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Expression unleashed: The evolutionary and cognitive foundations of human communication

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Abstract

Human expression is open-ended, versatile, and diverse, ranging from ordinary language use to painting, from exaggerated displays of affection to micro-movements that aid coordination. Here we present and defend the claim that this expressive diversity is united by an interrelated suite of cognitive capacities, the evolved functions of which are the expression and recognition of informative intentions. We describe how evolutionary dynamics normally leash communication to narrow domains of statistical mutual benefit, and how expression is unleashed in humans. The relevant cognitive capacities are cognitive adaptations to living in a partner choice social ecology; and they are, correspondingly, part of the ordinarily developing human cognitive phenotype, emerging early and reliably in ontogeny. In other words, we identify distinctive features of our species' social ecology to explain how and why humans, and only humans, evolved the cognitive capacities that, in turn, lead to massive diversity and open-endedness in means and modes of expression. Language use is but one of these modes of expression, albeit one of manifestly high importance. We make cross-species comparisons, describe how the relevant cognitive capacities can evolve in a gradual manner, and survey how unleashed expression facilitates not only language use, but also novel behaviour in many other domains too, focusing on the examples of joint action, teaching, punishment, and art, all of which are ubiquitous in human societies but relatively rare in other species. Much of this diversity derives from graded aspects of human expression, which can be used to satisfy informative intentions in creative and new ways. We aim to help reorient cognitive pragmatics, as a phenomenon that is not a supplement to linguistic communication and on the periphery of language science, but rather the foundation of the many of the most distinctive features of human behaviour, society, and culture.

1. Introduction

Why is human expression so rich and multifaceted? Living things communicate in a great variety of ways, from the quorum sensing of bacteria, to songbirds, to the gestural and vocal communication of primates, but humans are expressive in ways and to an extent that is clearly distinctive. There is language use of course, but also points, nods, winks, and other behaviours that although not linguistic are still conventionalised; and also many ad hoc, improvised behaviours, such as a small hand gesture used to visually park a topic of ongoing conversation, subtle body movements that connect dance partners, and the open-ended expressiveness of music, painting, and other art forms (Green, 2007). It is likely that humans are not naturally sensitive to many forms of interaction in nonhumans, and as such there is much still to discover from a comparative perspective; but at the same time, nonhuman expression is, on all available evidence, limited to finite domains. Bees, for instance, communicate about the location of flowers and the quantity of their nectar but, apparently, little or nothing else. The gestural communication of nonhuman great apes is more diverse and flexible than most other cases (Cartmill & Byrne, 2010; Fröhlich & Hobaiter, 2018; Graham, Hobaiter, Ounsley, Furuichi, & Byrne, 2018), but its scope is still clearly limited relative to humans.

In explaining the open-endedness of human communication, many researchers emphasise the combinatorial and generative quality of natural language: The fact that individual constituent parts can be recombined in many ways, making infinite use of finite means (e.g., Chomsky, 1965; Jackendoff, 1997). An emphasis on combinations and codes is, moreover, sometimes linked with particular assumptions about evolution: That as complex systems of words, rules, and combinations, natural languages are enrichments of the communication systems of other species (e.g., Leroux & Townsend, 2020; Nowak, Plotkin, & Jansen, 2000; Planer & Sterelny, 2021; Progovac, 2015). This picture is attractive because it describes

human and nonhuman communication systems in terms that appear continuous. However, as a broad explanation of human expression, this focus on the evolution of combinatorics faces a number of fundamental problems, of which we here highlight two. First, it says very little about quasi- and non-linguistic means of communication and expression. Second, the evolutionary story of complex combinations evolving from more simple ones does not address the "central problem" (Maynard Smith & Harper, 2003, p. v) for the evolution of communication, namely stability in the face of incentives to deceive. This is not an incidental critique. On the contrary, the problem of evolutionary stability is, we shall shortly argue, fundamental, because it holds expression on a leash, keeping it constrained to narrow domains of statistical mutual benefit (sect. 2). In consequence, explaining evolutionary stability and explaining expressive versatility are deeply interlinked problems. One cannot be resolved without the other.

