

**Communication without meaning or information: Abandoning language-based and informational constructs in animal communication theory**

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## I. Introduction

Contemporary research in animal communication is heavily influenced by analogy to human language and language-related information constructs: it focuses on establishing the meaning of animal signals or how they encode and transmit information. This approach feels so natural that few stop to consider that linguistic and informational constructs are not givens (*a priorisms*) in animal communication, but represent a significant departure from the anchoring concepts of earlier research (Owren & Rendall, 2001; Owren *et al.*, 2010). In fact, language-based and informational constructs became common in animal communication only with the rise of cognitivism in the middle 20<sup>th</sup> century.

However, the result has been a double-edged sword. On the one hand, linguistic and informational constructs have had significant heuristic value, spurred considerable research interest, and dramatically raised the profile of the field. On the other hand, while the constructs being invoked appear straightforward, they are not—at least as typically presented. We suggest they are fundamentally ambiguous, and put researchers out-of-step with core tenets of evolutionary biology. Hence, they are not strong conceptual pillars for a maturing science of animal communication.

To flesh-out this argument, we first examine the origins of key ideas about information and cognitive representation in computer science, linguistics, and psychology and their subsequent adoption by animal communication researchers. We then elaborate some problems inherent to these ideas, not only in the field of animal communication, but also in the disciplines they were borrowed from. Finally, we outline a class of alternative frameworks for studying animal communication that are both more consistent with core tenets of biological and evolutionary explanation, and more in-step with current research concerning the organization of brains, bodies and behaviour.

## II. Language, minds, and computers: circular metaphors of the cognitive revolution

Linguistic and informational constructs now dominant in animal communication can be traced to two mutually reinforcing developments that sparked the ‘cognitive revolution’ (Miller, 1956; Chomsky, 1959; Neisser, 1967). One key development was technological—the advent of computer-based information-processing as a synthesis of formal logic (Turing, 1950) and physical symbol systems (*sensu* Newell & Simon, 1976). With enough time and power, such systems could solve any logical problem. The other was the emergence of Chomskyan linguistics, based on the premise that language was an organic example of a physical symbol system that through formal, syntactical processing rules (Chomsky, 1965) could generate an infinite variety of meaningful utterances. Exactly how symbolic and syntactic processes might be realised in a brain versus a computer was, and still is, a thorny problem.

Nonetheless, the parallels between computer systems and language systems made the computer an appealing metaphor for language. For example, quantitatively oriented linguists embraced the potential offered for formal logical and mathematical analysis of

language structure. The key to such analysis lay in the combinatorial power of syntax operating over arbitrary symbols. Such systems are computationally tractable so long as the forms of the symbols themselves are completely arbitrary and do not muddy the computations by having a logic of their own independent of the logic of the syntax that governs them. This emphasis helped to consolidate Saussure's (1916) classic dictum of the 'arbitrariness of the sign'. Simply put, the approach became one of arbitrarily structured symbol tokens stored and manipulated via rule-governed syntactical processes to create meaningful expressions that convey information. Language was seen as a natural system of information processing and transmission, and the computer metaphor was eponymously reified as "computational linguistics."

The success of metaphorical, computer-based approaches to language also encouraged and reinforced tendencies to think about the brain (or mind) in a similar way. This emerging cognitivist approach in psychology thus also relied on computer metaphors, here too grounded in the supposition that mental processes can be modelled as a form of symbol manipulation via abstract rules. Later characterized as the "computational theory of mind," this approach went beyond metaphor. Over time, the view was not just that the mind is *like* a computer, but that it effectively *is* a kind of computer. With computer metaphors forming a common ground, these conceptions of language and brain become intertwined and mutually reinforcing. Indeed, mental processes were subsequently cast as a kind of "language of thought" (Fodor, 1975).

### **III. Cognitive ethology and the rethinking of animal communication**

The promise of Chomskyan linguistics and digital computing for understanding the architecture of mental processing and complex behaviour was not lost on scientists of animal behaviour. Historically, issues concerning animal mental life had been central to comparative psychology, and after decades of the strictures of behaviourism, researchers were ready to embrace this prohibited topic once again. Just as language was seen to reveal the workings of human minds, communication systems in animals were seen as privileged windows on their psychological processes (Griffin, 1974, 1995). Indeed, animals were proposed to be demonstrating complex cognition in proportion to the degree to which their communication showed evidence of language-like properties. Language thus quickly emerged as a core metaphor for understanding animal communication, and was readily connected to the information-processing metaphors emerging in the study of cognition (Marler, 1961). The two emphases came together in the new field of "cognitive ethology," a synthesis of animal behavior and psychology.

The new approach took a large leap forward through seminal work on primate vocal communication by Robert Seyfarth, Dorothy Cheney and Peter Marler. That work showed that vervet monkeys give acoustically distinct alarm calls to different types of predator and that the alarm calls alone elicit functionally differentiated escape responses (Seyfarth *et al.*, 1980). Hence, the calls appeared to function much like humans words as symbolic labels for the predators. Because the calls did not sound like the predators themselves, they also seemed to exemplify the arbitrariness that Saussure

proposed for symbolic language. Here, then, was evidence of language-like communication in a monkey, with the promise of similarly human-like cognitive complexity. The implications for language evolution were tantalizing, and the prospects for the broader enterprise of language-oriented research in animals equally rich.

#### **IV. Animal signalling and language**

It is difficult to overstate the influence of the vervet monkey research. It sparked a virtual explosion of like-minded research on primates searching for additional parallels to language and complex cognition. Soon, this approach spread to work on many other species (see Table 1), including animals with very different nervous systems and behaviour. More than 30 years on, however, vervet alarm calling remains not only the best-known and widely cited instance of language-like communication in animals—it *is* the best example. Despite intense interest, language-like, representational signalling has been reported in only some animals, and then in just a fraction of those species' signal repertoires, almost exclusively only in the relatively rare context of encountering predators. By far the majority of vocal signals are used to mediate routine social interactions, courtship, and daily travel and foraging activities, and evince no evidence of language-like representation. Arguments against continued reliance then on language-based metaphors in animal communication have been made in detail elsewhere (Rendall *et al.*, 2009; Owren *et al.*, 2010). Here, we highlight only some of the problems triggered by these critiques.

***Intentionality.*** Among the most revealing conclusions to emerge from primate research is the lack of key social cognitive abilities that undergird human sociality and language. In language, for example, words are imbued with meaning through the underlying intentionality in both speakers and listeners. Speakers understand that words stand for, or represent, things in the world. Listeners also understand this representational relationship, and it is their shared understanding with speakers that allows productive communication about things in the world. In short, word meaning hinges on implicit, reciprocal attributions about mental states, including what others do and do not know about the world, and how that knowledge can be modified through the use of words with shared representational value (Grice, 1957).

In contrast, these social cognitive abilities are absent in nonhuman primates. With the possible exception of some of the great apes, these animals do not attribute mental states to one another and, in their signalling, do not show sensitivity to the needs of perceivers (Cheney & Seyfarth, 1998, 2005). In fact, nonhuman primates appear to act largely in ignorance of the mental states and communicative needs of conspecifics in both signalling and wider patterns of social behaviour (Penn & Povinelli, 2007). Perhaps ironically, primate signallers appear to be ignorant even of the communicative value that their own signals can nevertheless have (Cheney *et al.*, 1996; Rendall *et al.*, 2000).

***Development and neuroscience.*** This shortcoming is buttressed by neuroanatomical research showing that the mechanistic underpinnings of communication in human and

nonhuman primates are, in fact, quite different. For example, speech production in humans is critically dependent on auditory experience and motor practice, is importantly governed by cortical circuits in the temporal and frontal lobes, and is volitionally controlled (Lieberman, 2002). In monkeys, however, vocalizations routinely emerge without any evident need to hear the sounds from others or to practice making them. Calling is furthermore governed primarily by subcortical structures of the limbic system, midbrain and brainstem, and is largely unaffected by cortical stimulation or damage (Jürgens, 2008). Overall, vocal production in primates is modulated primarily by involuntary processes and is relatively impervious to experiential modification. The processes involved therefore appear far more similar to relatively involuntary emotional expressions in humans, such as laughter and crying, than they do to those involved in language (Owren *et al.*, 2011).

As a result, a growing realization is that, despite superficial resemblances between some primate vocalizations and human words, the underlying mechanisms involved are fundamentally different in the two cases. Indeed, more than a decade ago, Cheney and Seyfarth (1996, 1998) themselves concluded as much and have reiterated this conclusion more recently ‘we conclude... that nonhuman primates’ inability to represent the mental states of others makes their communication fundamentally different from human language’ (2005, p. 135). Others have echoed this conclusion (Tomasello, 2008; Hauser, 2009). However, this insight has had surprisingly little effect on the field as a whole. Instead, many primate researchers remain committed to interpreting signals as representational events, although with the qualification that the reference involved is only ‘functional’ rather than truly language-like. In other words, researchers acknowledge that communication in primates is quite unlike language, yet still put comparisons to language in a central role. The unfortunate effect is to continue to imply a substantive connection to language even in the face of contrary evidence regarding intentionality, vocal development, and neuroscience.

