

To appear in *ELT* 2023

Informational communication and metacognition

Joëlle Proust

Institut Jean-Nicod, ENS, Paris

joelle.proust@gmail.com

Abstract

Procedural metacognition is the set of affect-based mechanisms allowing agents to regulate cognitive actions like perceptual discrimination, memory retrieval or problem solving. This article proposes that procedural metacognition has had a major role in the evolution of communication. A plausible hypothesis is that, under pressure for maximizing signalling efficiency, the metacognitive abilities used by nonhumans to regulate their perception and their memory have been re-used to regulate their communication. On this view, detecting one's production errors in signalling, or solving species-specific trade-offs between informativeness, processing effort, clarity, or urgency depend on a form of procedural metacognition, called "metacommunication". How does this view relate to Gricean theories of human communication? A parallel between procedural trade-offs and conversational maxims is discussed for its evolutionary implications. Rather than accepting radically discontinuist interpretations, in which mindreading operates a full reorganization of pragmatics, it is proposed that procedural forms of regulation are entrenched in all forms of human communication. According to contextual demands, humans adopt and monitor more or less demanding informational goals, such as factual updating, clarifying, explaining, proving, and reaching consensus in collective matters. Under time pressure, only part of these goals require adopting others' viewpoint. Efficiency in collective decision-making, in particular, might have been considerably raised by an ability to interpret others' intentions and motivations.

Keywords

Evolution of communication, animal signalling, procedural metacognition, cognitive goals, relevance, ostension, signalling trade-offs, informativeness, effortfulness, deception.

Introduction

The expression of "informational communication" (from now on: IC) refers to all kinds of productions – oral (non phonated), vocal (phonated), gestural, etc. – in which an agent actively transmits a specific kind of information to a recipient. Calls, whether produced in the context of mating, foraging, predation or territorial claims, have an informational goal to the extent that they signal a change in the environment that is relevant to the receivers' welfare. A natural question, then, is *whether signalling requires a specific cognitive equipment whose function is to control and monitor progress to goal*. If the response is positive, capturing recipients's attention, selecting efficient ways of conveying information, attending to signals, would be subserved by a form of metacognitive control. The goal of this article is not to provide comprehensive evidence in favor of this hypothesis, but rather to present an empirically plausible picture as to how *metacommunication* (understood as the metacognitive control of communication¹) might shape senders' and receivers' signalling activities.

This topic is relevant to evolutionary linguistics. Studies have recently focused on the extent to which rules of syntax, semantics and pragmatics organize signal use in various nonhuman species (Freeberg & Lucas, 2012, Schlenker, 2018). Granting that these rules have co-evolved with the informational properties of the vehicles (for example, phonation and auditory reception), it is plausible that signal systems have been selected to be user-friendly: they should minimize producers' and recipients' processing effort, and maximize beneficial effects on their fitness. This line of reasoning leads to examine how *signalling systems and human speech co-evolved with procedural metacognition* – i.e., the ability to control and monitor one's own cognitive activity (for example, in perceptual discrimination, learning and problem solving). The hypothesis considered here is that affective predictions (solving procedural trade-offs) are used by individual communicators in signal selection and reception in various phyla (including birds and mammals). A speculative evolutionary pathway would be that metacognitive predictions, initially developed to support perceptual discrimination or memory for foraging spots, apt partners, etc. allowed producers to learn how to signal, and

¹ This term has been coined following an established usage in other metacognitive domains, such as metaperception, metamemory or metareasoning. In this sense, *metacommunication* does not mean "communication *about* communication", but rather "control and monitoring in communication".

recipients to attend to relevant sequences. This remains at this stage a speculation that needs to be backed up by detailed ethological and neuroethological analysis.² Paul Cisek's detailed reconstruction of the evolution of control in the primate lineage from simple feedback loops to sophisticated forms of action fulfils these two conditions (Cisek, 2007, 2022). Granting the functional connection between action control and metacommunication, the present proposal can be seen as a modest and preliminary attempt to extend Cisek's proposal to the control of communication.

From information to communication

Information theory tells us that the informational content of a cue consists in how this cue affects response probabilities. The quantity of information carried by a cue is measured by "how far it moves probabilities", i.e., how it helps receivers predict environmental changes (Skyrms, 2010, 34). Organisms' brains, however, can only detect and store a relatively limited set of predictive cues: those that are fitness-relevant. Teleosemantics, pioneered by Fred Dretske (1981, 1988) and Ruth Millikan (1984), spells out the embedded causal mechanisms at work in the construction of meanings. In Dretske's approach, *indicators* (cues with a predictive potential) become *representations* (stored predictive cues) when they acquire a specific function in controlling behavior. In other words, representations are selected through their positive effects on agents' fitness. In a similar vein, brain evolution theorists observe that the evolution of nervous systems reflects "a continuous extension of behavioural feedback control further and further into the world" (Pezzulo & Cisek, 2016). Teleosemantics also applies to communication. Signals are not merely selected on the basis of the information they carry. They are also selected on the basis of the effects they have in stabilizing communication exchanges.

How to define communication?

The definitions of communication offered in the literature have tended to focus on a single dimension of communication. An "informational" definition states that an act is communicative if its function is to reliably reduce recipients' uncertainty about a fitness-relevant external property (Marler, 1967, Hauser, 1996). Recipients' behaviour, on this view,

² On the crucial role of neuroethology in evolutionary reasoning, see Margoliash & Nusbaum, 2009.

is a consequence of information being transmitted, not part of the definition of communication. According to the “Machiavellian intelligence” theory,³ in contrast, communication consists in altering the behavior of others to the producer's own advantage. On this "adaptationist" definition, an act is communicative if its function is to influence the recipients' behavior, and if the recipients' response evolved in order to respond to it (Maynard-Smith and Harper, 2003, Rendall et al., 2009). Let's pause on this divergence.

Consider the sirens' call in *The Odyssey*: wanting to hear the sirens' song is known to lead sailors to shipwreck on sirens' rocks. Ulysses' dilemma is that of information mining: exploring can be highly beneficial, but highly costly too. Adaptationists concentrate on how sirens attract sailors to feast on them, and on how cueing reliable testimony can help detect and remedy manipulation. Information theorists focus on the song: what information are recipients interested in? Is a signal accurate? What kind of action-guidance is to be expected from learning? From a teleosemantic viewpoint, however, the function of a signal and its informational value both play their role in the selection process. To be followed by behavioural effects in the receivers, announcements must be often generally accurate and easy to understand. For a signal to be stabilized, senders must be rewarded for their calling behavior.

From a functional-evolutionary viewpoint, then, both approaches need to be used. On the one hand, a metacognitive approach teams up with an adaptationist definition of communication to emphasize the *motivational* components of signals. Alarm vocalizations have the function of controlling recipients' behaviour in order to optimize fitness. On the other hand, they do so in virtue of signals' acoustic features – abrupt onsets, broadband noise spectra, processing dynamics – suited for eliciting in recipients immediate attention capture and adaptive response. These acoustic features *explain why* they are selected across phyla: the signals have an immediate *arousal* effect; they are *easily* discriminable; they trigger *prompt* responses even in *naïve* individuals; they allow recipients to *accurately* encode and retrieve fitness-relevant situations. Behavioural control, then, presupposes receivers' metacognitive sensitivity. On the view defended here, the two definitions of communication refer to distinct levels of analysis of one and the same phenomenon.

It could be objected, however, that an ambiguity affects the notion of metacognitive sensitivity. In a first interpretation, as a joint product of genetic transmission and individual

³ See Whiten & Byrne, eds., (1997)

learning, metacognitive sensitivity refers to how signalling systems have been shaped to be optimally efficient with respect to species' fitness issues. A first interpretation focuses on typical communicative agency in a population. Genetic selection shapes at the population level the most efficient balance between informational complexity, learnability and behavioral efficiency. In a second interpretation, metacognitive sensitivity refers to the varying ability of individuals to communicate efficiently. Abilities to send or attend to signals vary with the amount of social knowledge acquired by individuals. Variability across ontogeny will be occasionally pointed out. We will concentrate, however, on the first interpretation: how does a species control and monitor its signalling activity? Do communicative actions adjust to environmental circumstances, recipients' subjective uncertainty and needs?

Metacommunication belongs to procedural metacognition

An evolutionary approach to metacommunication is served by the discovery that there is more to metacognition than "knowing what one knows", a definition that suggests that only humans are able to evaluate their own cognitive actions (because only humans can refer to their own mental states and interpret them as beliefs and desires).⁴ In recent studies, "metacognition" is used to refer to a set of predictive abilities allowing cognitive agents (non-verbal or verbal) to control and monitor their own activity in domains such as memory, perception, reasoning, or communication (for a review, see Proust, 2019). On this view, procedural metacognition refers to the subset of evaluative abilities that guide decision-making on the basis of affects – through "internal reinforcement learning" (Daniel & Pollmann, 2012, Hisey et al., 2018). Comparing expected and observed internal feedback generates metacognitive feelings, such as feelings of knowing, of error, of familiarity, of ease or difficulty and of confidence (Koriat, 2000). These feelings have the function of predicting feasibility of an action, detecting mistakes, allocating effort, and selecting the most promising ways of acting.⁵

How can it be demonstrated that procedural metacognition has shaped the production and reception of signals in nonhumans? There are a number of research issues to be

⁴ For a detailed critical discussion of this view, see Goupil & Proust, 2022.

⁵ It is still controversial whether nonhumans' metacognitive regulation involves a subjective experience similar to humans' conscious feelings. An increasing number of theorists, however, defend that the two domains in which a subjective experience is likely to be involved are sensory perception and action evaluation. See Browning & Birch, J. (2022), Godfrey-Smith, (2017).

addressed: one needs to investigate what are the beneficial consequences that allowed a signalling system to stabilize in a given species. The trade-offs at work in structuring repertoires, call duration, amplitude or complexity need to be differentiated and if possible, related to corresponding selective pressures. If communicators are able to learn and extend call repertoires, one needs to know whether they detect their performance errors and have been tutored to correct them. Similarly, we need to know whether and how receivers learn how to attend to signals and react appropriately.

Given these general goals, what is the range of evidence to be relied upon? Although there is much to learn from homology about the evolution of language, data from nonprimate species such as birds, bats, or dogs have been claimed to be relevant to tracing this evolution (Fitch, 2017). The same observation also holds for the evolution of communication. Evidence from multiple phyla offers insight about the kinds of evolutionary pressures that can explain how metacommunication works *in a given species*.⁶

Based on these considerations, our exploration will develop in three steps. A first section will review the evidence for metacognitive skills in nonhumans, including their variations across species. A second section will discuss the extent to which signallers control their communicative actions, and will explore the trade-offs on which communicative efficiency is based. A third section will examine whether and to which extent these trade-offs generalize to human IC. A major contrast between humans and nonhumans might not consist so much in the pragmatic role of intention recognition in communication, as is often claimed, than in goal recognition across contexts. A rich and open-ended language use being available, human producers do not merely aim at reducing recipients' present uncertainty about the environment; they also entertain new communicative goals related to knowledge and collective decision-making. The implications of this expansion for procedural metacommunication will be discussed.

I - Metacognition in nonhumans

⁶ As emphasized by a reviewer, as a consequence of the species-specificity of the selective pressures imposed on communication, one should not expect that all the modes of signalling that have been useful to a species in an environment should persist in new species and environments. There is no progressive complexity to be expected, but rather specific interactions of environmental challenges, genetic endowment and communicative goals.

I.1. Experimental evidence

Although the subject of nonhuman metacognition has long been controversial, comparative, neurophysiological and developmental evidence now suggests that procedural metacognition is part of a genetic endowment allowing agents to select and monitor their informational goals. Nonhuman primates, rodents, birds and dolphins reliably predict and evaluate their own cognitive actions on the basis of nonconscious predictive heuristics and comparators and the latter's conscious affective outputs. Such evaluative predictions can be made before engaging in a task, during engagement or once the task is completed. The metacognitive feelings so generated in turn contribute to motivate decision-making as a function of their valence and intensity.⁷ They have been elicited in laboratory tasks targeting a specific action segment:

a) inviting animals to choose or decline trials, or to *wager predictively* about their potential success (Hampton, 2009).

b) testing animals' online sensitivity to ignorance and error, and their ability to seek information ("hint seeking"), or revise their errors (Kornell et al., 2007).

c) inviting animals to *wager retrospectively* about the decision they made, or to cash out their gains, and thus express their confidence in having made a correct decision (Zakrzewski et al., 2014).

