the rival’s mating song, preventing the female from replying to the rival (Cooley & Marshall, 2001). In a leafhopper, males that detect a male–female vibrational duet produce a series of rattling pulses, timed to overlap with the male signal or the female response (Mazzoni et al., 2009a); so effective is this signal at disrupting courtship that playback of artificial ‘disruptive signals’ can prevent reproduction in these grapevine pests (Mazzoni et al., 2009b).
rivals. Currently, the literature on animal communication treats the examples of competitive masking and other forms of interference as signals (using terms such as ‘masking signals’ or ‘disturbance signals’). Likewise, the issue of signal timing within choruses is simply treated as a general issue in communication, of when a signal should be produced to maximise its effectiveness (Greenfield, 2002). But if the response of an ‘information’ proponent to the masking signals of *T. gibbera* is to argue that they are not signals, then this response also requires the development of a new classification scheme, separating out signals from other signal-like behaviours. Ultimately the distinction would have to rely on function: if the function of a signal-like behaviour is to interfere with communication, then it is not a signal. In operational terms, this will depend largely on timing. For *T. gibbera*, the whine component of the advertisement signal and the masking signal are both sinusoidal vibrations with a fundamental frequency around 500 Hz. If a male *T. gibbera* produces a 500-Hz vibration that is followed by a series of pulses, and does not overlap with the pulses of another male, it is a signal; if it overlaps with the pulses of another male and is not itself followed by a series of pulses, it is a non-signal. For chorusing species, a mating song produced in isolation is a signal, but one produced immediately before the mating song of a rival has both signal and non-signal functions.

We suggest that it would be arbitrary to exclude ‘interference’ from the list of possible signal functions, or to classify similar phenotypes into signals and non-signals based on their timing relative to the signals of competitors. A strict information view would seem to require this approach. In contrast, the view that signals evolve to influence the behaviour of receivers allows us to view all of these phenomena as signals under one theoretical umbrella, and in so doing better reflects the complexity of communicative interactions.

10.3 An informative signal

In this section, we briefly review the honeybee waggle dance, one of the most widely known examples of animal signalling. We discuss it here because we think that it provides a particularly clear instance of the utility of the term ‘information’ in explanations of animal signalling.

Honeybee scouts that return to the colony after foraging in a flower patch may advertise their find with a waggle dance, performed on the vertical surface of the comb. The dance is a ‘miniaturised reenactment’ (Seeley, 2010) of the trip to the patch of flowers, with the direction and distance to the patch reflected in the dance. The dance consists of a series of straight waggle runs, during which the dancer runs forward for a few centimetres while vibrating its body from side to side and buzzing, then circles around to the beginning (von Frisch, 1967). The
direction of the waggle runs relative to vertical is correlated with the direction to the flower patch with respect to the Sun; for example, when the dance is oriented straight up, the patch is directly in line with the Sun. The duration of the waggle runs is correlated with the distance to the patch (Seeley, 1995). During a dance, one or more potential recruits follow closely behind the dancing forager (von Frisch, 1967).

For a human observer, the dance contains enough information to plot the colony’s foraging locations on a map. The information is obtained not only by human observers, but also by bees. When dance followers were captured upon leaving the hive and released some distance away, their flight paths took them straight to what would have been the location of the experimental feeder (Riley et al., 2005). Importantly, dance followers sample the odour present on the dancing forager (Díaz, Grüter & Farina, 2007), and they engage in a localised search for flowers with that odour once they have arrived at the target location (Seeley, 1995). Dance followers are flexible in how they integrate the information from floral cues and waggle run angle and duration; individuals that had previously foraged at flowers with a similar odour, but at a different location, may disregard the vector information from the dance and leave the hive to forage at the familiar location (Grüter, Balbuena & Farina, 2008).