## **V. Problems with information**

While communication research on nonprimates has not been so heavily influenced by the aura of human language, reliance on information-processing constructs is virtually ubiquitous (see Table 2). Indeed, such constructs dominate to such a degree that most formal definitions of animal communication are made explicitly in terms of information (see Table 1 in Rendall *et al.*, 2009). Similarly, most research is guided by a general informational model of communication like that depicted in Figure 1. Here again, this focus feels natural and intuitive and has become deeply entrenched. So much so that few reflect on the validity or historical origins of this approach. However, recalling the points made earlier, the two emphases are importantly linked. Specifically, the current centrality of informational constructs derives directly from the synergy among the notions of language, computer and mind that characterized the cognitive revolution. The outcome there was wholesale adoption of the view that minds are information-processing systems, with language, and communication more generally, functioning to transmit that information. In other words, even when communication in a given species

is not interpreted in language-based terms, closely associated notions of information-processing typically remain central. The problems involved are again reviewed in detail elsewhere (Rendall *et al.*, 2009; Owren *et al.*, 2010), with only a truncated discussion here.

**“Information” is ambiguous.** One fundamental problem is that the information construct, as used in animal communication, is inherently ambiguous. Although communication is frequently defined in informational terms, information itself is seldom defined or operationalised.<sup>1</sup> The most natural sense would be the one associated with formal information theory and the advent of digital computing where information was defined in quantitative terms as uncertainty reduction (Shannon & Weaver, 1949). Information in this mathematical sense can be applied productively in animal communication research (e.g., Beecher, 1989). Indeed, given that the focus on information importantly derives from the information-processing perspectives associated with digital computing, that should arguably be the sense intended. Strangely, precisely the opposite is the case. Information is instead almost always used in the loose, metaphorical sense that mirrors casual discourse. Here, information becomes effectively equivalent to *meaning*: the information that a signal contains or transmits is what the signal *means*. However, the construct of meaning is notoriously slippery, and, as just reviewed, does not apply in its linguistic sense to animal communication. As a result, while being careful not to claim that animal signals convey meaning in a linguistic sense, researchers are then unable to explain what they do intend. Because terms such as information and meaning lie at the heart of current conceptions of animal communication, the field itself now rests on constructs that its practitioners do not, and possibly cannot, define.<sup>2</sup>

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<sup>1</sup> In this sense, information has become the new phlogiston, something that cannot be seen, defined, measured or quantified but that is central to everything. The history of phlogiston theory should make us wary of such loose, sweeping constructs. We should be especially wary of the argument that information is a useful construct because it has supported a great deal of research in animal communication and can account for a great number of its findings (Seyfarth *et al.*, 2010). The same was once said of phlogiston, a flat-earth, and geocentrism.

<sup>2</sup> For example, Seyfarth *et al.* (2010) offer a recent defense of the information construct, yet similarly fail to define the term information. Instead, they appeal to a looser, informal conception of information based on an analogy they draw to animal learning research. They argue that just as a light predicts shock to a laboratory rat, so too does an alarm call predict the presence of an eagle to a wild vervet. Hence, signals can be said to encode information anytime there is a predictable relationship between a signal and some event or state of the world that receivers can pick up on. It is, of course, obvious that there is information in the world in the sense that predictive relationships like these abound and can be learned by animals (see Scott-Phillips, 2010 for more on this point). However, it is equally clear that such information does not reside in the signals themselves but rather in the relationship between them and the events they co-occur with. This is evinced by the fact that naïve rats, in fact, do not avoid the light at first and, similarly, naïve infant vervets do not respond appropriately to eagle alarm calls at first (Seyfarth & Cheney, 1986). In both cases, the predictive relationship between the calls and events in the world must be learned through a history of experience with the associations. The signals, by themselves, do not contain this information. To say that they do is to spirit into the signal itself the relationship it shares with events in the world and thus to fundamentally obscure the mechanisms by which signals function. Importantly, although vervet alarm calls do not actually contain information in the loose sense ascribed to them, we have argued elsewhere that their structure is nevertheless well designed to influence infant vervets in ways that facilitate their learning predictive relationships about predators and thus acquiring appropriate escape responses that they specifically lack when young (Owren & Rendall, 2001; Rendall *et al.*, 2009; Owren *et al.*, 2010).

**“Coding” is problematic.** Other core constructs of informational perspectives are similarly problematic. For example, informational characterizations of animal communication typically invoke some form of code. The information content of the transmitted message is said to be encoded in the details of the signal’s physical form, with listeners then decoding that signal to recover its message. As with the term information, references to encoding and decoding are common (see Table 2), but are seldom developed explicitly. The notions remain tacit, with little attempt to explain what the unencoded or decoded versions of a message might be like.

In standard usage, the concept of encoding involves some process of signal translation or transduction: content in one domain is translated into a different, but corresponding form. The Language of Thought hypothesis (Fodor, 1975) is similar, proposing that mental information takes a different form than the concrete version realized in spoken language. Hence, speech communication is taken to involve an encoding process that translates thoughts into words, an idea that lies at the heart of Chomsky’s (1965) theory of transformational or generative grammar. This theory argued for a fundamental distinction between the deep structure of language as it exists in mental form and the surface structure that results when these mental representations are transformed into overt communication. Neither the deep structure nor the process of translation to surface structure could ever be substantively described, however, as is also the case for analogous notions of mental representation and encoding of animal signals.

**“Coding” is unnecessary.** More importantly, perhaps, there is often no need to appeal to an encoding process in animal signalling. Many signals mediate common social contexts such as aggressive competition for resources or attracting mates. Here, signals are proposed to encode information about relevant social or physical characteristics of signallers, such as their age, sex, body size, individual identity, emotional state or physical condition (see Table 2). However, in these and other common signalling contexts, there is no need to invoke an encoding process – the dimensions are signalled directly. For instance, a large body naturally allows for a large vocal apparatus, and a large vocal apparatus naturally produces low frequency sounds (Fitch & Hauser, 1995). Hence, low frequency sounds are not somehow an *encoded translation* of large size. They are simply the direct acoustic manifestation of large size. They are what large size sounds like. Similarly, idiosyncrasies in development of the vocal apparatus among individuals naturally yield subtle, idiosyncratic differences in the sounds those individuals produce (Rendall *et al.*, 1998). Those acoustic differences do not then somehow *encode information* about individual identity. They are just the acoustic manifestations of individual identity. In like fashion, particular emotional or motivational states can affect aspects of physiology (e.g., respiration) in ways that influence structural characteristics of vocal sounds produced; and variation in physical condition can influence the susceptibility of such sounds to perturbations induced by effortful performance displays. In all of these cases, the structural differences in signals that are traditionally held to *encode* these different dimensions of size, identity, emotional state

or physical condition are, in reality, just direct manifestations of the dimensions themselves. There is no need to posit an intervening translational process—there is no code involved. Instead, “the medium *is* the message” (McLuhan, 1964).

Similar points can be made about the other side of the information-transmission equation, where a separate, decoding process may rarely be required. Instead, signals can have relatively direct influence on receiver sensory systems, physiology and behaviour.<sup>3</sup>

***Distinctive features and context.*** By emphasizing the notion of encoding and decoding, informational approaches strongly encourage a view that the signal itself bears most of the load in communication. One consequence is that signals are seen as bundles of distinctive features, each one of which can be dissected out as a carrier of potentially unique information (see Table 2). The result is that there is relatively little emphasis on more holistic or integrated patterns of signal production and perception. A second, related effect is that researchers downplay or overlook that many other factors can influence communication. These include a host of features of the social or environmental context that accompany signalling, as well as the variety of proximate motivations, predispositions and biases that signallers and receivers bring to the interaction (Smith, 1977; Leger, 1993).

## **VI. Language is not a “fixed code”**

The view of language that emerged through the work of Chomsky (1965) and others was both compatible with, and quickly became enmeshed in, contemporaneous computational and information-processing perspectives. It was argued, for example, that language is just too difficult for children to learn, and that the speech input children receive is impoverished relative to the speech they eventually produce. To account for the surprising ease of language learning, Chomsky (1965) proposed an innate, and uniquely human, language acquisition device (LAD). The LAD was further argued to be an embodiment of “universal grammar” (UG), innate knowledge of the basic principles of grammar that underlie all languages. Early linguistic development is thus a process of

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<sup>3</sup> Well-documented examples of such direct influence occur in a variety of fish, frogs, birds and insects (Endler & Basolo, 1998; Ryan & Rand, 2003; Cheng & Peng, 1997; Wilczynski & Chu, 2001; reviewed in Ryan, 1998), as well as in artificial neural networks (Enquist & Arak, 1993) and listener gene expression (Mello *et al.*, 1995). In a classic example, spectral characteristics of the courtship signals of male túngara frogs, *Physalaemus pustulosus*, are proposed to have evolved to match pre-existing auditory sensitivity of conspecific females (Ryan, 1990). Female attraction to male calls is explained mechanistically by the way distinct components of the male call have evolved to maximally stimulate two complementary inner organs of females (reviewed in Ryan & Rand 2003). Less dramatically, alarm vocalisations and common social calls produced by nonhuman primates (Owren & Rendall, 1997, 2001; Rendall & Owren, 2010) are not arbitrarily structured—as initially proposed—for instance most often being short, with abrupt onsets and broadband noisy spectra. These widely shared features are ideally suited for capturing and manipulating listener attention and arousal through direct links between the auditory periphery and brainstem regions regulating attention and arousal (also see Hartshorne, 1973; Searcy, 1992). Vocalisations can also have significant self-stimulation effects. For instance, Cheng (1992) found that the “nest” coos of female ring doves stimulate hormone release in the caller herself, thereby helping to advance the courtship and mating process.



setting language-specific parameters in the LAD rather than learning grammar from scratch. Hence, language functions similarly for every speaker and language structure is fundamentally predictable across all environments. This perspective constitutes a “fixed-code” view of language (Harris, 1998), one in which grammar is rule-bound, words have fixed, universal meanings that encode abstract semantic constructs of thought, and the individual sounds of language form well-defined categories with specifiable acoustic and articulatory features. Yet, there are significant problems with the fixed-code approach at each of these levels.

