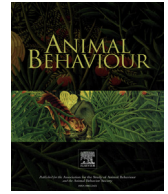Contents lists available at ScienceDirect

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The origin of meaning in animal signals

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Over 40 years ago, Peter Marler proposed that animal signals were adaptive because they provided listeners with information (Marler, 1961, *Journal of Theoretical Biology*, *1*, 295–317). But what was the nature of this information? How did it influence behaviour? And how might the information in animal signals compare with the information in human language? Here we review evidence that signals in a variety of social contexts are adaptive because they convey information. For recipients, meaning results from the integration of information from the signal and the social context. As a result, communication in animals — particularly in long-lived, social species where the same individuals interact repeatedly — constitutes a rich system of pragmatic inference in which the meaning of a communicative event depends on perception, memory and social knowledge. In the human lineage, pragmatics served as a precursor to the later evolution of semantics and syntax. Among primates, there is a striking difference in flexibility between constrained call production and more flexible perception and cognition. However, call production is more flexible in the wild, where it is affected by contextual cues, than in laboratory studies where contextual cues have been removed. Monkeys and apes may overcome the limits of constrained vocal production by producing composite signals in the same and different modalities.

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In this essay we focus on an issue that was central to Peter Marler's research on animal communication: the meaning of animal signals.

Research on animal communication has made almost no progress in understanding the semantics of natural signaling behavior because it is an exceedingly difficult problem in both practical and theoretical terms. … There is an irresistible tendency to use language as a model, either for comparison or contrast. This would be more appropriate if we really understood human semantics and the processes by which language acquires meaning in the course of our own early development. In many respects our picture of how words acquire meaning in human infancy is hardly any clearer than our understanding of the meanings of signals for animals … In both human and animal studies, for example, there are assertions of the overwhelming importance of contextual cues in understanding meaning (Smith, 1977), but precisely how the context influences meaning in particular cases has hardly been explored.

(Marler, 1983)

Marler's interests in the meaning of animal signals brought him squarely into the revolution in neurobiology, psychology, linguistics and cognitive science. When he began his research in the 1950s, questions about the 'minds' of animals had largely been ignored, because both psychologists like Skinner and ethologists like Tinbergen thought they were unanswerable and hence unsuited to scientific inquiry (Boakes, 1984; Burkhardt, 2005). Over the years, Marler developed a different view (Marler, 1961). He thought that, regardless of whether or not they were voluntary or intentional, animal signals provided listeners with information. But what was the nature of this information? Was it stored in memory so that it could affect future interactions? And particularly in monkeys and apes, could we find evidence for something like the 'mental representations' that were currently coming to light in human psychology, linguistics and cognitive science?

Here we review progress that has been made in answering these questions in the years since Marler first drew attention to them. We begin with evolution. Communication has been shaped by natural selection. Signallers would not produce signals if doing so were not beneficial to them, and receivers would not respond if doing so were not beneficial to *them*. But the signaller and the recipient are sometimes competitors, sometimes cooperators, and often a bit of both. How does communication achieve these two, sometimes

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contradictory, benefits? Studies of baboons and macaques, together with theoretical models, demonstrate how cheap signals that convey reliable information can become evolutionarily stable in social groups where competition and cooperation are inextricable entwined.

Next, we consider the link between communication and cognition. Following Marler and many others, we argue that most communicative events are adaptive for both signaller and recipient because signals reduce the uncertainty inherent in any social interaction. They do so by providing information. Where does it come from? We argue that, whereas some signals by themselves can provide recipients with specific information, many signals are vague. Signals do not occur in a vacuum, however. They are, instead, embedded in a rich social context where animals know each other and have a long history of interaction. This contextual information frames each communicative event, enormously enriching what a signal means. Borrowing a term from linguistics, we propose that animal communication constitutes a rich pragmatic system. The ubiquity of pragmatics, combined with the relative scarcity of semantics and syntax, suggest that as language evolved semantics and syntax were built upon a foundation of sophisticated pragmatic inference (Seyfarth & Cheney, 2014a, in press).

Finally, as Marler (1965) first noted, vocal production in nonhuman primates – and indeed most mammals – is highly constrained. How, he wondered, could such a limited system of production function in such a richly varied, ever-changing social environment? Subsequent research has shown, as Marler first predicted, that call production is not as rigid and reflexive as originally believed: contextual cues can affect call type, call acoustics, and whether an animal calls or remains silent. Marler also suggested that nonhuman primates overcome the constraints imposed by a limited vocal repertoire both by combining calls with visual signals and by combining different call types with each other ('composite' signals: Marler, 1965). Here again, his suggestions have proved prescient: we discuss some recent examples.