The evidence collected so far indicates that a number of nonhuman species reliably evaluate their perception or their memory in a predictive, on-line or a retrospective way (for a review, see Proust, 2019). Single-cell neural recordings in rodents and monkeys show that uncertainty is computed on the basis of the dynamics of the accumulation of information in dedicated neural assemblies (Kepecs & Mainen, 2012, Middlebrooks & Sommer, 2012). Frontopolar cortex activity in monkeys tracks differences between incorrect and correct trials before receipt of feedback rather than differences in reward (Tsujimoto, Genovesio, & Wise, 2010).

An online predictive form of procedural metacognition – detecting information gaps – (which triggers feelings of curiosity), has been shown to be available to non-human animals and to human infants : infants request information appropriately long before they can express their need in speech (Goupil & Kouider, 2019). Three-year-old children become progressively

⁷ As will be discussed in section II.3, metacognitive predictions are integrated with value predictions in decision-making.

able to reliably assess their memory (Balcomb & Gerken, 2008) and their perception (Bernard et al, 2015, Paulus et al., 2013) by accepting or declining a trial, while at chance in their verbal reports.

Recent studies document the role of dopamine in procedural metacognition. In humans and nonhuman primates, dorsolateral self-evaluations depend on dopamine release in the medial prefrontal and orbitofrontal cortex. The posterior orbitofrontal cortex is taken to be the primary region for the primates' perception of emotions (Barbas 2007). In zebra finches, new technologies based on optogenetics demonstrate that dopaminergic neurons are involved in the detection of performance prediction errors in vocal copying. A circuit involving the ventral tegmental area (VTA) and its projections to area X (an area functionally similar to mammalian basal ganglia) is hypothesized to mediate the kind of *internally* reinforced learning that comparing present song with song memory involves (Hisey et al., 2018).

These data have a threefold significance for the present study. First, they confirm behavioural evidence for procedural metacognition beyond primates and mammals (Terrace & Son, 2009). Second, they demonstrate that dopaminergic neurons evaluate fluctuations in performance quality in the domain of communication learning, which is our present target (Xiao et al., 2018, Duffy et al 2022). Third, the implication of dopaminergic activity suggests that procedural metacognition – including implicit metacommunication – depends on subjective evaluations integrating different affordances (Lak et al., 2014).

Comparing neural correlates in human adults with our closest primate relatives, the chimpanzees and the bonobos, on the other hand, suggests that enrolling sociocognitive beliefs and theories in cognitive decision-making might be specifically human. The human prefrontal cortex differs from that of other primate species in its lateral regions, with an emerging right-left asymmetry related to language (Broca area being located in the dominant hemisphere), and in a polar region subserving counterfactual reasoning (Koechlin, 2014). In comparison to other primates, human cognitive control has been considerably enhanced by an ability to store predictive cues at longer time-scales (Koechlin & Summerfield, 2007). In parallel with a stronger capacity for response inhibition, reasoning about their own self-efficacy has enabled human agents to adaptively overcome feeling-based decisions. Higher forms of control being more costly, however, procedural know-hows are routinely preferred (Aguirre et al., 2022, Barr & Kayser, 2002) (on this issue, see section III below).

I.2. Species differences in procedural metacognitive skills

To examine the potential specialization of procedural metacognition in a species, we will use the time-based distinction mentioned above (section I.1): pre-performance, (or prospective) evaluation, online evaluation during test, or post-performance evaluation. Prospective and/or retrospective evaluation have been experimentally elicited in apes, rhesus monkeys, rodents, dolphins and corvids (Beran & Smith, 2011). Among the latter group, large-bill crows manifest retrospective sensitivity to correctness in memory tasks (Goto & Watanabe, 2012).

The on-line ability to detect an informational need and to repair it through information seeking has been tested in several species by presenting to animals two or more opaque tubes (some empty, some baited), with or without a perceptual access to the baiting event: would they inspect tube opening as a function of the observed/hidden baiting event? In contrast to apes and rhesus monkeys (Call 2012, Rosati et al., 2016), ravens (Lambert et al., 2020), scrubjays (Watanabe & Clayton, 2016), and capuchin monkeys do not attempt to inspect tube contents before reaching (Basile, Hampton, Suomi, and Murray, 2009). As will be seen below, the metacognitive difference between two primate groups, rhesus and capuchin monkeys, can throw some light on the underlying selective processes.

Pigeons' skills in information-seeking cannot rival that of primates and corvids (Sutton & Shettleworth, 2008), but they turn out to be higher than initially thought. In a matching-to-sample test, they fail to inspect the sample to be matched when performing the task, thus displaying insensitivity to its informational role (Roberts et al., 2009). In spite of their initial lack of sensitivity to information, however, pigeons can be trained to seek information, and also to adaptively choose memory tests as a function of their own predicted performance (Santi & Adams, 2010). Capuchin monkeys display a higher awareness of the informational demands of a task than pigeons, but in contrast to rhesus monkeys, they stop inspecting the sample when the task includes additional challenges (Beran & Smith, 2019). Similarly, although rats and dogs do not voluntarily seek information by moving through space, they make an adaptive choice when forced to choose between stimuli that do or do not yield information about location of a food reward (Roberts et al., 2012).

Two insights from comparative research are to be kept in mind in our present discussion. First, metacognitive abilities may also vary *within* all the species studied so far. Some capuchin monkeys, for example, perform better than the poorest-performing rhesus (Beran & Smith, 2019). Similarly, individual human performers present substantial variations in their

metacognitive skills (Fleming et al., 2010). It is at this stage unknown whether such diversity reflects multiple evolutionary pressures (favouring fast or precise decision-making), developmental differences, or is merely a byproduct of genetic diversity in the brain structures subserving, for example, working memory and self-evaluation, in interaction with associative learning. Second, identifying the specific pressure(s) explaining how a given set of metacognitive skills emerged in a given species may be doomed to circularity, as long as the past environment that shaped the brain of a given species is merely inferred from present data.

This complexity may be somewhat reduced when considering two primate groups, such as rhesus and capuchin monkeys, that present striking differences in their metacognitive skills. Even in such a favorable case, a variety of factors are worth considering. Metacognitive skills might have adapted to

- the variability and amount of food resources in their respective foraging environments – an *ecological* property (Schwartz 2019),
- the opportunity to learn basic survival skills by observation – a set of *sociocognitive and cognitive* properties,
- social factors such as group size and amount of competition for more or less limited resources – a *socioecological property* (Cunningham & Janson, 2007). In this case, monitoring reliably one's memory or one's perception might significantly improve survival rate when food search extends to larger territories and/or involves more unpredictable casualties (as might be the case for rhesus monkeys), or when a number of food caches needs to be monitored and protected against pilfering (as is the case for scrubjays).

Further research might help clarify distinct evolutionary scenarii for enhanced metacognitive control and sensitivity.

II – Implicit metacommunication in nonhumans

Assuming that cognition is metacognitively regulated and controlled in a given species, we need to explore to which extent metacognitive sensitivity might regulate informational communication in this species. To demonstrate the relevance of this exploration, we must demonstrate that nonhuman signalling can be under the communicators' control. Second,

there must be evidence of individual metacognitive monitoring. In humans, specific brain connections in the frontopolar area are known to allow agents to adjust their cognitive actions to context. In non-humans, the neural subsystems involved in metacommunication start being explored (see section I.1).⁸ We must also review behavioral evidence of signalling flexibility based on error detection and feedback reliance.

II.1. Can nonhumans control their signalling behavior?

Both stereotypic and flexible kinds of communicational adaptation are exemplified in animal and human communication. The present investigation presupposes reconsidering what counts as "flexible" or "voluntary signalling".

We will first expose the (neo)Gricean criteria that have been advanced to distinguish informational from communicational behavior (II.1.1), then offer an alternative definition of communication (II.1.2) allowing us to operationalize intentional signalling (II.1.3).

II.1.1. Ostensive communication as a cue for intentional communication

Relevance theory, in the human case, takes voluntary signalling to be functionally dependent on having intentions to communicate, and making these intentions manifest to an audience (Sperber & Wilson, 1986/1995). Human communication presupposes that an "ostensive" component manifests a second-order intention: beyond the first order (world-directed) intention to communicate, the second-order intention aims to inform recipients about the producer having this informative intention. The rationale for such a construct is the following: Relevance is defined as the optimization of the trade-off between ease of processing and cognitive positive effects. This needs to be understood by receivers, and it is part of what the producers needs to convey : to the extent that their second-order intention justifies the mental effort expended in producing the first-order message, recipients are in turn justified in inferring that this message is worth being attended to. Ostension (i.e. the manifestation of the second-order intention), then, allows recipients to form "a presumption of relevance" (Sperber & Wilson 1995, 2002).

We will concentrate for now on the validity of this higher-order approach for nonhuman signalling: is an ostensive higher-order signal required to qualify a signal as intentional and

⁸ Gadagkar et al., (2016).

deserving attention? The primatologist Juan Gómez (1996) follows Sperber & Wilson in attributing a basic role to ostension: a hearer should recognize that the speaker intends to communicate, and interpret *on the basis of this recognition* the meaning of a signal. But this recognition, he proposes, can be secured in orangutans by eye contact and gaze following: these cues are *functionally* equivalent to attributions of second-order intentions. On this view, metarepresentations of a first-order intention to communicate do not need to be operative in identifying a signal and understand it.⁹

Against this line of reasoning, it has been objected that there is no behavioural evidence yet demonstrating that non-humans "communicate with Gricean meaning" (Scott-Phillips, 2016). Attributing intentions to communicate to animal signallers, on this view, is rejected for two reasons. First nonhumans are merely genetically programmed to produce signals. Second, these signals have the function of influencing receivers, not informing them (Dawkins & Krebs, 1978, Rendall et al., 2009). These two reasons are resisted in this article. First, genetic endowment does not need to result in inflexible behaviors. Second, stabilized influence, in metacognitive species, presupposes that informational needs are satisfied. Two types of stability constraints, then, are at work: statistical predictive accuracy and functional effects on receivers' behavior (Shea, Godfrey-Smith and Cao, 2018). Various selective pressures may have favored, across signal systems, higher or lower forms of goal asymmetry between producers and receivers (the former expecting a given response, the latter a reliable message). But the amount of asymmetry is highly context-sensitive: food calls, alarm calls, proximity calls, in a given species, tend to present a different ratio of informing and influencing messages. The same holds for receivers: in many species, they typically take contextual cues into consideration when deciding what to do with a signal.

II.1.2. Re-defining communicative actions

These clarifications allow us to address the objection that voluntary signalling should depend on manifesting one's intention— through ostension. A first step in our response is to deny that ostension is needed in human communication.¹⁰ Humans deliberately produce messages without having signalled any intention to communicate. Utterances such as "watch!", "stop thief!" as well as non-human alarm calls functionally exclude an ostensive

⁹ On the role of ostension in communication see Moore (2016), Planer (2017b), Proust (2016).

¹⁰ Sperber (2019) admits the existence of weaker forms of relevance presumption based on "proto-ostension".

preface. An emotional signal rather expresses an emergency that recipients are equipped to identify, based on prior signalling episodes and/or on innate affective reactivity. In impulsive actions (in contrast with mere reflexes), mechanisms of cognitive control guide behaviour in a split second: ducking to avoid being hit, correcting a word, taking a second look (Inzlicht et al., 2015). Impulsive calls similarly broadcast an imminent danger or a transient opportunity; they can, however, be accurate and precise: vervet monkeys, for example, produce impulsive vocalisations with predator-specific contents, that reliably guide recipients' flight (Cheney & Seyfarth, 1990).

A second step in our response proposes a different construal of communication as a goal-oriented action. What defines any action is not that it results *from* a specific cause – such as having a prior intention. As defended by the philosopher Harry Frankfurt (1988), an action is defined by the mechanisms that *guide* its execution: in any action, a compensatory activity must be available to adjust or restore the course of the action if it deviates from its goal. From this control viewpoint, then, communicative actions are, on the sender's side, characterized by context-sensitive flexibility, rather than by advertising an intention through an ostensive marker. Evidence for the voluntary control of communicative actions, then, includes, on the senders' side, the identification of persistent communicative goals and their adjustable control. On the receivers' side, message relevance influences behavior as a function of their individual circumstances and acquired knowledge. There is now a wide agreement, among comparative psychologists, that the study of intentional communication in animals can be *operationalized* in non-Gricean terms, without an ostensive component (Townsend et al., 2017).

