The Evolution of Primate Communication and Metacommunication

JOËLLE PROUST

Abstract: Against the prior view that primate communication is based only on signal decoding, comparative evidence suggests that primates are able, no less than humans, to intentionally perform or understand impulsive or habitual communicational actions with a structured evaluative nonconceptual content. These signals convey an affordance-sensing that immediately motivates conspecifics to act. Although humans have access to a strategic form of propositional communication adapted to teaching and persuasion, they share with nonhuman primates the capacity to communicate in impulsive or habitual ways. They are also similarly able to monitor fluency, informativeness and relevance of messages or signals through nonconceptual cues.

1. Introduction

How deep is the gulf between non-human signalling and human communication? In addressing this question, comparative psychologists and evolutionary theorists have relied on diverse, often incompatible views about the concept of communication.1 Some have taken animal signalling to be an evolved behaviour meant to manipulate the receivers' responses, eschewing the need of represented information as a mediator.2 On this view, signals are supposed to directly exert an influence on the receivers' neural system.3 Others take animal signalling to involve messages sent and reconstructed by receivers, either through coding-decoding mechanisms4 or through context-sensitive cognitive processes.5 Human communication, on the other hand, is claimed to be unique in its motivation for sharing information and cooperating. It makes no central use of fixed codes, but rather massively relies on

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Address for correspondence: Institut Jean-Nicod, Department of Cognitive Studies, Ecole Normale Supérieure, 29 Rue d’Ulm, 75005 Paris, France.

Email: joelle.proust@ehess.fr

1 Corballis, 2010; Fitch, 2010; Hauser, 1996; Hurford, 2007; Seyfarth and Cheney, 1997; Tomasello, 1999.
2 Dawkins and Krebs, 1978.
3 Rendall et al., 2009.
4 For a study of the waggle dance in bees, see von Frisch, 1967.
5 Seyfarth et al., 2010.
inferential capacities. This in turn is generally taken to require senders to make their intention to communicate manifest to their audience. Ostensive communication, on this view, involves two steps: 1) Letting the addressees understand that a current gesture or verbal utterance, is performed in order to communicate something to them. This first step allows the receivers 2) to interpret the message more or less as it was intended to be understood.

Granting this diversity of views, it is barely surprising that little consensus has yet prevailed about such central issues in the evolution of communication as the pervasiveness of the role of information, of shared representations, and of inferences in securing stability in the signal-response pairings. In philosophy, three strategies have been proposed to plug the gap between nonhuman and human forms of communication. A first strategy minimizes the role of inference in communication: communication in both non-humans and humans has the function of conveying meaning from a producer to a consumer (Millikan, 1998). This function is fulfilled in a direct, quasi-perceptual way, because producers and receivers have been attuned to use signs similarly. Even when communication is based on conventions, as in language, Millikan claims, these conventions can be applied without interpreting a sender’s mental states: natural conventions ‘do not require coordinations, regular conformity, or rational underpinnings’. They consist, rather, in patterns that can be reproduced, and that are reproduced because of the weight of precedent. On this view, then, every form of communication relies on coding/decoding processes. Pragmaticians and biologists, however, have offered at least three reasons for rejecting this line of argument. First, the function of communication evolved from more or less inflexible, recurrent signalling, to flexible communication. Hence, whereas coding-decoding processes merely involve associations between cues, extracting a message content across contexts of production requires complex inferential abilities. Second, such flexibility is rooted in a properly human function: to deliberately exchange information in the context of cooperative actions. A flexible, deliberate message, however, cannot be phylogenetically engineered, nor stabilized through ritualization. Metapsychological abilities must instead be present to establish whether coordination is appropriate. Third, new evolutionary pressures derive from the demands of flexible communication. An honest sender who says everything she knows, like a non-selectively trusting receiver, can easily be taken advantage of. These three characteristics explain why metapsychological competences have

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6 Sperber and Wilson, 1986/1995; Origgi and Sperber, 2000.
7 See also: Burge, 1993; Millikan, 1984, 2005; Recanati, 2002, 2004.
8 Millikan, 1998, p. 162.
9 A good example is offered by intention-movements in nonhumans: see Tinbergen, 1952; Tomasello, 2008.
10 Origgi and Sperber, 2000; Recanati, 2007; Tomasello, 2008.
11 Krebs and Dawkins, 1984.

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developed, in humans, to address the challenges that the new communicational capacities have generated. An alternative continuist strategy has emerged, however, attempting to attribute a more limited role to the inferences involved in human communication. François Recanati has argued that, in many cases, human communication does not need to be inferential (in the sense of deriving conclusions from premises), but rather relies on purely associative ‘primary’ pragmatic processes. Such primary inferences are on a continuum with the inferences subserving perception. Human communication could have initially been confined to processes extracting speaker’s meaning through primary pragmatic associations. Metapsychological abilities (such as attributing communicative and informative intentions) are only required in exceptional cases, such as communicative failure.

Another way of defending an evolutionary continuity in communication has consisted in extending a Gricean analysis of communicative acts to non-verbal, embodied conditions of satisfaction to which children and primates could be sensitive. An act of communication, according to Juan Gómez (1994), entails that a hearer should recognize that the speaker intends to communicate, and interpret on the basis of this recognition what it is that the speaker intends to communicate. Perceiving embodied counterparts of these embedded intentions, such as eye contact and gaze following, might be functionally equivalent to higher-order attributions of Gricean intentions. On this view, however, second-order metarepresentations may not be needed to make sense of what the producer means to say or to gesture.

A final reason for defending continuity in the evolution of communication is based on the recognition of a duality in human communication. Even though humans are able to communicate their propositional thoughts to others, they also have an alternative communication medium available, by expressing their emotions with respect to a given situation. This has led Dorit Bar-On (2013) to hypothesize that expressive behaviour is a significant stage in the emergence of linguistic communication, and that it plays an important role both in human and nonhuman communication.

Three basic ideas from these proposals might be freely combined in the following way. 1) Understanding an intention to communicate might consist merely in

12 These competences are involved in 1) inferring—as a receiver—the speakers’ intentions and in predicting—as a speaker—the receiver’s inferring abilities, 2) appreciating to what extent informational cooperation is beneficial or risky in a context, and hence, 3) exercising ‘epistemic vigilance’ to distinguish trustworthy, informed and benevolent informants from uninformed talkers or deliberate cheaters: Sperber and Wilson, 2002; Sperber et al., 2010.