**Grammar.** While Chomsky’s proposals had immense influence, it subsequently proved impossible to specify the fixed, universal language features instantiated in UG. Resulting changes have included abandoning the distinction between deep and surface structure, and an increasingly diluted body of principles and parameters (Chomsky, 1995). Even more damaging is that language is being found to be eminently learnable from typical input.<sup>4</sup>

**Words.** Words have also been considered fixed, in that they represent stable units with agreed upon meanings. However, this view has been strongly opposed by integrational linguists, who emphasize the role of individual experience and context. Harris (1981, 1998), for example, characterizes the fixed-code approach as one of publicly invariant meanings that then allow encoding and decoding of thoughts by those who know the code. The contrasting, integrational perspective is that word meanings are routinely context-dependent and changeable based on each individual’s experience with the language, the social circumstances in which words are used, and the semantic, grammatical, and prosodic aspects of the utterances in which they are embedded (Cowley & Love, 2006). Hence, word meaning is inherently slippery and fluid rather than stable and invariant due to extra-linguistic factors such as context and pragmatics (Ogden & Richards, 1923).

**Speech sounds.** Historically, the earliest, and perhaps most devastating challenge to the fixed-code approach arose in the search for invariance at the level of individual speech sounds. From the earliest stages, psycholinguists were discovering that neither the phones nor phonemes of a given language in fact provided invariant acoustic cues (Lisker & Abramson, 1967). Although speech might be psychologically experienced as a series of discrete phonemes, syllables, and words, the physical signals themselves cannot be parsed into corresponding, individual units. Speech acoustics are actually far more variable and continuous over time, with phonetic “segments” overlapping forwards-and-backwards in the speech waveform.

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<sup>4</sup> Here, neural networks can detect and ‘learn’ grammatical structure from statistical regularities in larger corpuses of language material and relatively rich semantic knowledge can be developed through associative processes operating over very large corpuses of language material (Landauer and Dumai, 1997). In humans, even preverbal infants have been found to be sensitive to the statistical regularities of the speech stream (Saffran *et al.*, 1996)—which now appears to be much less impoverished than previously believed. Indeed, research has shown such structure to exist at multiple organisational levels, which can serve to bootstrap language learning (Kuhl, 2000).

This lack-of-invariance problem inspired a proposal that humans are innately endowed with a phonetic module—akin to Chomsky’s LAD—that does the listener’s difficult perceptual work automatically. The early discovery of categorical perception (CP) appeared to illustrate the operation of such a phonetic module in showing that, despite continuous variation in the speech waveform, stop-consonants such as /ba/ and /pa/ were perceived as falling into discrete categories (Liberman *et al.*, 1957). This was exactly the sort of specialization expected of a native language endowment, one that could parse the complex and continuous speech stream into its distinctive and invariant, information-bearing phonemic elements. But this “speech is special” view has also not fared well. For example, it was subsequently found that the same consonants were subject to categorical perception when presented to rodents and monkeys (Kuhl & Miller, 1975; Kuhl & Padden, 1982). The long-term lesson has been that only written language can be said to be relatively discrete and particulate, spoken language is not (Port, 2010).

**Speech and computers.** The real-world difficulties of the fixed-code approach to language are illustrated by the decidedly mixed results of machine production and recognition of speech.<sup>5</sup> Nowhere has the effort been as great, or the returns as small, as in the continuing quest to develop computer speech recognition which has been critically hampered by the lack of invariance problem. While commercial speech-recognition software is now available, it functions by computing statistical best-guesses about speech input, which are often wrong. To achieve any significant level of success the programs have to be restricted to recognizing either a very small number of possible words, or a larger number of words from a very small number of speakers. The most successful approach has been to restrict the speech input to a single speaker who also first trains the software on his or her pronunciations of a known set of words. These modifications represent attempts to create a fixed speech code, but the fact that they are needed at all simply illustrates that, in real life, human speakers and listeners do not depend on such codes and that speech perception is far more holistic, episodic and contextual in nature (e.g., Palmeri *et al.*, 1993; Nygaard *et al.*, 1994; Johnson, 1997).

**Implications for fixed coding.** In spite of having deep, intuitive appeal, the fixed-code, particulate approach to language appears to fail at multiple levels of analysis (Harris, 1981, 1998; Cowley & Love, 2006; Kravchenko, 2007; Port, 2010). The organization and endowment of language no longer seems so plausibly to lie in a set of narrowly circumscribed and innately specialized computational and perceptual modules. Instead,

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<sup>5</sup> While public agencies and private companies have long tried to develop machines capable of producing and comprehending fluent speech, the actual results have been modest with problems arising at each of the levels outlined above. Spoken language is, for example, rarely as well-structured as written versions. Here, human listeners can take contextual factors into account to easily follow the broken and incomplete sentences that often characterize real-world speech. Machines cannot. The importance of semantic and other forms of context become quite obvious in machine translation of language. Performance can be reasonably effective for short, simple sentences that can be treated literally. However, even moderate complexity in the original material soon results in garbled output.

it seems to recruit a broad range of psychological capabilities, including simple but powerful associative and statistical learning abilities and complex, context-based inference. In other words, while viewing the human language faculty as a discretely organized system is intuitive and compelling, this analogy to digital information-processing seems to have little to say about how language production, perception, and comprehension actually happens in the brain.

## **VII. How the mind ~~works~~ does not work**

Developments in language theory have been paralleled (naturally) by developments in theories of mind. The computer metaphor of mind, so intuitive in the early days of cognitivism, is now seen to have many critical limitations and is gradually being eclipsed<sup>6</sup>. Foremost among its limitations is the emphasis on cognition as a disembodied, in-the-head phenomenon. In this view, perceptual input from the outside world is fundamentally transformed in creating an abstract mental code that is the basis of internal processing. Behavioural responses then require a converse transformation from that code into motor commands. However, this “brain-as-computer” model appears adequate only for certain “representation-hungry” tasks such as playing chess, doing mental long-division, or imagining the number of windows in one’s house (Clark, 1997). But these are relatively artificial and rarefied tasks. The bulk of quotidian behaviour and cognition is quite different, and is not well accommodated by the symbol-manipulation model of mind (Searle, 1980; Brooks, 1991; Clark, 1997; Dreyfus, 1999). Instead, ordinary behaviour and cognition is appreciated to be far more embodied and to involve processes for behavioural control that entail relatively direct engagement with the environment via perception-action circuits that effectively bypass any need for internal representation, symbol transduction and processing. In addition, a great deal of what we have traditionally modelled as cognition is now believed not to occur exclusively in one’s head, but rather to be distributed to the world or to our interaction with it (Hutchins, 1995; Clark & Chalmers, 1998; Wheeler & Clark, 2008; Clark, 2008). Indeed, a great deal of what we think of as uniquely human and complicated involves off-loading the demands of intensive internal processing to external supports in the environment.<sup>7</sup>

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<sup>6</sup> “Interestingly, Claude Shannon, one of the developers of the mathematical theory of information, was skeptical that the brain was an information processor; he believed that processing information required a transmitter, a receiver, and an agreed-upon code, none of which is found in the brain.” [Alva Noe 2009, p. 156]

<sup>7</sup> For example, rather than commit to memory shopping lists, phone numbers, and passwords, we commit them to pieces of paper or computer files, from which they can be retrieved whenever needed. We similarly store important personal items such as keys and glasses in locations that ensure we routinely encounter them on route to the habitual activities that will require them rather than in any number of other safer hiding places that are actually quite hard to remember! These are routine ways we off-load cognitive processing by marking the environment through our behaviour – sometimes deliberately, sometimes not – in ways that allow us simply to re-perceive, rather than remember (represent), important things. We also create a diversity of cognitive artifacts, like symbol manipulating calculators and computers, specifically to avoid cognitively demanding symbol manipulation tasks. In fact, perhaps our penchant for externalized symbol manipulating systems arises precisely to compensate for the weak symbol manipulation capacities of our brains.

***Developments in artificial intelligence and robotics.*** This conclusion is buttressed by research in artificial intelligence (AI) and robotics. These fields arose in conjunction with computer technology and were thus originally based on the same logic of symbol processing. They were widely anticipated to solve the problem of intelligence and to yield all manner of useful devices, but practical successes were slow to come (Dreyfus, 1999). This failing is argued to reflect their focus on symbol-crunching computational processes that, while generic and powerful in their way, create insurmountable informational bottlenecks. Even simple tasks are hamstrung by the need to first re-represent internally many features of the external environment and, based on this, perform an exhaustive, internal search of knowledge for that which is most relevant to the situation in order to select among appropriate response options. By the time a command for action has been processed, the situation has changed! In contrast, modern research in AI and robotics shows that this classic emphasis on representation and symbol manipulation is unproductive and unwarranted (Brooks, 1991; Dreyfus, 1999). For many everyday tasks, it just gets in the way. Instead, for many quotidian tasks, functional behaviour can be achieved by peripheral perception-action loops that largely forego representing the external world and instead capitalize on natural regularities and affordances inherent in the environment. In the words of Rodney Brooks, “the world is its own best model” (Brooks, 1991). There is no need to re-represent it. Just act on it.