II.1.3 Operationalizing the presence of first-order intentionality in communication

Operationalization is clearer if we distinguish the significant dimensions of adjustable control in senders' initiation of signalling episodes and in receivers' responses. Four types of *senders'* communicative behavior provide evidence of intentional signalling.

1. *Communication inhibition*: Birds' nestlings remain silent until prompted to beg by a parent's provisioning call (Magrath et al., 2010). Alarm calls are withheld in many species as a function of the risks incurred (Seafarth & Cheney 2003, Marler et al., 1991). Chimpanzees keep silent when patrolling (Mitani & de Watts, 2005).

2. *Sensitivity to recipients*: Primates stop or perseverate signalling as a function of the recipient's behavioural response (Hobaiter & Byrne, 2017).
3. *Audience effect*: the ability of nonhumans to adjust their calls to the presence of specific recipients suggests that signals are emitted strategically, as a function of the recipients' attention, quality and motivations (Zuberbühler, 2008). Marmosets adjust their responses to caller's identity (Miller & Thomas, 2012). Apes (Byrne et al., 2017), monkeys, ground squirrels, downy woodpeckers, sparrows, adjust their signals to the presence of social companions, amount of food available, etc. (Cheney & Seafarth, 1990). Chimpanzees only use silent visual gestures when intended recipients look at them (Hobaiter & Byrne, 2017). Nonhuman primates can also produce strategic calls, meant to manipulate recipients' reactions, for example by deliberately exaggerating scream amplitude to recruit help (Whiten & Byrne, 1988, Slocombe & Zuberbühler, 2007).
4. *Signal learning*: Voluntary communication is also manifested in the ability to invent or to learn new signals (from conspecifics or from human caretakers), as exemplified by dialect variation in marmosets (Eliades & Miller 2016), mocking birds, nightingales (Petkov & Jarvis, 2012), zebra finches (Gadagkar et al., 2019), humpback whales (Allen et al., 2018) and elephants (Poole et al., 2005). Although it was at first hypothesized that apes cannot control and hence, cannot learn new vocal signals, they have been shown to learn new oral (non phonated) signals such as the raspberry, used to solicit grooming attention (chimpanzees: Hopkins et al., 2007) or in the context of nest building and infant retrieval (orangutans: Lameira, 2017). Immigrant captive adults have been shown to adopt the acoustic pattern of local food calls once they are socially integrated (Watson et al., 2015). Chimpanzees, in addition, can readily learn a sign language; they spontaneously use quantitative modulation (repetition of a sign) to indicate emphasis or assent, as young children do (Chalcraft & Gardner, 2005). They do not seem to spontaneously enlarge their innate repertoire of gestures, however (Byrne et al. 2017). In contrast, orangutans are able to invent arbitrary calls, and to spread them through social learning. (Wich et al., 2012). Captive gorillas also involve new signals to attract their caregivers' attention (Salmi et al., 2022).

The evolutionary significance of signal learning in the primate lineage has recently been emphasized by comparing the neural correlates of signalling in marmoset

monkeys and human infants (Takahashi et al., 2015, Hage 2018). In both cases, vocal development is driven by learning. Prior to learning, both species produce protophones (such as speech-like babbling in infants) and affective vocalizations (such as moaning and crying). Learning from parental auditory feedback results in the ability to voluntarily and flexibly control signalling. Marmosets reduce noise in their calls and learn to make a context-relevant use of call types. In human infants, babbling becomes increasingly speech-like. A major difference in learning, however, is that young marmoset monkeys can learn how to adjust usage, focal duration, amplitude and frequency of their calls, but *do not learn novel patterns*, as human infants do. Still, both marmosets and humans have been claimed to have *two vocal neural networks available* for jointly controlling their vocal productions (a similar duality is also present in birds, see Jarvis, 2013). An ancient vocalization system – the primary vocal motor network – located in subcortical structures, generates innate signals. With learning, it comes under the control of a volitional articulatory motor network originating in the prefrontal cortex. This functional contrast might be a preadaptation in the primate lineage for speech acquisition in humans (Hage & Nieder, 2016).

On the *receivers'* side, flexibility seems to be less restricted than in senders. Far from automatically adopting pre-wired behaviors, receivers integrate the contextual cues available to them, as a function of the affordance that a signal predicts.¹¹ Examples discussed in the literature suggest that receivers, when deciding what to do with a signal, learn to differentiate the informational core¹² of a signal and use it to their own advantage (Wheeler and Fisher,

¹¹ The integration mechanisms are briefly described in section I.1. Receivers' flexibility might be the result of selective pressures favoring resistance to manipulation. (see section II.3.3.4 below on deception).

¹² There is at present no agreement about the best way to characterize the semantics of this informational score (What Suzuki, 2016, calls "the representational ideation of senders". There is also non consensus about "functional reference" amounts to in a given signalling system. Some researchers take signals to refer to external entities in a non-structured way, as language refers to entities through proper names and definite descriptions (Macedonia & Evans, 1993). Others hypothesize rather that signals have an internal structure, involving unarticulated constituents such as "here" and "now" (Millikan, 2005, Proust (2016, 2023). The latter articles propose that signals have a structured semantics derived from their role in action control systems: signals predict the presence here and now of specific affordances with their associated behavioral commands. In the present paper, no specific commitment concerning the functional reference in animal signalling will be discussed.

2012, Scarantino & Clay, 2015). This flexibility is predicted by game theoretic modelling of the dynamics of signal systems (Skyrms, 2010).

Taken together, these findings suggest that there is much more continuity between nonhuman and human IC than previously anticipated. Intentionality of communication can be detected in its flexible adjustment to circumstances, whether or not the communicative act ostensibly advertises its own intentional character (for a similar argument, see Townsend et al., 2017).

II.2 Medium-dependent efficiency: evolutionary preconditions for individual control and monitoring processes

Efficiency in communication is defined as the probability that successful information transfer occurs with minimal processing effort. Information transfer is successful when the information in fact extracted from a signal by a recipient is equal to the information made available by the signal. Granting that a number of nonhuman species use signalling systems, we need to explain what makes communicative efficiency possible for them.

A first response is that IC efficiency is based on biological adaptations: communication efficiency would be impossible without animals' capacity to extract probabilistic information from the environment (Franke & Jäger, 2016, Gallistel, 2020). Affordances in a context, then, structure signal meanings available in a predictable way. In languages, syntax, semantics and pragmatics have been demonstrated to be biologically shaped to optimize efficiency (Gibson et al., 2019). In human speech, for example, frequent words such as "the", "and", "or" but also shortened words as "chimp" conform to a principle of least effort as a function of their contextual predictability. This "Zipf Law" is observed in animal vocalizations (Kershenbaum et al., 2021). Efficiency also requires effort to be proportional to message informativeness, and relevance, except for urgent signals, that need to be easy to process. For example, vitally relevant information has shaped short, long-range alarm calls in all communication systems. A trade-off between informativeness and complexity also applies to communication vehicles. For example, a signal for *predator* is less informative than a signal for *aerial predator*. Enhanced informativeness – reduction of ambiguity in predictions – increases complexity by the additional processing efforts and potential learning costs and predictive errors that it may generate. Redundancy may seem to contradict informativeness, but here again, a trade-off steps in: in noisy environments, or in far-range communication redundancy facilitates the

extraction of information. In all these cases, efficiency does not seem to require individual regulation any more than perception and memory.

This objection, however, ignores that there are regulative steps that involve individual agency. For example, learning how to communicate requires communicators to monitor their performances, detect and revise their errors, until they acquire the desired level of competence. More generally, signal production and reception also engage individual forms of selection, error-monitoring and revision, i.e., of procedural metacommunication.

II.3 Functional components of procedural metacommunication in nonhumans

II.3.1 A functional duality

Granting the articulation in nonhuman communication of an informational action (informing a recipient) with a pragmatic action (e.g., enhancing food intake) *two systems must independently regulate a given signalling episode*. A functional analysis of communication indeed distinguishes an "external" reinforcement system that governs pragmatic pay-offs from an "internal" reinforcement system that optimizes the informational quality of transmission and reception in individual agents (Duffy et al., 2022, Hisey et al., 2018). Let us comment on this important duality.

- Pragmatic efficiency

A value monitoring system surveys the conformity of observed pragmatic effects to expected ones. Vocalizers, then, need to monitor the *relevance* (based on affordance detection) *and pragmatic efficiency* of their own message: did the intended recipients flee (warning call), approach food (food call), express mating availability (courtship twitters)? Recipients, on the other hand, monitor the *value* of past signals from sender S: how urgent or beneficial has been the communicated affordance?

- Informational efficiency

A metacognitive monitoring system surveys the *informational efficiency of these messages*. In producers, errors are monitored in song learning and production; recipients monitor their attention to a signal as a function of its complexity and relevance. As will be seen later, birdsong imitation in nestlings is revised with or without parental tutoring.

This contrast is exemplified in the Ulysses and the Sirens episode. The Sirens' song is informationally recipient-efficient, in fully producing the expected level of delight and trance

in listeners. It is pragmatically producer-inefficient, if the predatory goal can be effortfully neutralized, as done by Ulysses.

One might object, however, that these two evaluative systems cannot fully *independently* regulate a given signalling episode: a flexible action system needs to balance anticipated gain against resource expenditure, including opportunity costs (i.e. the alternative goals that might have been pursued instead).¹³ This holds for communication. *Predicted effort*, before and during a cognitive task, engages a form of pragmatic sensitivity

Let us observe, however, that anticipated effortfulness impacts selection of action and resource engagement, rather than uncertainty monitoring.¹⁴ Furthermore, in primates, gaining information is an intrinsic source of pleasure, even in the absence of a reward. This justifies maintaining a functional distinction between our two types of efficiency. The two regulative systems are sensitive to different kinds of efficiency, without confusing them. Even though decision-making combines their respective outputs (Tang et al, 2022). For example, alarm signalling, from Belding ground squirrels to primates and birds, has a nepotist function – protecting kins from predators, and is generally produced appropriately (Sherman, 1977). In some conditions, however, a potential signaller may choose to flee silently (Seyfarth & Cheney, 2003). Indeed, alarm calls help predators locate signallers.

Learning how to signal requires informational motivations, for example identifying what *needs to be learned* (Kuchling et al, 2022). Signalees' feedback (their degree of responsiveness) helps a signaller adjust intensity, clarity or accuracy in its call as a function of specific classes of recipients. Learning how to signal is also pragmatically motivated: in blackbird songs, highly fitness-relevant sequences – "sexy" rapid high frequency twitters – combined with low frequency, far ranging whistles, determine males' reproductive and territorial success (Hesler et al., 2012).

II. 3.2 The puzzle of communicative deception

¹³ For a defense of effort in terms of opportunity costs, see Kurzban et al., 2013.

¹⁴ Koriat et al. 2006 studied learning confidence across conditions with different incentive levels. They show that the relative calibration of confidence is unaffected but the level of effort involved in learning, although the individual judgements of learning are (correctly) increased as a function of effort.

On recipients' side, a major aspect of pragmatic efficiency has to do with reliability. A signal that misinforms to receivers' detriment and to senders's benefit, is a case of deception. On this definition, withholding information is not a case of deception.¹⁵

The duality of pragmatic and informational goals has been a major source of puzzlement for evolutionary theorists. On the one hand, it is rational, for a sender, to take advantage of the predictive structure of a call to use it to its own advantage. On the other hand, how can signals, in the absence of any guarantee that they are reliable, be valued by recipients (Maynard-Smith & Harper, 2003, Skyrms, 2010)? For example, chimpanzees frequently send a deceptive signal to distract a recipient away from a foraging site (Whiten & Byrne, 1988). Male mourning cuttlefish (*Sepia Plangon*) often simultaneously display a male courtship pattern on the side of their body facing the female, and a female pattern on the side facing a rival male (Brown et al., 2012). Why should recipients trust signals?