THE EVOLUTION OF SOCIAL SIGNALS

Animals are often involved in overtly competitive interactions: over food, territory, or mates. But rather than immediately escalating to physical fighting, competition is more likely to take the form of displays, like the roars of red deer, *Cervus elaphus* (Clutton-Brock & Albon, 1979), the jousting of stalk-eyed flies (Wilkinson & Reillo, 1994), the croaking of male frogs (Ryan, 1985), or the loud wahoo calls of male baboons (Fischer, Kitchen, Seyfarth, & Cheney, 2004; Kitchen, Seyfarth, Fischer, & Cheney, 2003). Thanks to decades of empirical research (reviewed in Bradbury & Vehrencamp, 2011; Searcy & Nowicki, 2005) and pioneering theoretical work (Enquist, 1985; Grafen, 1990; Maynard Smith, 1991; Zahavi, 1975), we now have an explanation of why these displays are evolutionarily stable. To cite just one example, in red deer the fundamental frequency (F0) – or, more accurately, formant spacing – in a male's roar is constrained by his body size, which in turn predicts his competitive ability (Reby et al., 2005). Formant spacing is an honest, unfakeable cue because small males cannot make deep-pitched roars. And because formant spacing accurately predicts competitive ability, selection has favoured listeners who decide to escalate or retreat based in part on this acoustic cue. From the listener's perspective, honest signals provide a reliable way to assess an opponent quickly and with minimal risk (Searcy & Nowicki, 2005). If the listener cannot make an assessment (because, for example, roars are so alike that they cannot be distinguished), the interaction escalates to include additional signals or behaviour that reduce the participants' uncertainty, like the 'parallel walk' in red deer (Alvarez, 1993; Clutton-Brock & Albon, 1979; see Searcy & Nowicki, 2005, for further discussion).

But what about the many other signals that animals use in less competitive, more cooperative circumstances? Can the same argument be applied? Consider, for example, the grunts given by female baboons (*Papio cynocephalus ursinus*) as they approach mothers with young infants. Like all female primates, female baboons are highly attracted to infants; however, mothers are often reluctant to allow access to their infants, particularly when the approaching individual is of higher dominance rank (Silk, Rendall, Cheney, & Seyfarth, 2003). Mothers rarely initiate interactions with prospective handlers, and when other females approach them, mothers' reactions range from passive acceptance to overt avoidance (Silk et al., 2003). For all of these reasons, the individuals involved in this communicative event are, in a mild way, competitors.

At the same time, infant handling is common among females and occurs even when the two females are highly disparate in rank. It is often accompanied by grooming and occurs at high rates among individuals that may live for many years together in groups where repeated interactions are common and long-term social bonds with consistent partners are positively correlated with reproductive success (Silk et al., 2009, 2010a, 2010b). For all of these reasons, the individuals involved are not exactly competitors – in many respects their interests overlap.

Grunts facilitate infant handling. When a female gives a series of grunts as she approaches a mother with infant, the mother is significantly less likely to move away than if the approaching female remains silent (Cheney, Seyfarth, & Silk, 1995). How do grunts achieve this outcome? In a study of rhesus macaques, *Macaca mulatta*, where females' interest in infants is also high and grunt and girney vocalizations facilitate infant handling, Silk, Kaldor, and Boyd (2000) found that grunts and girneys accurately predicted the approaching female's subsequent behaviour: if she grunted, aggression was significantly less likely and grooming was significantly more likely than if she did not. In other words, there was a contingent, predictable relation between the approaching female's vocalizations and what she did next. Mothers had come to recognize this contingency and treated grunts and girneys as honest indicators of the approaching female's benign disposition. Just as in any learning experiment – or any competitive interaction – mothers acquired information from signals. This information reduced their uncertainty and affected their behaviour.

Following Maynard Smith (1991, 1994), Silk et al. (2000) developed a model demonstrating that honest, low-cost signalling can be an evolutionarily stable strategy (ESS) even when there is conflict of interest between the individuals involved, as long as the individuals interact repeatedly. Such signalling is particularly likely to evolve when individuals rank the value of possible outcomes in the same order (for example, by preferring a friendly outcome over an aggressive one) or evaluate outcomes differently but place some value on coordination. This result is important because it suggests that honest, low-cost signalling can evolve under a wide variety of conditions. Indeed, the conditions that are most favourable to its evolution are those commonly found in groups of social mammals.