Dancing bees influence the behaviour of their nestmates; and in addition to any motivational effect of their dancing on dance followers, it would be difficult to provide an account of the evolution of the dance language without reference to the information receivers gain about the location of the flower patch and the scent of the floral resource. Accordingly, while the lesson we drew from the duetting example was that the term ‘information’ should not be required in all accounts of animal signals, the lesson we draw from this one is that neither should we exclude information from all accounts of animal signals.

10.4 Informative signals from uninformed signallers

Our third example illustrates that the idea that an animal can gain information from a signal does not require the assumption that animals send information in signals (Morton & Coss, Ch. 8 of this volume; Bradbury & Vehrencamp, 2011).

The example we focus on here is collective signalling by broods of offspring of the thornbug treehopper, Umbonia crassicornis. Female thornbugs lay a single clutch of eggs on a host-plant stem, and then remain on that stem for the rest of their lives, caring for their offspring (Wood, 1983). After hatching, the offspring cluster together around the stem, feeding through incisions in the bark made by the female. The nymphs are frequently attacked by invertebrate predators such
as wasps and stink bugs, and their only defence is the mother’s active protection (Wood, 1976; Cocroft, 2002).

Immature thornbugs solicit the mother’s protection with collective signals. When a predator approaches, the nearest individuals produce signals with two components. One is a substrate-borne vibrational ‘chirp’ (Cocroft, 1996); the other is a tactile signal consisting of a side-to-side movement of the abdomen (Borduin et al., 2008). Signals of the first individuals initiate a wave of signalling that sweeps through the group. Although the vibrational chirps are transmitted within a millisecond or two throughout the 10–20-cm-long aggregation, the wave of signalling takes up to half a second to reach the other end of the group; the spread of signalling within the group depends largely on the transmission of tactile signalling behaviour from each individual to its immediate neighbours (Borduin et al., 2008; Cocroft et al., in preparation). The result of this spread of signalling across a group is a collective, group signal that is longer and higher in amplitude than the individual signals; indeed, individual signals can no longer be distinguished within the group signal, except for one or two that occur at the beginning or end (Figure 10.2A). Alarmed groups produce collective signals every 1–2 seconds (Cocroft, 1999). Note that only the few initiators of the collective signal are responding directly to perception of a predator; most of the individuals producing the signal are responding only to the behaviour of their neighbours.

Female thornbugs are normally sedentary, facing their offspring from a few cm away (Figure 10.2B). In response to collective signals, a female will walk into the brood and attempt to locate the predator. The female must approach the predator closely, because her defences (wing-buzzing and kicking) work only at very close range (Wood, 1976). The farther an attacked nymph is from the female, the longer it takes the female to arrive and the less likely the nymph is to survive the attack (Cocroft, 2002). Because the female must approach the predator to drive it away, and because her movement is relatively slow, there is a premium on efficient localisation of the predator. If the female can see the predator from a distance she will move directly towards it, but with small, inconspicuous predators such as stink bugs, the female relies on the offspring signals for clues to the predator’s location. Almost all predator attacks occur on one of the two ends of the cylindrical aggregations (Cocroft, 2002), so the female’s main problem is to determine which end has been attacked.

Females use the offspring’s collective signals to locate the predator (Ramaswamy & Cocroft, 2009). How is this possible, given that most of the offspring have no personal information about the predator’s presence or location? First, females respond only to collective signals, and not to single or uncoordinated signals (Cocroft, 1996). And given the dynamics of how collective
signals are generated, the properties of the overall signal reveal the predator’s location within the brood (Ramaswamy & Cocroft, 2009). A number of aspects of the collective signals are correlated with the predator’s location, one of which is a signalling gradient. Because there is a process of attrition as the signalling behaviour is transmitted across the brood, individuals closer to the predator are more likely to participate in a given collective signal (Figure 10.2C; Ramaswamy & Cocroft, 2009). In the absence of any cues apart from the offspring signals, females can locate a ‘virtual predator’ using this signalling gradient (K. Ramaswamy & R. B. Cocroft, unpublished data).