Distinguishing communication games on the basis of the kind of reinforcement learning accessible to participants proposes an interesting solution (Skyrms, 2010). Let us consider repeated communication conditions, in which communicators are unaware of the structure of the game; suppose further that receivers learn by reinforcement the degree to which they should act on a signal. Modelling shows that signallers are reinforced to deceive within these limits (Skyrms, 2010).¹⁶ In animals able to represent the possibility of deception, unreliable signallers tend to be identified and punished by social exclusion (Cheney & Seyfarth, 2003), violent reprisal and other deterrent measures (Brown et al., 2012).

In conclusion, deception does not need to threaten communication stability: it can rather work as one of the conditions of stability. Evolutionary stable strategies (ESS) emerge at a population level whenever the inclusive benefit-cost ratio of honest signalling is slightly higher than that of deceptive signalling. (see II.3.3.4)

II.3.3. Selecting and monitoring informational goals

Independently of the trade-offs between pragmatic and informational efficiency examined above that have shaped signal systems over time, it is worth considering how

¹⁵ Shea et al., (2018). Hauser (1997) defends rather that strategic withholding of information (e.g. food calls) is a form of deception that, being difficult to detect, "tends to be more prevalent than active falsification" (p.114). Still, no false signal is sent.

¹⁶ For a detailed analysis of the "hybrid equilibrium" conditions in which a communication game tolerates deception, see Shea et al, (2018), pp. 1025 sq.

nonhuman signallers regulate their *individual* communicative acts. The jury is still out about the question whether metacognition so engaged is domain-specific (such as assessing one's own auditory discrimination), or domain-general (such as assessing one's uncertainty). In human cognitive actions, both types seem to be co-activated (Morales et al., 2018). Research on artificial grammar learning in various species suggests that the mechanisms for syntactic learning are not specific to language, but apply to musical tone, picture and sign sequences (Fitch & Friederici, 2012). Some main types of metacommunicative regulation accessible to nonhumans are explored below.

II.3.3.1 Metalearning

Learning requires an ability to detect performance errors, based on a sensitivity to negative feedback. Metalearning allows learners to discriminate and memorize learnable signal sequences, including their composition rules, but also to detect and revise errors, and assess learning progress. A nestling who learns a song by trial and error must be able to detect its learning errors and to stop learning in due time (Konishi, 2004). The neural correlates of metalearning have been explored in zebra finches. When the birds are confronted with their own song auditory feedback, their dopamine activity correlates with the fluctuations of their own performance. The retrospective timing of this activity is consistent with song *evaluation* rather than production: it is modulated as a function of observed error response magnitude. This demonstrates that birds monitor their learning performance (Duffy et al., 2022, Gadagkar et al., 2016) as mammals do (Tian et al., 2016).

Similar convergence across species is found when manipulating metalearning in monkeys and in humans (Ferrigno et al. 2017). Experimentally manipulating the perceptual properties of informational input (e.g. modifying size, colour contrast, auditory volume) leads human subjects to misjudge that the corresponding items are easy to learn. They tend accordingly to dedicate less effort to (re-)studying fluently processed stimuli (Rhodes & Castel, 2009). In monkeys, similar fluency-based illusions have been found in prospectively or retrospectively betting about correct learning: their learning confidence is influenced by subjective fluency (Ferrigno et al., 2017). However, monkeys' higher sensitivity to the differential complexity of images restricts the amplitude of their overconfidence, compared to humans.

II. 3.3.2 Informativeness versus complexity (effortfulness)

Just as metalearning seems to be a functional precondition for IC, a sensitivity to informativeness needs to be present for communicators to select appropriate signals or understand them. Informativeness refers to the amount of surprising evidence offered by a signal. In animal IC, a call is informative if it allows recipients to detect an environmental affordance that they would not have detected otherwise. Calls routinely allow them to obtain benefits (food, mating), to escape from predators, or defend their territory against intruders. Granting that affordances can be generic (predator) or specific (aerial predator), predictive cues as well as signals can vary in the information conveyed. A principle of economy for selecting the appropriate level of informational specificity is needed in signal systems that use a number of different call types, thus enhancing potential complexity in calls (where concatenation of signals "means" a conjunction of properties). For example, Campbell's monkeys can add suffixes to their vocalizations (Ouattara et al., 2009). In chickadees, the calls are open-ended (up to 45 notes); some species, such as Carolina chickadees, have a huge encoding capacity. Their calls have a form of "phonological syntax" (Berwick et al., 2012), which allows signals to vary in length, note composition, repetition and acoustic parameters, as a function of the context of use. They convey a variety of messages, such as predator, distance from signaller, predator size and status – perched or in flight – food, etc. (Freeberg & Lucas, 2012).

How is the trade-off between informativity and complexity (i.e. processing effortfulness) settled by individual communicators in specific signalling episodes? Philippe Schlenker, Klaus Zuberbühler and their groups hypothesize that primates apply a "principle of informativity": Informativeness is balanced against message complexity, leading to select the call (and interpret it) in the way that offers the most specific prediction (Schlenker et al., 2016). Campbell's monkeys are particularly interesting, because two different groups respectively live in the Tai forest and in Tiwai Island, where predators are, respectively, either both terrestrial (leopards) and aerial (raptors), or only aerial. In the Tai forest, adults call 'krak' for leopard, 'hok' for raptors, and add the suffix "-oo" for characterizing unspecific or weaker risks. They also use 'boom' for non-predatory alert: falling tree, neighbouring groups, etc. Comparing call use in these two environments throws light on the trade-off informativity/complexity. Call meanings appear to be regulated by a dominance relation. In the Tai forest, if I call 'krak', understand: 'not Krak-oo' and 'not hok'. If I say 'hok', understand

‘not hok-oo’. On Tiwai, if I say ‘krak’, understand ‘eagles or any other alert’: it is used as a general alert signal. ‘Hok’ is also used non-specifically.

From a theoretical viewpoint, these studies suggest that the principle of informativity works as a “primate implicature” in monkeys (Schlenker, 2018). Signallers select the call that is maximally informative in a context. Recipients use this implicature to interpret the affordances conveyed by a signal. For example, a specific signal is sent only in a situation of serious aerial danger. This example illustrates the point made above (section II.3.1.) that the informational trade-off between message complexity and informativeness interacts with the pragmatic trade-off between effort allocation and expected value in signal production and reception.

Evidence suggests that curiosity also engages a trade-off between expected processing effortfulness and informativeness (Goupil & Proust, 2023, Oudeyer & Smith, 2016). Nonconscious heuristics elaborated through internal reinforcement allow agents to compute the contextually optimal trade-off; in favorable cases, the trade-off produces in humans a conscious feeling of curiosity whose function is to contextually motivate exploration. Although there is no consensus yet about non-human conscious awareness of their metacognitive predictions, animal sentience and self-awareness are now gaining momentum. (Lage et al. 2022). This suggests that nonhumans can also rely on conscious metacognitive feelings to produce or interpret signalings.

II.3.3.3 Comparative urgency

Urgency is one of the dimensions of relevance, as already observed by Grice (1989, p.27). Urgency determines order in signal constituents, independently of the potential proto-syntactic properties of signal sequences. Arnold and Zuberbühler (2012) observed that putty-nose monkeys’ calls conveying information about a threat *come before* those that don't. The function of this “urgency principle” is to allow recipients to promptly prepare an adaptive motor response: being predictive, information is distributed over time in conformity to its expected effects. A similar urgency principle applies, in bird songs, to threatening sequences. Long-range matching songs (whose function is to signal a territorial conflict) precede the close-range aggressive “soft songs” and wing-waving, which prepare an attack (Akçay et al., 2013). This sequence provides competitors ways of appreciating their respective aggressive dispositions, and introduces a welcome diplomatic distance between communicating and

acting.

II.3.3.4 Accuracy versus deception

As observed in the case of meta-learning, nonhumans can detect and revise their errors when learning their species-specific signals, alone or under the tutelage of proximal adults. Are they also able to monitor the accuracy of their own signal productions: for example, can they detect when they have been wrong to call for a raptor? In other terms: can they monitor the *quality* of their calls – in analogy to Grice's maxim of conversation?

The analogy implied by this question, however, is slightly problematic, because of the epistemic difference between truth and informativeness. Informativeness is the functional outcome of mechanism whose function is to detect and broadcast environmentally significant events.¹⁷ A predator signal is objectively informative when it is caused by a predator, which raises the probability of receivers' escaping predation. Truth is the norm that regulates and justifies beliefs and assertions. From an evolutionary viewpoint, the normative use of truth is a product of human cumulative culture (see section III.4). It evolved, along with the evaluative methods of explicit metacognition (Shea et al., 2014), when verbal inquisitive behavior became available in human cooperative groups (Proust, 2022). As a result, deception can be defined either as a manipulation of information to the detriment of receivers, or as presenting as true what is actually false. Granting that nonhumans communication does not involve propositions,¹⁸ their deceptive behavior consists in misinforming receivers, by sending a signal in the absence of what the call signals, for its own benefit.

Signallers and signallees having different interests, signalling should reflect these differences. Abstract modelling of communication games (Shea et al., 2018, Skyrms 2010) distinguish instances of call suppression (senders fail to call in the presence of its "functional referent" – leopard, eagle, etc.), "half true signals" that allow two interpretations from deceptive signals, only one which serves the receivers' interests.¹⁹ In the first two cases, no deception occurs, because absence of a signal or weakening of its informativeness do not,

¹⁷ On functional deception, see Hauser (1997).

¹⁸ On a proposal defended in Proust (2015, 2016, 2023), nonhuman signalling and part of human communication have the function of conveying affordance detection, rather than descriptions of the environment. An affordance semantics, similar to Strawson's feature-placing semantics, is claimed to form the representational medium of utility based and cognitive thinking in humans and non-humans.

¹⁹ Cheney & Seafarth, 1990, discussed in Skyrms, 2010, p.73.

properly speaking, carry *misinformation*. Deception occurs only when a signal is sent in the absence of its referent to the benefit of the sender and the detriment of the receiver.

Granting that, in most cases, communicators' interests diverge, how can signalling systems resist the threat of deception (senders manipulating receivers by inappropriate calls, receivers adapting, by turning misinformation into useful information)? When communication involves mixed interests, a combination of partial alignment and partial divergence occurs. In other terms, informativeness occurs often enough to maintain stable signalling (Skyrms, 2010, p.79). As a result, signalling systems tend to flourish when the equilibrium depends on information pooling: the sender misinforms receivers in a way that secures to both a payoff higher than absence of signal would offer. Many species seem able to modify their signalling system in responses to changes in environmental conditions and associated signalling payoffs.

Comparative evidence confirms that, in many species, deceptive IC is part of an innate or acquired behavioral repertoire.²⁰ This case is exemplified by the double display delivered by courting cuttlefish described above (Brown et al., 2012), or by the “broken wing” display in plovers and many other bird species. The distribution of this display in various avian species suggests that it has been phylogenetically selected for on the basis of predation pressures but also higher latitudes, where nests are more exposed (de Framont et al., 2022). In other species, reinforcement learning allows individuals to learn how to produce deceptive behaviors, and receivers to resist them. The case of the bluestreak cleaner wrasse (*Labroides dimidiatus*), is particularly striking. Wrasses from high density coral reefs are able to deceptively advertise a cooperative food preference when a by-stander observes a cleaning event – eating only the client’s ectoparasites, instead of its nutritious but protective mucus (Pinto et al., 2011). Cleaner wrasses from low density, isolated patches, in contrast, do not attempt to raise a bystander’s image score by advertising “proper” food preferences. This difference originates in the respective learning opportunities of the two social environments. It takes experience to learn the costs and benefits to be drawn from cheating (Wismer et al., 2014). Among primates, chimpanzees have been singled out for their ability to deceive others strategically, for example to signal (when out of sight) for an attack when there is none (Whiten & Byrne, 1988). One might again suppose that chimpanzees have discovered from

²⁰ See Searcy & Nowicki, 2005.

experience that cheating about signalling, in some conditions, is safe and pays well.

Our initial question, in this section, was: are non-humans able to monitor the accuracy of signal productions, for example, to detect when, as senders, they have been wrong to call for a raptor? Field evidence remains to be collected on this issue. Evidence for metalearning, however, suggests that they can notice and repair their signalling errors. As receivers, are they able to recognize that they have been manipulated? A positive answer can be offered. Game-theoretic modelling and comparative evidence suggest that nonhumans manifest a sensitivity to deception by ignoring informers' behavioral imperatives when they do not receive the expected payoffs.