The upshot is that models of mind based on the computer and on disembodied information processing and symbol manipulation increasingly appear to be substantively incomplete—if not largely wrong. They are appropriately giving way to alternatives that stress the active nature of cognition, and its more embodied and distributed nature. Such models of cognition are taking hold in research on human psychology but have yet to gain much purchase in the field of animal cognition, although there have been a few seminal empirical and theoretical forays over the years (Grasse, 1959; Gallese *et al.*, 1996; Barrett, 2011).

### **VIII. Metaphors, phenomenal models and explanations**

Metaphor can be an important reasoning tool. In fact, metaphor might be a common and uniquely powerful mode of human thought (Lakoff & Johnson, 1980) that naturally and inevitably infects scientific thought. There is no doubt that metaphors can be productive in science. They might often have special heuristic value in the early stages of a discipline. Without a mature theoretical edifice in place, young disciplines frequently turn to other fields for constructs with which to provide initial characterizations of their own field.

***“The price of metaphor is eternal vigilance”<sup>8</sup>*** However, metaphors come at a price. One is the risk of that the metaphors become circular and self-sustaining like those of

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<sup>8</sup> This quote is often attributed to Arturo Rosenbleuth and Norbert Weiner but typically either without citation details or with details that do not actually contain the quoted material. We have tried unsuccessfully to find the

the cognitive revolution. There is also the risk of unwarranted, and often times unwitting, reification. Over time, a metaphor becomes so familiar that it elides gradually into a literal account of core phenomena. Hence, “the price of metaphor is eternal vigilance”. Regular re-evaluation of explanatory constructs is needed to avoid these pitfalls. In the normal course of things, as disciplines mature, the metaphors evolve and ultimately give way entirely to more concrete accounts of focal phenomena.

In animal communication, language-based metaphors had heuristic value during an important stage in the development of the field. The focus on language properties in the early vervet monkey research made good sense. Language was of course familiar to us and provided a ready benchmark for comparison in a field just finding its feet. It also made sense to seek evolutionary precursors to language among nonhuman primates. Following the expanding appeal of computer technology and information processing models of communication systems and cognitive processes, the importation of derivative information processing constructs into animal communication research more broadly also seemed natural.

**Abandoning language and information metaphors.** However, a variety of evidence now suggests that the language and information metaphors that have coloured research in animal communication have run their course, have confronted their limits, and should be abandoned. The evidence of their limitations comes from both directions: from within the field of animal communication itself where the metaphors have been applied, and from the domains of human language and cognition whence the metaphors originated and were borrowed.

From within animal communication, the constructs have proved both too loose and too restrictive to cover the broad range of animal signalling phenomena. They are too restrictive because their common language-based and informational focus unduly narrows the focus of study and limits the range of questions asked, problems investigated and alternatives considered (Rendall *et al.*, 2009).

The constructs are simultaneously too loose because their core linguistic and informational explanatory constructs – *meaning, information, encoding, decoding* – are only ever vaguely defined and operationalised, or, more often than not, left entirely tacit. As a result, fundamental research emphases (e.g., functional reference) often blur important distinctions in ethological and evolutionary enquiry such as between the mechanisms and functions of signals, or between the potentially disparate roles of signallers and receivers.<sup>9</sup> Ultimately, the constructs cannot be cashed-out in terms of

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original quote. Given that, we simply continue the tradition of attributing the aphorism to them because it carries the same cautionary value no matter the source.

<sup>9</sup> The incoherence is most simply illustrated in a concurrent conceptual development, specifically the proposal that the meaning of animal signals can be conceived of as lying on a continuum between endpoints anchored by purely motivational signals and purely referential ones (Marler *et al.*, 1992). According to this proposal, the motivational end of the continuum involves signals that simply reflect and convey the internal emotional or motivational state of the signaler, while the referential end reflects the extent to which receivers can draw inferences about external

standard constructs used in biological and evolutionary theory. As a result, they operate only in support of ‘as if’ theories that focus on putative functional abilities but masquerade as accounts of the underlying mechanisms involved.

Hence, at best they serve as phenomenal models that provide a functional, systems-level descriptive account of some phenomenon and allow some predictive capacity about how the system will behave under some conditions (Craver, 2006). In this sense, they are temporary place-holders for true explanations which require not just a functional, systems-level description of a phenomenon but must account in far more detailed fashion for the actual mechanisms governing it. In other words, as phenomenal models they ultimately fail as scientific accounts because they address only ‘*how WE CAN UNDERSTAND that*’ and not ‘*how it IS that*’.<sup>10</sup>

From outside the field of animal communication, the traditional Chomskyan model of language and the related computational, information processing metaphors of mind are now regarded as quite incomplete even as models for human language and human minds for which they were originally intended. They are, at best, caricatures promoted by the disembodied information-processing logic of the computer, and they are slowly being abandoned in favour of alternative and more pluralistic approaches that are markedly different from those that spawned the cognitive revolution. Hence, it is deeply ironic that research in animal communication continues to adhere to explanatory metaphors largely abandoned in the fields they were borrowed from.

## **IX. Alternative approaches to animal communication**

Thus far, our focus has been a critique of the use of non-native linguistic and informational constructs in animal communication research – in effect, emphasizing how research should not be organized and conducted. In closing, we want to shift this

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events upon hearing the signals. In other words, one end of the continuum concerns the mechanisms underlying signal production, and the other concerns the functional consequences for listeners of receiving and interpreting the signals. The notion that a given signal can be attributed meaning and placed at a single location on this continuum thus involves blending the mechanisms of signalling with its potential functions, and merges the distinct roles of signaller and receiver in the process. As a result, either the distinction between the motivational and referential endpoints evaporates and with it the entire notion of a continuum between them, or any given signal must be said to exist simultaneously at multiple locations on the continuum depending on whose perspective is being considered and whether one is focused on either the mechanisms or the functions of signalling.

<sup>10</sup> Notably, this weakness mirrors one that has plagued the Chomskyan account of language. That account hinged on a postulated mentalistic language *competence* to account for the routine functional *performance* of everyday language users. This emphasis was classically Cartesian in its appeal to some kind of mental stuff distinct and separate from body and behaviour stuff. Of course, some kind of mental stuff is required in the sense that routine language performance obviously hinges on a variety of brain states (as well as some other states of physiology, body, and context) in order to coordinate acts of language production and comprehension. But such brain states were not the stuff of the putative mentalistic language competence. That competence was proposed to exist in some other more abstracted mentalistic form distinct from physical brain (and body) states. However, the nature and ontological status of that abstracted mentalistic competence has never been specified, even in principle, making continued appeal to it as somehow necessarily separate or distinct from performance seem increasingly illusory. There might be no real distinction between competence and performance. Instead, it might be performance all the way down.

emphasis to consider briefly how research could be organized instead which we try to outline schematically in Figure 2.

**Functional re-orientation around influence rather than information.** For starters, we suggest a fundamental functional re-orientation of research. In addition to the many inherent ambiguities reviewed briefly here and in more detail elsewhere (Rendall *et al.*, 2009; Owren *et al.*, 2010), informational perspectives entail additional commitments that are incompatible with fundamental tenets of ethological and evolutionary explanation. Specifically, they require cooperative scenarios for the evolution of communication in order to produce in signallers and receivers the matched encoding and decoding systems and representational processes needed to share information. Cooperation is certainly possible in some signalling contexts where signaller and receiver interests overlap substantially. However, the bulk of signalling behaviour, even among closely related individuals, occurs in contexts where signallers and receivers have at least modestly, and often markedly, divergent interests (Trivers, 1974). Therefore, and leaving aside their many other problems, informational perspectives can only ever hope to account for a minority of signalling phenomena that are clearly cooperative.

We suggest instead that research in animal communication be re-oriented around the broader functional principle that signal evolution is organized by the benefits that signalling has for signallers, most often by influencing receivers (but see below). For signals to evolve, this influence must ultimately be beneficial to the signaller itself and it may also be beneficial to receivers in some contexts but it need not be. In this, we are simply suggesting a return to a broader foundational principle of natural selection, namely that adaptations, whether they be of morphology, physiology or behaviour, are shaped by the functional benefits they provide to their bearers. We see no reason to assume that communication is somehow a special domain of biology and behaviour that contradicts this fundamental evolutionary tenet.<sup>11</sup> Of course, others have emphasized this point (e.g., Dawkins & Krebs, 1978; Owings & Morton, 1997, 1998), and so, in this, we are simply re-asserting what was a common focus of earlier research in animal communication prior to the wholesale importation of linguistic and informational constructs.