13 See Recanati, 2002, 2004.

14 These ‘inferences in the broad sense’ are unconscious associations between nonconceptual (e.g. saturation of a schematic meaning) or conceptual representations (e.g. enrichment), but, in both cases, they fail to be truth-preserving relations among propositions.

15 Recanati, 2002, pp. 113ff., 2004; see also Pettit, 1987.

16 See also Moore, submitted.

17 Bar-On, 2004, 2013, sect. 4.4. See also Green, 2007.
anticipating an overt communicational action on the basis of nonconceptual cues. 2) Linguistic and non-linguistic forms of communication might both involve associative cues. 3) Emotions might have a crucial structuring role in the production and reception of shared meanings.

This general line of thinking, however sketchy, seems a promising way of characterizing a possible common basis of nonhuman and human primate communication. Several questions, however, are left unaddressed. 1) What is the basis of the functional equivalence between an embodied attention getter and an ostensive signal? 2) What kind of animal signals would count as intentional? 3) Granted that expressive behaviour constitutes a common form of communication across primates, what is its representational structure?

Three kinds of issues, then, will be addressed below. Investigating the existence and scope of intentional communication in non-humans will address the first two questions (Section 2). An analysis of the representational structure of animal signals will address question 3 (Section 3). Finally the contribution that inferences and associations should make in interpreting a call will be discussed (Section 4). Addressing these issues will provide a basis for assessing to which extent nonhuman and human communication share some of their basic processes.

2. Intentional Communication

In the first step of human ostensive communication, in its standard account, producers are supposed to let the addressees understand that a current gesture or verbal utterance is performed in order to communicate something to them. Does this step require that producers should form and express a prior intention to communicate? Do they need to consciously plan their message? A positive response to these questions encounters a major difficulty; it conflicts with a well-known trade-off that applies to action and decision-making, and hence, to communicational actions. The latter are subject to an economy principle, according to which any action must find the proper compromise, in a given context, between expected effort and predicted outcome. As shown in more detail in Proust, 2014, three stable trade-offs between time (i.e. effort) and stake (reward or risk) respectively govern three systems of intentional action. Applying this tripartition to communicational actions clarifies the analysis of intentionality in signal production:

1) In impulsive communication, producers express—rapidly and at a low cognitive cost—an affective attitude towards a situation requiring prompt action from receivers, with stakes varying from high to moderate. In nonhuman primates, alarm calls, in humans, facial and arm gestures, interjections, intonation, emotional words and expressive speech acts are serving this function.

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18 Chaiken et al., 1996; Proust, 2014.

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2) In *habitual* communication, such as affiliative displays, primate grooming, human politeness, a recurrent social situation prompts a reactive action. These communicational actions favour not so much rapidity as cognitive economy for low stake contexts. Accordingly, they do not rely on intense emotional reactions, but rather on innate or implicitly learned behavioural patterns. They have an emotional valence, however: having a directive component, habitual communication triggers in others expected reactions with the appropriate affective and motor dispositions.

3) In *strategic* communication, non-urgent, moderate to high stakes justify engaging effortful, cognitively demanding representations and inferences. Control is no longer reactive, but ‘proactive’, i.e. anticipatory. Belief-based inferences are used (by the producer) to predict the likely cognitive and socio-affective effects of the communicated act, and, (by the receiver) to reconstruct its motivations. This pro-active communicational dimension may have the function of securing adequate teaching, persuasion and collective planning in complex environments.

The upshot of our tripartition is that ostensive communication, being based on inferences, may suit the needs of strategic communication, without fitting those of impulsive and routine communication. A new research question, then, is that of how intentionality is conveyed in the latter two cases. Before raising it, however, we must ask whether impulsive and habitual communication are intentional.

It might indeed be objected that impulsive signalings are automatic reflexes. A reflex does not qualify as an action because it is irrepressible and non modifiable. For example, the acoustic startle response caused in an individual by an auditory stimulus greater than 80 decibels carries information about this individual’s being surprised, but does not have the function to indicate it. It thus fails to be a case of intentional communication. It has been hypothesized that alarm calls are of this kind. Drew Rendall and colleagues, for example, have claimed that ‘primate vocalizations should not be attributed world-like meanings. They are rather modulated primarily by involuntary processes involving subcortical brain structures such as the limbic system, midbrain and brainstem.’ Similarly, routine forms of communication may be seen as mere conditioned responses, unintentionally produced. It was noted, for example, that primate gestures are dyadic, and aim to

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19 Most routine communicational actions are generated, fully or partly by reinforcement, model-free conditioning.

20 Motivation in routine action is typically modular and short-sighted, in contrast with motivation in strategic action. See Niv et al., 2006.

21 In reactive control, agents respond to present imperative or recurrent events. In proactive control, agents prepare upcoming actions by planning them in more or less detail.

22 See Dretske, 1988.

23 For a discussion of the representational content of alarm calls, see Fitch, 2010, pp. 189–91.

24 Rendall, Owren and Ryan, 2009, p. 235.
attract the attention of others to the self, but rarely if ever to an outside entity.\textsuperscript{25} In addition, captive apes, when begging for food, seem to rely on crude indicators for visual attention in recipients.\textsuperscript{26}

Other theorists, however, pointed out that flexibility in message content or production was incompatible with a non-intentional view of primate auditory and gestural communication. First, Seyfarth, Cheney and Marler (1980) showed that vervet monkeys’ vocalisations are flexible, in the sense that they carry various predator-specific contents (eagles, leopards, and snakes), to which the receivers are able to react differentially. Such flexibility indicated that alarm calls can both be emotional and carry information that receivers are able to interpret. Second, there is flexibility in auditory signal production and reception: according to context, acoustically similar calls can elicit different responses, while acoustically different calls can elicit similar responses.\textsuperscript{27} Alarm calls can, furthermore, be suppressed in an adaptive way.\textsuperscript{28} Third, alarm calls turned out to be semantically structured. A semantic analysis of the alarm calls used by Campbell’s monkeys in the Tai forest and on Tiwai island suggests that the meaning of the roots differ in Tai and Tiwai, and that these roots can be combined and associated with an attenuating suffix.\textsuperscript{29} Fourth, callers have been shown to control their vocalisations as a function of the contextual risks.\textsuperscript{30} Finally, alarm calls can be accommodated to fit an intended audience. Male blue monkeys adjust their alarm calls to the distance of their females and offspring to a predator, regardless of their own.\textsuperscript{31} Apes are more likely to produce alarm signals for snakes in the presence of group members who are unaware of the danger than in the presence of aware group members.\textsuperscript{32}