We present and develop an alternative explanation of the zoological distinctiveness and open-ended richness of human expression, based not on combinatorics but on cognitive pragmatics. That is, we describe the evolution of distinctly human means of communication – sometimes called an "interactional engine" (Levinson, 2006, p. 39) – as the evolution of mechanisms of social cognition targeted at navigating distinctive features of the human social ecology; and we specify how these cognitive mechanisms in turn unleash expression. More specifically, we argue that expression can be unleashed in partner choice social ecologies where it is simultaneously adaptive (1) for interpretative inferences to be predicated on spontaneous prior assumptions that communicators are cooperative, and (2) for expressive behaviour to exploit this assumption. Natural languages, in all their combinatorial richness, are a means by which we *exploit* unleashed expression, rather than being the source of unleashed expression. If we are right about this, then our account provides an overtly adaptationist and cognitive answer to the "Why humans?" question about language origins, that is clearly different to prominent biolinguistic approaches (e.g., Berwick & Chomsky, 2016, 2017; Hauser et al., 2014).

These contributions substantially enrich previous insights that human communication is evolutionarily grounded in cooperative social ecologies, and that key cognitive processes involved in communication derive, evolutionarily, from *non*-communicative aspects of social cognition shared with other primates (e.g., Arbib, 2012; Dor, Knight, & Lewis, 2014; Frith & Frith, 2010; Fitch, Huber, & Bugnyar, 2010; Hrdy & Burkart, 2020; Hurford, 2007; Johansson, 2021; Levinson & Holler, 2014; Moore, 2017; Scott-Phillips, 2015; Seyfarth & Cheney, 2018; Sperber, 2000; Sterelny, 2012; Tomasello, 2008; Wheeler & Fischer, 2012; Zlatev, Żywiczyński, & Wacewicz, 2020). Going beyond this point of agreement, we provide an especially focused description of the relevant cognitive capacities, grounded in a precise theory of cognitive pragmatics. In other words, we "scratch beneath the surface" (Graham, Wilke, Lahiff, & Slocombe, 2020), to describe the computational tasks the interactional engine must perform. We also describe how these cognitive capacities are employed for use in a wide range of domains, extending far beyond how communication is ordinarily construed. In doing this we do not make recourse to notions such as "we-intentionality," which is, in our view, not a cognitive process but a behavioural phenomenon that is itself in need of explanation.

The structure of the paper is illustrated in Figure 1. As it suggests, we elaborate on the problem of leashed expression in the next section, and we explain how it is resolved (sect. 5) after we have provided a taxonomy of ways in which individuals can affect the minds of others (sect. 3), and make adaptive inferences based on others' behaviour (sect. 4).

2. Expression leashed

We use "expression" to describe any trait or behaviour whose function is to inform others. This characterisation is solely *functional* in nature, and not mechanistic.[1] In this way, it is sufficiently broad to be inclusive of whatever means this function might be achieved, including, for instance, emotional expression; but also sufficiently narrow so as not to include any and all cases of information flow, regardless of function. In this section we describe how expression in this functional sense is leashed rather than freely open-ended. In later sections we focus on one specific manifestation of expression, namely behaviours that result from informative intentions.[2]

Crucially, an organism's expressive range is limited by the fact that only a specific and finite range of stimuli will actually generate a psychological reaction in other organisms. After all, organisms attend only to a limited subset of other organisms' behaviour, and will take from this only a limited range of information. This makes expression about, for instance, future events, or the location of far away food sources, effectively impossible without mechanisms of interpretation that complement mechanisms of production. Consider bee dance: It would not – and could not – express the location of pollen if other bees had no mechanisms specifically dedicated exactly to interpreting dances as indicators of the location of pollen.

