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Informational communication and metacognition

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Abstract

Procedural metacognition is the set of affect-based mechanisms allowing agents to regulate their cognitive actions (such as perceptual discrimination, memory retrieval or problem solving). Against the view that nonhumans merely use innate codes, it is argued that a number of species are able to learn to communicate, and to contextually regulate their signaling activity. A plausible evolutionary hypothesis is that, under pressure for maximizing efficiency, metacognitive abilities already used by nonhumans to regulate their perception and their memory were applied to communication. On this view, detecting and revising learning errors, converging on the species-specific trade-offs between informativeness and processing effort depend on a form of procedural metacognition, called metacommunication. The implications of this view for the evolution of human communication is raised. Against the expressivist view that, in human language use, relevance is extracted from affective content cues, it is proposed that the affects engaged in informational appraisal are mostly derived from processing properties. Against the intellectualist view that relevance requires second-order representations of producers' intentions, it is proposed that procedural heuristics allow recipients to select intended interpretations at a lesser cognitive cost.

Keywords

Evolution of communication, animal signaling, procedural metacognition, cognitive affordances, relevance, informativeness.

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 deliberately transmits a specific kind of information to a recipient. In this article, we examine

the following research question: granting that the calls produced in the context of mating, foraging, predation or territorial claims have such an informational goal, they should involve a specific cognitive equipment whose function is to control and monitor progress to goal. On this hypothesis, learning how to capture recipients's attention, selecting efficient ways of conveying information, would be subserved by a form of metacognitive control called "metacommunication". The goal of this article is to explore the extent to which metacognitive sensitivity (to informativeness, ease of processing, urgency) has shaped – and routinely controls – signaling activities. This research goal is relevant to evolutionary linguistics. Studies have recently focused on the extent to which rules of syntax, semantics and pragmatics organize signal use in 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 *signaling systems and human speech co-evolved with procedural metacognition* – the ability to control and monitor one's own cognitive activity (for example, in perceptual discrimination, learning and problem solving).

How to define communication?

The metacognitive dimension of communication depends on one's working definition of communication. The Machiavellian intelligence theory¹, for example, takes communication to consist 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 alter the recipients' behavior, and if the recipients' response evolved in order to respond to it (Maynard-Smith and Harper, 2003, Rendall et al., 2009). An "informational" definition, in contrast, states that an act is communicative if its function is to reliably reduce recipients' uncertainty about a fitness-relevant external property (Hauser, 1996). Recipients' behaviour, on the latter view, is a consequence of information being transmitted, not part of the definition of communication. Let's pause on this duality.

¹ See Whiten & Byrne, eds., (1997)

Consider the sirens' call in *The Odyssey*: wanting to hear the sirens' song is known to lead sailors to shipwreck on sirens' rocks.² 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 how reliable testimony can help detect and remedy manipulation. Metacognitive studies focus on the song: what information are recipients interested in? Why is a signal or a message attractive or boring? What kind of action-guidance is to be expected from learning?

Does a metacognitive theory need to endorse the informational definition? Both approaches focus on the constraints that optimize efficiency in processing signals and messages. Metacognitive theory, however, also teams up with the adaptationist definition to emphasize the motivational components of signals. Alarm vocalizations have the function of controlling recipients' behaviour. They do so, according to metacognitive theorists, in virtue of signals' acoustic features – abrupt onsets, broadband noise spectra, processing dynamics – suited for eliciting in recipients immediate attention capture and adaptive response. The metacognitive properties of 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 fitnessrelevant situations. When focusing on behavioural control, then, an adaptationist theory of IC, more or less tacitly, needs to presuppose specific forms of metacognitive sensitivity to explain recipients' manipulation. On the view defended here, the two definitions refer to different levels of analysis of one and the same phenomenon.

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). “Metacognition” is now 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

² In Homer's *Odyssey*, Ulysses resists the bewitching song of the mermaids by being tied up to the mast by his crew while they are ordered to wax up their ears so as not to hear the song.

to the subset of evaluative abilities that guide decision-making through a process of "internal reinforcement learning" – on the basis of affects (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. These feelings have the function of predicting feasibility of an action, detecting mistakes, differentially allocating one's own effort, and selecting the most promising ways of acting.³

How can it be demonstrated that procedural metacognition has shaped the production and reception of information in nonhumans? Here are central questions that need to be addressed: Are there different specific evolutionary pressures that apply to successful signaling in a given species? Can we identify the comparators used in non-human IC: do signalers assess clarity, informativeness, relevance of a call? Are trade-offs specifically at work in structuring repertoires, call duration, and amplitude? Are communicators able to learn their signaling repertoire, and detect their performance errors? Do they learn how to attend to signals and to respond to them?

Given these general goals, what is the range of evidence to be relied upon? Although there is much to learn about the evolution of language from homology, 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. Collecting evidence from multiple phyla will offer insight about the kinds of evolutionary pressures that can explain how metacommunication works in a given species.

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 signalers exert a voluntary control on their communicative actions, and distinguish signaling evolution-based efficiency of a communication system from individual signalers' efficiency. This distinction is a key to understanding how signalers experience communication as an activity, and allocate their production and reception effort across survival contexts and noisy environments. Various trade-offs involved in signal use will be discussed. A third section will examine whether

³ 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, (2022), Godfrey-Smith, (2017)

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 role of intentions in communication, as is often claimed, than in the function of metacommunication. A rich and open-ended language use being available, human producers do not merely aim at reducing recipients' uncertainty about the environment; they also aim at advertising that they do, and can let recipients infer by themselves information implicit in their message. This opens up the field of pragmatics far beyond nonhuman communicators' reach. This should not lead us to ignore the role that procedural evaluation has had in shaping Gricean style conversation maxims.