This emphasis on signaller influence does not mean that receivers are somehow passive participants in communication, which seems to be a common confusion. On the

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<sup>11</sup> In a recent response to these arguments, Seyfarth *et al.*, (2010) demur that our proposed focus on influence is inappropriate. In support, they cite an example we have often used, namely of the conflict that routinely occurs even between mothers and offspring over the timing and amount of investment provided by mothers, particularly at the stage when they are weaning offspring. In this context, offspring of many species produce long bouts of loud, harsh chaotically structured calls that we have argued are not well designed to transmit information but are well-designed to stimulate maternal attention and arousal, to preclude habituation to their noxious effects, and ultimately to wear-down maternal resistance. Seyfarth *et al.* argue that it is wrong to characterize this interaction, and many others, as involving conflict and influence because all infants ultimately do get weaned. This argument patently conflates the outcome of a process with the process itself. If it were valid, then it would also be true that because the Great War ultimately ended there was in fact no conflict or influence ever involved.

contrary, selection obviously acts on all parties. To the extent that the influence exerted on receivers is not ultimately in their interests, there will, of course, be counter-selection on them to resist such influence. However, it cannot simply be assumed *a priori* that selection on receiver resistance always trumps selection on signaller influence. This assumption has become entrenched in some contemporary communication frameworks where signal honesty is offered as a putative axiom of communication (Zahavi & Zahavi, 1977; Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005). However, as with cooperation, honesty is only one possible signalling outcome. There are many others, where signalling systems deviate from honest equilibria due to a host of factors including historical contingency, latent sensory biases, physiological and neurological constraints, or perceptual sensitivity tradeoffs (Ryan, 1990, 1998; Guilford & Dawkins, 1991; Cummings, 2007). As a result, while the focus on honesty gives veto power to receivers and yields a relatively one-sided view of the communication process, the focus on influence is much broader and more widely applicable. It acknowledges that signalling is often dynamic in real-time, with important and potentially distinct roles for signallers and receivers engaged in an iterated process of reciprocal influence and resistance (Owings & Morton, 1998). It also acknowledges that signalling systems are dynamic in evolutionary time as well.

***Mechanistic re-orientation.*** We suggest an associated mechanistic re-orientation away from the symbolic and representational processes that have been an explicit focus of some specifically language-oriented research and that are, in fact, also an implicit focus of work grounded in informational constructs. Whether they know it or not, in focusing on how signals encode information and how receivers decode signal content, researchers are positing perceptual and cognitive representational relationships that are, as reviewed, unwarranted and outdated (Owren *et al.*, 2010).

We suggest that research should instead update its views on perception and cognition. In keeping with points made above, research needs to move away from the passive, disembodied, and exclusively 'in-the-head' views of cognition inspired by the computer metaphor and embrace alternative perceptual-cognitive frameworks that emphasise the more dynamic, embodied and distributed nature of perception, cognition and action (e.g., Thelen & Smith, 1994; Hutchins, 1995; van Gelder, 1995; Dreyfus, 1999; Noe, 2009; Clark 2001, 2008). The latter frameworks are grounded in the elemental and unassailable logic that all organisms are characterized by a fundamental ongoing integration and engagement with themselves, with others, and with the physical environment around them, and, therefore that their basic challenge is to monitor and manage this engagement in ways that minimize perturbation to themselves. This focus entails a number of subsidiary emphases including how affective and motivational systems complement cognitive processes in stimulating behaviour and in influencing and impelling responses to the behaviour of others; how such systems are influenced and primed by contextual factors; how quotidian tasks may be organized by fairly direct links between perception and action that bypass the need for more central, evaluative cognitive processes; and how proximate sensory and perceptual biases can facilitate



some opportunities for action and constrain others. It might also include increased consideration of the extent to which behaviour, including communication, serves important self-regulatory or self-stimulatory functions (cf. Cheng, 1992).

Finally, we suggest that research in animal communication look beyond the physical signals themselves to take greater account of the diversity of contextual factors that can influence communication. Contextual factors have sometimes been studied to good effect but have not been a continuing priority in animal communication research because, as noted earlier, informational perspectives have assumed that the signals are doing the bulk of the work. The physical signals are, of course, central and must be a continuing focus of study. However, it is well-established that social and environmental factors can influence physiological, perceptual and motivational systems instrumental in an organism's ongoing flow of behaviour (e.g., Seigel *et al.*, 2000; Galef & Laland, 2005).

Taken together, we are advocating a broad functional re-orientation of animal communication research around the notion of influence, with signallers and receivers engaged in a dynamic and iterated process of reciprocal influence and resistance. This process is affected by their individual and species histories, which equip them with a variety of proximate sensory, motivational and behavioural response tendencies and biases. These are part of a larger integrated system of perceptual and behavioural control functionally dedicated to managing engagement with the world and others in it and regulating one's own systems. All are potentially influenced and primed by a variety of contextual factors.

We do not suggest that this scenario is somehow complete, or even necessarily very novel. Indeed, some of what we propose represents a return to past emphases in the study of behaviour, perception and cognition or updated incarnations of them (von Uexkull, 1910; Gibson, 1979; Jarvilehto, 2009), and some are well known and widely practised by some researchers. However, we do see the KIND of approach we are advocating as markedly different and both more pluralistic and more plausible than traditional language-based and informational perspectives that reduce this great variety of factors and the myriad possible interactions among them to unitary and enigmatic constructs like meaning or information. The latter kind of explanatory reduction may be a great simplification, in some sense, but ultimately it is one that grossly underspecifies and obscures most of what needs explaining about animal communication and takes the study of it well outside the realm of normative ethological and evolutionary enquiry.

Table 1. Examples of linguistic and informational constructs characterized loosely to support comparisons of animal signals to language. Examples trace the spread of such constructs from research on primates to research on other animal taxa.

Author(s)	Explanations of signals, signalling, or communication
<p>Seyfarth <i>et al.</i> (1980) Vervet monkey alarm calls: Semantic communication in a free-ranging primate. <i>Animal Behaviour</i>, 28: 1070-1094.</p>	<p>“The qualitatively different responses elicited by experimental playbacks of leopard, eagle, and snake alarms demonstrate that alarm calls alone... <i>provided the monkeys with sufficient information</i> to make distinct and apparently adaptive responses. ... It is, of course, a difficult task to establish the precise <i>meaning</i> to the monkeys of each alarm type... There are limits to how far a <i>semantic</i> analysis of signals can be carried when it is based solely on the responses that those signals evoke. Nevertheless, it seems appropriate to conclude that the alarm calls of vervet monkeys <i>designate particular external referents</i>. Certainly the calls are <i>arbitrary</i> and <i>non-iconic</i>... one criterion for differentiating <i>symbols</i> from <i>icons</i> .... This view of alarm calls as a form of <i>semantic</i> signalling, probably involving the formation of internal perceptual <i>concepts</i>, or <i>symbols</i>, contrasts with earlier interpretations. .... It therefore seems appropriate to interpret arousal-related properties of alarm calls as ancillary to more specific call features, supplementing and enriching the <i>meaning</i> of calls rather than serving as a primary basis for <i>meaning</i>. ... Having shown that alarm calls, whatever their motivational basis, can be used to <i>convey information</i> about external events, our next stop is to investigate whether calls used during social interactions function in a similar manner.”</p>
<p>Cheney &amp; Seyfarth (1988) Assessment of meaning and the detection of unreliable signals by vervet monkeys. <i>Animal Behaviour</i> 36: 477-486.</p>	<p>“Humans make judgments about the similarity or difference between words on the basis of an abstraction, their <i>meaning</i>.... One method for determining how group-living animals assess the <i>meaning</i> of calls is through their ability to detect anomalous or unreliable signals. The results presented here suggest that the detection of unreliable signals is influenced by the ways in which animals assess and compare signals based upon their <i>meaning</i>.... In the case of vervet monkeys, and perhaps other primates as well, selection may have favoured the ability to recognize 'spheres' of <i>meaning</i> and the <i>transfer of information</i> gained in one sphere to other, related ones. Individuals who have come to recognize that one type of call by a given signaller is unreliable appear to transfer their scepticism to other calls of broadly similar <i>meaning</i>, but not to calls whose <i>referents</i> are different.”</p>
<p>Cheney &amp; Seyfarth (1996) Function and intention in the calls of nonhuman primates. <i>Proceedings of the British Academy</i> 88: 59-76.</p>	<p>“The alarm and contact calls of monkeys <i>provide information</i> about the signaler's current physical and mental states, but they are not deliberately given to inform or instruct others. Instead, listeners appear to <i>extract relevant information</i> about a call's function based on behavioral contingencies and their own experiences.”</p>
<p>Zuberbuhler (2000) Interspecies semantic communication in two forest primates. <i>Proceedings of the Royal Society B</i> 267: 713-718.</p>	<p>“From the perspective of the call recipient, however, the difference between primate alarm calls and human linguistic utterances are less explicit. In this and other studies, it was the <i>meaning</i> of the stimuli, but not the acoustic features that explained the subjects' response patterns. These results extend this finding ... by showing that <i>semantic understanding can be based on arbitrary signals, as it is [sic] the case for word meaning</i>.”</p>
<p>Cheney &amp; Seyfarth (2005) Constraints and preadaptations in the earliest stages of</p>	<p>“Here we review research on the vocal communication and cognition of nonhuman primates ... we conclude, first, that nonhuman primates' inability to represent the mental states of others makes their</p>