Female thornbugs, then, gain information about the existence of a predator, and about its location, from the signalling behaviour of their offspring. On the
Bradbury and Vehrencamp account of information, there is a change in the female’s estimated probability that there is a predator, and a change in her estimated probability of the location of the predator. However, there are many signallers rather than one, and the feature(s) of the signal that reveal the predator’s location are a property of the collective signal, not the individual signals. Although one could argue that the ‘information’ account works here if one considers the collective signal rather than the individual signallers, it remains true that the signal giving the female information about predator presence and location is not sent by a signaller who possesses that information; there is no signaller that has the information, encodes it and sends it along to the female. Very few of the signalling nymphs can see the predator; the rest are signalling either in response to the chirping and tactile signalling of a neighbour, or to the chirping of many individuals in the group. It is the signalling of the group as a whole that provides information to the mother; the signalling of those few nymphs who know of the existence and location of the predator is not enough. So there is no signaller who sends or encodes the information that is gained by the mother.

10.5 Human language and mental state attribution

Some participants in this debate think that differences between animal and human communication are relevant to whether we can speak of animal signalling in terms of information. In this section we focus on one purported difference, that humans intend to provide needed information whereas animals do not. Rendall, Owren & Ryan (2009) say that “the failure of calling animals to take account of the informational needs of listeners corroborates a growing literature showing that non-human primates show little of the perspective-taking and mental state attribution abilities considered to be foundational to the referential quality of human language” (p. 235). We do not believe it has been established that perspective-taking and mental state attribution abilities are foundational to the referential quality of human language, and we do not think that the failure of animals to take into account the informational needs of listeners provides evidence that can be used to determine whether we can speak of animal signalling in terms of information. In our opinion, there is evidence that some human language users – speakers with Autism Spectrum Disorder (ASD) – have limited ability to attribute mental states, and thus limited ability to identify what information is needed by a listener, and yet use referential language. Our final example makes this point. Furthermore, we believe that it remains to be seen to what extent non-human primates can take the perspective of another, or attribute mental states to another. We conclude that
there is as yet no reason to think that this particular difference between typical humans and animals is relevant to the question of whether animals gain information from signals.

Rendall et al. (2009) argue that animals do not have the mental capacities that underlie human communication; they argue that a series of studies have shown an “absence of the intent to inform by calling animals (D. Cheney & Seyfarth 1990; D. L. Cheney et al. 1996; D. Rendall et al. 2000)” and that “callers prove to be fundamentally unaware of the informational value of their own signals” (p. 235). Owren et al. (2010) argue that

[Human] communication shows intentionality. In other words, humans routinely taking [sic] the beliefs, motivations, and knowledge of listeners into account when speaking to them, thereby communicating more effectively and efficiently. (pp. 768–769)

In contrast,

non-human primates have limited understanding of the mental states of others – an ability considered fundamental in using language. (p. 769)

Similarly, Cheney and Seyfarth (2005) argue that

If, as Grice (1957) and others have argued, true linguistic communication cannot occur unless both speaker and listener take into account each other’s state of mind, then monkeys cannot be said to communicate unless they use calls like contact barks with the intent to provide information to others. (p. 138)

Cheney and Seyfarth go on to argue that baboons do not communicate with contact barks; their evidence is that female baboons answer contact barks from a relative only when the answerer is separated from the group, not when the answerer is herself at no risk of becoming lost. Thus both proponents of signalling as influence and proponents of signalling as information have a shared assumption about human communication – that it requires the capacity to take into account the state of mind of the listener, and thus take into account what information he or she needs. Furthermore, humans, but not animals, have the intent to provide needed information.

Both Rendall et al. and Cheney and Seyfarth are motivated in part by Grice, who held that for a person to mean something by what she says, she must have communicative intentions towards her audience (Grice, 1989). But the Gricean account is far from accepted doctrine. Human conversation is a highly complex form of behaviour. To participate fully and smoothly in a conversation, a speaker must grasp the syntax and semantics of a language, and have
substantial pragmatic ability; she must be capable of assessing how much or little to say, when to say it, how to say it and so on. Competence with pragmatics clearly requires the ability to consider what another believes or knows. But we have little reason to suppose that the ability to represent the state of mind of a listener is a prerequisite for the acquisition of the syntax and semantics of a natural language; so we do not have the evidence required to support the thesis that having communicative intentions towards an audience is necessary for what one says to mean something.