I - Metacognition in nonhumans

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 motivate decision-making as a function of their valence and intensity. 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 participants 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-yr-old children become progressively 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, it demonstrates that dopamine 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 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).

2. Species differences in procedural metacognitive skills

To examine the potential specialization of procedural metacognition across species, we need to classify metacognitive skills with reference to specific evaluative steps: 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). Large-bill crows, for example, 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 two or more opaque tubes (some empty, some baited) to animals, with or without a perceptual access to the baiting event: would the animals 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, this difference between two closely related primate species 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 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 vary widely *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. 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 reduced when considering two closely related 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 of corvids).

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

II - Metacommunication in non humans

Granting that nonhumans' cognition is metacognitively regulated and controlled, we need to explore to which extent metacognitive sensitivity to informativeness, ease of processing, or environmental urgency regulates nonhuman informational communication. To demonstrate the relevance of this exploration, we must demonstrate that nonhuman signaling can be under the communicators' voluntary or intentional 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).⁴ There is also behavioral evidence of signaling flexibility based on error detection and feedback reliance. The ability to learn from experience, flexibly repair one's errors, select proper signaling sequences, and invent new sequences, then, need to be investigated.

1. Can nonhumans control their signaling behavior?

This investigation must start with re-examining what counts as "voluntary signaling". Relevance theory, in the human case, takes voluntary signaling to be functionally dependent on having intentions to communicate, and making these intentions manifest to an audience (Sperber & Wilson, 1986/1995). In humans, an "ostensive" component is taken to manifest 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 is the following: Relevance is defined as the optimization of the trade-off between ease of processing and cognitive positive effects. This should be 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, then, allows recipients to form "a presumption of relevance" (Sperber & Wilson 1995).

The validity of this higher-order approach of communication has first been discussed in the context of nonhuman signaling: is an ostensive higher-order signal required to qualify as

⁴ Gadagkar et al., (2016).

“intentional”, i.e., individually controlled? 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 orang-utans by eye contact and gaze following: these cues are *functionally* equivalent to attributions of second-order intentions. On this view, metarepresentations are not needed for a recipient to identify a signal and understand it.⁵ 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). They might not have, after all, any intention to communicate at all.

A first response to this objection has been to deny that ostension *defines* active communication. Even humans deliberately produce messages without having formed any prior intention to communicate. Utterances such as “watch!”, “stop thief!” as well as non-human alarm calls functionally exclude an ostensive preface. The emotional signal rather expresses an emergency that recipients are equipped to identify, based on prior signaling 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 vocalisations with predator-specific contents, that reliably guide recipients' flight (Cheney & Seyfarth, 1990).

A second response consist in proposing that voluntary signaling is manifested by context-sensitive flexibility in signaling, along four main dimensions.

- 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 signaling as a function of the recipient's behavioural response (Hobaiter & Byrne, 2017).

⁵ For a detailed discussion of the role of ostension in communication see Proust (2016).

- 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 & Seafearth, 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, Zuberbühler, 2008).
- 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 (for chimpanzees) or during nest building (for orangutans) (Hopkins et al., 2007, Lameira, 2017). Chimpanzees, however, 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).

The evolutionary significance of signal learning for voluntariness has recently been emphasized by comparing the neural correlates of signaling 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 signaling. It is manifested in marmosets by a reduction of noise in their calls and 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 *two vocal neural networks available* for 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 is considered to be a preadaptation in the primate lineage for speech acquisition in humans (Hage & Nieder, 2016).

This finding leads to suspect that there is much more continuity between nonhuman and human IC than anticipated. It adds a final reason to reject the view that ostension should be a precondition for context-sensitive efficiency.

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 minima processing effort. Information transfer is successful when the information in fact extracted from a signal by the recipient is equal to the information made available by the signal. Granting that a number of nonhuman species manifest a form of vocal decision-making, we need to explain what makes communicative efficiency possible.

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 also been 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 (Lameira 2021). Efficiency also requires effort to be proportional to message informativeness and relevance. 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 to recommend an amount of redundancy in signaling, in order to facilitate the extraction of information in noisy environments, or in far-range communication. 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., procedural metacommunication.

3. Functional components of procedural metacommunication in nonhumans

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 signaling episode*. A functional analysis of communication indeed distinguishes an "external" reinforcement system that governs pragmatic pay-offs from a second "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.

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, however, in the sense that the predatory goal that the song is supposed to mediate is neutralized.

While the two regulative systems are sensitive to different kinds of efficiency, they combine their respective influences in decision-making (Tang et al, 2022). For example, the degree of recipients' subjective uncertainty about signalers' reliability combines with the fitness-significance of a signal. Alarm signaling, from Belding ground squirrels to primates and birds, has a nepotist function – protecting kins from predators (Sherman, 1977). In some conditions, however, a potential signaler may choose to flee silently (Seyfarth & Cheney, 2003). Indeed, an alarm call often helps a predator locate the signaler.