These data suggest that our first two types of communicational actions, respectively instantiated in primate calls and gestures, are intentional to some degree. Impulsive alarm calls can be flexible enough to be called ‘intentional’, because they satisfy minimal constraints for flexibility in their semantic and pragmatic conditions of production. Communicational gestures involved in play, grooming, nursing, sexual and agonistic contexts, however, are comparatively more controlled and flexibly used than auditory signals.\textsuperscript{33} As was the case for calls, the same gesture can be

\textsuperscript{25} Pika \textit{et al.}, 2007; the authors note that infant chimpanzees’ gestures for begging food (palm-up gestures) are indeed triadic, because the thing to obtain is indicated in the gestures. Gómez (2007) however, suggests that only protodeclarative gestures are referential.

\textsuperscript{26} Povinelli and Giambrone, 2000.

\textsuperscript{27} Seyfarth \textit{et al.}, 2010.

\textsuperscript{28} See Seyfarth and Cheney, 2003, p. 41; Papworth \textit{et al.}, 2008.

\textsuperscript{29} Schlenker \textit{et al.}, 2014. See a further discussion of these data below in Section 4.2.

\textsuperscript{30} Auditory signals can be withheld or modulated in many species, including monkeys, ground squirrels and songbirds. See Seyfarth and Cheney, 2003, p. 41; Papworth \textit{et al.}, 2008; Papworth \textit{et al.}, 2013.

\textsuperscript{31} Papworth \textit{et al.}, 2008.

\textsuperscript{32} See the experiments by Crockford \textit{et al.}, 2012.

\textsuperscript{33} Tomasello and Zuberbühler, 2002.

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used for different ends, and different gestures for the same goal.34 In contrast with alarm calls, they might be individually learned through ontogenetic ritualization.35 Human-raised apes can learn human-like habitual gestures.36 When gesturing, apes monitor the attention of recipients.37 Contrary to earlier suppositions, chimpanzees are able to select vocal or manual begging gestures as a function of their human caretaker's attention (vocal requests are more frequent if the human is not looking).38 An auditory begging signal, then, belongs to habitual communication (in contrast with an anger shout, which is impulsive).

Granting that communication in nonhuman primates may be intentional, how do recipients recognize impulsive or habitual signals as signals? The first part of the response is simple: they do it because these signals form a typical, recurrent class of events. Given the fitness significance of calls and gestures for themselves, receivers learn to be sensitive and to respond adequately to them during their own development. In the case of impulsive signals, the recognition of their communicational content is tightly associated with their triggering congruent emotions in attuned receivers.

One could object at this point that primate communication might also instantiate a strategic form of control. On this view, producers would not merely react to a presently felt emergency or recurrent opportunity. They would be able, when stakes are sufficiently high, to set the stage for anticipated events. Observations of feral apes and monkeys suggest that primates have the capacity to collectively plan to raid cornfields at night. They can also plan their future tool use.39 Some signals, then, might be of a strategic variety. First, primates might use specific vocalizations to signal an upcoming coordinated activity. Chimpanzees’ travel hoo40 and gorillas’ grunts might both indicate their own readiness to depart and assess that readiness in others.41 Second, gestural attention-getters might express the producer’s intention to attract a receiver’s attention in a causal sequence leading to the intended interaction.42 In the interpretation proposed by Gómez (1994), eye contact and gaze following might work as an ostensive signal for an upcoming message production. Incipient actions used in greetings and grooming might also be seen as produced in

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34 Tomasello, 2008.
35 Tomasello, 2008. For a defense of the claim that apes’ gestural signals are rather based on a species-typical repertoire, see Genty et al., 2009.
36 Pika et al., 2007, p. 39.
37 Attention monitoring is an important primate skill, crucially involved in subordinates’ foraging decisions based on what the dominant chimpanzees can or cannot see: cf. Tomasello et al., 2003. For attention in the orangutans, see Call and Tomasello, 1994; for the gorillas, see Gómez, 2007.
38 Tomasello, 2008.
39 Osvath et al., 2008.
40 Gruber and Zuberbühler, 2013. See also: Boinski and Campbell, 1995; Stewart and Harcourt, 1994.
41 Stewart and Harcourt, 1994.
42 Pika et al., 2007, p. 42.
order to convey the agent’s desire to initiate upcoming bouts of social interaction. A stylized arm raise, for example, might mean an intention to start an upcoming play-hitting episode.

It can be objected, however, that these signals should be interpreted as part of an on-going action rather than of a planned event. The temporal continuity between the signal produced and the interaction that it motivates suggests that these calls and gestures respond to habitual rather than to strategic intentions. Furthermore, travelling together to new grounds, playing together, etc. are habitual affordances, which again suggests a more parsimonious, reactive type of communication.

The discussion above suggests that the mere opposition between (human) inference-based and (nonhuman) association-based communication is too simplistic. Impulsive communication plays an important role in human exchanges: it is instantiated in interjections, expressive speech acts, and in facial gestures. Habitual acts are exemplified, in humans, by conversational gestures, pointings, iconic or modelling gestures, and by verbal greetings. Human producers can perform several acts in parallel: for example intonation may add an emotional content to a strategic utterance, which can itself be clothed as a routine greeting.

Granting the descriptive adequacy of our hypothesis, our next task is to identify the representational structure that is engaged in each mode. It is often claimed that, to the extent that nonhumans can represent others’ motivations, they do so by means of unstructured representations, lacking compositionality and recursion. Our proposal consists rather in extending the scope of structured representations, by recognizing that lacking propositional compositionality and recursion does not amount to absence of structure. Our hypothesis is that reactings are evaluative representations, with a gradient-based associative structure motivating specific graded dispositions to act.