Still, anticipating that signals produce responses in recipients does not amount to knowing *why* signals produce these responses – which mental states explain lapses in reliable signalling (Hauser, 1997). An explicit metacognitive monitoring and control of higher epistemic norms such as truth or plausibility co-evolved with a capacity to metarepresent one's own and others' beliefs, motivations and intentions. It is therefore more than doubtful that deceptive IC of this strategic kind is accessible to non-human agents.

II.3.3.5 Clarity as ease of processing

Grice's maxim of manner recommends communicators to be perspicuous, by avoiding obscurity, ambiguity, and unnecessary prolixity. Manner reflects the trade-off between clarity of a message and ease of processing: a clear message may require a longer signalling event (see Table 1 below). In some noisy contexts, redundancy serves clarity, in others it unnecessarily increases signal length.

Sensitivity to clarity is specifically demonstrated in bird signalling. Environmental noise influences songbirds' vocal behavior. To maintain the quality of their signals, they may change the temporal pattern of their vocalizations, or shift the frequency and amplitude of their signals (Brumm & Slabbekoorn, 2005). Birds tend to avoid singing overlap with other birds, conspecifics or not. More generally, both in the case of nonhuman primates (Schel et al., 2010), and in the case of chickadees, the balance between economy and prolixity seems to depend on predation pressure. Owing to the higher number of food competitors and predators, Carolina chickadees have a larger and less redundant vocal repertoire than black-capped chickadees (Freeberg & Lucas, 2012).

III - From nonhuman to human informational communication: the evolution of metacommunication

III.1. From procedural to explicit metacommunication

How closely do the various procedural trade-offs discussed in the preceding section match those that are implicit in conversational maxims? Table 1 presents central functional analogies.

Regulative dimension	Procedural rules or trade-offs	Conversational maxims
Quality	transmit predictive information about current affordances.	<i>Try to make your contribution one that is true.</i>
Quantity	prefer informative signals that are easy to acquire and process	<i>Try to make your contribution as informative as required</i>
Relation	<ul style="list-style-type: none"> • Prefer signals with immediate instrumental value • Prefer signals with contextually maximal informational value • order signal sequences as a function of response urgency 	<ul style="list-style-type: none"> • <i>Be relevant!</i>
Manner	<ul style="list-style-type: none"> • adjust signal discriminability to local noise. • Adjust processing difficulty to environmental requirements 	<ul style="list-style-type: none"> • <i>Be perspicuous!</i>

Table 1 – Functional analogies between procedural trade-offs applying to signal systems and conversational maxims.

Table 1 confronts procedural metacommunication, on the left-hand column, with explicit metacommunication, on the right-hand column. The left-hand column lists the trade-offs and repairs that nonlinguistic animals perform on the basis of genetic endowment, social learning and reinforcement. The conversational maxims listed on the right-hand column turn these regulations into explicit, concept-based norms of cooperation.²¹ The notion of a

²¹ See a detailed analysis of conversation maxims in Grice (1989).

"functional analogy", then, refers to the fact that informational efficiency can be served by metacognitive sensitivity or through explicit rules.

Two alternative views of the evolution of communication can be defended on the basis of Table 1.

- On a discontinuist view of communication, human communication *replaces* procedural processes with interpretive processes: humans' ability to transmit information beyond the narrow set of fitness-relevant affordances requires a distinctive cognitive equipment that only humans possess. Hence, pragmatics is a properly human affair.
- On a continuist view, there is a *cumulative entrenchment* between procedural and explicit metacommunication: procedural tools are available to active communicators as a function of their specific contexts, genetic endowments and reinforcement schedules. In the human case, these tools combine feelings with concept-based and explicit conversational norms.²²

The two viewpoints are discussed in the following sections. They are represented respectively by a modularist and a metacognitive conception of communicative control.

III.2. Discontinuist view: a metacommunicative module

A discontinuist might argue that, once a shared language is available, procedural sensitivity is no longer involved. Relevance theorists might recognize that procedural metacognition plays a role in evaluating information-seeking actions in non-human signalling. For example, Sperber (2000) acknowledges that animal signallers, having a fixed and limited repertoire, might predict *cognitive* relevance based on the *cognitive trade-offs* listed in the left-hand side of Table 1. Human communication, in contrast, having no repertoire limitation, is claimed to require flexible reasoning abilities in order to interpret a speaker's informational intentions. This is why a *communicative principle of relevance*, called "presumption of relevance", is needed over and above the low-level mechanisms of cognitive relevance in order to test alternative interpretations and to stop interpreting at the right level. What are the additional mechanisms involved?

²² This hierarchical cumulative continuity evolved in other domains of human cognitive control, such as informational seeking, metaperception, metamemory or metareasoning.

Developmental evidence shows that children can converse long before they theorize about mental states.²³ Hence, Sperber & Wilson (2002) propose that an innate metacommunicative module (MM), "a submodule of the mind-reading module", allows human communicators to understand utterances or communicational gestures without reasoning about the speaker's mental states (Sperber, 2000, Sperber & Wilson, 2002). The main function of MM is to automatically enable conversational agents to:

- a) follow a path of least effort in computing cognitive effects
- b) use least effort as the principle for solving interpretive ambiguities about reference and implicatures.
- c) stop when expectations of relevance are satisfied.

III.3. A continuist proposal: metacognitive processes

Continuists about procedural pragmatics recognize that language allows communicators to generate and interpret messages much more diverse and complex than non-verbal signalings.²⁴ Human messages differ from animal signals in terms of lexicon acquisition, revision and innovation, diversity of contexts, multiple embedding of meanings, use of indirect or ironic utterances, etc. They are not convinced, however, that a specific submodule of a theory of mind -- "with its own proprietary concepts and mechanisms"²⁵ -- explains how the four steps listed above are processed.

- a) Follow a path of least effort in computing cognitive effects

Granting that MM includes this rule, a question remains: how does MM apply a scale of difficulty to alternative interpretations? *Relevance* offers an explanation in terms of an innate ordering of contents based on their logical structure. According to contemporary metacognitive studies, ease of processing, i.e. effortfulness, is rather computed on the basis of the dynamics of the target brain activity, including its onset, its duration and the amplitude of neural activity that it involves (Kepecs & Mainen, 2012). Such heuristics are not limited to utterance processing; they apply to any form of cognitive engagement. Effortfulness is often claimed to be inversely correlated with motivation for a given decision (Schwarz & Clore, 2007).

²³ Liszkowski et al. 2008, Abbott-Smith et al., 2022.

²⁴ Sign languages, having a language-like structure, have their own grammatical rules. Structural properties of emissions have a crucial role both in the expansion of reference and in the reduction of complexity.

²⁵ Sperber and Wilson, 2002, p. 12.

But rewarded effort can itself become attractive (Converse and DeSchon, 2009), which suggests that felt effort results from various predictive cues, (such as interest, importance, or self-representation).

Curiosity is another case in point of the trade-off between ease of processing and cognitive effects. Agents only feel curious if they anticipate that they can learn what they need, but they do so as a function of the anticipated effort to be invested. Curiosity, as a result, requires a minimal amount of knowledge to arise, and it stops when the information need is satisfied (Goupil & Proust, 2023, Kang et al., 2009).

- b) Use least effort as the principle for solving interpretive ambiguities about reference and implicatures.

As seen in the preceding comment, the brain automatically achieves these tasks. No "principle" needs to be made salient by a specialized module, because economy is part of the evaluative apparatus that allows action selection in all kinds of behavioral control.

- c) Stop when expectations of relevance are satisfied.

This command is also built into the regulative apparatus for cognitive actions. When exploring new information, agents are sensitive to their learning-rate, and more generally to the time they spend on cognitive tasks – from learning (Koriat & Ackerman, 2010) to remembering (Koriat et al, 2008) and problem-solving (Ackerman, 2014). A *stopping criterion* motivates agents to stop trying either when the goal is reached or in case no progress is registered. In the latter case, the stopping criterion can, in addition, include opportunity costs: "don't spend additional time on a goal if progress is low and there is more to be gained elsewhere" (Kurzban et al, 2013). Interestingly, in intense cognitive effort (for example, in problem solving, or when trying to make sense of an obscure utterance), the stopping criterion is *lowered*: agents may decide to accept a solution or an interpretation despite the low confidence they have in being right. (Ackerman, 2014).

In summary, *the three rules claimed to be implemented by MM are standard metacognitive processes* that control and monitor cognitive decision-making in cognitive actions. They are based on nonconscious predictive heuristics, which in turn generate specialized feelings (see I.1.). The astonishing flexibility of human metacommunication, then, might be rooted in part on the same procedures as those involved in nonhuman metacommunication.

Note that an entrenchment account of Table 1 does not need to offer additional evidence of the role of the procedures listed above in computing implicatures and disambiguation, because, *ex hypothesi*, they perform functions attributed to MM. However, in agreement with the continuist hypothesis, there is ample evidence that a submodule of mind-reading often fails to be used in human communication. Receivers tend to rely on their own first-order representation of the environment to interpret others' utterances (Aguirre et al., 2022). Children and adult speakers alike do not respond to routine *wh*-questions based on a representation of the questioner's specific knowledge and ignorance, but on their own relevant factual knowledge. The same applies to conversational anchoring: receivers tend to interpret the referential value of expressions from their egocentric viewpoint, not on the basis of the common ground of the current conversation (Barr and Keysar, 2002)²⁶. These observations suggest that "a language processing system is "optimal" not because it guarantees mutual understanding, but because it provides adequate real-time understanding at a minimal cognitive cost" (Barr and Keysar, 2002, p. 392).

While the trade-off mechanisms described above emerged before mindreading abilities, the latter undeniably raised the stakes of communication, by allowing meaning to be kept implicit in utterances. Producers were thus able to mask their manipulative intentions (Reboul 2011). In conjunction with symbolic communication, mindreading expanded the domain of social learning, and generated cumulative culture. In human conversation, however, egocentric, first-order context representations may become more salient than mind-reading inferences under the influence of the trade-offs listed above: they offer an economical way of generating a subjective, but sometimes inadequate, form of comprehension. What seems easy to me may not be easy to you.

III.4 How do continuists explain conversational flexibility?

If Table 1 is used to defend a continuist viewpoint in pragmatics, defenders owe their opponents an account of the amazing, although partly unstable flexibility of human communication. To clarify: continuists are expected to explain how procedural

²⁶ Keysar et al. (2003) demonstrate egocentric interpretations of receivers in a communication game where senders have a restricted knowledge of the objects involved.

metacommunication, based on the trade-offs discussed above, evolved to enable a comparatively more flexible regulation of linguistic communication of this new medium.

This question becomes more tractable when additional metacognitive structure is introduced in pragmatics (Kissine, 2016). First, let us observe that cognitive acceptances (the regulative outputs of cognitive actions) are governed by different epistemic norms, and, consequently, involve different regulative procedures (Proust, 2013). In the domain of IC, for example, ignoring cases of deception, communicators can try to

- inform or to cautiously accept information about a fact
- Accurately inform or be accurately informed.
- Entertain or be entertained (fiction, music, poetry)
- come up with a consensual view (science)
- persuade or be persuaded by consistent arguments (science, law)
- explain, understand an explanation

This multiplicity of regulative standards parallels the multiple trade-offs listed above. Note, however, that most of these goals involve explicit metacognition, i.e the ability to distinguish the differences of acceptability conditions between truth, plausibility and coherence.

At this point, a pressing question is to know how a given standard is selected (by producers) and recognized (by receivers). In a nutshell, the most plausible hypothesis is that *conversational contexts* have been shaped around specific sociocognitive goals, by cultural accumulation. Knowing how to identify, in practice, the currently active norm (factual, explanatory, etc.), is one of the central epistemic aims of the social division of labour (Proust, 2022). Still, even these new forms of regulation build in part upon metacommunicative processes already used by nonhumans, as proposed by Table 1.