An ability to distinguish the two types of (in)efficiency is a functional precondition for learning. Learning how to signal requires a motivation that can be intrinsically informational, or pragmatic, or both; it also requires identifying what *needs to be learned* (Kuchling et al, 2022). Signalees' feedback (their degree of responsiveness) helps a signaler adjust intensity, clarity or accuracy in its call as a function of specific classes of recipients. Blackbird songs, for example, develop over time through phrase combination, repetition, and inclusion of new material. Learning to combine highly fitness-relevant sequences – "sexy" rapid high frequency twitters with low frequency, far ranging whistles is a key to blackbirds' reproductive and territorial success (Hesler et al., 2012).

3.2 The puzzle of communicative deception

On recipients' side, a major aspect of pragmatic efficiency has to do with trustworthiness. The duality of pragmatic and informational goals has been a major source of puzzlement for evolutionary theorists. Granting that communicative deception exists, how can signals, in the absence of any guarantee that they are reliable, be valued by recipients (Maynard-Smith & Harper, 2003)? 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 at all?

In response to this puzzle, a prevalent hypothesis is that animal signaling is regulated as a Nash equilibrium, i.e. as an evolutionary stable strategy in which both producers and recipients maximise their gains: honest signaling is stable whenever the benefit-cost ratio of honest signaling is higher than that of deceptive signaling (Maynard-Smith & Price, 1973). Nash equilibria do not all require individual actions to be taken – they can be fulfilled at a population level. However, field evidence suggests that in many species, recipients keep track of individual callers' reliability statistics. Unreliable signalers tend to be punished by social exclusion (Cheney & Seyfarth, 2003), violent reprisal and other deterrent measures (Brown et al., 2012).

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 nonhuman signalers 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). As will be seen below, research on artificial grammar learning in various species suggests that the mechanisms for syntactic learning are not specific to language, but apply to musical tones, pictures and animals signaling sequences. Some main types of nonhuman metacommunicative regulation are explored below.

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. 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 fluency. However, their higher sensitivity to the differential complexity of images restricts the amplitude of the illusion in their case, compared to humans.

3.3.2 Informativeness versus complexity

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 signaler, predator size and status – perched or in flight – food, etc. (Freeberg &

Lucas, 2012).

How is the trade-off between informativity and complexity settled? Research conducted by Philip Schlenker, Klaus Zuberbühler and their groups hypothesizes that primates apply a “principle of informativity”: Informativeness is balanced against message complexity, leading to select the call that most specifically predicts a type of affordance (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 both terrestrial (leopards) and aerial (raptors), and (in Tiwai), 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 cases throws light on the trade-off informativity/complexity work. 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). Signalers select the call that is maximally informative in a context. Recipients use this implicature to interpret affordances. For example, a specific signal is sent only in a situation of serious aerial danger. This example further illustrates the point made above (section 3.1.) that the informational trade-off between message complexity and informativeness interacts in signal production and reception with the pragmatic trade-off between effort allocation and expected value.

Appraising comparative informativeness in the context of curious exploration is performed in nonhumans as it is in infants (Goupil & Proust, submitted, Oudeyer & Smith, 2016). This suggests that the trade-off between complexity and informativeness is performed in the same way by non-human and human communicators: nonconscious heuristics elaborated through internal reinforcement underly the sensitivity to informational value, and settle the trade-off through a conscious feeling of understanding (i.e., adequate processing).

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 in putty-nose monkeys' signaling that calls that convey information about the nature or location of 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.

3.3.4 Information quality: error versus deception

As observed in the case of meta-learning, nonhumans can detect and revise their errors when learning species-specific signals. Are they also able to monitor the accuracy of their signal productions, for example, 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 first maxim of conversation?

This analogy, however, is questionable, because of the epistemic difference between truth and accuracy. Accuracy is the functional outcome of a detection mechanism.⁶ A predator signal is objectively accurate when it is caused by a predator, which raises recipients' probability of escaping predation. In contrast, a perceptual discrimination is assessed as accurate by a perceiver when a given threshold of subjective certainty obtains. Truth, in contrast, makes the relation between an assertion and what is objectively the case explicit. It 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. It evolved, along with the evaluative methods of explicit metacognition (Shea et al., 2014), in the course of verbal inquisitive behavior in human cooperating groups (Proust, 2022).

Let us focus, then, on the range of functional deception in nonhumans. Whenever signaling directly depends on the output of detection mechanisms, informational quality of a signal reflects the signaler's own detection abilities modulo its willingness to signal. Refraining

⁶ On functional deception, see Hauser (1997).

from communicating does not amount to sending a signal which the recipients knows to be false. Some species are unable to perform deceptive calls (although they can deceive through their bodily appearance). In some species, however, signaling is not constrained by signalers' perception of the environment. How is this possible? The usual explanation is that signalers functionally adjust their signals to their own interests by signaling false motivations or bodily dispositions.

Some species are indeed so equipped. In many species, deceptive IC is part of an innate behavioral repertoire. 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 (de Framont et al., 2022). In other species, reinforcement learning allows individuals to learn how to produce deceptive behaviors. 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 experience that cheating about signaling, in some conditions, is safe and pays well.