INFORMATION

Evolutionary models of communication invoke the concept of information, but their exclusive focus on function leaves them agnostic about the content of information or how it is acquired. Grafen (1990, page 521), for example, stated that 'at ESS the receivers will have adjusted their assessment rule so that they determine correctly the true quality of a male', but he did not

specify the content underlying the assessment rule or how its adjustment is achieved. For Grafen, all that mattered was that the assessment rule focused on a stimulus that was correlated with the signaller's quality.

Learning theory helps to clarify the content of information and how it is acquired. Indeed, there is a striking convergence in the language used by evolutionary biologists and learning theorists when they describe signallers' displays and receivers' assessments. Just as biologists discuss 'persuasive' attempts by signallers that try to influence the behaviour of recipients (Grafen, 1990, page 529), learning theorists propose that, with experience, animals acquire information about the relationship between their own acts and particular outcomes (Gleitman, Gross, & Reisberg, 2011, pp. 278ff; Tolman, 1932). And just as biologists propose that receivers 'adjust their assessment rule', learning theorists state that 'expectations [are] shaped, trial by trial, by an adjustment process that brings the expectations into line with reality … [so] the animal's behaviour ends up fully in accord with the probabilities in its environment' (Gleitman et al., 2011, page 274; Kamin, 1968; Rescorla & Wagner, 1972).

Given these converging perspectives, we can combine evolutionary theory, animal learning and some recent field experiments to address questions that were fundamental to Marler's research, such as what information is acquired from signallers, how that information is organized and stored in memory and how the information contained in animal signals relates to the information contained in human words (Marler, 1961, 1982, 1985).

What Determines the Information That Recipients Acquire from a Signal?

Properties of the signal

Three factors shape the acquisition and content of information acquired by animals. The first is a signal's informative value (Seyfarth & Cheney, 2003). Whenever there is a predictable relation between a particular signal and a specific individual or social situation, the signal has the potential to provide listeners with information. A light that predicts shock, an alarm call that predicts the presence of an eagle, or an individually distinctive scream all have the potential to provide a listener with specific information because they are reliably associated with a narrow range of contexts (Rescorla, 1988; Seyfarth & Cheney, 2003; Seyfarth et al., 2010).

The second factor is the breadth of stimuli that elicit a signal, or its referential specificity (Seyfarth & Cheney, 2003). Some animal vocalizations are elicited by a broad array of stimuli whereas others are highly stimulus specific. For example, both suricates (*Suricata suricatta*) and female Diana monkeys, *Cercopithecus diana*, give 'alert' calls to a wide variety of stimuli, including mammalian and avian predators, large nonpredatory animals, falling trees and social disturbances within the group (Gautier & Gautier, 1977; Manser, 2001; Zuberbühler, Noë, & Seyfarth, 1997). These general alerting signals differ from two acoustically distinct calls given by the same species to specific types of predator, snakes and raptors. Whereas such predator-specific calls have the potential to provide information that is relatively precise, general alert calls provide a listener with information that is more vague.

The third factor is signal specificity. How easy is it to distinguish a particular signal from others in the signaller's repertoire? Among vervet monkeys (*Chlorocebus aethiops*), for example, the acoustically distinctive 'terrestrial predator alarm' given by adult females provides listeners with specific information because it not only predicts the presence of a predator and is elicited by a narrow range of stimuli but also because it is acoustically distinct from other calls in the vervets' repertoire (Price et al., 2015; Seyfarth, Cheney, & Marler, 1980). By contrast, the alarm call given by adult female vervets to snakes satisfies the first two criteria because it is reliably elicited only by snakes; however, it overlaps in its acoustic features with the threatening chutter calls that vervet females give during conflicts with members of their own and other groups (Price et al., 2015; Struhsaker, 1967). As a result, the information potentially available to a listener who hears a snake alarm may be somewhat more ambiguous, and the listener's response may depend more on accompanying contextual cues — although the possibility remains that vervets can discriminate among calls that, by our acoustic measurements, seem to overlap (e.g. Fischer, 1998).

Some animal signals satisfy all three criteria for specific, highly informative signals. They are reliable predictors, elicited by only a narrow range of stimuli, and they are easy to distinguish from other signals. As a result, they have the potential to provide recipients with specific information. Other signals satisfy some, but not all, of the requirements, so the information they can potentially provide is precise along some dimensions and vague along others. A listener, for example, may hear a vocalization that recognizably comes from individual X but be unable to determine from the call alone exactly what X is doing or communicating about. What determines a recipient's response in these uncertain circumstances?