3. The Semantic Structure of Primate Communicational Signals

3.1 A Semantic Proposal

In a nutshell, our proposal is that impulsive and habitual signals have a common representational-evaluative structure, conveying to others what a situation affords, and thereby motivating an immediate response in attuned receivers. The mental

43 For a discussion of these two interpretations in the case of gestures, see Tomasello, 2008.
44 See for example La Fontaine’s fable The Crow and the Fox: ‘Mister Crow, good day to you. You are a handsome and good-looking bird! In truth, if your song is as beautiful as your plumage, you are the Phoenix of this forest’. A highly strategic message, disguised as habitual greeting and felt reactive emotion.
45 See, for example, Sperber, 2000, p. 118.
46 For a detailed analysis, see Proust, 2013, 2014, 2015. Similar views are defended in Allen, 2013; Cussins, 2012; Scarantino, 2013; and Seyfarth et al., 2010.
states mediating signal production and reception are affordance-sensings. Their general function—detecting and assessing opportunities—is exercised independently from communication.

‘Affordance’ here is freely borrowed from Gibson to refer to a perceived opportunity, represented as positive (something to approach or use) or as negative (something to avoid and flee from). Affordance-sensing is based on perceptual cues predicting benefits or risks. While organisms perceptually inspect their environment, they routinely attempt to predict what kind of positive or negative utility a given perceived situation involves. These can concern either fitness-relevant opportunities (for impulsive actions), or opportunities associated with social interactions or instrumental conveniences (for habitual actions). Being ex hypothesi, common to all individuals in a species, affordances provide an adequate representational structure for a signal to be fluently produced and understood as an action trigger.

Affordance-sensings are close to Ruth Millikan’s ‘pushmi-pullyu representations’ (‘PPRs’), advertised as ‘more primitive than either purely directive or purely descriptive representations’. On the present view, this dual role is captured by their evaluative function. Affordance-sensings indicate a graded intensity in arousal and in positive or negative utility (valence): this is their directive content. Arousal and valence markers are associated with a presently sensed affordance: this is their descriptive content. In contrast with PPRs, they have an indexical structure, to the extent that they describe an occurrent property in the presently perceived situation. What is indexed is an occurrent (relational) affordance, rather than an individual event or object. Given this contrast, signal indexicality does not instantiate reference as usually understood.

Additional arguments in favor of the existence, in humans, of a nonconceptual representational structure, working in parallel with propositional attitudes such as beliefs and desires, have been detailed elsewhere. In summary: impulsive affordance-sensings occur very early in the perceptual flow, long before a conceptual categorisation of the input has been performed. They are available to young children even before they can form beliefs about a situation, and have been claimed to form—under another label—the cognitive basis of early forms of communication in human ontogeny. Throughout life, they can influence

47 On non-Gibsonian usages of ‘affordance’ in philosophy, see Dreyfus and Kelly, 2007; Scarantino, 2003.
48 Millikan, 1995.
49 Millikan, however, did not try to characterize further the semantic content of PPRs, nor did she relate their dual role to their having a specific type of nonpropositional content. Gendler’s aliefs, defined as ‘innate or habitual propensities to respond to a stimulus that are associative, automatic and arational’ (2008) are close to our two varieties of affordance-sensings.
50 Section 3.2 below will develop this point.
51 See Proust, 2014, 2015. See also Dreyfus and Kelly, 2007; Griffiths and Scarantino, 2009; Zajonc, 1980.
52 Barrett and Bar, 2009.
53 Trevarthen and Aitken, 2001.
decisions in spite of an agent’s having contrary beliefs. They lack the generality and inferential promiscuity of conceptual thinking. Habits, once acquired, also tend to persist despite an agent’s awareness of diminishing returns. All reactivings are typically action-oriented and myopic about long-term consequences.

Our proposal, then, is that affordance-sensings with the following hypothetical structure are involved in producing and in understanding reactive communicational actions:

$$\text{Affordance}_a \{ \text{Place} = \text{here}, \ \text{Time} = \text{Now/soon}, \ \text{Valence}_a = + \text{or}--- \text{with gradient v}, \ \text{Intensity}_a \text{with gradient t} \} \ \text{[motivation to act with degree}_a \text{according to action program}_a \}.$$ 

The subscript ‘a’ is meant to indicate that all the elements having this subscript characterize the same perceived ‘affordancea’. An alarm call reflects the valence and intensity of the affordance. The orientation of the producer’s body and gaze determines the area where the affordance is located.

On the present view, evaluative cognition enables both impulsive and routine communication: non-conceptual needs and motivations are as swiftly accessed by receivers as they are sensed by producers. The specialized bodily markers involved in sensing an affordance are often amplified for communication purposes. They tend to pre-activate the bodily segments for the specific act that they motivate. Gestural signals transmit an opportunity for interaction, the intensity of a request related to it and of its valence through incipient action icons. Distinctive embodied cues make a gesture into a pleasurable invitation or into a threat. Alarm calls, in contrast, elicit behavioural dispositions from call types, call loudness and vocalization sequence in the absence of visual contact. In both impulsive and habitual cases, then, communication is neither general (it does not involve inferences from receivers), nor referential (properties, rather than objects are in focus).

### 3.2 Inferences or Pattern Completion?

We now are in a position to start addressing one of the questions raised at the end of Section 1. Are inferential capacities involved in interpreting alarm calls? Granting a sharp distinction between inferences and associations, they do not need to be. One or two cues are sufficient, through pattern completion, to retrieve an affordance, when it belongs to the receiver’s repertoire. Propositional inferences are not needed, then, to mediate expression and content. In some cases, however,

54 Gendler, 2008.
55 See Gendler, 2008; Proust, 2015; Griffiths and Scarantino, 2009
56 Griffiths and Scarantino, 2009; Pacherie, 2002; Proust, 2015.
57 See Arnold and Zuberbühler, 2006.
the purpose of communicating is to make a new (or a complementary) affordance salient in a recipient, rather than merely convey one’s own sensed affordance. Active touch, for example, may elicit in the recipient a being-groomed affordance, distinct from the producer’s own grooming disposition. Similarly, an angry call is not meant to produce anger in the recipient, but rather fright and submissive behaviour. In all these cases, there is a common although complementary affordance-script that can be read in a single signal.