Communication is thus, in our terms, a subset of expression. Although expression is the production of stimuli the function of which is to generate a psychological reaction, communication involves the production of stimuli the function of which is to generate a reaction *by the particular means of* stimulating complementary mechanisms of interpretation (Scott-Phillips, Blythe, Gardner, & West, 2012). By "complementary," we mean that each mechanism can perform its function only under conditions when the other mechanism is in place. Bee dance, for instance, is communication because it generates a reaction by means of stimulating complementary mechanisms of interpretation; and those mechanisms of interpretation can only perform their function (to learn about pollen) if bee dance actually takes place. In contrast, frightening behaviour can be expressive but not communicative: It can generate a reaction, but not necessarily by stimulating *complementary* mechanisms of interpretation. The

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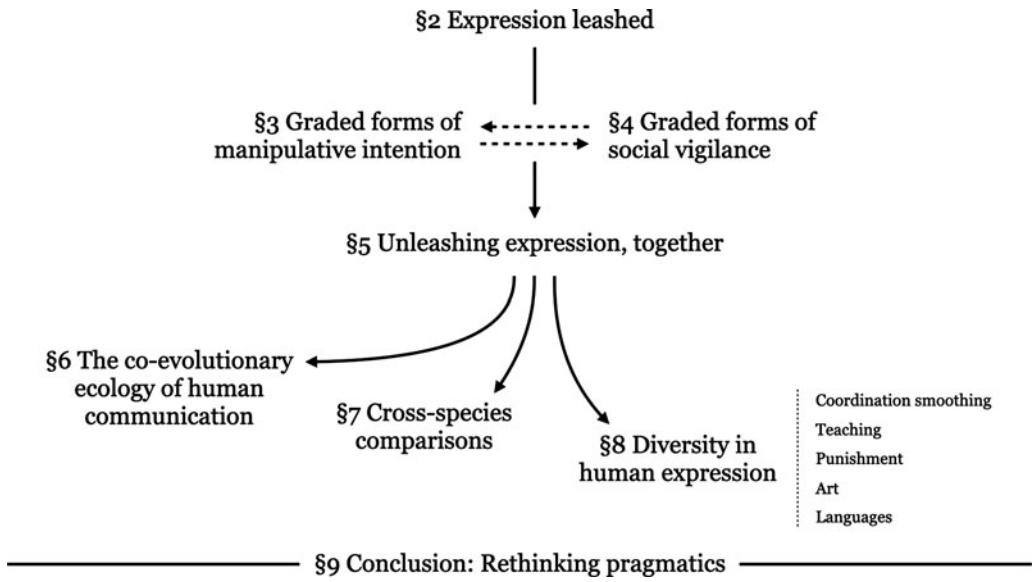

Figure 1. Structure of the article. We first elaborate on how the key problem of evolutionary stability leashes expression (sect. 2). We then describe a series of successively embedded, graded subsets of the different ways in which individuals might affect the minds of others (sect. 3), and make adaptive inferences based on the behaviour of others (sect. 4). We bring these two sides together by describing how the innermost subsets on each side of the equation combine to unleash expression (sect. 5). Three further sections elaborate and enrich this point in different ways. We identify the social ecology in which the relevant cognitive mechanisms are mutually supportive and can hence gradually co-evolve (sect. 6); we make relevant comparisons with other species, chimpanzees in particular (sect. 7); and we describe how the framework presented here unifies and provides new insights on otherwise diverse and disparate means of human expression (sect. 8). As the figure suggests, the arguments made in these later sections are mutually supportive but largely independent of one another. To conclude, we summarise how this evolutionary and cognitive perspective redefines the domain and goals of pragmatics as a scientific discipline (sect. 9).

great ape behaviours commonly known as "attention-getters" are another possible example: They appear to trigger a mixed set of mechanisms that may not be complementary in the relevant way (see, e.g., Tomasello & Call, 2019).

Correspondingly, we characterise communicative stimuli as those that generate a reaction by triggering complementary mechanisms of interpretation; and we characterise non-communicative stimuli as stimuli that generate a reaction by triggering other mechanisms, with different functions. Expression thus involves producing either communicative or non-communicative stimuli to change others' psychological states, while communication involves producing specifically communicative stimuli for the same function. As such, the evolutionary emergence of mechanisms of interpretation in audiences enriches expression because they complement mechanisms of production, producing communication systems as a result. (This is *not* the same as unleashing expression: see below.) This distinction between expression and communication is useful and important because it frames the important questions in the right way. First, it raises the question of whether or not an expressive function is met communicatively, that is, by means of triggering the audience's dedicated interpretative capacities. Second, it raises the questions of how and why expressive and interpretative capacities might co-evolve.