Properties of the context

We now know that animals can acquire very precise information from an otherwise imprecise signal by incorporating information from the context in which the signal is given (Smith, 1977). The importance of context immediately becomes apparent when one considers that most communication among animals occurs in stereotypical situations where the kinds of information that might be transmitted are sharply reduced. When a territorial songbird sings, or a female baboon grunts to a mother with an infant, the song and the grunt occur in common, highly stereotyped contexts (or 'frames', to borrow a term from cognitive science) where the scope of possible information — what the signal could possibly mean — is limited. The bird's song might provide information about the singer's intention to defend his territory or court a female (Searcy, Akçay, Nowicki, & Beecher, 2014), but in this particular context it is unlikely to predict the singer's feeding behaviour or the presence of a predator. A baboon's grunt as she approaches a mother with infant predicts her benign intent, but it is unlikely to provide information about anything else.

The incorporation of contextual information (or 'framing') is especially prevalent when the individuals involved recognize one another and have had a history of interaction. Under these circumstances, the context of a signal expands to include all of the information stored in the animals' memories, enormously enriching the variety of information that a signal can convey. Consider, for example, the reconciliatory grunts given by female baboons after an aggressive interaction.

Many primates 'reconcile' with an opponent by touching, hugging or behaving in a friendly way towards the opponent after aggression (Aureli, Fraser, Schaffner, & Schino, 2012; Cords, 1992; de Waal, 1996). Such reconciliatory signals may be adaptive because they minimize the disruptive potential of aggression by bringing opponents back to baseline levels of interaction. In baboons, reconciliation often takes the form of grunts; following roughly 10% of aggressive interactions between adult females, the aggressor grunts to her former victim soon after aggression (Silk, Cheney, & Seyfarth, 1996). Audio playback experiments confirm that these grunts function as reconciliatory signals: playback of the aggressor's grunt increases the likelihood that the victim will approach her former opponent or tolerate her opponent's approach (Cheney & Seyfarth, 1997; Cheney et al., 1995). By contrast, playback of a grunt from another higher-ranking individual not previously

involved in an aggressive interaction with the victim produces no such changes in behaviour (Cheney & Seyfarth, 1997). The grunts of a close relative of the aggressor can also reconcile opponents: in other playback experiments, victims of aggression were more likely to tolerate their opponent's proximity in the hour after aggression if they have heard the grunt of their opponent's relative than if they had heard the grunt of a more dominant individual belonging to a different matriline (Wittig, Crockford, Ekberg, Seyfarth, & Cheney, 2007).

Considered in isolation, baboon grunts are very general, nonspecific signals. They are acoustically similar; occur in a variety of contexts; and do not necessarily predict any particular sort of behaviour (Cheney et al., 1995; Rendall, Seyfarth, Cheney, & Owren, 1999; Silk et al., 2003). They are also individually distinctive (Owren, Seyfarth, & Cheney, 1997). Beyond the identity of the signaller, however, grunts by themselves provide listeners only with general information about the likelihood that the signaller will be aggressive.

But grunts do not occur in a social vacuum. Each grunt occurs in circumstances where the recipient is free to supplement information acquired from the call itself with information acquired from the context. In the case of reconciliatory grunts, experiments that systematically manipulate call and context demonstrate that listeners' responses – our best measure of the information they acquire from grunts – depend on information derived from the call itself (call type, caller identity) combined with information derived from the context, particularly the memory of past interactions and knowledge of the social relationship between the caller and individuals with whom the recipient has recently interacted (see also Das, 2000; Judge & Mullen, 2005). By incorporating information from these contextual cues, listeners transform a signal that, by itself, provides only vague information about benign intent into one whose meaning is very specific.

Similar data come from experiments that examine baboons' responses to aggressive calls. When female baboons heard the threat-grunts of a higher-ranking female, they were more likely to move away from the area if they had recently received aggression from that female than if they had recently groomed with her (Engh, Hoffmeier, Cheney, & Seyfarth, 2006). Subjects also responded more strongly when they heard threat-grunts from a relative of a former opponent than when they heard threat-grunts from a higher-ranking individual who was unrelated to their former opponent (Wittig, Crockford, Seyfarth, & Cheney, 2007). Once again, a signal that occurs in many different contexts, and hence provides by itself only general information, becomes a signal that conveys highly specific information as a result of the listener's integration of information from the call, from her observation of recent events and from her knowledge of others' relationships.

