Animal Behavior and Cognition
ABC 2024, 11(4):432-439
DOI: https://doi.org/10.26451/abc.11.04.06.2024

Signaler-Receiver "Exchangeability" Promotes Information Exchange in Animal Communication

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Citation – Francescoli, G., & Hare, J. F. (2024). Signaler-Receiver "Exchangeability" Promotes Information Exchange in Animal Communication. *Animal Behavior and Cognition, 11*(4), 432-329. https://doi.org/10.26451/abc.11.04.06.2024

Abstract – Signals that inform prospective receivers of potential contingencies associated with the signaler or its environment may be innate, or may rely upon repeated association between signal production and a context relevant to the receiver, or theory of mind, such that signalers and/or receivers infer the state or contextual situation communicative partners find themselves in. While theoretical discourse on the information content of signals has focused on the coevolution of signalers and receivers as distinct entities, the fact that individuals often act both as receivers and signalers in similar communicative contexts over the course of their lives presents the possibility that signals emitted in a given context may reflect the signaler's own experience as a receiver in the same or similar contexts. This process, which we term "Exchangeability," would allow signalers to encode appropriate information in signals and receivers to extract meaningful information without conditioning or recourse to theory of mind. We propose that Exchangeability readily accounts for the expression of true communication, where both signalers and receivers benefit, eavesdropping, where receivers alone benefit, and manipulation, where signalers benefit at the expense of receivers, thus providing a previously overlooked mechanism via which information can be encoded and decoded in animal communicative exchanges.

Keywords – Animal communication, Exchangeability, Information, Meaning, Semiosis, Signaler-receiver.

Actions of signalers that affect receiver behavior (signals) evolve by exploiting pre-existing receiver sensory biases or via fitness benefits associated with receiver responses to actions that are reliably associated with certain signaler states or environmental contingencies (influence versus information respectively, *sensu* Owren et al., 2010; Scarantino, 2010; Stegmann 2013). As such, signals may come to have meaning for signalers and receivers alike (Amphaeris et al., 2023; Carazo & Font, 2010; Danchin, 2013; Font & Carazo 2010; Jablonka 2002; Seyfarth et al. 2010), though that meaning may differ for participants within a communicative bout owing to the multifaceted nature of both communicative interactions and meaning itself (Amphaeris et al., 2023; Marler, 1961; Rendall et al. 2009).

Previous research has implicated repeated pairings of a particular signal type with a given context or outcome (i.e., conditioning, *sensu* Shriner, 1999) to explain predictable receiver responses to specific signals, or has invoked theory of mind (Hare et al., 2000; Premack & Woodruff, 1978; Royka & Santos, 2022; Thom & Clayton, 2013) to account for intentional communication (Graham et al., 2019; Zuberbühler & Gomez, 2018). As individuals often act as both signaler and receiver in communicating with others they may also ascribe meaning to signals based on their own experience producing and receiving them, a process that we term "Exchangeability". We propose that this previously overlooked dimension of the signaler-

receiver dynamic allows information to be encoded and decoded by signalers and receivers respectively. Thus, this process represents a more general case of what Hockett (1963) termed Interchangeability – the ability of individuals to produce any linguistic signal they can receive – in outlining the design features that distinguish language from communication in the broad sense.

Exchangeability refers to the capability of an individual to act as both signaler and receiver in the same situation, either serially or at disjunct points in time. In turn, the individual, consciously or unconsciously, interprets the scenario and can do so again when confronted with either that same situation in the future, or with the signal previously associated with that situation. Further, where signal production and perception are congruent for signalers and receivers, signalers can use signals related to a given context to manage receivers through expected receiver behavior based upon the signaler's previous behavior in that same context (Guilford & Dawkins, 1991; Miller & Bee, 2012).