As a case in point, it is interesting to examine how epistemic regulation may have co-evolved with humans' cumulative culture (Proust, 2022).²⁷ *Curiosity-based* exploration, present in nonhumans, allows one of the first cooperative kinds of linguistic exchange, called *inquisitive behavior (from now on: IB)*, to develop.²⁸ In IB, senders question receivers in order to reduce their subjective uncertainty about a given topic. A question has a *focus* (e.g., a new

²⁷ For alternative approaches, see Dunstone & Caldwell (2019), Heyes et al., (2020), Shea et al. (2014)

²⁸ For a detailed functional-developmental analysis of curiosity, see Goupil & Proust, (2023)

object in the environment). It also evokes a range of "contrastive topics" to be narrowed down concerning the focus (e.g. name, function, place, time) (Roberts, 2012). Adequately answering a question, then, requires receivers to identify its focus along with a set of topical alternatives. But it also requires for both senders and/or receivers to detect and revise failures, lack of information, lack of comprehension, and learning-rate. This first structure for *exchanging factual information* motivated subsequent kinds of corrective or elaborative uses. First comes *clarificatory questioning* (how to understand a word, a sentence, a grunt, a gesture?). Second, *explanatory questioning* aims at enriching one's own inferential potential. A final decisive step involves *group decision-making*, in which tracking of individual beliefs and commitments are a key to mutual trust. On the view proposed, attribution of beliefs to senders and receivers exert a selective pressure in favour of mental state attribution in order to optimize consensual decision-making.

Note that, in all these cases, error-detection-and-repair are cumulatively re-deployed at any level in the hierarchy of cognitive actions:

- in basic questioning *informativeness* regulates the exploration/exploitation trade-off
- in dyadic communication, *expressive clarity* secures alignment on focus and referential idiom.
- in group decision-making, *argumentative clarity* regulates optimal communication.

On this view, as observed by Kissine (2016), context dependence applies not only to how to interpret words (such as "bank"), but also to the goals pursued in a given exchange. For each goal type, there is a specific mode of regulation shared by producers and receivers. They can monitor validity through context-selected epistemic or merely informational criteria. For example, factual questioning might, in ordinary daily conversation, merely involve informativeness and ease of processing. In a legal context, it might require more sophisticated standards such as truth, consistency, etc.

To recap: how do communicators select or recognize a communicational goal, in order to apply to it the relevant epistemic standard? A plausible response is that communicational context automatically prioritizes a salient type of acceptance, along with its metacommunicative regulation (Kissine, 2016, Proust, 2022). Epistemic standards expected to be used at school, in a shop, in the street, in a court of law, in a literary circle or in a scientific

meeting engage different trade-offs, some of which favor speed of processing, others complexity, including metarepresentational inferences. Those that favor speed of processing are those where egocentric reception takes precedence on allocentric interpretation. When messages are redundant, recipients may also stop processing a given message before the end of the message.²⁹

Concluding speculations

This article defended the continuity of procedural processing from non-human to human communication. Let us summarize some significant metacognitive properties in this multifaceted evolution. First, signal systems are selectively shaped to enhance learnability, discriminability, informativeness and pragmatic efficiency. Second, the ability to deliberately control signalling events is diversely manifested by receivers across species – *when* they should be produced or suppressed, to *which targets* they should be directed, and *how* (with which frequency, duration, details). Third, recipients are differentially sensitive not only to message contents, but also to how they are conveyed. The hypothesis defended here is that vehicle-based affective predictions (procedural trade-offs) have guided signal selection and reception in various phyla (birds and mammals). Metacognitive predictions – initially developed to support perceptual discrimination or memory retrieval in foraging – might have been reused by producers to learn how to signal, and by recipients to attend to relevant sequences. A common preference for minimal effort was used to make informational content easily transmissible at the minimal cost compatible with the epistemic goal. Fourth, diversified, specialized communication repertoires developed in human languages as a natural consequence of having specialized epistemic goals (such as: educational, political, legal, religious, etc.)

In the proposed framework, maxims of conversation or relevance rules are conceptual counterparts of general procedural constraints on metacommunication at work in species endowed with cognitive control. But the right-hand side of Table 1 should include, in addition, the various forms of acceptance that human IC required, from simple factual questions, to clarification, explanation, hypothesizing, justification, etc. These alternative informational

²⁹ See Pulvermüller & Grisoni, (2021).

goals manifest properly human communicative flexibility, a flexibility rooted in the specific selective pressures of cooperation of large groups in structured societies.

Where Grice and neo_Gricean pragmaticians spell out the higher-order inferences involved in selecting and interpreting message contents, our proposal is that verbal and non-verbal communication is largely regulated on a leaner basis, through basic structural properties of signal processing. The point of proceduralizing pragmatic rules is not to deny any role to mindreading in IC. It is to make the case that the ability to recognize communicative intentions is a later acquisition, both in phylogeny and in ontogeny (Aguirre et al., 2022, Proust, 2012, Wu et al., 2013). In this evolution, a major role should be recognized to the control and monitoring of collective decision-making.

Granting the overall validity of this hypothesis, much remains to be done to substantiate it. First, animal calls are about *what to do here and now* – no such limitation applies to human IC. Second, only a *fixed number of affordances* is expressible in nonhuman signal systems. In contrast, speech can represent past, present or future situations in a “detached” way (believed, desired, planned, etc.). The cognitive routes for bridging these discontinuities are still debated. A plausible speculation emerges from an analysis of the specific informational demands that elicited detached representations. Genetic endowment and cultural acquisition might have interacted to favor this crucial step in communication (Avital & Jablonka, 2000), possibly 500 000 years ago, when *Homo heidelbergensis* and early Neanderthals learned how to haft prepared stones to wooden handles using adhesive peck (Haidle et al, 2015). Technological gesture sequences had to be memorized and planned. These needs, in a prosocial context, might have enhanced protolanguage use to monitor cooperative activity, as well as critical goal appraisal (Sterelny, 2016, Planer, 2017a). A metacognitive preference for novelty seems to have developed in humans at this time (Harcourt, 2015), in contrast with chimpanzees' relative conservatism and "dormant" curiosity (van Schaik et al., 2019).

Another hypothesis is that detached communication reflects a reduction of the signalling biases caused by human "self-domestication" (Deacon, 2010). Just as the song of domestic Bengalese finches has progressively been made more varied by new brain systems, symbolically mediated affordances might have liberated the human symbolic repertoire from the high-arousal states associated to innate constraints. Consonant with this view is the observation that, once teaching and language became instrumental in acquiring new

techniques, individual curiosity and cumulative culture developed in parallel (Burkart et al., 2018, Planer, 2017a). Human inquisitive behavior, first aimed at environmental properties, progressively evolved in adversarial forms of verbal communication. At this point, communicators became sensitive to multiple epistemic goals and associated norms. Whether correct or not, these speculations point to the need to theorize further about the variability of human culture as well as its cumulative character.

Acknowledgments

The author warmly thanks Maël Leroux, Howard Nusbaum, Anne Reboul and Nicholas Shea for their thoughtful critical observations and suggestions. This work has been supported by the institutional grant ANR-17-EURE-0017 FrontCog.

References

- Abbot-Smith, K., Schulze, C., Anagnostopoulou, N., Zajączkowska, M., & Matthews, D. (2022). How do 3-year-olds use relevance inferencing to interpret indirect speech?. *First Language, 42*(1), 3-21.
- Ackerman, R. (2014). The diminishing criterion model for metacognitive regulation of time investment. *Journal of experimental psychology: General, 143*(3), 1349-1368.x
- Aguirre, M., Brun, M., Reboul, A., & Mascaro, O. (2022). How do we interpret questions? Simplified representations of knowledge guide humans' interpretation of information requests. *Cognition, 218*, 104954.
- Akçay, Ç. L., Tom, M. E., Campbell, S. E., & Beecher, M. D. (2013). Song type matching is an honest early threat signal in a hierarchical animal communication system. *Proceedings of the Royal Society B: Biological Sciences, 280*(1756), 20122517.
- Allen, J. A., Garland, E. C., Dunlop, R. A., & Noad, M. J. (2018). Cultural revolutions reduce complexity in the songs of humpback whales. *Proceedings of the Royal Society B, 285*(1891), 20182088.
- Arnold, K., & Zuberbühler, K. (2012). Call combinations in monkeys: compositional or idiomatic expressions?. *Brain and language, 120*(3), 303-309.
- Avital, E., & Jablonka, E. (2000). *Animal traditions: Behavioural inheritance in evolution*. Cambridge University Press.
- Balcomb, F. K., & Gerken, L. (2008). Three-year-old children can access their own memory to guide responses on a visual matching task. *Developmental science, 11*(5), 750-760.
- Barbas, H. (2007). Flow of information for emotions through temporal and orbitofrontal pathways. *Journal of anatomy, 211*(2), 237-249.
- Barr, D. J., & Keyser, B. (2002). Anchoring comprehension in linguistic precedents. *Journal of Memory and Language, 46*(2), 391-418.
- Basile, B. M., Hampton, R. R., Suomi, S. J., & Murray, E. A. (2009). An assessment of memory awareness in tufted capuchin monkeys (*Cebus apella*). *Animal Cognition, 12*(1), 169-180.
- Beran, M. J., & Smith, J. D. (2011). Information seeking by rhesus monkeys (*Macaca mulatta*) and capuchin monkeys (*Cebus apella*). *Cognition, 120*(1), 90-105.

Beran, M. J., French, K., Smith, T. R., & Parrish, A. E. (2019). Limited evidence of number–space mapping in rhesus monkeys (*Macaca mulatta*) and capuchin monkeys (*Sapajus apella*). *Journal of Comparative Psychology*, *133*(3), 281-293.

Bernard, S., Proust, J., & Clément, F. (2015). Procedural metacognition and false belief understanding in 3-to 5-year-old children. *PloS one*, *10*(10), e0141321.

Berwick, R. C., Beckers, G. J., Okanoya, K., & Bolhuis, J. J. (2012). A bird’s eye view of human language evolution. *Frontiers in evolutionary neuroscience*, *4*, 5.

Brown, C., Garwood, M. P., & Williamson, J. E. (2012). It pays to cheat: tactical deception in a cephalopod social signalling system. *Biology letters*, *8*(5), 729-732

Browning, H., & Birch, J. (2022). Animal sentience. *Philosophy Compass*, *17*(5), e12822.

Brumm, H., & Slabbekoorn, H. (2005) Acoustic communication in noise. *Advances in the Study of Behavior*. San Diego: Elsevier Academic Press Inc. pp. 151–209.

Burkart, J., Martins, E. G., Miss, F., & Zürcher, Y. (2018). From sharing food to sharing information: cooperative breeding and language evolution. *Interaction Studies*, *19*(1-2), 136-150.

Byrne, R. W., Cartmill, E., Genty, E., Graham, K. E., Hobaiter, C., & Tanner, J. (2017). Great ape gestures: intentional communication with a rich set of innate signals. *Animal cognition*, *20* (4), 755-769.

Call, J. (2012). Seeking information in non-human animals: weaving a metacognitive web. In M. Beran, J. Brandl, J. Perner & J. Proust eds.), *Foundations of metacognition*, Oxford : Oxford University press, 62-75.

Chalcraft, V. J., & Gardner, R. A. (2005). Cross-fostered chimpanzees modulate signs of American Sign Language. *Gesture*, *5*(1-2), 107-132.

Cheney, D. L., & Seyfarth, R. M. (1990). *How monkeys see the world: Inside the mind of another species*. University of Chicago Press.

Cisek, P. (2007). Cortical mechanisms of action selection: the affordance competition hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1485), 1585-1599.

Cisek, P. (2022). Evolution of behavioural control from chordates to primates. *Philosophical Transactions of the Royal Society B*, *377*(1844), 20200522.

Converse, P. D., & DeShon, R. P. (2009). A tale of two tasks: reversing the self-regulatory resource depletion effect. *Journal of Applied Psychology*, *94*(5), 1318.1324.

Cunningham, E., & Janson, C. (2007). Integrating information about location and value of resources by white-faced saki monkeys (*Pithecia pithecia*). *Animal cognition*, *10*(3), 293-304.

Daniel, R., & Pollmann, S. (2012). Striatal activations signal prediction errors on confidence in the absence of external feedback. *Neuroimage*, *59*(4), 3457-3467.

Dawkins, R., & Krebs, J. R. (1978). Animal signals: Information or manipulation? In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (Vol. 2, pp. 282–309). Blackwell Scientific Publications.