It is tempting to equate an ability to produce deceptive signals with lying, i.e. presenting a content as true in order to produce a false belief in recipients. Still, anticipating that signals produce responses in recipients does not amount to knowing *why* signals produce these responses – which motivations may govern alternative signals (Hauser, 1997). As seen above, a sensitivity to truth norms first emerges in human inquisitive behaviour. In inquisitive behaviour, a recipient has the explicit informational goal of *learning something* about a specific topic (it is curiosity-driven), not that of *obtaining a reward* (utility-driven questions) from an informer. It is plausible that increased social complexity of human groups imposed explicit truth commitments in order to secure cooperation between non-kin communicators (Sterelny, 2014). Specialized cultural practices (based on institutions, rituals and celebrations)

have been relied upon to externalize commitments into normative networks of prescription, involving evidence checking, trustworthiness, etc. (Poirier et al., 2021). According to this hypothesis, there is more to manipulating the informational quality of one's own messages than monitoring signal's accuracy or trying to influence recipients' behavior by signal distortion. It requires an ability to explicitly represent one's own, and others' epistemic awareness, an ability that co-evolved with collective decision-making (Proust, 2022, Shea et al., 2014). An explicit metacognitive monitoring and control of higher epistemic norms such as truth or plausibility might have co-evolved with a capacity to metarepresent one's own and others' beliefs, motivations and intentions. It is therefore doubtful that deceptive IC of this kind is accessible to non-human agents.

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 inevitable trade-off between clarity of message and ease of processing: a clear message may require a longer signaling 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 signaling. 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.

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

1. From Grice's maxims to procedural metacognition and back

How closely do the procedural trade-offs discussed in the preceding section match those that are implicit in Grice’s conversational maxims? Table 1 presents some of the most plausible functional equivalences.

Regulative dimension	Grice’s maxim	Procedural trade-off
Quality	<i>Try to make your contribution one that is true.</i>	transmit predictive information about current affordances.
Quantity	<i>Try to make your contribution as informative as required</i>	prefer informative signals that are easy to acquire and process
Relation	<i>Be relevant!</i>	<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
Manner	<i>Be perspicuous!</i>	<ul style="list-style-type: none"> • adjust signal discriminability to local noise. • Adjust processing difficulty to environmental requirements

Table 1 – Functional equivalences of Grice’s conversational maxims and procedural trade-offs applying to signal systems.

This table must be read in the following way: the function of procedural metacommunication in signal systems, in contrast to its conceptual Gricean counterpart, consists in balancing trade-offs or repairing misfirings, *not in interpreting them*. The set of preferences and adjustments in the procedural section are learned by reinforcement, on the basis of preexisting innate sensitivities to signaling structure: nonhumans’ preferences, very similar to humans’ musical preferences, motivate and guide adaptive IC behavior. Gricean and neo-Gricean pragmatics applied to human communication, in contrast, assume that maxims observance is expected from producers, and used as a premiss by recipients to infer

the implicatures of a given assertion. Relevance theorists propose that a relevance principle is sufficient to account for the data. This assumption is based on an important pragmatic distinction.

As a *cognitive trade-off*, relevance is the optimal ratio between positive cognitive effects gained and processing effort expended. This trade-off is implemented in mechanisms whose function is to automatically monitor cognitive activities. In information-seeking actions, for example, specific metacognitive heuristics predict informational efficiency by balancing cognitive effort against cognitive effects. This trade-off is used as input to assess the expected instrumental value of the exploration leading to these cognitive effects. (see section ? above). Cognitive trade-offs, then, are among the evaluative tasks of procedural metacommunication. Although Sperber & Wilson take contextual effects and processing effort to be non-representational dimensions of mental processes" (..) based "in the monitoring of physico-chemical parameters". (Sperber & Wilson 1986/1995, p. 131), it is now accepted by pragmatist theorists that they are monitored by metacognitive processes (Kissine, 2016).

According to Relevance theory, cognitive relevance is insufficient to account for human communication: a *communicative principle of relevance*, called "presumption of relevance" is needed over and above the automatic mechanism of cognitive relevance, because human communication does not consist in transmitting signal-based, coded information, but in interpreting a speaker's informational intentions. From this viewpoint, cognitive relevance as assessed in a context may violate its expected trade-off. This should lead the recipient to either reject the utterance, or to process it more deeply to recover additional cognitive effects. Hence the communication trade-off explains apparent exceptions to the cognitive trade-off by justifying the additional processing effort needed in special contexts and circumstances. An often quoted example from Grice (1975) is that of the reference letter for a philosophy position. A letter exclusively praising a candidate for her "excellent command of English" (CE) implicitly communicates that her competence in philosophy is rather poor (not CP). Understanding the implication in this particular utterance, is taken to require a mental state attribution, a counterfactual reasoning ability, in addition to specific background knowledge. The role of such inferences should not be minimized in highly strategic cases.

It can be objected, however, that interpretive norms involving a speaker's intentions are only required in specific contexts such as reference letters. In many daily cases, the structure of *informativeness dominance* exemplified in Campbell's monkeys' implicatures (see above,

section ?) might help human communicators to grasp a number of indirect speech acts without having to perform higher-order reasoning. It is sufficient to be exposed to a familiar context to derive effortlessly the relevance of an utterance. In support of this view, human children understand indirect speech acts such as “can you shut the door?” long before they can reason on others’ intentions (Abbot-Smith, et al., 2022).

There is also evidence that children and adult speakers alike do not respond to routine wh-questions based on a representation of the questioner’s specific knowledge and ignorance; they tend to rely on their own first-order representation of the environment (Aguirre et al., 2022). This suggests that trade-off mechanisms securing quick and costless informational transmission between producers and recipients evolved long before mindreading abilities. Mentalizing abilities subsequently 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) – a specifically human concern.