The ability of animals to learn and unlearn associations between salient stimuli and events in their environment, which also confers the ability to predict how others are likely to behave in the same scenario (Emery & Clayton, 2001; Kano et al. 2019), suggests that individuals may take into account experiences they have had when acting as receivers, and apply those when acting as signalers (Miller et al., 2009). Exchangeability, in this sense, refers to exchanging signal perception with subsequent signal production, which would require individuals to "know" what they are doing when signaling, yet need not invoke the attribution of mental states to others, at least in the sense we presume humans do, either consciously or unconsciously (de Sousa, 2008). To meaningfully encode information employing Exchangeability, individuals would require: 1) the sensory and neural mechanisms to perceive the signal (perceptual architecture), 2) the capacity for categorical thinking, attributing objects, internal states, and events to mental categories, relating those to particular signals they have experienced in the past, 3) mid- to long-term memory capability so as to recall what signal had been used by signalers confronted with the same environmental contingency, situation or stimuli in the past, and, 4) the neural and physical substrate (productional apparatus) to control signal production.

We propose that signalers encode information in a signal because as subjects, their relationship to an object is not direct, but instead is mediated by something new: a sign or signal (Hofkirchner, 2011). Signalers thus relate the signal, and the context in which it is emitted, with their memories of similar situations/contexts when they were a receiver. However, this does not necessarily mean that the signaler infers information the actual receiver of its signal has in mind, or how that receiver will interpret the information. This process is independent of the signaler possessing theory of mind regarding potential receivers (Lurz et al., 2022; Penn & Povinelli, 2007; Seyfarth & Cheney, 2003, Skyrms, 2010), and may also be independent of the receiver's reaction to the signal. If the signaler acts through the process of Exchangeability, it will encode information relevant to the situation at hand based on its own memories regarding past similar situations, and its signal usage or interpretation (attribution of meaning to the signal) as signaler or receiver in those situations.

Exchangeability would allow receivers to decode signals based upon their own experience with signal production, particularly where signals conform to Morton's motivation-structural rules (Morton 1977), such that the signal's characteristics reflect the intrinsic state of the signaler. This is likely to be the case in that signals ultimately have their genesis in intention movements, displacement activities or activation of the autonomic nervous system (Bradbury & Vehrencamp 1998). As such, manifesting overt behavior or a particular physiological response in the presence of a certain stimulus or context would provide the association between that behavior/response (incipient signal), the stimulus/context at hand, and the state of the individual at the point the incipient signal was broadcast. Subsequent perception of that signal would presumably then allow the individual, as a receiver, to exchange their past experience as a signaler (producer) with their perception of that signal at present (receiver), assuming they possess the four attributes outlined above (perceptual architecture, memory capability, capacity for categorical thinking, and productional apparatus).

The four attributes that are requisite to employing Exchangeability are presumably widespread across taxa. Animals have evolved the necessary sensory and perceptual mechanisms to respond in an organized fashion to relevant stimuli in their environment (von Uexküll, 1926), along with mechanisms

necessary to produce signals that are detectable to receivers in sensory modalities selected for by the interaction of signaler and receiver anatomy and physiology and the nature of the physical environment through which signals are conveyed (Bradbury & Vehrencamp 1998). Further, the capacity for categorical thinking, such that objects, events and internal states are ascribed to mental categories, has been documented repeatedly among insects, anuran amphibians, birds, and mammals (Bruni, 2008; Ehret, 1990; Francescoli, 2021; Hare & Atkins, 2001; Hauser, 1996; Miller & Bee, 2012; Nelson & Marler, 1989; Prather et al., 2008, Prather et al., 2009; Reznikova, 2007; Snowdon, 1990), as has the ability to recover past associations and experiences from memory (Billard et al., 2020; Clayton & Dickinson, 1998; Clayton et al. 2001; Godfrey-Smith, 2014; Guilford & Dawkins, 1991; Pavlov, 1927; Shriner, 1999; Skyrms, 2010; Spear et al., 1990; Thorndike, 1898). Lasting associations between extrinsic or intrinsic stimuli, receiver responses and the production of certain signals on the part of signalers, or between those stimuli and signaler behavior on the part of receivers, constitute information available to receivers and signalers alike (Fischer, 2011).