Deacon, T. W. (2010). A role for relaxed selection in the evolution of the language capacity. *Proceedings of the National Academy of Sciences*, *107*(supplement_2), 9000-9006.

de Framond, L., Brumm, H., Thompson, W. I., Drabing, S. M., & Francis, C. D. (2022). The broken-wing display across birds and the conditions for its evolution. *Proceedings of the Royal Society B*, *289*(1971), 20220058.

Dretske, F. (1981). *Knowledge and the Flow of Information*. Cambridge: Cambridge University Press

Dretske, F. (1988). *Explaining Behavior*. Cambridge, Mass: MIT Press.

Duffy, A., Latimer, K. W., Goldberg, J. H., Fairhall, A. L., & Gadagkar, V. (2022). Dopamine neurons evaluate natural fluctuations in performance quality. *Cell reports*, 38(13), 110574.

Dunstone, J., & Caldwell, C. A. (2018). Cumulative culture and explicit metacognition: A review of theories, evidence and key predictions. *Palgrave Communications*, 4(1), 1-11.

Eliades, S. J., & Miller, C. T. (2017). Marmoset vocal communication: behavior and neurobiology. *Developmental neurobiology*, 77(3), 286-299.

Ferrigno, S., Kornell, N., & Cantlon, J. F. (2017). A metacognitive illusion in monkeys. *Proceedings of the Royal Society B: Biological Sciences*, 284(1862), 20171541.

Fitch, W. (2017). Empirical approaches to the study of language evolution. *Psychonomic bulletin & review*, 24.1: 3-33.

Fitch, W. T., & Friederici, A. D. (2012). Artificial grammar learning meets formal language theory: an overview. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1598), 1933-1955.

Fleming, S. M., Weil, R. S., Nagy, Z., Dolan, R. J., & Rees, G. (2010). Relating introspective accuracy to individual differences in brain structure. *Science*, 329(5998), 1541-1543.

Franke, M., & Jäger, G. (2016). Probabilistic pragmatics, or why Bayes' rule is probably important for pragmatics. *Zeitschrift für Sprachwissenschaft*, 35(1), 3-44.

Frankfurt, H. G. (1988). *The importance of what we care about: Philosophical essays*. Cambridge University Press

Gadagkar, V., Puzerey, P. A., Chen, R., Baird-Daniel, E., Farhang, A. R., & Goldberg, J. H. (2016). Dopamine neurons encode performance error in singing birds. *Science*, 354(6317), 1278-1282.

Gadagkar, V., Puzerey, P. A., & Goldberg, J. H. (2019). Dopamine neurons change their tuning according to courtship context in singing birds. *bioRxiv*, 822817

Gallistel, C. R. (2020). Where meanings arise and how: Building on Shannon's foundations. *Mind & Language*, 35(3), 390-401

Gibson, E., Futrell, R., Piantadosi, S. P., Dautriche, I., Mahowald, K., Bergen, L., & Levy, R. (2019). How efficiency shapes human language. *Trends in cognitive sciences*, 23(5), 389-407.

Godfrey-Smith, P. (2017). The evolution of consciousness in phylogenetic context. In *The Routledge Handbook of philosophy of animal minds* (pp. 216-226). Routledge.

Gómez, J. C. (1996). Ostensive behavior in great apes: The role of eye contact. *Reaching into thought: The minds of the great apes*, 131-151.

Goto, K., & Watanabe, S. (2012). Large-billed crows (*Corvus macrorhynchos*) have retrospective but not prospective metamemory. *Animal Cognition*, 15(1), 27-35.

Grice, P. (1989). *Studies in the Way of Words*. Harvard University Press.

Eliades, S. J., & Miller, C. T. (2017). Marmoset vocal communication: behavior and neurobiology. *Developmental neurobiology*, 77(3), 286-299.

Frankfurt, H. (1988). *The Importance of what we care about*, Cambridge : Cambridge University Press.

Freeberg, T. M., & Lucas, J. R. (2012). Information theoretical approaches to chick-a-dee calls of Carolina chickadees (*Poecile carolinensis*). *Journal of Comparative Psychology*, 126(1), 68-81.

Godfrey-Smith, P. (2017). The evolution of consciousness in phylogenetic context. In *The Routledge handbook of philosophy of animal minds* (pp. 216-226). Routledge.

Gómez, J. C. (1996). Ostensive behavior in great apes: The role of eye contact. *Reaching into thought: The minds of the great apes*, 131-151.

Goupil, L., & Kouider, S. (2019). Developing a reflective mind: from core metacognition to explicit self-reflection. *Current Directions in Psychological Science*, 28(4), 403-408.

Goupil, L., & Proust, J. (2023). Curiosity as a metacognitive feeling. *Cognition*, 231, 105325.

Hage, S. R. (2018). Dual neural network model of speech and language evolution: new insights on flexibility of vocal production systems and involvement of frontal cortex. *Current opinion In behavioral sciences*, 21, 80-87.

Hage, S. R., & Nieder, A. (2016). Dual neural network model for the evolution of speech and language. *Trends in neurosciences*, 39(12), 813-829.

Haidle, M. N., Bolus, M., Collard, M., Conard, N. J., Garofoli, D., Lombard, M., Nowell, A., Tennie, C. & Whiten, A. (2015). The nature of culture: an eight-grade model for the evolution and expansion of cultural capacities in hominins and other animals. *Journal of Anthropological Sciences*. Vol. 93 (2015), pp. 43-70.

Hampton, R.R. (2009). Multiple demonstrations of metacognition in nonhumans: Converging evidence or multiple mechanisms? *Comparative Cognition and Behavior Reviews*, 4, 17-28.

Harcourt, A. H. (2015). *Humankind*. New York: Simon and Schuster.

Hauser, M. D. (1997). Minding the behaviour of deception. In Whiten & Byrne (eds.), *Machiavellian intelligence II: Extensions and evaluations*, 12, 112-143.

Hesler, N., Mundry, R., & Dabelsteen, T. (2012). Are there age-related differences in the song repertoire size of Eurasian blackbirds?. *Acta ethologica*, 15(2), 203-210.

Heyes, C., Bang, D., Shea, N., Frith, C. D., & Fleming, S. M. (2020). Knowing ourselves together: The cultural origins of metacognition. *Trends in Cognitive Sciences*, 24(5), 349-362.

Hisey, E., Kearney, M. G., & Mooney, R. (2018). A common neural circuit mechanism for internally guided and externally reinforced forms of motor learning. *Nature neuroscience*, 21(4), 589-597.

Hobaiter, C., & Byrne, R. W. (2017). What is a gesture? A meaning-based approach to defining gestural repertoires. *Neuroscience & Biobehavioral Reviews*, 82, 3-12.

Hopkins, W. D., Tagliabata, J. P., & Leavens, D. A. (2007). Chimpanzees differentially produce novel vocalizations to capture the attention of a human. *Animal behaviour*, 73(2), 281-286.

Inzlicht, M., Bartholow, B. D., & Hirsh, J. B. (2015). Emotional foundations of cognitive control. *Trends in cognitive sciences*, 19(3), 126-132

Jarvis, E. D. (2013). Evolution of brain pathways for vocal learning in birds and humans. *Birdsong, speech, and language: exploring the evolution of mind and brain*, 63-107.

Kang, M. J., Hsu, M., Krajbich, I. M., Loewenstein, G., McClure, S. M., Wang, J. T. Y., & Camerer, C. F. (2009). The wick in the candle of learning: Epistemic curiosity activates reward circuitry and enhances memory. *Psychological Science*, 20(8), 963-973.

Keysar, B., Lin, S., & Barr, D. J. (2003). Limits on theory of mind use in adults. *Cognition*, 89(1), 25-41.

Kepecs, A., & Mainen, Z. F. (2012). A computational framework for the study of confidence in humans and animals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1594), 1322-1337.

Kershenbaum, A., Demartsev, V., Gammon, D. E., Geffen, E., Gustison, M. L., Ilany, A., & Lameira, A. R. (2021). Shannon entropy as a robust estimator of Zipf's Law in animal vocal communication repertoires. *Methods in Ecology and Evolution*, 12(3), 553-564.

Kissine, M. (2016). Pragmatics as metacognitive control. *Frontiers in psychology*, 6, 2057.

Koechlin, E. (2014). An evolutionary computational theory of prefrontal executive function in decision-making. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369(1655), 20130474.

- Koechlin, E., & Summerfield, C. (2007). An information theoretical approach to prefrontal executive function. *Trends in cognitive sciences*, 11(6), 229-235.
- Konishi, M. (2004). The role of auditory feedback in birdsong. *Annals of the New York Academy of Sciences*, 1016(1), 463-475.
- Koriat, A. (2000). The feeling of knowing: Some metatheoretical implications for consciousness and control. *Consciousness and cognition*, 9(2), 149-171.
- Koriat, A., & Levy-Sadot, R. (1999). Processes underlying metacognitive judgments: Information-based and experience-based monitoring of one's own knowledge. In S. Chaiken & Y. Trope (Eds.), *Dual Process theories in social psychology* (pp. 483–502). Guilford.
- Koriat, A., & Ackerman, R. (2010). Metacognition and mindreading: Judgments of learning for self and other during self-paced study. *Consciousness and cognition*, 19(1), 251-264.
- Koriat, A., Ma'ayan, H., & Nussinson, R. (2006). The intricate relationships between monitoring and control in metacognition: lessons for the cause-and-effect relation between subjective experience and behavior. *Journal of experimental psychology: general*, 135(1), 36-69
- Koriat, A., Nussinson, R., Bless, H., & Shaked, N. (2008). Information-based and experience-based metacognitive judgments: Evidence from subjective confidence. In J. Dunloski and R.A. Bjork, (eds.) *A Handbook of Memory and Metamemory*, Psychology Press, 117-136.
- Koriat, A. (2008). Subjective confidence in one's answers: the consensuality principle. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 34(4), 945-959.
- Kornell, N., Son, L. K., & Terrace, H. S. (2007). Transfer of metacognitive skills and hint seeking in monkeys. *Psychological Science*, 18(1), 64-71.
- Kuchling, F., Fields, C., & Levin, M. (2022). Metacognition as a consequence of competing evolutionary time scales. *Entropy*, 24(5), 601
- Kurzban, R., Duckworth, A., Kable, J. W., & Myers, J. (2013). An opportunity cost model of subjective effort and task performance. *Behavioral and brain sciences*, 36(6), 661-679.
- Lage, C. A., Wolmarans, D. W., & Mograbi, D. C. (2022). An evolutionary view of self-awareness. *Behavioural Processes*, 194, 104543.
- Lak, A., Stauffer, W. R., & Schultz, W. (2014). Dopamine prediction error responses integrate subjective value from different reward dimensions. *Proceedings of the National Academy of Sciences*, 111(6), 2343-2348.
- Lambert, M. L., & Osvath, M. (2020). Investigating information seeking in ravens (*Corvus corax*). *Animal Cognition*, 23(4), 671-680.
- Lameira, A. R. (2017). Bidding evidence for primate vocal learning and the cultural substrates for speech evolution. *Neuroscience & Biobehavioral Reviews*, 83, 429-439.
- Lizkowski, U., Carpenter, M., & Tomasello, M. (2008). Twelve-month-olds communicate helpfully and appropriately for knowledgeable and ignorant partners. *Cognition*, 108(3), 732-739.
- Macedonia, J. M., & Evans, C. S. (1993). Essay on contemporary issues in ethology: Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology*, 93(3), 177-197.
- Magrath, R. D., Haff, T. M., Horn, A. G., & Leonard, M. L. (2010). Calling in the face of danger: *in the Study of Behavior* (Vol. 41, pp. 187-253). Academic Press.
- Margoliash, D., & Nusbaum, H. C. (2009). Language: the perspective from organismal biology. *Trends in cognitive sciences*, 13(12), 505-510.
- Marler, P. (1967). Animal Communication Signals: We are beginning to understand how the structure of animal signals relates to the function they serve. *Science*, 157(3790), 769-774.

predation risk and acoustic communication by parent birds and their offspring. In *Advances* Marler, P., Karakashian, S., & Gyger, M. (1991). Do animals have the option of withholding signals when communication is inappropriate? The audience effect. In C. A. Ristau (Ed.), *Cognitive ethology: The minds of other animals: Essays in honor of Donald R. Griffin* (pp. 187–208). Lawrence Erlbaum Associates, Inc.