Pragmatics is the subfield of linguistics that examines how context contributes to meaning. By this definition, it seems clear that communication in animals – particularly long-lived, social species where individuals interact repeatedly with the same partners – constitutes a rich pragmatic system. The ubiquity of pragmatics in animal communication, combined with the relative scarcity of semantics and syntax, is important for those interested in the evolution of language because it suggests that, as language evolved from prelinguistic systems of communication, semantics and syntax were built upon a foundation of rich pragmatic inference.

Information has content

In evolutionary models of communication, information is an abstraction whose content remains unspecified. The experiments reviewed above, however, suggest that we can begin to determine, through experimentation, the content of information contained in a signal. Attempting to specify such information is not an exercise in anthropomorphism (cf. Rendall, Owren, & Ryan, 2009); it merely applies to naturally occurring communicative acts the same concepts and methods used in traditional experiments in classical conditioning.

Consider, for example, a straightforward Pavlovian test with simple signals and simple contextual cues. Colwill and Rescorla (1985) trained rats to press a lever for food and pull a chain for liquid sucrose. When the rats subsequently learned that the food was unpalatable, they ceased pressing the lever but continued to pull the chain. When they learned that the liquid was unpalatable, the opposite occurred. The experimenters concluded that, before the devaluation of food or water had occurred, the rats had learned not just that lever pressing and chain pulling were rewarding but also that each behaviour was associated with a specific outcome. On the basis of their immediate perception (i.e. the signal) and their prior experience (i.e. the context), the rats had formed an *expectation* of what they would receive if they pressed a lever or pulled a chain. In other words, they had acquired information *about* bar pressing and chain pulling.

By studying the content of an individual's expectations we can begin to specify some of the information a recipient has acquired from a signal in a particular context. When a female monkey with an infant hears grunts from an approaching female, her response suggests that she has formed an expectation that the caller is likely to be friendly (Cheney et al., 1995; Silk et al., 2000). When a male sparrow hears the song type that it just sung 'matched' by a neighbouring male, his response suggests that he has formed an expectation that escalated aggression is imminent (Beecher & Campbell, 2005; Molles & Vehrencamp, 2001; Searcy et al., 2014; Vehrencamp, Hall, Bohman, Depeine, & Dalziell, 2007). When a vervet monkey hears an adult female's leopard alarm, her reaction suggests that she has formed an expectation that some terrestrial predator is in the area (Price et al., 2015; Seyfarth et al., 1980). In each case, the recipient's expectations help to clarify the information she has acquired from the signal.

Information is structured

Even in highly restricted laboratory experiments, Pavlovian conditioning is not limited to the formation of associations among simple pairs of elements. Instead, learning can lead to 'a hierarchical organization in which associations among some pairs of items yield new entities that themselves can enter into further associations' (Rescorla, 1988, page 155).

Under natural conditions, several observations support the view that, even if it begins with relatively simple Pavlovian associations, the social knowledge of primates is rapidly organized into units of thought that resemble our concepts (Dasser, 1988; Seyfarth & Cheney, 2014b). Consider, for example, the speed of animals' reactions to events. When a baboon hears a sequence of vocalizations that suggests that an aggressive interaction is occurring that violates the dominance hierarchy, she responds within seconds (Cheney & Seyfarth, 2007). When a macaque or capuchin monkey involved in a fight tries to recruit an ally, she seems already to know which individuals would be the most effective partners (Perry, Barrett, & Manson, 2004; Schino, Tiddi, & Polizzi di Sorrentino, 2006; Silk, 1999). The speed of these reactions suggests that animals are not searching through a massive, unstructured database of simple dyadic associations but have instead organized their knowledge about individuals into categories, including what we call dominance hierarchies and matrilineal kin groups.

Bergman, Beehner, Cheney, and Seyfarth (2003) used a violation of expectation method to test this hypothesis. As background, recall that rank relations among females are generally stable over time, with few reversals occurring either within or between families.

However, when reversals do occur, their consequences differ significantly depending on who is involved. For example, if the third- ranking female in matriline B (B3) rises in rank above her second-ranking sister (B2), the reversal affects only these two individuals; the family's rank relative to other families remains unchanged. However, a rank reversal between two females from different matrilines (for example, C1 rising in rank above B3) potentially affects both families, since all members of the C matriline are likely to rise above all the members of the B matriline (Cheney & Seyfarth, 2007).