The meaning attributed to a signal by a receiver (the relationship between a signal and the category or categories it represents in the receiver's mind) would be the same or similar to the one it attributes to that signal when it broadcasts the signal as a signaler, owing to what Francescoli (2021) termed "semiotic canalization", which describes the progressive encapsulation of signal meaning by signalers and receivers over the course of development. In the context of Exchangeability, this could be based on a comparison and self-assessment process like the one that occurs in social eavesdropping (Doutrelant et al., 2001), or through self-monitoring (Allen, 1999). Thus, it is analogous to the self-referent phenotype matching mechanism underlying kin recognition, in which individuals use cues emanating from themselves to form a template allowing the subsequent discrimination of kin from non-kin (Dawkins, 1982; Holmes & Sherman, 1982; Neff & Sherman, 2005).

As suggested by Scarantino (2010), signals may convey the internal state of the signaler to receivers. A clear way of interpreting this is through the Exchangeability process we have described, because an animal that has used signals to encode referential information about an internal state (motivation), and in parallel, sensed that state through proprioception or self-monitoring (Allen, 1999), could subsequently decode the signal and interpret its meaning in an empathic way when acting as a receiver. The neurophysiological basis of this process may involve neural mechanisms such as those described by Prather et al. (2008, 2009) that affect song learning and production in swamp sparrows (*Melospiza georgiana*), or the development of mirror neurons (Keysers, 2009), which have been postulated to promote the exchange of interpretations and responses to signals in a given context within the individual's brain when that individual acts as both a receiver and signaler, thus representing a process at the root of what we call empathy (Gallesse, 2003) or ‘associative explanation’ (Heyes, 2014; but see Heyes & Catmur, 2022 for a contemporary account of documented mirror neuron function).

Regardless of the underlying mechanism, both the productional repertoire of signalers, and the perceptual abilities of receivers, co-evolve through repeated interactions between those parties that are often exchangeable: the same individual can play both roles at different times, allowing individuals to act as, what Smith (2007) termed, ‘introspective obverters’. In that sense, even if an individual can never be sure of the true meaning of a signal, because he/she cannot directly access the mind of another individual, repeated signal exchanges in particular situations with experience as both signaler and receiver would allow an individual to relate a category or categories of event(s) with a signal, and thus interpret or attribute meaning to the signal (not to the mental contents) emitted by another individual. This mechanism, a fundamental component of our proposed Exchangeability concept, promotes flexibility in signal meaning, leading to the development of complex signaling systems (Francescoli, 2021; Menant, 2003; Smith, 2007).

Exchangeability would allow the ascription of meaning to signals in the three possible contexts that Wiley (1983) outlined as encompassing animal communication: where both the signaler and receiver benefit (true communication), where signalers benefit at the expense of receivers (manipulation), and where receivers benefit at the signaler's expense (eavesdropping). For instance, female Belding's ground squirrels (*Urocitellus beldingi*) emit vocal "trills" that warn conspecifics of the presence of terrestrial predators (Leger et al., 1984). Receivers of trills benefit by being alerted to potential terrestrial predators, while signalers benefit via enhanced survivorship of female kin alerted to those predatory threats by trills

(Sherman, 1985). Here, receivers come to associate the trill vocalization with terrestrial threats, and thus are expected to selectively broadcast that vocalization type upon detection of a terrestrial threat given the benefit of promoting an appropriate behavioral response to the threat at hand among kin. The selective emission of the trill call to terrestrial predators would, in turn, predispose individuals to perceive the presence of a terrestrial threat when they detect trill calls broadcast by conspecifics. Association of a particular alarm signal with evasive responses of conspecifics, however, may inadvertently provide signalers with the experience necessary to manipulate others, as has been demonstrated for certain insects (Lloyd, 1975) birds (Flower, 2011; Flower et al., 2014; Møller, 1988), ungulates (Bro-Jørgensen & Pangle, 2010), and non-human primates (Wheeler, 2009) that broadcast false signals for their own benefit. Indeed, the manipulative bioluminescent signals of the femme-fatale firefly (*Photuris versicolor*) that attract *Photinus* males to their death are produced facultatively by the femme fatales, who eavesdrop on *Photinus* males (Lloyd 1975). Exchangeability here may provide the basis both for the perception of *Photinus* mating signals by *Photuris* femme fatales (eavesdropping), in that receivers come to associate the species-specific *Photinus* bioluminescent signals that reliably correlate with the presence of attractable males (Magrath et al., 2015), and for the production of the correct species-specific counter-signal that serves to attract those *Photinus* males (manipulation), given the signaler's experience in producing bioluminescent signals attracting conspecific males as mates, and attracting allospecific males of several *Photinus* species as prey.