language evolution. <i>Linguistic Review</i> 22: 135-139.	communication fundamentally different from human language. Second, while nonhuman primates' production of vocalizations is highly constrained, their ability to <i>extract complex information</i> from sounds is not. Upon hearing vocalizations, <i>listeners acquire information</i> about their social companions that is <i>referential, discretely coded, hierarchically structured, rule-governed, and propositional.</i> "
Slocombe & Zuberbühler (2007) Chimpanzees modify recruitment screams as a function of audience composition. <i>Proceedings of the National Academy of Sciences</i> 104: 17228-17233.	"Our first goal was to examine to what degree chimpanzee victim screams <i>conveyed information</i> about the nature of the conflict, thus <i>providing valuable information</i> for nearby receivers <i>deciding</i> whether or not to interfere. Previous research on macaques has revealed that callers produce acoustically distinct screams types that are <i>meaningful to listeners.</i> "
Evans & Evans (1999) Chicken food calls are functionally referential. <i>Animal Behaviour</i> 58: 307-319.	"Food-associated vocalizations have also been of interest for research addressing proximate questions, especially efforts to understand the <i>meaning</i> of animal signals. Some food calls may have properties like those of the highly specific alarm calls described in birds and monkeys and may <i>provide information</i> sufficient to evoke anticipatory feeding behaviour from conspecifics. If so, such food calls would be ' <i>functionally referential</i> '."
Bugnyar <i>et al.</i> (2001) Food calling in ravens: Are yells referential signals? <i>Animal Behaviour</i> 61: 949-958.	" <i>Signals may encode information</i> about attributes of the sender ... and about stimuli or events in the environment ... If such <i>signals provide receivers with sufficient information</i> to determine the context underlying signal production ... the signals are regarded as <i>functionally referential...</i> "
Manser <i>et al.</i> (2002) Suricate alarm calls signal predator class and urgency. <i>Trends in Cognitive Sciences</i> 6: 55-57.	"Recent work on suricates, an African mongoose, shows that animal alarm calls simultaneously <i>encode information</i> about both predator type and the signaler's perception of urgency."
Templeton <i>et al.</i> (2005) Allometry of alarm calls: Black-capped chickadees encode information about predator size. <i>Science</i> 308: 1934-1937.	"If a species is preyed upon by different predators that use different hunting strategies or vary in the degree of danger they present, selection can favor variation in alarm signals that <i>encode this information</i> . Such variation in alarm signals can be used to <i>transfer information</i> about the type of predator, the degree of threat that a predator represents, or both."

*Table 2.* Examples of broader use of informal informational constructs in current animal communication research. This sample is drawn from the flagship journal *Animal Behaviour* and is limited to articles related to animal communication published in the first five issues of the journal in 2011 (January – May). These were simply the issues from that year that were available at the time this chapter was drafted. The examples cover a wide range of species and signalling topics. The quoted material is drawn from the Abstract, Introduction or Discussion sections that provided general characterizations of the communication problems being studied. In no case were the core informational constructs being used further clarified or defined, and none of the studies used information in its understood formal quantitative sense. In some cases, additional cognitive constructs were invoked also without definition or clarification (e.g., decision, evaluation).

Author(s)	Topic and Taxon	Explanations of signals, signalling, or communication
Jordan <i>et al.</i> (2011: 31-42)	Scent marking in mongoose	“To understand fully the function(s) of scent marking we need to consider not only the broad spatial patterns of scent deposition, but also both the <i>information content</i> of olfactory signals... In general, glandular secretions tend to contain stable <i>category-specific information</i> ... and are less likely to convey <i>information</i> on, and vary with, reproductive physiology... Excretory products are more likely to <i>contain and convey information</i> on reproductive state.”
Whattam & Bertram (2011: 135-144)	Signals of condition in field crickets	“Content-based signals are thought to evolve because of the <i>information content</i> they <i>provide</i> to the receiver. Such signals may function as multiple messages, each <i>relaying different information or types of information</i> .”
Judge (2011: 185-194)	Effect of age and quality on male courtship success in field crickets	“In the fall field cricket, <i>G. pennsylvanicus</i> , age <i>information</i> is conveyed through calling song... a longitudinal analysis may detect relatively subtle age-related changes in calling song, but these changes may not <i>convey enough information</i> for females to predict male age.... To examine the <i>amount of information</i> about male age relative to male morphology that is conveyed in song, I conducted three sequential canonical correlation and redundancy analyses.”
Green & Field (2011: 205-209)	Status signalling in wasps	“Visual status signals are small patches of colour that <i>convey information</i> about an individual’s competitive ability, or resource-holding potential (RHP), to an opponent.”
Berg <i>et al.</i> (2011: 241-248)	Individual recognition in parrotlets	“Contact calls function to coordinate activities between two or more individuals in many social animals... <i>Signature information</i> seems particularly important when individuals need to identify each other in crowded, noisy or dangerous reproductive contexts. Green-rumped parrotlets have large, albeit poorly known, vocal repertoires and could have individual <i>information encoded</i> in additional call types.”
Gordon & Uetz (2011: 367-375)	Multimodal communication in spiders	“... multimodal communication, in which communication is defined by signals that <i>convey information</i> in more than one sensory modality or communication channel... Interest in multimodal signalling has resulted in numerous (nonexclusive) hypotheses concerning the origin, nature

		and content of multimodal signalling: (1) signals in different sensory modes <i>contain the same information</i> ... (2) signals in different sensory modes each <i>provide different information</i> ... (3) signals in different sensory modes <i>contain information intended</i> for different receivers, or are used in different contexts ...”
Chaine <i>et al.</i> (2011: 447-453)	Multiple status signals in sparrows	“In birds, research on status signals has largely involved the colour and area of distinct feather patches... Multiple signals are traits that show some phenotypic independence and <i>convey either independent information</i> to the same receiver or <i>different information</i> to different receivers.”
Nunes <i>et al.</i> (2011: 463-467)	Nestmate recognition in stingless bees	“The cuticle of stingless bees, as in other social insects, is a rich source of <i>information</i> that is important for the regulation of their society... Each individual in a colony presents a blend of compounds on its cuticle that may also <i>carry information</i> regarding its sex, age, caste, group task as well as colony”
Antunes <i>et al.</i> (2011: 732-730)	Individual variation in acoustic signals of sperm whales	“Securing the benefits of group living often requires mechanisms for group cohesion. These require the <i>exchange of information</i> through some form of communication.... With this in mind, we hypothesized that variation in particular coda types could potentially <i>carry information</i> about individual identity and therefore codas could <i>contain both group- and individual-level information</i> . ... The present study also suggests that codas are <i>hierarchically coded signals</i> in which individuality <i>information</i> is <i>encoded</i> in finer variations in timing around the stereotyped rhythm of a given coda type. We suggest that studies of animal communication will benefit from considering the possibility of subtle <i>information coding</i> at different hierarchical levels that may otherwise be overlooked.”
Barrera <i>et al.</i> (2011: 779-787)	Predator avoidance in doves	“Animals identify potential risk by assessing various cues such as alarm calls and predator vocalizations... However, these different cues provide <i>different information</i> .... We first demonstrated that predator-elicited wing whistles in zenaida doves are alarm signals... Then, we studied the <i>relative information content</i> of these signals compared to vocalizations from a common predator, the red-tailed hawk... Given that our results showed a greater reaction to predator sounds, we infer that the nonvocal wing whistle was less reliable, suggesting that reliability influences the receiver’s <i>evaluation of the relative information content</i> .”
Karubian <i>et al.</i> (2011: 795-800)	Sexual signalling in fairy wrens	“In the red-backed fairy-wren, bill coloration (and perhaps behaviour) appears to <i>provide information</i> on current status during the breeding season ... whereas plumage coloration <i>provides information</i> on condition, circulating levels of androgens and, potentially, status during moult prior to the breeding season. These findings are consistent with the ‘multiple messages hypothesis’, which proposes that different ornaments <i>provide information</i> about individual quality at different stages of life .”