In one set of trials, subjects heard an apparent rank reversal involving two members of the same matriline: for example, female B3 giving threat-grunts while female B2 screamed. Later, the same subjects heard an apparent rank reversal involving the members of two different matrilines: for example, female C1 giving threat-grunts while female B3 screamed. As a control, subjects heard a fight sequence that was consistent with the female dominance hierarchy. As in prior tests (e.g. Cheney et al., 1995), listeners responded with apparent surprise to sequences of calls that appeared to violate the existing dominance hierarchy, suggesting that their expectations included information about the relative ranks of the individuals involved. In addition, between-family rank reversals elicited a consistently stronger response than did within-family rank reversals (Bergman et al., 2003), suggesting that expectations also included information about matrilineal kinship and about the nested relationship of kinship and rank (see Schino et al., 2006 for similar observational results).

The Neural Basis of Information

If information has content and is structured in memory, it should be possible to identify the brain mechanisms that underlie the processes of encoding and storage — that is, to identify the neural instantiations of information. Although we are presently far from achieving this goal, recent studies of birds, fish and humans suggest that it may ultimately be possible.

Consider, for example, the neural mechanisms involved in the recognition of song by zebra finches, *Taeniopygia guttata*. When one male hears another sing, this causes the expression of an immediate early gene, *egr1*, which would otherwise be inactive. But this gene expression is not just a response to an auditory stimulus. Instead, like the behavioural response of baboons to a reconciliatory grunt, gene activation depends upon the bird's integration of information from call, context and the memory of past interactions. If the singing male is unfamiliar to the listener, the *egr1* response is stronger; if the male is familiar, the response is weaker (Dong & Clayton, 2008; Mello, Vicario, & Clayton, 1992; reviewed in; Robinson, Fernald, & Clayton, 2008).

Cichlid fish provide another case study in which the memory of past interactions combined with the acquisition of new information affect brain activity. In one experiment, a female was first exposed to two different males and expressed a preference for one by swimming towards him. Then the female saw her preferred partner either win or lose an aggressive contest with another male. If she saw her partner win, this information activated immediate early gene expression in brain areas associated with reproduction; if she saw her partner lose, this produced activation in brain areas associated with anxiety (Desjardins, Klausner, & Fernald, 2010).

This result is important because it demonstrates that, given a particular behavioural history, the acquisition of information *by itself* can cause changes in an individual's brain. Indeed, just observing behaviour can be as powerful as active participation in generating brain activity. And this, in turn, reveals intriguing continuities between the role of information in animal interactions and the role of knowledge acquisition in human clinical studies.

Compare, for example, the conclusion that in cichlid fish 'social information alone, independent of actual social interactions, activates specific brain regions that differ significantly depending on what the female sees' (Desjardins et al., 2010, page 21176), with the conclusion from human clinical studies that 'subjective perceptions of the external social environment (e.g. as being friendly versus hostile) appear to be more strongly related to genome-wide transcriptional shifts than the actual social-environmental conditions themselves' (Slavich & Cole, 2013, page 341).

Finally, while we are only beginning to understand how information is encoded in the brains of any species, several recent studies of monkeys provide new insights into the neural encoding of information about numerosity (Neider & Miller, 2004), abstract rules (Miller, Freedman, & Wallis, 2002) and the network of brain regions involved perception of features of the social environment (reviewed in Platt, Seyfarth, & Cheney, 2016), while MRI-based studies of human cognition offer new data on the ways in which humans encode information about objects (Chao & Martin, 2000), number (Cantlon et al., 2009; Nieder & Dehaene, 2009), words that vary in semantic precision (Musz & Thompson-Schill, 2015) and conceptual processing of nouns and verbs (Boylan, Trueswell, & Thompson-Schill, 2015). These results provide further evidence that both the content of information and its underlying mechanisms can be studied empirically. Comparative studies of humans and animals may ultimately allow us to consider the broader, fundamental question: how does the encoding of information differ between organisms with and without language?

CONSTRAINED VOCAL PRODUCTION

In human language, meaning is a two-way street: signaller and recipient are equally flexible in production and perception, and they typically exhibit 'semantic parity', sharing a common representational framework that underlies each person's comprehension of what the other means (Fitch, 2010).