Concluding Summary

Exchangeability proposes that an individual's experience as a signaler and receiver would prove sufficient to encode and decode the information contained in signals. This previously overlooked process does not necessitate theory of mind for animals to ascribe meaning to signals, relying instead on more modest cognitive processes, including the capacity for categorical thought and memory, in addition to the sensory and perceptual mechanisms underlying signal perception and production.

Exchangeability can readily account for true communication, manipulation and eavesdropping among signalers and receivers based on an individual's garnering experience in either of those roles and subsequently applying their experience in the complementary role in a communicative exchange. As such, Exchangeability represents a more general case of Hockett's Interchangeability concept (the ability to produce any signal that can be received in the context of human language), and yet a more specific case of what Lurz & Krachun (2019) describe as experience projection (predicting how others are likely to behave in a given context based on past experience they have had in that same context), here, involving the projection of experience between the signaler and receiver role in a communicative context.

Non-human animals communicate in ways that defy, or at least cast serious doubt, on purely mechanistic explanations (e.g., audience effects: Doutrelant et al., 2001; Dzieweczynski et al., 2005; Evans & Marler, 1994; Le Roux et al., 2008, Townsend & Zuberbühler, 2009; content attribution: Ostojic et al., 2013; Price & Fischer 2014; concept formation: Hare & Atkins, 2001; Thompson & Oden, 2000; Wasserman, 1995; Wasserman et al. 2023; Zuberbühler et al., 1999; and controlled signal production: Miller et al., 2009; Snowdon, 1998). Exchangeability provides a simple mechanism via which individuals can process information about a situation, and relate that to similar situations recovered from memories stored in the context of their past participation as a signaler or receiver in a communicative context (Bruni, 2008; Francescoli, 2021; Prather et al., 2008, 2009; Reznikova, 2007).

The outstanding challenge, having recognized that an individual's experience as a signaler or receiver can inform their production or perception of signals in the complementary communicative role, is to obtain empirical evidence of Exchangeability affecting signal production and/or perception. This will require controlling an individual's experience with itself in terms of signal production and perception, necessitating clever manipulation of the developing individual's sensory experience (e.g. Gottlieb, 1966) and capacity to produce signals (e.g. Glassey & Forbes 2002), yet will undoubtedly shed important light on the mechanism underlying the attribution of meaning in animal communication.

Acknowledgements

We thank multiple anonymous reviewers and Editor-In-Chief Lydia Hopper for helpful comments that have allowed us to refine and clearly communicate our notion of Exchangeability in animal communication.

Author Contributions: GF: Original Conceptualization, Writing - Original Draft, Writing - Review and Editing; JFH: Supplementary Conceptualization, Writing - Original Draft, Writing - Review and Editing.

Funding: Gabriel Francescoli thanks Sistema Nacional de Investigadores (SNI), Programa de Desarrollo de las Ciencias Básicas (Pedeciba), and Universidad de la República through Comisión Sectorial de Investigación Científica (CSIC), Uruguay for financial support through the development of his ideas and research. James Hare appreciatively acknowledges financial support provided by the Natural Sciences and Engineering Research Council of Canada through Discovery Grant Funding over the course of his research program.

Conflict of Interest: The authors declare no conflict of interest.

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