A caveat: our proposal is not meant to describe a primitive state of cognitive systems. It does not claim, in particular, that evaluators are unable to form beliefs and inferences. Our claim is, rather, that evaluative processes do not need to draw on beliefs. Relying on an independent type of information, they can be exercised when agents have beliefs related to a target situation, or when they don’t.58

Our semantic proposal is compatible with Seyfarth and Cheney’s observation that, in monkeys and suricates, separate processes are used to produce and to understand an alarm call.59 Producers are calling because of an emotional reaction of fear to a current situation. But the function of the call is not merely that of venting an emotion. If a call merely propagated an emotion, receivers would not be able to react adaptively as they do.60 Granting that affordance-sensings have a dual pushmi-pullyu evaluative structure, there is no cut-off point allowing theorists to distinguish an informative from a directive signalling function.

This view is also compatible with the wide recognition of the role of non-inferential, associative processes in human cognition. Associative processes have been shown to promote model-free learning and guide decisions in a number of domains, such as reward probability, working memory, recognition, sense of agency, mirror neurons, imitation, causal reasoning, prediction error, and social behaviour.61

3.3 Pointing to Affordances

Affordance-sensings, being non-propositional attitudes, offer an alternative explanation of the contrast between imperative and declarative pointing in apes and humans. Wild apes do not seem able to point declaratively, as human children do.62 Informing others about what is the case is not something apes are motivated to do. Apes rather aim to have others do what they want.63 Some contrary observations have

58 For example, chess players may select a move through an affordance-based evaluation, in spite of having a number of beliefs about the present game configuration. See Proust, 2014, 2015.
59 Seyfarth and Cheney, 2003.
60 In particular Allen, 2013; Seyfarth et al., 2010. For a discussion of the continuum between emotional and referential calls, see Macedonia and Evans, 1993.
61 Behrens et al., 2008; Heyes, 2012; Penn and Povinelli, 2007; Shanks, 2010.
62 On this distinction, see Bates et al., 1975.
63 Leavens et al., 1996; Tomasello, 2008.
been reported, however, of apparently declarative pointing by Kanzi’s mother, a bonobo, and by Chantek, a language-trained orangutan.64 A wild bonobo has also been taken to point to a distant threatening object.65 Except for these exceptional and controversial cases, pointing by apes has been said to function like a referring expression, despite not being produced with a referential intention. The same kind of explanation has been used to characterize alarm calls elicited by a distinctive type of event and motivating a specific adaptive response.66 A signal $S$ functionally refers to an entity $O$ when it is regularly triggered by $O$ and has the function to evoke the appropriate responses associated with $O$. In contrast, a signal genuinely refers to $O$ if the representational subsystem involved in the communicational act has the function of representing $O$ on different occasions as one and the same individual entity, or as belonging to the same category of entities. Note, however, that genuine reference requires a propositional mode of representation, where objects are subsumed under concepts.67 Granting that functional reference does not qualify as genuine reference, what is its cognitive status? Our semantic proposal offers an answer: what an ape is pointing to is an affordance, rather than an object falling under a concept. This explains why captive apes do not generalize their understanding of human declarative pointing from a competitive to a cooperative context: in apes’ repertoire, there is no habitual disposition to share a foraging opportunity. Hence, no communication for a help-in-foraging-sensed affordance can be elicited.68

The ability to learn opportunity-based affordances also explains why feral apes do not point, while hand-reared apes do. As Leavens et al. (1996) have noted, wild apes, being free to move, do not need to attract others’ attention to obtain objects that would otherwise be unattainable.69 Captive apes, like human infants, in contrast, need help to reach an object of interest, when a barrier prevents them from obtaining it. In such contexts, they readily learn to point imperatively by mere reinforcement: it pays to point.70 Talking about ‘objects pointed at’, however, is semantically improper. On the present view, apes’ imperative pointings have the function of highlighting an opportunity, with its associated motivation to act, rather than highlighting an object subsumed under a concept.

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64 Leavens, 2004. A precondition for apes’ declarative pointing seems to be a close emotional bond between the animal and his/her human caregiver.
65 Véa and Sabater-Pi, 1998.
66 Macedonia and Evans, 1993.
67 For a classical defence of an alternative nonpropositional semantics, where properties, rather than objects are represented, see Strawson, 1959, and its discussion in Proust, 2013. See also Adrian Cussins’ nonreferentialist semantic proposal in Cussins, 2012.
68 See Tomasello et al., 2003; Herrmann and Tomasello, 2006. For a different view, according to which chimpanzees understand cooperative pointing, see Russell et al., 2011. In our present framework, apes might be trained to sense a cognitive affordance even in a cooperative context.
69 See also Leavens et al., 2005.
70 Hand-reared apes also easily pick from their caretakers the habit to point imperatively. See Tomasello, 2008, p. 34.
This hypothesis can be generalized to human infant pointing. Why is it that, in some ontogenetic contexts, infants fail to point? In their environment, imperative pointings are not produced because there is no salient opportunity for being helped. Similarly, why should triadic joint attention be interpreted as securing co-reference to one and the same object? Again, sensing an affordance does not entail that a child has formed a belief of a certain kind. On our proposal, triadic joint-attention should be seen as a form of shared affordance-sensing rather than of shared perceptual belief. In virtue of our trade-off, pointing is more likely to be part of an impulsive or habitual communicational act than of a strategic, belief-based, communicational act.

Recent evidence about children’s pointing can be more readily explained in these terms. Three motives have been found to elicit declarative pointings: a social motive of sharing with an adult one’s own interest for an object or an event, a desire to inform the addressee about something that the latter does not know, and a desire to know more about the target. Although this evidence is generally interpreted in referential terms, a non-referential interpretation makes more functional sense. The child first points to an event or a property in the environment because it is sensed as new and interesting (environmental affordance), which triggers a disposition to communicate about it. If it is not reinforced, the behaviour will tend to disappear. If it is encouraged by adults, new positive affordances can be sensed: an affordance for sharing congruent emotions with the adult (social affordance), an affordance for conveying new information to an addressee (communication affordance), and an affordance for receiving more information (epistemic affordance). These four affordances combine their respective valence gradients to elicit pointing gestures in a given context. If something is both attractive and familiar, both new and dull, or if no one is around, a child will not be motivated to point to it. On this view, sensing these affordances does not need to engage a metapsychological skill for metarepresenting others’ perceptions and beliefs. What we need to explore, however, is how informativeness can be sensed as an affordance in the communicational and in the epistemic senses.