One line of evidence against the Gricean account comes from language development in young children. On the Gricean account, in order to mean something, a speaker must intend that a listener form a belief, and furthermore, she must intend that the listener form that belief because he recognises that the speaker intends that he form that belief. This is a complex intention, and it has been argued that young children become competent with syntax and semantics before they become capable of having such a complex intention (Risjord, 1996). A second line of evidence comes from research on language development in speakers with ASD, which suggests that syntax and semantics can be acquired without at least some elements of the capacity that typically developed adults have to represent the state of mind of a listener. This is the example we focus on here. Competence with syntax and semantics is sufficient to provide information, even though it is not sufficient to provide the most apt information. So while we agree with Rendall et al. that effective and efficient human communication seems to depend on a rich ability to attribute mental states to others, that is not to say that we cannot glean information from speakers who are not fully sensitive to the mental states of others.

ASD is a developmental disorder with onset before the age of three; it is characterised by qualitative impairment in social interaction, qualitative impairment in communication, and restricted, repetitive and stereotyped patterns of behaviour, interests and activities (American Psychiatric Association, 2000). There are two features of ASD that are of particular interest here, mind-blindness and impairment in communication.

Baron-Cohen, Leslie and Frith (1985) first proposed that children with autism lack a theory of mind; to have a theory of mind is to be able to ascribe psychological or mental states such as beliefs and desires to themselves and others (Premack & Woodruff, 1978). Someone who lacks a theory of mind cannot use beliefs and desires to predict and explain the behaviour of others (Baron-Cohen et al., 1985). Baron-Cohen et al. held that to be capable of attributing a belief, one must be capable of attributing a false belief, so on their view, the inability to attribute a false belief indicates the lack of a theory of mind. In Baron-Cohen et al.’s study, 85% of neurotypical children could attribute a false belief to others.
or to themselves, as could 86% of children with Down’s syndrome, but only 20% of children with ASD could do this.

With regard to communication, people with ASD exhibit a broad range of ability with language, as DeVilliers et al. explain:

Though some individuals with ASD, especially those with Asperger’s syndrome, are able to develop typical speech and language abilities, many speakers with ASD have immense trouble understanding metaphor, irony, sarcasm, indirect speech acts\(^3\), and conversational implicature\(^4\). In contrast, even these pragmatically challenged speakers often exhibit surprising competence when it comes to abilities that are widely assumed to be properly linguistic, for example, complex syntax, phonology, and compositional semantics. They may exhibit some difficulties, specifically flat intonation and some highly idiosyncratic meanings for lexical items. Notoriously as well, many speakers with ASD exhibit delays in acquiring language. However, for the most part, the language-related difficulties of so-called high functioning individuals with autism do not lie on the ‘encoding/decoding’ side; instead, they have to do with appropriate use. (DeVilliers, Stainton & Szatmari 2007, p. 296)\(^5\)

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\(^3\) An example of an indirect speech act is “Can you pass the salt?” which has the sentence structure of a question but is usually meant as a request. More generally, indirect speech acts are speech acts where the force of the speech act is not encoded by a performative verb in the sentence (such as ‘order’, ‘ask’, ‘inform’) or by a sentence type (the three major sentence types in English being the imperative, interrogative and declarative). See Levinson (1983).

\(^4\) A speaker conversationally implicates that q by saying p by exploiting conversational maxims (Grice, 1989). For example, it is a maxim that one should be as informative as is required. Failing to follow this maxim can communicate information. For instance, if Grice is asked to provide a recommendation letter for an applicant for an academic job, and the letter says only that the applicant has good handwriting, he fails to follow the maxim and conversationally implicates that the applicant is not a good candidate for the job.