In summary, it has been hypothesized that communicative relevance might be related to the cognitive goals typically pursued in a given communication context. Selecting or recognizing a goal, however, can be context-dependent. In this case, a presumption of relevance would only be needed when a goal cannot immediately be derived from the situation in which a conversation takes place. Relevance at school, in a shop, in the street, or in a literary circle, might be based on different trade-offs, some of which favor speed of processing, while others favor complexity, i.e., metarepresentational inferences (Kissine, 2016).

2. Detecting relevance

How, then, – by which mechanisms–, can a recipient detect the relevance of a given utterance? Note that Table 1 has three procedural entries for the maxim of relevance: instrumental, informational, and temporal – three ways in which fitness issues contextually constrain IC. If we look for a single representational format that may be used to integrate opportunities and risks, an affect-based format recommends itself. Affects are able to promptly appreciate valence and intensity of inputs in these three dimensions. Several proposals have been made to substantiate the role of affect in allowing recipients to extract the point of a message from its content.

2.1. Expressive theories

An interesting complement to Relevance Theory proposes that affective information is not confined to a biasing role among competing premisses for relevance – as suggested by Sperber & Wilson (2015). It results in part from a trade-off between processing effort and *affective positive* effects (Wharton & Strey, 2019, Saussure & Wharton, 2020). Nonpropositional utterance components such as “total *prick*”, “*bloody class*”, interjections such as “*Ouch*” or “*Yugh*” express directly the attitude of the speaker, without describing it. Being natural signs, these components are of the same variety as non-human calls and signals: they are both spontaneously emitted in response to a given situation and have the function to signal it. The authors theorise that the procedural information so encoded will activate a form of processing that is either *about* mental states, or that *elicits* them: in such cases, a specific attitude is directly perceived and experienced by recipients. Emotional contagion, then, is the crucial mechanism that allows expressives to compete with propositional reasoning in driving relevance. Expressives, in contrast to their conceptual redescription, are not truth-conditional (they cannot be proven false). They are effects of sensations and feelings, rather than “cognitive effects”. Still they motivate specific lines of reasoning. They can even function as sub-intentional procedures that make recipients sensitive to positive emotional effects through inferential heuristics, and hence, can influence propositional inferences themselves.

A similar account of the function of emotion in communication has been applied to animal signaling as well as to some aspects of human communication (such as protolanguage “fossils”) (Arnold & Bar-On, 2020). In this account, emotions elicited by the environment, such as fear, have a more central role in driving relevance in nonhuman signaling and in human speech. Expressivism is the view that an expressive content is *needed* to directly extract the survival significance of a call. A bird's alarm call both expresses fear and points to a specific predator. On this view, animal calls *both* reveal the producer's psychological states, *and* changes the recipients' psychological states. The authors speculate that animal signals have evolved to orient group members' behavior – a distal function – by openly revealing their psychological states – a proximal function (ibid., p.126). This proximal function, however, is claimed not to require access to a theory of mind. Rather, producers' emotions are

experienced by recipients of expressive calls. In humans, expressive communication might have underlain mutual comprehension in protolanguage. Granting that conversational relevance requires reading a producer's intention to communicate, an expressive protolanguage might have provided an evolutionary basis for language understanding,

The evolutionary hypothesis according to which affective signaling has persisted in human gestural and verbal communication is further strengthened by studies analysing its role in human conversational gestures and prosody (Proust, 2013, ch.13). In conversation, for example, facial expressions emphasize important words with forceful prosody and concomitant brow movements. Raised eyebrows have been hypothesized to be a signal produced in analogy with the natural startle reaction (Bavelas and Chovil, 2000). They invite the recipients to expect a surprising and relevant information. Prosody – variations in pitch and loudness in verbal vocalizations – might express anger, frustration, sadness, perplexity, as well as composure, pleasure, joy and certainty (Patel et al., 2011).

Expressivism might be a solution to the puzzle of communication discussed above. Affects are subjective responses to external conditions, that can be elicited in group members confronted with the same fitness needs. In addition, promptness and gradiency of emotional responses might justify its role in orienting relevance assessments. To be convincing however, an expressivist theory of relevance needs to address two questions. First, are affective mechanisms necessary for grasping relevance? Second, are they sufficient?

2.2. Are emotions necessary for a message to be understood?

What makes emotion a necessary component in the evolution of communication, for expressivists, is that an emotional signal, or an interjection directly communicate states of mind to recipients. Although she herself does not endorse expressivism, Ruth Millikan's argument against the role of mentalizing inferences in language understanding is used to support the immediacy of expressive communication. What is Millikan's own view on this matter?

In her recent book, she writes: "Learning language is learning to identify without inference various things in one's world" (Millikan, 2017, p.185). Such learning depends on predictive cues that Millikan calls "infosigns". On her analysis, then, language understanding is achieved by the same processing channel as perceptual understanding: the sensory input is

"translated" into affordances (perceptual) judgments (Millikan, 2017, p.185.). Millikan, however, does not identify affective signs as an interesting category of infosigns. From her viewpoint, infosigns communicate situational affordances here and now. Hence, mental states and situational affordances are directly accessible through perception. Emotion is part of what is perceived, not what makes direct perception possible.