4. Cognitive Affordance-Sensings and the Evolution of Metacommunication

A propensity to perform declarative pointing indicates that even young human communicators can appreciate the interest of a given percept and want to share their

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71 See Leavens, 2004.
72 Tomasello, 2008.
73 Liszkowski et al., 2008.
74 Kovács et al., 2014.
75 For a general defense of domain general, ‘submentalizing’ processes, see Heyes, 2014.

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appreciation with others. The social motivation for pointing is thus mediated by a metacommunicational ability that is worth exploring for its role in primate communication. Granting that a communication action may vary in importance and urgency (see Section 2), the way it is monitored should vary accordingly. On the present view, affordance-sensings can also be elicited in metacommunication. On the proposed hypothesis, informational properties with a positive or a negative valence, a given gradient, and an associated disposition to act (such as clarity/unclarity, novelty or familiarity) can be swiftly extracted and used to monitor communication, both in humans and non-humans.

4.1 Communication Monitoring: Strategic or Reactive?
Let us turn again to our economy principle for acting. Does it also apply to communication monitoring? Consider first the human case. Are the stakes high, with moderate or low time constraints? On a standard view, the motivation to accurately understand what is meant by a given utterance should mobilize the system of related beliefs. On the basis of metarepresentations of one’s own and others’ beliefs and desires, an interpretation of the producer’s communicational intention might be reliably reconstructed. The relevant interpretation would be computed as the optimal trade-off between the effort required by a given depth of processing and the cognitive effects that it produces. Such a view has been defended in great detail by Sperber and Wilson (1986/1995, 2002, 2012) as applying to all forms of human non verbal and verbal communication, including irony and metaphor.76 Crucially, the relevance trade-off is said to be computed by a dedicated metacommunication module, whose function is, for the producer, to select appropriate utterances and, for the receiver, to determine the proper inferential outputs.77 The rough convergence of producers and receivers, in this process, is secured by mental architecture. Starting with the logical form of a linguistic expression (which, ex hypothesi, is common to speakers and receivers), the same explicatures (i.e. the inferences inherent to the logical form) help derive the same sequence of implicatures (i.e. the inferences that are contextually inferred). As a consequence, assuming that producers and receivers have roughly the same background beliefs, the same point in the sequence should be reached as optimally fulfilling the trade-off.78 Arguably, the computations involved in the relevance trade-off are elusive and under-described. Moreover, the speed and efficiency are expected to result from a modular processing, but the underlying mechanisms remain largely mysterious.79

76 See also Sperber et al., 2010.
77 Sperber, 2001. Sperber and Wilson, 2002, pp. 11–12; 2012, p. 269.
78 Sperber and Wilson, 1987, p. 703; 1986/1995, p. 39.
79 See Apperly, 2011, p. 87, for a similar argument, applied to mindreading: ‘A “mindreading module” is not an explanation for speed and efficiency. Rather, it presupposes that the task of mindreading can be rendered in a way that makes it tractable to fast, efficient computation’.

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Are the stakes moderate or low, with high constraints on time or resources? By analogy with the selection of a given type of communication action, the metacommunication device should also rely on affordance sensings. This assumption, however, may prima facie look unlikely: higher-order properties of mental contents, such as ease of processing, informativeness, or relevance seem to require metarepresenting what one wants to say or what one understands. In response to this worry, let us observe that the function of affordance-sensings is not to describe states of affairs or states of mind, but rather, to evaluate opportunities for acting, including conversing. Mental states do not have to be metarepresented for monitoring a cognitive affordance such as the amount of effort involved in processing an utterance. Affordances for communicating are another type of affordance, not a higher-order kind of representation.

There are two convergent reasons for endorsing the existence of cognitive affordance-sensings. First, they account for the tractability of metacommunication. This tractability can be explained in terms of a dual mode of processing, shown to apply, among others, to subjective confidence in one’s own epistemic decisions. When the stakes involved in a cognitive task are low, and/or when cognitive resources are limited (divided attention) and/or under temporal pressure, people tend to rely on their metacognitive feelings, i.e. (in our terms), on cognitive affordance-sensings. For example, they can experience clarity of mind or confusion, have a feeling of effort while reading a text or hearing a speech, be uncertain that they can solve a problem, understand a narrative, etc. When stakes are high, and when time or cognitive resources are available, people tend to rely on explicit, rule-based judgments and stored beliefs to evaluate their confidence in a cognitive task. The competition between these two modes of processing, however, is modulated by an additional factor that often fails to be appreciated. Engagement in a cognitive task is able to elicit metacognitive evaluations that a mere conceptual representation of the task fails to elicit. For example, agents may reliably predict learning efficiency for specific word pairs only after they attempted to memorize them, not when merely watching other agents perform the task. This difference in outcome suggests that different processes are at work. When engaging in a task, associative cues from subpersonal heuristics are made available to predict outcome, and enable detection of cognitive affordances. Judging what might be the case if one engaged in a task, without actually engaging in it, however, fails to generate activity-dependent cues. Self- and others- attribution of capacity, in this case, taps into the agents’ higher-order beliefs and inferences, i.e.
on some form of mind-reading and conceptual self-prediction. Granting that dual processes offer different routes to self-prediction, they should also be in principle available to organize metacommunication. If communicational actions are either reactive or strategic, so could be their control and monitoring. Reactings, i.e. affordance-sensings, being activity-dependent, are obviously more adapted for on-line conversation monitoring than mindreading or a proposition-based metacommunication module. Strategic forms of communication control and monitoring might be selected in high-stakes written documents, such as scientific articles, legal agreements, etc.