\(^5\) At the time of writing, DSM-IV is the most recent edition of the American Psychological Association’s diagnostic manual for psychiatric disorders. The diagnostic criteria for ASD in DSM-IV require that there be at least one of the following impairments: (a) delay in, or total lack of, the development of spoken language (not accompanied by an attempt to compensate through alternative modes of communication such as gesture or mime); (b) in individuals with adequate speech, marked impairment in the ability to initiate or sustain a conversation with others; (c) stereotyped and repetitive use of language or idiosyncratic language; (d) lack of varied, spontaneous make-believe play or social imitative play appropriate to developmental level (p. 75). The diagnostic criteria for ASD are expected to be modified for DSM-V, which has an anticipated publication date of 2013.
The individuals with ASD who are of interest to the current topic are people whose syntax, phonology and compositional semantics are complete. Glüer and Pagin (2003) review the literature and show that there are individuals with ASD with intact syntax, phonology and compositional semantics who are incapable of attributing false beliefs to others; i.e. they do not have all the capacities of non-ASD human beings to take into consideration the state of mind of another, yet become competent with representational aspects of human language (Happeé, 1993, 1995; Baron Cohen, 1997). They can judge sentences as right or wrong, and distinguish between what is said to be the case and what is the case (Baron-Cohen, 1997), “thus indicating an understanding of the representational character of the utterances” (Glüer & Pagin, 2003, p. 33). Thus, contra Rendall et al., these speakers are competent with the referential qualities of human language, but have atypical ability to take someone else’s perspective, or attribute mental states to someone else. They may find it difficult to interpret metaphor (Happeé, 1993), identify a joke (Baron-Cohen, 1997), comprehend irony (Filippova & Astington, 2008) or contribute appropriately to a conversation. In short, speakers with ASD cannot fully take into account the informational needs of others; yet we can gain information from what they say. Thus we believe that the fact that animal signallers do not take into account the informational needs of others has no bearing on the question of whether animals can gain information from animal signals.

More recently, Wellman and Liu (2004) argue that theory of mind has a number of elements that develop in stages; typically developing children first understand that different people may want different things, then that different people may have different beliefs about the same thing, then that not seeing leads to not knowing, then they understand false belief, and then they understand that people can feel a different emotion from the one that they display. Peterson, Wellman & Slaughter (2012) found that the last two stages were reversed for ASD children. Thus passing the false belief task that played a key role for Baron-Cohen et al. (1985) is a relatively complex task, and an autistic speaker who cannot pass this task may nevertheless have a more limited theory of mind. One might speculate that the mental state attribution and perspective-taking that comes along with recognising diverse beliefs and with understanding that not seeing leads to not knowing would be enough to underpin the referential qualities of language that concern Rendall, Owren and Ryan.

However, this more nuanced conception of what constitutes a theory of mind does not undermine our main point, that there is no reason to suppose that the intent to provide needed information is relevant to the question of whether animal signals should be understood in terms of information. We have two reasons for thinking this. The first is that Peterson et al. (2012) controlled
statistically for individual differences in language ability, and showed that the
development of theory of mind represents conceptual developments other than
increasing language competence; so their study does not support the idea that
language development and theory of mind somehow develop in lockstep.
Second, Kaminski, Call & Tomasello (2008) and Hare, Call & Tomasello (2001)
have evidence suggesting that chimpanzees recognise that not seeing leads to
not knowing, the step on the Wellman and Liu scale that in typically developing
children falls right below false belief, and that chimpanzees recognise that
different chimpanzees have different beliefs depending on what they have
seen. If these are the abilities that are required for referential language, then
at least some non-human primates may have what it takes.