<p>Gruter &amp; Ratnieks (2011: 949-954)</p>	<p>Forager recruitment in bees</p>	<p>“In many social insects, successful foragers guide nestmates to food sources by <i>providing</i> route or location <i>information</i> (in their waggle dances) ... However, recent studies suggest that many workers that follow waggle dances ignore the vector <i>information</i> on leaving the nest... It seems that the floral odours on the dancing bee are important... Hence, social odour <i>information</i> can cause <i>informational ambiguity</i> if it is similar to private odour <i>information</i> linked to route memories.”</p>
<p>Balsby &amp; Adams (2011: 983-991)</p>	<p>Flockmate recruitment in conures</p>	<p>“Identifying which individuals will make good group mates requires the ability to communicate motivational state and/or identity prior to fission-fusion events... Vocalizations can <i>carry</i> a variety of <i>information</i>, including group/flock association, relatedness or geographical origin, as well as <i>information</i> on physical characteristics such as sex, age and condition, all of which may aid the <i>decision</i> of whether or not to recruit other individuals.... In fission-fusion societies, the <i>information exchanged</i> within a single vocal interaction may be sufficient to <i>decide</i> whether or not to recruit an individual or group.”</p>

## References

- Barrett, L. (2011) *Beyond the Brain: How Body and Environment Shape Animal and Human Minds*. Princeton, NJ: Princeton University Press.
- Beecher, M. D. (1989) Signaling systems for individual recognition: An information theory approach. *Animal Behaviour* **38**, 248-261.
- Brooks, R. (1991) Intelligence without representation. *Artificial Intelligence Journal* **47**, 139-159.
- Cheney, D.L. & Seyfarth, R.M. (1996) Function and intention in the calls of nonhuman primates. *Proceedings of the British Academy* **88**, 59-76.
- Cheney, D. L. & Seyfarth, R. M. (1998) Why animals don't have language. In: *The Tanner Lectures on Human Values* (Ed. by G.B. Pearson), pp. 174-209, Salt Lake City: University of Utah Press.
- Cheney, D.L. & Seyfarth, R.M. (2005) Constraints and preadaptations in the earliest stages of language evolution. *Linguistic Review* **22**, 135-159
- Cheney, D. L., Seyfarth, R. M. & Palombit, R. (1996) The function and mechanisms underlying baboon 'contact' barks. *Animal Behaviour* **52**, 507-518.
- Cheng M.-F. (1992). For whom does the female dove coo? A case for the role of self-stimulation. *Animal Behaviour* **43**, 1035-1044.
- Cheng M.-F. & Peng, J.P. (1997) Reciprocal talk between the auditory thalamus and hypothalamus: an antidromic study. *NeuroReport* **8**, 653-658.
- Chomsky, N. (1959) Review of Verbal Behavior, by B.F. Skinner. *Language* **35**, 26-57.
- Chomsky, N. (1965) *Aspects of the Theory of Syntax*. Cambridge, MA: MIT Press.
- Chomsky, N. (1995) *The Minimalist Program*. Cambridge, MA: MIT Press.
- Clark, A. (1997) *Being There: Putting Brain, Body, and World Together Again*. Cambridge, MA: MIT Press.
- Clark, A. (2001) *Mindware: An Introduction to the Philosophy of Cognitive Science*. Oxford: Oxford University Press.
- Clark, A. (2008) *Supersizing the Mind: Embodiment, Action, and Cognitive Extension*. Oxford: Oxford University Press.
- Clark, A. & Chalmers, D. (1998) The extended mind. *Analysis* **58**, 7-19.
- Cowley, S. & Love, N. (2006) Language and cognition, or, how to avoid the conduit metaphor. In: *Bridges and Walls in Metalinguistic Discourse* (Ed. by A. Duszak & U. Okulska), pp. 135-156. Frankfurt/Main: Peter Lang.
- Craver, C.F. (2006) When mechanistic models explain. *Synthese* **153**, 355-376.
- Cummings, M. E. (2007) Sensory trade-offs predict signal divergence in surfperch. *Evolution* **61**, 530-545.
- Dawkins, R. & Krebs, J. R. (1978) Animal signals: information or manipulation. In: *Behavioural Ecology: an Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 282-309. Oxford: Blackwell Scientific.
- Dreyfus, H. (1999) *What Computers Still Can't Do*. Cambridge, MA: MIT Press.
- Endler, J.A. & Basolo, A.L. (1998) Sensory ecology, receiver biases and sexual selection. *Trends in Ecology & Evolution* **13**, 415-420.
- Enquist, M. & Arak, A. (1993) Selection of exaggerated male traits by female aesthetic senses. *Nature* **361**, 446-448.

- Fitch, W.T. & Hauser, M.D. (1995) Vocal production in nonhuman primates: Acoustics, physiology and functional constraints on 'honest' advertising. *American Journal of Primatology* **37**, 191-219.
- Fodor, J. (1975) *The Language of Thought*. Cambridge, MA: Harvard University Press.
- Galef, B. G., Jr. & Laland, K. N. (2005) Social learning in animals: empirical studies and theoretical models. *Bioscience* **55**, 489-499.
- Gallese V, Fadiga L, Fogassi L, Rizzolatti G. (1996). Action recognition in the premotor cortex. *Brain* **119**, 593-609.
- Gibson, J.J. (1979). *The Ecological Approach to Visual Perception*. Boston: Houghton Mifflin.
- Grasse, P.P. (1959). La reconstruction du nid et les coordinations inter-individuelles chez *Bellicositermes natalensis* et *Cubitermes* sp. La theorie de la stigmergie: Essai d'interpretation des termites constructeurs. *Ins. Soc.* **6**, 41-83.
- Griffin, D.R. (1974) *The question of animal awareness*. New York: Rockefeller University Press.
- Griffin, D.R. (1995) Windows on animal minds. *Consciousness and Cognition* **4**, 194-204.
- Grice, P. (1957) Meaning. *The Philosophical Review* **66**, 377-388.
- Guilford, T. & Dawkins, M. S. (1991) Receiver psychology and the evolution of animal signals. *Animal Behaviour* **42**, 1-14.
- Harris, R. (1981) *The Language Myth*. London: Duckworth Publishers.
- Harris, R. (1998) *Introduction to Integrational Linguistics*. Oxford, UK: Pergamon Press.
- Hartshorne, C. (1973) *Born to Sing*. Indiana University: Bloomington
- Hauser, M.D. (2009) The possibility of impossible cultures. *Nature* **460**, 190-196.
- Hutchins, E. (1995) *Cognition in the Wild*. Cambridge, MA: MIT Press.
- Jarvilehto, T. (2009) The theory of the organism-environment as basis for experimental work in psychology. *Ecological Psychology* **21**, 112-120.
- Johnson, K. (1997) Speech perception without speaker normalization: An exemplar model. In: *Talker Variability in Speech Processing*, (Ed. by K. Johnson & J. Mullenix), pp. 145-166. New York: Academic Press.
- Jürgens, U. (2008). The neural control of vocalization in mammals: a review. *Journal of Voice* **23**, 1-10.
- Kravchenko, A. V. (2007) Essential properties of language, or, why language is not a code. *Language Sciences* **29**, 650-671
- Kuhl, P. K. (2000). A new view of language acquisition. *Proceedings of the National Academy of Science* **97**, 11850-11857.
- Kuhl, P. K., & Miller, J. D. (1975). Speech perception by the chinchilla: Voiced-voiceless distinction in alveolar plosive consonants. *Science* **190**, 69-72.
- Kuhl, P. K., & Padden, D. M. (1982). Enhanced discriminability at the phonetic boundaries for the voicing feature in macaques. *Perception & Psychophysics* **32**, 542-550.
- Lakoff, G. & Johnson, M. (1980) *Metaphors We Live By*. Chicago: University of Chicago Press.
- Landauer, T.K. & Dumais, S.T. (1997) A solution to Plato's problem: The latent semantic Analysis theory of the acquisition, induction, and representation of knowledge.



- Psychological Review* **104**, 211-240.
- Leger, D.W. (1993) Contextual sources of information and responses to animal communication signals. *Psychological Bulletin* **113**, 295-304.
- Lieberman, A. M., Harris, K. S., Hoffman, H. S. & Griffith, B. C. (1957). The discrimination of speech sounds within and across phoneme boundaries. *Journal of Experimental Psychology* **54**, 358–368.
- Lieberman, P. (2002) On the nature and evolution of the neural bases of human language. *Yearbook of Physical Anthropology* **45**, 36-62.
- Lisker, L. & Abramson, A.S. (1967). Some effects of context on voice onset time in English stops. *Language and Speech* **10**, 1–28.
- Marler, P. (1961) Logical analysis of animal communication. *Journal of Theoretical Biology* **1**, 295-317.
- Marler, P., Evans, C. S. & Hauser, M. D. 1992. Animal signals: Motivational, referential, or both? In: *Nonverbal vocal communication: Comparative and Developmental Approaches* (Ed. by H. Papousek, U. Jürgens, & M. Papousek), pp. 66-86, Cambridge: Cambridge University Press.
- Maynard Smith, J. & Harper, D. (2003) *Animal Signals*. Oxford: Oxford University Press.
- McLuhan, M. (1964) *Understanding Media: The Extensions of Man*. New York: McGraw Hill.
- Mello, C., Nootebohm, F., & Clayton, D. (1995) Repeated exposure to one song leads to a rapid and persistent decline in immediate early gene's response to that song in zebra finch telencephalon. *The Journal of Neuroscience* **15**, 6919-6925.
- Miller, G. A. (1956) The magical number seven, plus or minus two: Some limits on our capacity for processing information. *Psychological Review* **63**, 81–97.
- Neisser, U. (1967) *Cognitive Psychology*. New York: Apple-Century-Crofts.
- Newell, A. & Simon, H. (1976) Computer science as empirical enquiry: Symbols and search. *Communications of the Association for Computing Machinery* **19**, 113-126.
- Noe, A. (2009) *Out of Our Heads*. New York: Hill and Wang.
- Nygaard, L. C., Sommers, M. S., & Pisoni, D. B. (1994). Speech perception as a talker-contingent process. *Psychological Science* **5**, 42-46.
- Ogden, C.K. & Richards, I.A. (1923) *The Meaning of Meaning*. New York: Harcourt Brace.
- Owings, D. H. & Morton, E.S. (1997) The role of information in communication: An assessment/management approach. In: *Perspectives in Ethology: Volume 12. Communication* (Ed. by D.H. Owings, M.D. Beecher & N.S. Thompson), pp. 359-390, New York: Plenum Press.
- Owings, D. H. & Morton, E. S. (1998) *Animal Vocal Communication: A New Approach*. Cambridge: Cambridge University Press.
- Owren, M.J. & Rendall, D. (1997) An affect-conditioning model of nonhuman primate vocalizations. In: *Perspectives in Ethology, Vol. 12 Communication* (Ed. by D.H. Owings, M.D. Beecher & N.S. Thompson), pp. 299-346. New York: Plenum Press.
- Owren, M.J. & Rendall, D. (2001) Sound on the rebound: Returning form and function to the forefront in understanding nonhuman primate vocal signaling. *Evolutionary Anthropology* **10**, 58-71.