Crucially, however, the emergence of communication systems does not usually *unleash* expression, because communication systems are tied to domains of statistical mutual benefit (e.g., Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005; *inter alia*). This is because the interdependence of mechanisms of production and mechanisms of interpretation means that for communication to be stable, it must be beneficial, on average, to both communicator and audience. This does not imply that communication is always of mutual benefit, or that deception never occurs. However, it does imply that communication must be sufficiently beneficial, sufficiently often, for both parties, otherwise it would collapse. Explaining why this does not happen is *the* central theoretical issue in animal signalling theory (Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005). Answers to this question are usually developed in the context of evolution by natural selection, but pairs of mutually stable mechanisms of production and comprehension can also emerge across the lifespan, such as in the case of ontogenetic ritualisation (see, e.g., Halina, Rossano, & Tomasello, 2013, for description).

In some cases this mutual benefit derives from genetic relatedness, such as with ant pheromones or bee dance. In other cases it derives from direct fitness effects on communicator and audience. For instance, the pattern on the wings of many poisonous butterfly species communicates their non-palatability to potential predators, because this is beneficial to both the butterfly and the potential predator. The function of the pattern is to inform the potential predator, and the function of the predator's reaction is to avoid feeding on such butterflies. Clearly deception can occur: Other species of butterfly can be and have been selected to mimic the focal species, even if they (the other species) are not themselves poisonous. Missing out on the possibility of preying on the mimic species is an opportunity cost for the predator, but this is outweighed by the benefits of avoiding poisonous butterflies. If this were not so – if, in other words, the same pattern is used by so many actually palatable organisms that the predator's opportunity costs outweigh the risks of eating unpalatable prey – then the communication system would collapse. The predator will, under these circumstances, not evolve any mechanism for attending to the signal in the first place; or, if they already have such a mechanism, it will be selected against (Scott-Phillips et al., 2012). These and other dynamics, such as those associated with the differential costs of signalling (Lachmann, Szamado, & Bergstrom, 2001;

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Scott-Phillips, 2008), leash communication to relatively narrow domains of statistical mutual benefit.

Human communication appears to be in flagrant violation of this limitation. Its range is certainly not restricted to any particular topic: Humans can communicate about potentially anything. Moreover, we commonly and ordinarily take people at their word, even for statements that can have immediate and serious fitness consequences, such as, for instance, a doctor's medical diagnosis and prescriptions. Moreover, humans frequently communicate about phenomena for which no directly observable evidence could ever be provided, such as statements about past or future events. Given this vast expressive range, audiences should be massively vulnerable to misinformation and deception; and what should follow, on ordinary evolutionary logic, is the collapse of the communication system itself (see above). Yet this does not happen. Explaining why this is so is, we believe, not only necessary for explaining the evolution and the expressive richness of human communication, but also being fundamental.

Let us summarise. Expression can be enriched when supplemented with complementary mechanisms for interpretation, generating a communication system. This does not however *unleash* expression: This does not make expression open-ended. On the contrary, standard evolutionary considerations tell us that communication systems are still expressively limited because they are only evolutionarily stable when there is little gain (in the aggregate) to deception. Yet as a truly open-ended means of expression, human communication does not seem to be restricted in the same way. How is this paradox resolved? Why would it be adaptive for humans to have the sort of interpretative mechanisms they do, given the central evolutionary problem of stability? The assertion that human expressivity is enabled by combinatoriality offers no answer to this problem. We will provide an answer (sects. 3–7) by relating the evolution of human communication to the evolution of cognitive mechanisms that specifically function to allow humans to make the most informative use of social interaction. These mechanisms are, we shall argue, both a consequence and a cause of a partner choice social ecology.