Second, animal species unable to conceptually represent mental states as such are able to evaluate their own cognitive dispositions. Rhesus monkeys, when having to decide whether they want to perform cognitive tasks of varying difficulty (perceptual or memorial), opt out as a function of the gradient of difficulty of the proposed task.84 Their confidence in favor of a given decision is computed on the basis of two activity-dependent parameters of the corresponding neural activation: speed is an indicator of ease of processing; intensity of the accumulation of evidence is an indicator of informativeness.85 We have no way of ascertaining that monkeys have a subjective experience such as a feeling of confidence. But an inference to the best explanation is that they do rely on these feelings, which in humans, seem to play a mediating role between predictive cues and decisions.86

How then might a non-metarepresentational device be able to assess the reliability, clarity, correctness of a perception, a memory, or any other epistemic outcome? Although feeling-based cognitive monitoring does not depend on contents, it carries information about the operational status of these contents. This status does not tell the agent what the content consists in, still less provide a justification for its correction on incorrection. It only evaluates whether this operation is conducted in a way that predicts a correct outcome. This prediction is not made irrationally: it is based, and permanently updated, on past observed associations relative to this type of affordance-sensing.

If humans and non-humans share a nonconceptual, reactive sensitivity to the informational properties crucial for cognition, they should also be in a position to monitor ease of processing, informativeness, and relevance in communication. There is some experimental evidence supporting this hypothesis.

84 Animals can reliably assess their performance even when no trial-by-trial feedback is provided, i.e. independently of any reinforcement. Furthermore, they are able to transfer their evaluative ability to a new task—say, from memory to perception. For a review of the relevant studies, and of the controversies about methodological issues, see Beran et al., 2012; Hampton, 2009; and Kornell et al., 2007.

85 See Kiani and Shadlen, 2009. For more recent developments about the neuroscience of metacognition, see Fleming and Dolan, 2012. For the capacity of the brain to predict epistemic outcomes on the basis of patterns of dynamic activity, see Proust, 2013.

86 Koriat, 2000.
4.2 Evidence for Metacommunicational Reactive Devices

4.2.1 Fluency. Subjective ease of processing (or fluency) correlates with the comparatively shorter duration of the processing needed to complete a task.¹⁸⁷ Feelings of fluency are known to regulate infant and adult cognition. In the context of perceptual recognition, ease of processing triggers a feeling of familiarity. In a conversational context, fluency is the informational property underlying Grice’s maxim of manner: ‘be perspicuous’.¹⁸⁸ Felt fluency of a message, as suggested above, is influenced not directly, as Grice had taken for granted, by message content, but rather by message processing. Human adults present a high sensitivity to fluent communication: they are more inclined to accept statements whose fluency is enhanced by repetition, rhyming or more legible font.¹⁸⁹ When presented with written statements, such as ‘Osorno is in Chile’, adult participants take the statements with a higher visual fluency more likely to be true than the statements that are more difficult to read.¹⁹⁰ These participants, however, are unaware of the role that fluency has had in guiding their attributions of truth.¹⁹¹

Young children seem to be similarly sensitive to the auditory fluency of a verbal statement.¹⁹² Confronted with two informants’ incompatible messages of a different auditory fluency, four- and five-year-old children endorse more readily a fluent rather than a dysfluent statement. As predicted by our hypothesis, children’s sensitivity to fluency does not correlate with their performance in a false belief task. Feelings of fluency, then, are used reactively rather than strategically to control and monitor communication.

4.2.2 Informativeness and Relevance. What about sensitivity to informativeness in nonhumans and humans? Repetition of a message turns ease of processing into boredom. As Sperber and Wilson have emphasized,¹⁹³ an evaluation of relevance results from the trade-off between ease of processing and informativeness.¹⁹⁴ On the present view, however, relevance does not need to be computed on the basis of the logical form of the alternative interpretations (as described in Section 4.1). It is rather, a cognitive affordance, based on associative, low-level predictive cues guiding attentional processes. Infants sense gradients of informativeness when they adjust their looking times to familiar versus novel items.¹⁹⁵ So do infants when they point

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¹⁸⁷ For a review of the role of fluency in human metacognition, see Alter and Oppenheimer, 2009.
¹⁸⁸ Grice, 1969, p. 28.
¹⁸⁹ For rhyming: McGlone and Tofighbakhsh, 2000; for fluency in writing: Reber and Schwarz, 1999; for repetition: Schwarz, 2004.
¹⁹⁰ Reber and Schwarz, 1999.
¹⁹¹ For a discussion of the influence of a concept-based theory of the task on the interpretation of fluency, see Proust, 2015.
¹⁹² Bernard, Proust and Clement, 2014.
¹⁹³ See Sperber and Wilson, 1995.
¹⁹⁴ Grice’s maxim of relation, ‘Be relevant!’ meant something vaguer, like ‘stay on topic’.
¹⁹⁵ Roder et al., 2000.
In pointing, informativeness is bidirectional: Pointing to an event or a property is meant both to inform and to acquire affordance-related information. Preschoolers (aged 2 to 4) also have an epistemic motivation when they ask the same question until they get an explanation.

In both pointing and questioning, however, informativeness is only sensed in the course of a joint activity. This observation is coherent with the finding, discussed in Section 4.1, that engaging in a task offers access to associative cues that are not available to concept-based reasoning. One might conjecture, then, that nonhuman primates can also be nonconceptually sensitive to the informativeness of a call or gesture. The flexibility of alarm calls in apes and monkeys, examined in Section 2, suggests that they are able to monitor informativeness of signals, rather than being blindly influenced by them. Can primates also compute the relevant content of a call, when several interpretations are possible? A ground-breaking linguistic study of alarm calls in monkeys already mentioned in Section 2 suggests that they can. The alarm calls of Campbell’s monkeys from two African sites have been recorded. These sites (Tiwai and Tai) present different predation patterns: respectively only aerial, or both aerial and terrestrial. The monkeys’ innate alarm calls can be either general (signal for a predator) or specific (signal for an aerial predator). Which signals, then, are used in Tai for terrestrial predators? Evidence for call selection and reception is compatible with two interpretations. According to the first, a ‘Krak’ signal emitted in Tai differs in lexical meaning from a ‘Krak’ from Tiwai. Several semantic and pragmatic considerations, however, militate against this interpretation. According to the second, these roots have the same lexical meaning; but an optimization device allows more informative calls to suppress less informative calls in a context-sensitive way. For example, issuing a ‘Krak’ signal for general alert in Tai, where there are leopards, is strengthened into meaning [general alert and not aerial alert (expressed by ‘hok’) and not faint alert (expressed by ‘Krak-Oo’)]. In Tiwai, in contrast, only the unstrengthened meaning of ‘Krak’ as general alert is used. The flexible ability to compute the trade-off between informativeness, i.e. the cognitive value of the message, and ease of processing, i.e. the preference for minimizing cognitive resources, amounts to selecting the relevant meaning of a signal. This example illustrates that relevance can be computed by subpersonal mechanisms that track the ratio between informativeness and ease of processing.