By contrast, when Marler began his research on nonhuman primate vocalizations in the 1960s, the prevailing view held that call production in monkeys and apes was little more than an involuntary reflex — sounds just emerged in highly emotional circumstances (reviewed in Cheney & Seyfarth, 1990, pp. 98ff). Although recipients might extract complex information upon hearing a vocalization, there was little evidence that the signaller had voluntary control over his actions.

Marler was sceptical of this view, in part because it relied heavily on laboratory neurophysiological studies from which the social dimension had been removed (e.g. Ploog, 1981; see Jurgens, 2009 for a more recent review). How, he wondered, could a relatively inflexible system of production function in a complex, ever-changing social environment? Marler (1965) suspected that, when studied under natural conditions, primate call production might turn out to be more flexible than it appeared in the laboratory. What have we learned in the ensuing years?

There is, no doubt, a striking difference in flexibility between relatively constrained vocal production and more open-ended responses (Hammerschmidt & Fischer, 2008; Seyfarth & Cheney, 2010). Nonhuman primates, like most mammals, typically produce acoustically specific call types in specific social circumstances and show limited acoustic modification during development. Call combinations are rare (but see Arnold & Zuberbühler, 2012). By contrast, responses to calls are highly flexible and often involve learning.

But the mechanisms underlying vocal production are more complex than this sharp dichotomy suggests. In recent years, there have been several observations and experiments in which the production of a vocalization served as the dependent measure.

Some have focused on individuals' ability to modify call acoustics. For example, Herbinger, Papworth, Boesch, and Zuberbühler (2009) found that wild chimpanzees, *Pan troglodytes*, gave pant-hoot vocalizations in response to playback of calls from familiar individuals, but they gave screams in response to calls from neighbours or unfamiliar individuals. This result is consistent with the many studies showing that wild primates give acoustically different alarm calls when they see different predators (e.g. vervet monkeys: Seyfarth et al., 1980; Diana monkeys: Zuberbühler et al., 1997; see Evans, 1997 for review). Similarly, young marmosets alter the acoustic features of their phee calls in response to maternal feedback (Takahashi et al., 2015). When wild chimpanzees receive aggression, they modify the acoustic features of their screams depending on both the severity of the encounter and the presence of higher-ranking potential allies in their foraging party (Slocombe & Zuberbühler, 2007).

Other studies, building on the 'audience effect' first noted by Marler and colleagues (Karakashian, Gyger, & Marler, 1988), have focused on the contextual factors that affect whether an individual calls or remains silent. In field experiments on baboons, Rendall et al. (1999) found that subjects were more likely to grunt in response to playback of a grunt from another individual if the initial grunt had the acoustic features of a 'move' grunt and if the group was currently resting (see also Rendall, Cheney, & Seyfarth, 2000). Similarly, female baboons are more likely to grunt to individuals with whom they share a relatively weak bond, where the outcome of an interaction is uncertain, than to close kin like mothers and daughters, where the outcome of an interaction is almost always affiliative. Zuberbühler, Cheney, and Seyfarth (1999) found that wild Diana monkeys gave their species' leopard alarm calls when they heard a leopard growling, but they remained silent upon hearing the same growl if they already knew that a leopard was in the area. If they had previously heard a leopard, however, but then heard the call of an eagle, they gave their species' eagle alarm. Wich and de Vries (2006) exposed 12 different groups of Thomas's langur monkeys, *Presbytis thomasi*, to a model of a tiger. In each group, the male continued giving alarm calls until every other member of his group had also given at least one alarm. Finally, in two experimental studies conducted independently, chimpanzees were more likely to give alarm calls to a snake model when their audience was ignorant of the snake's location than when their audience had already detected the snake. Alarm calling was also more likely if the caller and the new arrival shared a close bond (Crockford, Wittig, Mundry, & Zuberbühler, 2012; Schel, Townsend, Machanda, Zuberbühler, & Slocombe, 2013). Similar results were obtained in a study of chimpanzees' food calls (Schel, Machanda, Townsend, Zuberbühler, & Slocombe, 2013).

Taken together, these studies support Marler's suspicions that, while primate vocal production might appear to be an involuntary, reflexive process in laboratory studies where contextual factors have been removed, under natural conditions call production — like animals' responses to calls — is crucially affected by the caller's integration of information from the social and ecological context. Contextual factors can affect not only a call acoustics but also the caller's decision to vocalize or remain silent. It is therefore inaccurate to describe call production in primates as an involuntary, reflexive process.