We wish to emphasise that we do not maintain that animals have the same
abilities in perspective-taking and mental state attribution as we do; and we
do not maintain that perspective-taking and mental state attribution are
completely irrelevant to the development of human language in children.
Furthermore, we do not maintain that human language could have evolved as
it has if humans did not have a rich theory of mind. Rather, we think that it has
not been established that perspective-taking and mental state attribution
are required in order for human language to have its referential properties.
The evidence that would be needed to support the thesis that the intent to
provide needed information is a marker that distinguishes animal communica-
tion and human communication is currently unavailable.

10.6 Conclusion

The strength of the ‘information’ approach is that, if we avoid assuming
that higher cognitive processes are necessary and use a clear definition that
focuses on what receivers can gain from signals, it allows us to talk about how
receivers assess signals in the same terms we use to talk about how they assess
other stimuli in their environment. Furthermore, for cases such as the honeybee
waggle dance, insisting on avoidance of the term ‘information’ would unneces-
sarily constrain our ability to describe the behaviour and its function in the life
of the colony. Animals can gain information from signals even if that informa-
tion is not packaged up by senders, as the collective signalling of treehopper
nymphs shows, and even if the sender cannot assess what information is
required by the receiver, as the case of human speakers with ASD shows.
The strength of the ‘influence’ approach is its fruitful emphasis on the mecha-
nisms and evolutionary history of signal production and perception. Because
only signals that influence receivers will be maintained by selection, a defini-
tion of communication based on ‘influence’ should extend to all examples
of communication. Furthermore, there are clear examples of animal signals, such as the masking signal of treehoppers, which influence the behaviour of receivers, but from which the receiver does not gain information. On the whole, then, we believe that the ‘influence’ approach provides a strong framework for understanding animal communication, but that it would be incomplete without the acknowledgement that providing information is one way that signallers can influence receivers.⁶

References


⁶ We thank Ulrich Stegmann, Ruth Millikan and two anonymous reviewers for comments.


Commentary

Horisk and Cocroft’s chapter offers us some fascinating examples of insect behaviour. I wonder, however, whether its central engagement is more than a verbal dispute. If every time you try to whisper sweet nothings in your darling’s ear, I screech so loud that she can’t hear you, is my screech a ‘signal’? It seems that you can use the word ‘signal’ that way if you want to. But in more usual cases there exists an answer to the question, what is the signal signalling? What is it a signal of, or a signal that?

Ruth G. Millikan

Response

We agree with Millikan that it is not unreasonable to consider a behaviour that interferes with signals as not itself being a signal. Furthermore, we are sympathetic to the idea that the choice to describe a phenomenon as a signal may be driven by the theoretical interests of the researcher more than by a robust reality to be found in the natural world. In that sense, this may be a verbal dispute. But the theoretical interests of researchers are legitimate considerations. Treating ‘interference’ as one of the possible functions of signals would bring a range of similar phenomena under the same theoretical umbrella. For example, in many chorusing species, individuals time their mating signals to interfere with those of others, and disrupting others’ signals contributes to mating success. Our approach allows one to consider interference to be one of the ways in which the mating signals enhance fitness, rather than requiring one to separate out the ways in which the behaviour is a signal and the ways in which it is not. In the insect example we described, there has been specialisation within the signal repertoire, such that some signals have evolved to be effective at interference, without the need to also be attractive to mates. These masking vibrations are similar to the mating vibrations in frequency, duration and amplitude, with the most striking difference being their timing relative to the rival’s mating signals. We prefer not to have to consider some of the vibrations as signals and others as non-signals, but instead to treat all of them as signals that differ in the means by which they influence fitness. One consequence of this view is that some signals exist that do not inform.

As to the question of what this is a signal of or a signal that, perhaps it is not a signal of or that anything. We wonder what is gained by considering the signals
of organisms such as insects, frogs, fish or cellular slime moulds as signals of something or signals that something occurs; we suspect those terms are conversational conveniences for biologists. In general, with possible exceptions like the vervet alarm calls, we are not convinced that it is usual for signals to be of, or that, something. On an influence approach, there is no need for signals to have that representational component.

Reginald Cocroft and Claire Horisk