96 From the age of 12 months, infants are claimed to be able to point to the location of an object that was displaced in the addressee’s absence: Tomasello et al., 2007, p. 714. Infants might rather point to a change in affordances. This interpretation also applies to evidence that chimpanzees can communicate about absent entities, see Lyn et al., 2013.

97 Frazier et al., 2009.

98 Akhtar et al., 1996; Moll and Tomasello, 2007.

99 See Schlenker et al., 2014, section 8.1.

100 Schlenker et al., 2014.

101 Subpersonal information from competing neural dynamics of the decision vehicles might, here also, allow the best prediction to emerge, and to guide decision. See Fleming and Dolan, 2012.
underlying scalar implicatures, i.e. those mechanisms in virtue of which, e.g., ‘some’ is understood to mean ‘not all’. Scalar implicatures, then, might be based not on explicit metapsychological inferences, but rather on a principle of competition for determining which signal in the repertoire best satisfies the trade-off between ease of processing and informativeness in a given context.

Another source of evidence about primates’ sensitivity to informativeness consists in rhesus monkeys’ ability to ask relevant questions in order to obtain memorial hints (against a payment) when needed in a memory task. Requesting hints is not merely an instrumental achievement. Such a request must be appropriate to the animals’ present memorial dispositions, and therefore must involve an evaluation of what they can or cannot remember.

In summary: if our proposal is on the right track, informativeness is a cognitive affordance that both task-trained primates and humans can evaluate. The corresponding affordance-sensings might thus serve metacommunication functions, such as selecting the relevant meaning of alarm calls or requesting hints.

Now an open question is whether informativeness and relevance are always sensed impulsively, by emotionally reacting to messages, or can also be sensed through learning—e.g. by calibrating cues correlated with communication contents. The examples of metacommunication given in this section seem compatible with both types of account.

A related question is whether, as speculated in Section 4.1, a single trade-off between time and effect should apply to communication and communication-monitoring (i.e. metacommunication). Should alarm calls, being impulsive, be monitored through feelings? Should gestural communication, being habitual, be monitored through opportunity cues? Although further investigation is needed, it does not seem to be the case. American Sign Language users occasionally have an impulsive tip of the finger experience just as oral communicators have a tip of the tongue experience. Apes might also use feelings to monitor their gestural communication, or conversely, might use opportunity cues to monitor their oral communication. In humans, the relevance of a given interpretation does not seem to be experienced differently in gestural behaviour and in oral utterances. Further experimental studies, however, are needed to adjudicate this issue.

A third unsolved issue has to do with the sharpness of the contrast proposed in Section 4.1 between reactive and strategic metacommunication. It was assumed that the speaker purposefully did not choose to use a more informative term on the same scale. For example, ‘some’ should be interpreted as ‘not all’.

102 A scalar implicature modulates the meaning of an utterance by allowing a hearer to suppose that the speaker purposefully did not choose to use a more informative term on the same scale. For example, ‘some’ should be interpreted as ‘not all’.

103 Schlenker et al., 2014, p. 4.

104 See Kornell et al., 2007: some metacognitive tasks require the monkeys to ‘request hints’, and to accept to pay a price in order to be reminded of an item in a sequence of icons previously presented, which they are expected to reproduce.

105 Emmorey et al., 2008.
above, following Sperber and Wilson, that the relevance trade-off might be based, at least occasionally, on propositional metarepresentations of the producer’s and the receiver’s beliefs and desires. It is unclear, however, that mental reasoning can be entirely performed in a propositional way. The contribution of noetic feelings might be required even within strategic metacommunication. It is plausible that, here too, the mental architecture for reasoning and communicating should take advantage of predictive evaluations from whichever source.

Finally, a fourth question to address in the future is whether nonhuman primates are able, as humans are, to ‘spontaneously’ convey their own cognitive affordances to conspecifics (i.e. discounting the experimental contexts where animals are trained to ask or to respond to questions). Humans have a rich repertoire of facial gestures and verbal utterances expressing the receivers’ own incomprehension, doubt, trust, relative to a given message, or the producer’s sense of offering important information, being unclear, boring etc.\textsuperscript{106} Many languages also syntactically require the speakers to specify whether they had direct or indirect access to the information they are reporting.\textsuperscript{107} Part of these human abilities are clearly derived from speech-related constraints. Still, it seems worth investigating whether primates learn to recognize unreliable messages or to identify untrustworthy signalers.

5. Conclusion

This article attempted to investigate continuities between nonhuman and human communication. Information and influence were claimed to have a combined role in primate communication. It was proposed that intentional actions, being subjected to temporal constraints, can also be initiated by nonpropositional evaluative attitudes, called ‘affordance sensings’, which can be impulsive (i.e. triggered by feelings), or habitual (i.e. triggered by innately detected or learned opportunities). Primate calls belong to impulsive communicational actions. Being impulsive does not rule out their intentional character: they can be suppressed and adjusted to circumstances. Primate communicative gestures belong to habitual communicational actions. These two reactive, non-reflexive types of communication are also present in humans.

On the proposed view, affordance-sensings can also be used in metacommunication. Cognitive affordance-sensings have a graded valence and intensity and associated dispositions to act, which explains how they can swiftly and reliably guide signal production and reception. It is plausible to speculate, then, that fluency, informativeness and relevance are used in guiding cognition, epistemic decision and communication across primate phylogeny. The extent and efficiency of such guidance, however, depend on socio-environmental constraints and species-specific

\textsuperscript{106} See Proust, 2013, ch. 13.
\textsuperscript{107} On the varieties of evidentials across languages, see Aikhenvald, 2004.
executive abilities. Cognitive affordance-sensings might belong to the ‘elements of
a language capacity’ present in monkeys and apes, hypothesized by some theorists as
having allowed protolanguage to develop in humans.\textsuperscript{108}

\textit{Institut Jean-Nicod}

\textit{Ecole Normale Supérieure, Paris}

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