This explanatory alternative can be illustrated through what is often presented as a manifestation of empathy: contagious crying in newborns. A first hypothesis is that contagious crying express a genetically inherited disposition to feel what others are feeling – here: distress. Subcortical affective resonances are hypothesized to enable primary empathic processes in the human species (Panksepp & Panksepp, 2013). Other studies, however, take empathy to be a functionally complex type of behavior. In the case of empathy for pain, there is an overlap between the empathic network and that of pain experience; but two different neural pathways are involved for action prediction and mental state attribution (Lamm et al., 2011). In addition, emotion sharing is not automatic. Social context and perceived agency modulate the neural circuits of empathy for pain (Akitsuki & Decety, 2009). Although modulated by social perception and mindreading, affective resonance does not seem to *lead to* "mind perception" or mental state attribution. Affective signaling, then, does not seem to have the distal function of revealing mental states.

An alternative explanation of newborns' empathy, the *Learned matching theory*, explains the propagation of crying without appeal to grasping *others'* distress: babies merely learn to associate *crying sounds of whichever source* with their own interoceptive experience of distress (Heyes 2018, see also Hatfield et al., 1994). In support for this hypothesis, incongruent training in human adults where pleasurable feedback is associated to others' signs of distress, (for example) can suppress or enhance emotional contagion, and even produce alternative emotional responses in participants. On a learning view, then, alarm calls are efficient in guiding behavior not because they have an intrinsically alarming content, but because recipients have learned to associate this call with a predator's presence. Consistent with this view, is the finding that younger tree swallow nestlings seem to be less receptive to the emotional value of alarm calls than older ones (Lock & Hauber, 2012).

What, then, are the crucial mechanisms involved in emotional communication? The appraisal theory of empathy addresses this question.

2.3. Appraisal theory of empathy: situation affordances

The appraisal theory of empathy (ATE from now on) is crucial to assess the value of expressivism in communication because it attempts to analyse *vicarious emotions*, i.e. the process through which an observer feels an emotion for someone else (Wondra & Ellsworth, 2015). Perceived emotion, on this view, is mediated by an *appraisal of the situation* to which the target emotionally reacts. As a consequence of this appraisal, however, the observer may feel *a similar or a dissimilar* emotion. Translating this in our framework: ATE takes situation affordances to mediate both producers and recipients' emotional states. In contrast to expressivism, however, ATE does not entail that producers and recipients need to share their appraisals, and the associated emotions.

Equipped with the cumulated findings of Learned matching theory and ATE, let us come back to our initial question: are affective markers necessary to detect relevance, as claimed by Saussure & Wharton & (2020)? On an appraisal theorist's view, affective markers predict, or report, the affordance to be expected in a context. This is why they efficiently guide action here and now. If a speaker says "Yuck", the recipient understands that an object smells awful; if she says "ouch", that she felt pain : If she says "bloody prick", that she was deceived or exploited by someone else, etc. Why do affective words help identify the affordance being appraised? Because they are associated with it through prior learning, not because of their intrinsic capacity to convey disgust or pain. Associative learning is facilitated by the fact that appraisals express what is good or bad "for me" [the signaler, the speaker) in a situation that is easily observable by recipients who also have their own interests vested in it. As a consequence, appraising a situation involves as many predictive dimensions as there are opportunities and risks associated to it.

Our question was: are emotions necessary for accessing relevance ? The phenomenon of vicarious empathy suggests that they are not (Wondra & Ellsworth, 2015). Recipients of an emotional signal do not need to feel the emotion experienced by the producer. This is a common experience: a producer's nonconceptual emphasis on how she feels about a situation may fail to be attended by recipients who appraise the situation differently. Learned matching theory predicts when mismatching should occur. Animal signaling offers many examples of mismatching: only recipients sharing both a signaling system *and* fitness issues can react to signals as anticipated. In avians, nestlings exemplify the first case, predators the second.

In summary, granting that emotional contents in communication are pointers to background appraisals of a situation, they *can* contribute to relevance detection. However, they do not offer a necessary route for understanding an utterance, and still less offer a direct access to others' mental states. The same line of reasoning shows that they are not sufficient either: an isolated emotional cue – i.e. a signal not associated with a specific affordance by recipients – would fail to be relevance-conducive.

Another argument against the sufficiency of nonconceptual *emotional contents* in securing relevance is that the relevance trade-off can be settled on an entirely different basis, the dynamics of the vehicles engaged in content *processing* by metacognitive appraisals.

2.4. Metacognitive appraisals: Cognitive affordances and relevance.

In analogy with the quality and quantity procedural trade-offs examined in section II, the trade-off involved in informational relevance can be automatically settled by an integration of several comparators for ease processing, informational and instrumental effects, including urgency and importance (see section III.1). The output of comparators, as we saw, consists in affects with a specific valence and intensity. Feelings of fluency (ease of processing), of interest (expansion of neural activity), and of understanding (reaching a threshold for decision-making) are necessary conditions for a message to be received. This affective dimension of communication success, however, is not directly related to *situation affordances*. The feelings elicited in metacommunication only depend on the *processing vehicle*, i.e., on how the co-activated neuronal assemblies process the information. How is the informational noise reduced, how sequences are easily parsed, how quickly assemblies converge to a given solution? Recipients' feelings of understanding are conscious indicators that processing was performed above a nonconscious expected threshold, providing a relevance criterion. These indicators allow a recipient to stop processing a given message, which may happen even before the end of the message, if it is redundant.⁷

Metacommunicative affects, then, appraise the cognitive affordances to be relied upon in communication. Exactly as situation affordances are extracted and stored to predict fitness relevant properties of the environment, cognitive affordances are extracted and stored to appraise informational inputs and guide processing. Metacommunicative affects, on this

⁷ See Grisoni et al. (2017).

view, are necessary conditions for learning how to communicate and monitor communication episodes. Are they sufficient conditions? Our discussion of animal signaling in section II suggests that metacommunication presupposes that the basic signaling system has itself been shaped in the course of evolution so as to allow optimal communication. Just as the emergence of action control presupposes antecedent agentive patterns, communication control and monitoring presupposes a common sensitivity to auditory frequencies and sequences in a group of communicators. To this extent, *affective appraisal is not sufficient to detect* relevance. There must already be established regularities in communicative practices for comparators to step in.