- Owren, M.J., Rendall, D. & Ryan, M.J. (2010) Redefining animal signaling: Influence versus information in communication. *Biology and Philosophy* **25**, 755-780.
- Owren, M.J., Amoss, R.T., Rendall, D. (2011) Two organizing principles of vocal production: Implications for nonhuman and human primates. *American Journal of Primatology* **73**, 530-544.
- Palmeri, T.J., Goldinger, S.D., & Pisoni, D.B. (1993) Episodic encoding of voice attributes and recognition memory for spoken words. *Journal of Experimental Psychology: Learning, Memory and Cognition* **19**, 309-328.
- Penn, D. C. & Povinelli, D.J. (2007) On the lack of evidence that chimpanzees possess anything remotely resembling a 'theory of mind.' *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences* **362**, 731-744.
- Port, R.F. (2010) Language as a Social Institution: Why Phonemes and Words Do Not Live in the Brain. *Ecological Psychology* **22**, 304-326.
- Rendall, D., Owren, M.J. & Rodman, P.S. (1998) The role of vocal tract filtering in identity cueing in rhesus monkey (*Macaca mulatta*) vocalizations. *Journal of the Acoustical Society of America* **103**, 602-614.
- Rendall D., Cheney D. L., & Seyfarth R. M. 2000. Proximate factors mediating 'contact' calls in adult female baboons and their infants. *Journal of Comparative Psychology*, **114**, 36-46.
- Rendall, D., Owren, M.J. & Ryan, M.J. (2009) What do animal signals mean? *Animal Behaviour* **78**, 233-240.
- Rendall, D. & Owren, M.J. (2009) Vocalizations as tools for influencing the affect and behavior of others. In: *Handbook of Mammalian Vocalization: An Integrative Neuroscience Approach*. (Ed. by S.M. Brudzynski), pp. 177-186. Oxford: Academic Press.
- Rosenbleuth, A. & Weiner, N. (1950) Purposeful and non-purposeful behavior. *Philosophy of Science* **17**, 318-326.
- Ryan, M. J. 1990. Sensory systems, sexual selection, and sensory exploitation. *Oxford Surveys in Evolutionary Biology* **7**, 157-195.
- Ryan, M.J. (1998) Receiver biases, sexual selection and the evolution of sex differences. *Science* **281**, 1999-2003.
- Ryan, M.J. & Rand, A.S. (2003) Mate recognition in tungara frogs: A review of some studies of brain, behavior, and evolution. *Acta Zoologica Sinica* **49**, 713-726.
- de Saussure, F. (1916/1986) *Course in General Linguistics*. C. Bally & A. Sechehaye, eds. Translated by R. Harris. La Salle, IL: Open Court Publishing.
- Scott-Phillips, T. (2010) Animal communication: Insights from linguistic pragmatics. *Animal Behaviour* **79**, e1-e4.
- Saffran, J.R., Aslin, R.N., & Newport, E.L. (1996) Statistical learning by 8-month-old infants. *Science* **274**, 1926-1928.
- Searcy, W.A (1992) Song repertoire and mate choice in birds. *American Zoologist* **32**, 71-80.
- Searcy, W. A. & Nowicki, S. (2005) *The Evolution of Communication: Reliability and Deception in Animal Signaling Systems*. Princeton, NJ: Princeton University Press.
- Searle, J. (1980) Minds, brains and programs. *Behavioral and Brain Sciences* **3**, 417-457.

- Siegel, S., Baptista, M. A. S., Kim, J. A., McDonald, R. V. and Weise-Kelly, L. (2000). Pavlovian psychopharmacology: The associative basis of tolerance. *Experimental and Clinical Psychopharmacology* **8**, 276-293.
- Seyfarth, R. M. & Cheney, D. L. (1986) Vocal development in vervet monkeys. *Animal Behaviour* **34**, 1640-1658.
- Seyfarth, R.M., Cheney, D.L. & Marler, P. (1980) Monkey responses to three different alarm calls: Evidence for predator classification and semantic communication. *Science* **210**, 801-803.
- Shannon, C. E. & Weaver, W. (1949) *The Mathematical Theory of Communication*. Urbana-Champaign, IL: University of Illinois Press.
- Smith, W.J. (1977) *The Behavior of Communicating*. Cambridge, MA: Harvard University Press.
- Thelen, E. & Smith, L. (1994) *A Dynamic Systems Approach to the Development of Cognition and Action*. Cambridge, MA: MIT Press.
- Tomasello, M. (2008) *Origins of Human Communication*. Cambridge, MA: MIT Press.
- Trivers, R. (1974) Parent-offspring conflict. *American Zoologist* **14**, 249-264.
- Turing, A.M. (1950). Computing machinery and intelligence. *Mind* **59**, 433-460.
- Van Gelder, T. (1995) What might cognition be, if not computation? *Journal of Philosophy* **92**, 345-381.
- Uexküll J. von (1910) Die Umwelt. *Die neue Rundschau* **21**, 638-649.
- Wheeler, M. & Clark, A. (2008) Culture, Embodiment and Genes: Unravelling the Triple Helix. *Philosophical Transactions of the Royal Society Series B* **363**, 3563-75.
- Wilczynski W. & Chu, J. (2001) Acoustic communication, endocrine control, and the neurochemical systems of the brain. In: *Anuran Communication* (Ed. by M.J. Ryan) pp. 23-35. Smithsonian Institution: Washington, DC.
- Zahavi, A. & Zahavi, A. (1997) *The Handicap Principle: a Missing Piece of Darwin's Puzzle*. Oxford: Oxford University Press.

## Figure legends

Figure 1. A schematic illustrating core features common to language-based and informational models of communication. Communication involves the transmission of information, from signaller to receiver. It starts with some form of ideation (thought, belief, motive) that is translated into a message that is encoded by the signaller in the details of a physical signal that is then transmitted to the receiver. The receiver receives the physical signal and decodes its information content to recover the intended message. The emphasis in communication is on the disembodied packet of information encoded in the signal that flows from signaller to receiver. Additional implicit assumptions are that the mechanisms of signal encoding and decoding are matched to ensure fidelity of information transmission and that the information being transmitted is honest, because receivers are free to discount anything else.

Figure 2. A schematic illustrating some important features of non-informational alternatives to animal communication. Functionally, communication is dynamic, both in real-time and in evolutionary time, and involves an iterated process of reciprocal influence and resistance by signallers and receivers with overlapping spheres of influence. The details of the physical signals are important and are central to the functions they serve which often entail having relatively direct influence on receiver sensory, motivational and cognitive systems. Signals may be honest because receiver resistance is an important pressure favouring honesty, but honesty in signalling is not assumed because historical mechanistic constraints and inevitable functional tradeoffs often leave receivers susceptible to signaller influence, such that signalling dynamics can deviate from honest equilibria. Signalling dynamics are importantly affected by a host of additional factors including the sensory, motivational, cognitive and behavioural biases and predispositions of signallers and receivers alike and how these have been shaped by their species (phylogenetic) and individual histories and are, in turn, modulated in real-time by specific features of the social and environmental context.

Figure 1

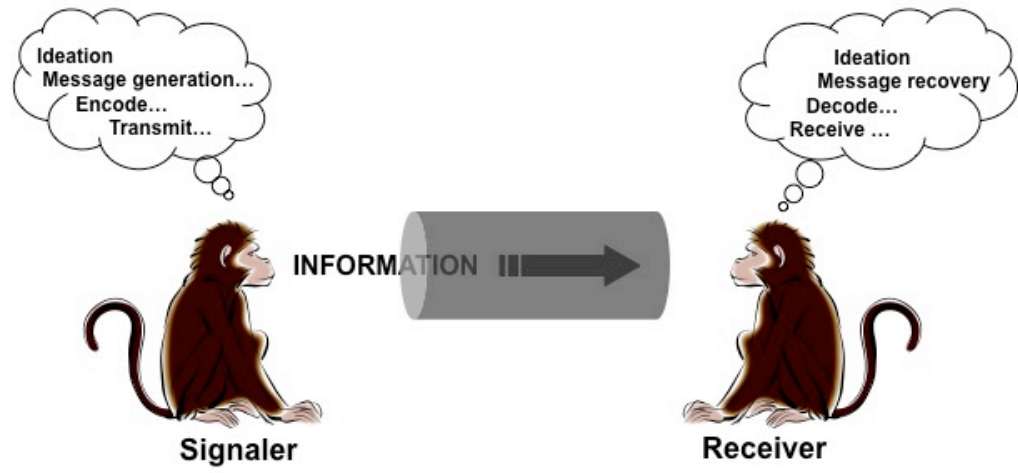


Figure 2