Maynard Smith, J. & Harper, D. (2003). *Animal signals*. Oxford University Press.

Middlebrooks, P. G., & Sommer, M. A. (2012). Neuronal correlates of metacognition in primate frontal cortex. *Neuron*, 75(3), 517-530.

Miller C.T. & Thomas A.W. (2012). Individual recognition during bouts of antiphonal calling in common marmosets. *Journal of Comparative Physiology*, 198: 337–346.

Millikan, R. G. (2017). *Beyond concepts: Unicepts, language, and natural information*. Oxford University Press.

Mitani, J. C., & Watts, D. P. (2005). Correlates of territorial boundary patrol behaviour in wild chimpanzees. *Animal Behaviour*, 70(5), 1079-1086.

Moore, R. (2016). Meaning and ostension in great ape gestural communication. *Animal Cognition*, 19(1), 223-231.

Morales, J., Lau, H., & Fleming, S. M. (2018). Domain-general and domain-specific patterns of activity supporting metacognition in human prefrontal cortex. *Journal of Neuroscience*, 38(14), 3534-3546

Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009). Campbell's monkeys use affixation to alter call meaning. *PloS one*, 4(11), e7808.

Oudeyer, P. Y., & Smith, L. B. (2016). How evolution may work through curiosity-driven developmental process. *Topics in Cognitive Science*, 8(2), 492-502.

Paulus, M., Proust, J., & Sodian, B. (2013). Examining implicit metacognition in 3.5-year-old children: An eye-tracking and pupillometric study. *Frontiers in Psychology*, 4, 145.

Petkov, C. I., & Jarvis, E. D. (2012). Birds, primates, and spoken language origins: behavioral phenotypes and neurobiological substrates. *Frontiers in evolutionary neuroscience*, 4, 12.

Pezzulo, G., & Cisek, P. (2016). Navigating the affordance landscape: feedback control as a process model of behavior and cognition. *Trends in cognitive sciences*, 20(6), 414-424.

Pinto, A., Oates, J., Grutter, A., & Bshary, R. (2011). Cleaner wrasses *Labroides dimidiatus* are more cooperative in the presence of an audience. *Current Biology*, 21(13), 1140-1144.

Planer, R. (2017a). Talking About Tools: Did Early Pleistocene Hominins Have a Protolanguage? *Biological Theory*, 12, 211-221.

Planer, R. (2017b). Protolanguage might have evolved before ostensive communication. *Biological Theory*, 12:72-84.

Poole, J. H., Tyack, P. L., Stoeger-Horwath, A. S., & Watwood, S. (2005). Elephants are capable of vocal learning. *Nature*, 434(7032), 455-456.

Proust, J. (2012) Metacognition and mindreading: one or two functions? in: M. Beran, J. Brandl, J. Perner & J. Proust (Eds.), *The Foundations of Metacognition*. Oxford: Oxford University Press, 234-251.

Proust, J. (2013). *The Philosophy of Metacognition*. Oxford University Press.

Proust, J. (2015). Time and action: Impulsivity, habit, strategy. *Review of Philosophy and Psychology*, 6(4), 717-743.

Proust, J. (2016). The evolution of primate communication and metacommunication. *Mind & Language*, 31(2), 177-203.

Proust, J. (2019). From comparative studies to interdisciplinary research on metacognition. *Animal Behavior and Cognition*, 6(4), 309-328.

Proust, J. (2022), The cultural evolution of information seeking, *Journal of Cognition and Culture*.

Proust, J. (2023), A semantics for affordances, *Philosophical Psychology*.

Pulvermüller, F., & Grisoni, L. (2020). Semantic prediction in brain and mind. *Trends in Cognitive Sciences*, 24(10), 781-784.

Reboul, A. (2011). A relevance-theoretic account of the evolution of implicit communication. *Studies in Pragmatics*, 13(1), 1-19.

Rendall, D., Owren, M. J., & Ryan, M. J. (2009). What do animal signals mean?. *Animal Behaviour*, 78(2), 233-240.

Rhodes, M. G., & Castel, A. D. (2009). Metacognitive illusions for auditory information: Effects on monitoring and control. *Psychonomic Bulletin & Review*, 16(3), 550-554.

Roberts, C. (2012). Information Structure: Towards an integrated formal theory of pragmatics. *Semantics and Pragmatics*, 5(0), 6:1-69.

Roberts, W. A., Feeney, M. C., McMillan, N., MacPherson, K., Musolino, E., & Petter, M. (2009). Do pigeons (*Columba livia*) study for a test? *Journal of Experimental Psychology: Animal Behavior Processes*, 35, 129-142.

Roberts, W. A., McMillan, N., Musolino, E., & Cole, M. (2012). Information seeking in animals: metacognition?. *Comparative Cognition & Behavior Reviews*, 7, 85-109.

Rosati, A. G., & Santos, L. R. (2016). Spontaneous metacognition in rhesus monkeys. *Psychological Science*, 27(9), 1181-1191.

Salmi, R., Szczupider, M., & Carrigan, J. (2022). A novel attention-getting vocalization in zoo-housed western gorillas. *Plos one*, 17(8), e0271871.

Santi, A., Adams, A., & Bassett, J. (2010). The role of keypecking during filled intervals on the judgment of time for empty and filled intervals by pigeons. *Learning & Behavior*, 38(1), 42-49.

Scarantino, A., & Clay, Z. (2015). Contextually variable signals can be functionally referential. *Animal Behaviour*, 100(100), e1-e8.

Schel, A. M., Candiotti, A., & Zuberbühler, K. (2010). Predator-detering alarm call sequences in Guereza colobus monkeys are meaningful to conspecifics. *Animal Behaviour*, 80(5), 799-808.

Schlenker, P. (2018). Iconic pragmatics. *Natural Language & Linguistic Theory*, 36(3), 877-936.

Schlenker, P., Chemla, E., & Zuberbühler, K. (2016). What do monkey calls mean?. *Trends in Cognitive Sciences*, 20(12), 894-904.

Schwartz, B. L. (2019). Using natural ecology to predict higher cognition in human and non-human primates. *Animal Behavior and Cognition*, 6(4), 344-354.

Schwarz, N., & Clore, G. L. (2007). Feelings and phenomenal experiences. In A. W. Kruglanski, & Higgins, (Eds.). (2013). *Social psychology: Handbook of basic principles*. Guilford Publications, 385-407.

Scott-Phillips, T. C. (2016). Meaning in great ape communication: summarising the debate. *Animal Cognition*, 19(1), 233-238.

Seyfarth, R. M., & Cheney, D. L. (2003). Signallers and recipients in animal communication. *Annual review of psychology*, 54(1), 145-173.

Shea, N., Boldt, A., Bang, D., Yeung, N., Heyes, C., & Frith, C. D. (2014). Supra-personal cognitive control and metacognition. *Trends in cognitive sciences*, 18(4), 186-193.

Shea, N., Godfrey-Smith, P., & Cao, R. (2018). Content in simple signalling systems. *The British Journal for the Philosophy of Science*, 69, 4.

- Sherman, P. W. (1977). Nepotism and the Evolution of Alarm Calls: Alarm calls of Belding's ground squirrels warn relatives, and thus are expressions of nepotism. *Science*, *197*(4310), 1246-1253.
- Slocombe, K. E., & Zuberbühler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences*, *104*(43), 17228-17233
- Skyrms, B. (2010). *Signals: Evolution, Learning, and Information*. Oxford: Oxford University Press.
- Sperber, D. (2000). Metarepresentations in an evolutionary perspective. In D. Sperber (ed.), *Metarepresentations: A multidisciplinary perspective*, Oxford: Oxford University Press, 117-137.
- Sperber, D. (2019). Personal notes on a shared trajectory. *Relevance, Pragmatics and Interpretation*. Cambridge University Press, Cambridge.
- Sperber, D., & Wilson, D. (1986/1995). *Relevance: Communication and cognition* (Vol. 142). Cambridge, MA: Harvard University Press.
- Sperber, D., & Wilson, D. (2002). Pragmatics, modularity and mind-reading. *Mind & language*, *17*(1-2), 3-23.
- Sterelny, K. (2016). Cumulative cultural evolution and the origins of language. *Biological Theory*, *11*(3), 173-186.
- Sutton, J. E., & Shettleworth, S. J. (2008). Memory without awareness: pigeons do not show metamemory in delayed matching to sample. *Journal of Experimental Psychology: Animal Behavior Processes*, *34*(2), 266-282.
- Suzuki, T. N. (2016). Semantic communication in birds: evidence from field research over the past two decades. *Ecological Research*, *31*(3), 307-319.
- Takahashi, D. Y., Fenley, A. R., Teramoto, Y., Narayanan, D. Z., Borjon, J. I., Holmes, P., & Ghazanfar, A. A. (2015). The developmental dynamics of marmoset monkey vocal production. *Science*, *349*(6249), 734-738.
- Tang, H., Costa, V.D., Bartolo, R., and Averbeck, B.B. (2022). Differential coding of goals and actions in ventral and dorsal corticostriatal circuits during goal-directed behavior. *Cell Rep*. *38*, 110198
- Terrace, H. S., & Son, L. K. (2009). Comparative metacognition. *Current opinion in neurobiology*, *19*(1), 67-74.
- Tian, J., Huang, R., Cohen, J. Y., Osakada, F., Kobak, D., Machens, C. K., & Watabe-Uchida, M. (2016). Distributed and mixed information in monosynaptic inputs to dopamine neurons. *Neuron*, *91*(6), 1374-1389.
- Townsend, S. W., Koski, S. E., Byrne, R. W., Slocombe, K. E., Bickel, B., Boeckle, M., ... & Manser, M. B. (2017). Exorcising Grice's ghost: An empirical approach to studying intentional communication in animals. *Biological Reviews*, *92*(3), 1427-1433.
- Tsujimoto, S., Genovesio, A., & Wise, S. P. (2010). Evaluating self-generated decisions in frontal pole cortex of monkeys. *Nature neuroscience*, *13*(1), 120-126.
- van Schaik, C. P., Pradhan, G. R., & Tennie, C. (2019). Teaching and curiosity: sequential drivers of cumulative cultural evolution in the hominin lineage. *Behavioral ecology and sociobiology*, *73*(1), 1-11.
- Watanabe, A., & Clayton, N. S. (2016). Hint-seeking behaviour of western scrub-jays in a metacognition task. *Animal cognition*, *19*(1), 53-64.
- Wheeler, B. C., & Fischer, J. (2012). Functionally referential signals: a promising paradigm whose time has passed. *Evolutionary Anthropology: Issues, News, and Reviews*, *21*(5), 195-205.

- Whiten, A., & Byrne, R. W. (1988). Tactical deception in primates. *Behavioral and brain sciences*, 11(2), 233-244.
- Whiten, A., & Byrne, R. W. (Eds.). (1997). *Machiavellian intelligence II: Extensions and evaluations*. Cambridge, Cambridge University Press.
- Wich, S. A., Krützen, M., Lameira, A. R., Nater, A., Arora, N., Bastian, M. L., ... & van Schaik, C. P. (2012). Call cultures in orang-utans?. *PLoS one*, 7(5), e36180
- Wismer, S., Pinto, A. I., Vail, A. L., Grutter, A. S., & Bshary, R. (2014). Variation in cleaner wrasse cooperation and cognition: influence of the developmental environment? *Ethology*, 120(6), 519-531.
- Wu, S., Barr, D. J., Gann, T. M., & Keysar, B. (2013). How culture influences perspective taking: differences in correction, not integration. *Frontiers in human neuroscience*, 7, 822.
- Xiao, L., Chattree, G., Oscos, F. G., Cao, M., Wanat, M. J., & Roberts, T. F. (2018). A basal ganglia circuit sufficient to guide birdsong learning. *Neuron*, 98(1), 208-221.
- Zakrzewski, A. C., Perdue, B. M., Beran, M. J., Church, B. A., & Smith, J. D. (2014). Cashing out: The decisional flexibility of uncertainty responses in rhesus macaques (*Macaca mulatta*) and humans (*Homo sapiens*). *Journal of Experimental Psychology: Animal Learning and Cognition*, 40(4), 490-501.
- Zuberbühler, K. (2008). Audience effects. *Current Biology*, 18(5), 189-190.