One might object, however, that there is little chance, in the human case, that comparators converge in their appraisals, given their various learning histories, cognitive capacities and knowledge background. How, then, can producers and recipients procedurally converge in detecting relevance? A response to this question has been given by metacognitive studies, the "consensuality principle" (Koriat, 2008). In a number of first-order tasks, such as guessing the meaning of foreign words, general information questions or sentence memory, metacognitive appraisals (predicting one's likely correction in solving a task) are based on properties of the response that "make it compelling to the majority of participants". (Koriat, 2008, p.954). Whether right or wrong, intuitive, fluency-dependent responses are held more confidently. A striking character of consensuality, especially in the context of communication, however, is that people agree unknowingly with others about the most correct guess or response. Extrapolating this finding to communication, an intuitive preference for fluent processing is the plausible basis for the sense of a understanding in conversational exchanges. Granting that a preference for fluency prevails in a group, procedural relevance appraisals work well and are reinforced. When communicators differ significantly in their communicative goals and practices, however, for example when the pragmatic rules do not favor the same informational or social norms, however, procedural methods will not result in consensual outcomes.⁸ More effortful, theory-based reasoning, in such cases, is called for in order to detect the cultural source of the divergence and infer speakers' meaning.

⁸ For examples of a crosscultural divergence in conversational rules, see Le Guen (2018).

Concluding speculations

This article has concentrated on the continuity of procedural processing from non-human to human communication. Let us summarize the most significant metacognitive steps in this evolution. The first consists in the emergence of signal systems shaped to enhance learnability, discriminability, informativeness and pragmatic efficiency. A second step consists in the ability to deliberately control signaling events – *when* they should be produced or not, to *which targets*, and *how* (with which frequency, duration, details). At this time, recipients are sensitive not only to message contents, but also to how the message is delivered. 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 – allowed producers to learn how to signal, and recipients to attend to relevant sequences. A common preference for minimal effort was used to make informational content easily transmissible and quickly used. A third step in the evolution of communication occurred when metacognitive predictions allowed human communicators to expand adaptively their communication repertoire on the basis of a more powerful syntactic processing and open-ended referential semantics.

In the proposed framework, Gricean maxims of conversation are conceptual counterparts of general procedural constraints on metacommunication at work in species endowed with cognitive control. While Grice spelled out the higher-order inferences involved in selecting and interpreting message contents, our proposal is that verbal and non-verbal communication has been regulated on a leaner basis, through basic structural properties of signal processing exploited by predictive heuristics. The point of proceduralizing Gricean maxims is not to deny any role to mindreading in IC. It is to make the case that the ability to recognize one's own communicative intentions – by reading one's own (and the recipient's) mind – is a later acquisition, both in phylogeny and in ontogeny (Aguirre et al., 2022, Proust, 2012, Wu et al., 2013). A dual-processing view of communication follows from the recognition of the regulative structure of communication.

Granting the overall validity of this hypothesis, much remains to be done to substantiate it. An emphasis on continuity should not lead to ignore two notorious discontinuities in the evolution of communication. 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.), while preserving a role to emotional appraisal and “attached” representations in prosody and paralinguistic communication. 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). 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 relaxation of selection (a reduction of the signaling biases) caused by human "self-domestication" (Deacon, 2010). Just as the song of domestic Bengalese finches has progressively been controlled by new brain systems, and made it more flexible and varied, 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). 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 norms (Kissine, 2016, Proust, 2013, submitted). Whether correct or not, these fascinating speculations point to the need to theorize further about the variability of human culture as well as its cumulative character.

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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.

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.

Akitsuki, Y., & Decety, J. (2009). Social context and perceived agency affects empathy for pain: an event-related fMRI investigation. *Neuroimage*, 47(2), 722-734.

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., & Bar-On, D. (2020). Primate pragmatics, expressive behavior, and the evolution of language. *Animal Behavior and Cognition*, 7(2), 117-130.

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.

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.

Bavelas, J. B., & Chovil, N. (2000). Visible acts of meaning: An integrated message model of language in face-to-face dialogue. *Journal of Language and social Psychology*, 19(2), 163-194.

Beran, M. J., & Smith, J. D. (2011). Information seeking by rhesus monkeys (*Macaca mulatta*) and capuchin monkeys (*Cebus apella*). *Cognition*, 120(1), 90-105.

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.

Bshary, R. (2011). Machiavellian intelligence in fishes. In C. Brown, K. Laland, & J. Krause, (eds). *Fish cognition and behavior*, Wiley-Blackwell, Oxford, pp. 277-297.

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.

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.

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.

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.

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., & Zuberbühler, K. (2013). Primate precursors to human language: Beyond discontinuity. *The evolution of emotional communication: From sounds in nonhuman mammals to speech and music in man*, 26-48.

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.

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.

Gottlieb, J., Oudeyer, P. Y., Lopes, M., & Baranes, A. (2013). Information-seeking, curiosity, and attention: computational and neural mechanisms. *Trends in cognitive sciences*, 17(11), 585-593.