Nevertheless, differences between production and perception in primate vocalizations remain a puzzle, in large part because the same animal is both a producer and a perceiver. Why should an individual who can learn an almost unlimited number of sound-meaning pairs be so constrained in her production of calls? The contrast between human and nonhuman primates in the mechanisms of production is particularly striking given these animals' close evolutionary relationship and the fact that, in both groups, communication is embedded in a rich social environment.

Marler also suggested that nonhuman primates might overcome the constraints imposed by a limited vocal repertoire both by combining calls with gestures, postures and other visual signals and by combining different call types with each other ('composite' signals: Marler, 1965). These suggestions have proved prescient. There is now an active area of research that examines the role of visual signals in primate social interactions (e.g. Genty, Clay, Hobaiter, & Zuberbühler, 2014), as well as a number of studies that examine the use of call combinations, particularly in forest monkeys (e.g. Arnold & Zuberbühler, 2012; Schlenker et al., in press). When individual callers use specific call combinations in particular social or ecological circumstances, as for example, in Ouattara, Lemasson, & Zuberbühler (2009) study of Campbell's monkey, *Cercopithecus campbelli*, a listener can acquire specific information about events in the world — information that goes beyond the information that might have been obtained from any one call type alone.

One recent example of call combinations, together with what may be call-and-answer exchanges, comes from the work of Schamberg, Cheney, Clay, Hohmann, & Seyfarth (2016) on wild bonobos, *Pan paniscus*. Like chimpanzees, bonobos live in a fission–fusion society in which all of the animals in a local area form a community, but within this community, individuals join and leave temporary subgroups or parties (Kano, 1992). Vocalizations appear to play an important role in facilitating movement between parties.

Bonobos have two vocalizations that can be heard over long distances, the whistle (W) and the high hoot (HH). They also occasionally combine these two (W+HH). Whether an animal gives an HH or a W+HH combination seems to reflect its motivation to join another party: joining is significantly more likely after a W+HH than after an HH alone (Schamberg et al., 2016).

But the caller's movement between parties is also strongly affected by whether or not its call is answered. If an HH alone is answered, joining occurs 27% of the time, but if an HH is unanswered, the caller never joins. If a W+HH is answered, joining again is much more common. Overall, both initial call type and the presence of an answer are significantly and independently correlated with the initial caller's movement between groups (Schamberg et al., 2016). Consistent with the view that giving a W+HH combination reflects a stronger motivation on the part of the caller to join another party than HHs given alone, callers were more likely to continue calling if a W+HH was unanswered than if an HH was unanswered (Schamberg et al., 2016).

Given these preliminary results, we may speculate that the bonobos' use of call combinations and their call-and-answer exchanges arise from several interacting selective pressures: the need to maintain contact and to coordinate movement between widely separated parties in a fission–fusion society, particularly in a rainforest environment where visibility is low; and the fact that there is inherent uncertainty whenever two individuals come together. Call combinations appear to reduce this uncertainty.

SUMMARY

Peter Marler led the way in posing thoughtful, challenging questions about the meaning of animal signals, the nature of the information they convey and their function in nature. He inspired and conducted experiments to test hypotheses about communication, the mind, and the differences between animal communication and language. Although he shyed away from general theories, we are, thanks to Peter and many others, now much closer to a broad view of how communication works in different species (Bradbury & Vehrencamp, 2011; Searcy & Nowicki, 2005).

Evolutionary theory predicts that, at equilibrium, signals will generally be honest indicators of one or more important properties of the signaller or its environment, and that recipients will assess signals on the basis of these properties. Contemporary animal learning, together with observations and experiments on monkeys, illustrate the proximate mechanisms that can underlie the convergence to an equilibrium state. Over time, signallers acquire information about the relationship between signals and outcomes, while receivers adjust their assessment rule to bring expectations in line with reality. Both signaller and recipient rely on the acquisition of information, which is acquired from the signal itself and relevant features of the context. Such pragmatic inference is particularly powerful in species in which individuals recognize each other, interact repeatedly and draw upon a long history of interactions in their assessment of a signal's meaning. In the primate lineage, pragmatic inference seems likely to have served as a precursor to the evolution of semantics, syntax and language among humans. Although in primates, as in most mammals, the production of vocalizations is highly constrained, it is not a fixed, reflexive process. Individuals overcome constraints on production by combining different call types with each other, by combining vocalizations with signals in other modalities and by using pragmatic inference to enrich the information conveyed by each signal.

Acknowledgments

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