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

Grisoni, L., Miller, T. M., & Pulvermüller, F. (2017). Neural correlates of semantic prediction and resolution in sentence processing. *Journal of Neuroscience*, 37(18), 4848-4858.

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

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.

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.

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.*

Hailman, J. P., Ficken, M. S., & Ficken, R. W. (1987). Constraints on the structure of combinatorial "chick-a-dee" calls. *Ethology*, 75(1), 62-80.

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.

Hare, B., Call, J., & Tomasello, M. (2001). Do chimpanzees know what conspecifics know?. *Animal behaviour*, 61(1), 139-151.

Hatfield, E., Cacioppo, J. T., & Rapson, R. L. (1994). *Emotional contagion: Cambridge Studies in emotion and social interaction*. Cambridge, UK: Cambridge University Press.

Hauser, M. D. (1996). *The evolution of communication*. Cambridge, Mass: MIT press.

Hauser, M. D. (1997). Minding the behaviour of deception. *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. (2018). Empathy is not in our genes. *Neuroscience & Biobehavioral Reviews*, 95, 499-507.

Hipólito, I., Ramstead, M. J., Convertino, L., Bhat, A., Friston, K., & Parr, T. (2021). Markov blankets in the brain. *Neuroscience & Biobehavioral Reviews*, *125*, 88-97

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.

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

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. (2008). Subjective confidence in one's answers: the consensuality principle. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *34*(4), 945-959.

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.

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

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.

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.

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.

Lamm, C., Decety, J., & Singer, T. (2011). Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. *Neuroimage*, *54*(3), 2492-2502.

- Le Guen, O., (2018), Managing epistemicity among the Yucatek Mayas (Mexico), in J. Proust & M. Fortier (eds.), *Metacognitive Diversity, an Interdisciplinary approach*. Oxford: Oxford University Press.
- Lock, J., & Hauber, M. E. (2012). A predation risk-and-avoidance model of nestling responses to parental vocalizations. *Evolutionary Ecology Research*, 14(2), 235-245.
- Magrath, R. D., Haff, T. M., Horn, A. G., & Leonard, M. L. (2010). Calling in the face of danger: predation risk and acoustic communication by parent birds and their offspring. In *Advances in the Study of Behavior* (Vol. 41, pp. 187-253). Academic Press.
- 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.
- 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
- Mouterde, S.C. (2020) in N. Mathevon, & T.Aubin (eds.) (2020). *Coding strategies in vertebrate acoustic communication, Animal signals and communication*, 7, pp. 203-230 St. Andrews, Fife, UK, Springer.
- 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.
- Panksepp, J., & Panksepp, J. B. (2013). Toward a cross-species understanding of empathy. *Trends in neurosciences*, 36(8), 489-496.
- Patel, S., Scherer, K.R., Bjorkner, E., Sundberg, J., (2011). Mapping emotions into acoustic space: the role of voice production. *Biological Psychology*, 87, 93–98.
- 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.
- 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.
- Poirier, P., Faucher, L., & Bourdon, J. N. (2021). Cultural blankets: Epistemological pluralism in the evolutionary epistemology of mechanisms. *Journal for General Philosophy of Science*, 52(2), 335-350.
- Poole, J. H., Tyack, P. L., Stoeger-Horwath, A. S., & Watwood, S. (2005). Elephants are capable of vocal learning. *Nature*, 434(7032), 455-456.
- Potts, C. (2007) The expressive dimension , *Theoretical Linguistics*, 33, 2, 2007, pp. 165-198.

- 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. (2018). Consensus as an epistemic norm for group acceptance. in J. A. Carter, A. Clark, J. Kallestrup, S.O. Palermos, and D. Pritchard (eds.), *Socially Extended Epistemology*, Oxford: Oxford University Press, 132-154.
- Proust, J. (2019). From comparative studies to interdisciplinary research on metacognition. *Animal Behavior and Cognition*, 6(4), 309-328.
- Proust, J. (2021). *Penser vite ou penser bien?* Paris, O. Jacob.
- Proust, J. (2018).
- Proust, J. (in print), The cultural evolution of information seeking, *Journal of Cognition and Culture*.
- Ramstead, M. J., Friston, K. J., & Hipólito, I. (2020). Is the free-energy principle a formal theory of semantics? From variational density dynamics to neural and phenotypic representations. *Entropy*, 22(8), 889, 1-29.
- 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.
- 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.
- de Saussure, L., & Wharton, T. (2020). Relevance, effects and affect. *International Review of Pragmatics*, 12(2), 183-205.
- 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.
- 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). Signalers 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.
- 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.
- Sperber, D., & Wilson, D. (1986/1995). *Relevance: Communication and cognition* (Vol. 142). Cambridge, MA: Harvard University Press.
- Sterelny, K. (2014). A Paleolithic reciprocation crisis: symbols, signals, and norms. *Biological Theory*, 9(1), 65-77.
- Sterelny, K. (2016). Cumulative cultural evolution, K 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.
- 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.
- 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.
- Wharton, T., & Strey, C. (2019) Slave of the Passions: Making Emotions Relevant. In R. Carston, B. Clark & K. Scott (eds.), *Relevance, Pragmatics and Interpretation*, 253–266, Cambridge: Cambridge University Press.
- 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.

- 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.
- Wondra, J. D., & Ellsworth, P. C. (2015). An appraisal theory of empathy and other vicarious emotional experiences. *Psychological review*, *122*(3), 411-428.
- 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.