The study of cognitive mechanisms for human expression is traditionally the domain of cognitive pragmatics: The study of the capacity of mind that facilitates human communicative competence. The relevant literature has its most important origins in the work of philosopher Paul Grice (1957, 1975, 1989). Grice was particularly concerned with meaning, and his key originality was to approach it as a primarily psychological phenomenon, and a linguistic phenomenon only derivatively. In particular he developed the idea that intentions might play a key role in determining meaning itself. This work provides the foundations on which a cognitive theory of communication and expression can be built, and since Grice an extensive literature has developed this approach in various ways, including from evolutionary and developmental perspectives (e.g., Bach & Harnish, 1979; Clark, 1996; Csibra & Gergely, 2009; Levinson, 2000; Moore, 2017; Scott-Phillips, 2015; Sperber & Wilson, 1986/1995; Tomasello, 2008; Wilson & Sperber, 2012; *inter alia*). Specific approaches differ from one another in some of the detail, but all agree that the expression, recognition, and epistemic evaluation of intentions together play a foundational role. In what follows we adopt and enrich the post-Gricean approach commonly known as relevance theory, which specifies key notions for communication ("communicative intention," "informative intention," "ostension" in computational terms (Carston, 2002; Clark, 2013; Padilla Cruz, 2016; Sperber & Wilson, 1986/1995; Wilson & Sperber, 2012; see also the *Relevance Theory Online Bibliographic Service*). Our analysis could potentially be adapted to fit with more classically Gricean or neo-Gricean approaches (for focused comparisons see, e.g., Carston, 2004; Sperber & Wilson, 2007).

3. Graded forms of manipulative intention

In a pair of seminal papers, Krebs and Dawkins characterised animal communication as an arms race between means of affecting the minds and behaviours of other organisms – labelled "manipulation" – and means of reacting in an adaptive way to the behaviour of others (Dawkins & Krebs, 1978; Krebs & Dawkins, 1984; see also Guilford & Dawkins, 1991). Manipulation is a broad term, to include, for instance, the handling of objects in a goal-directed way. Krebs and Dawkins's insight was to think of informing others as a means of "manipulating" their behaviour.[3] In this section we relate this teleological characterisation to the specific, cognitive mechanisms by which it is achieved in humans. In the next section we do the same for the audience side.

The specific mechanisms by which communication is achieved in the natural world are many and varied. They might be, for instance, physiological, as in the case of, say, butterfly wing patterns; or chemical, as in the case of, say, quorum sensing (Diggle, Gardner, West, & Griffin, 2007). Our focus is on cognitive means, and more specifically the expression and recognition of intentions. Specifically, we shall focus on informative and communicative intentions, which are proximate, cognitive processes for the functional tasks of expressing and communicating, respectively. We distinguish three embedded categories of manipulative intention, elaborating on each with examples (Fig. 2). Each of the following subsections begins with a concise statement of each category, followed by examples and elaboration.

3.1. Intentional action on others

The broadest set are behaviours that are intentional and manipulative. For instance, experimental studies show how orangutan mothers will, if necessary, use their offspring as physical tools (Völter, Rossano, & Call, 2015). Because of their small size, infants can reach food in locations that mothers cannot reach, so mothers can (and do) use them to reach the food, with the mother then consuming the food herself.

3.2. Action based on informative intention

In the second set are behaviours that intentionally change mental states, and which can do so without overtly bringing attention to the intention itself. We call the underlying intentions "informative intentions."[4] For instance, an individual might dress in a smart and conservative way, as a means to suggest to others competence and professionalism, yet without bringing excessive attention to oneself. Conspicuous consumption is intended to provide evidence of wealth and other markers of status, but without necessarily advertising this intent in a formally overt way. In the presence of others we might adopt a bodily posture that suggests, say, social ease and competence, and while this can be done in an overt or otherwise exaggerated way, it need not be. More generally, impression management – individuals presenting themselves in ways intended, subconsciously or otherwise, to generate and maintain a positive image in the eyes of others, but without

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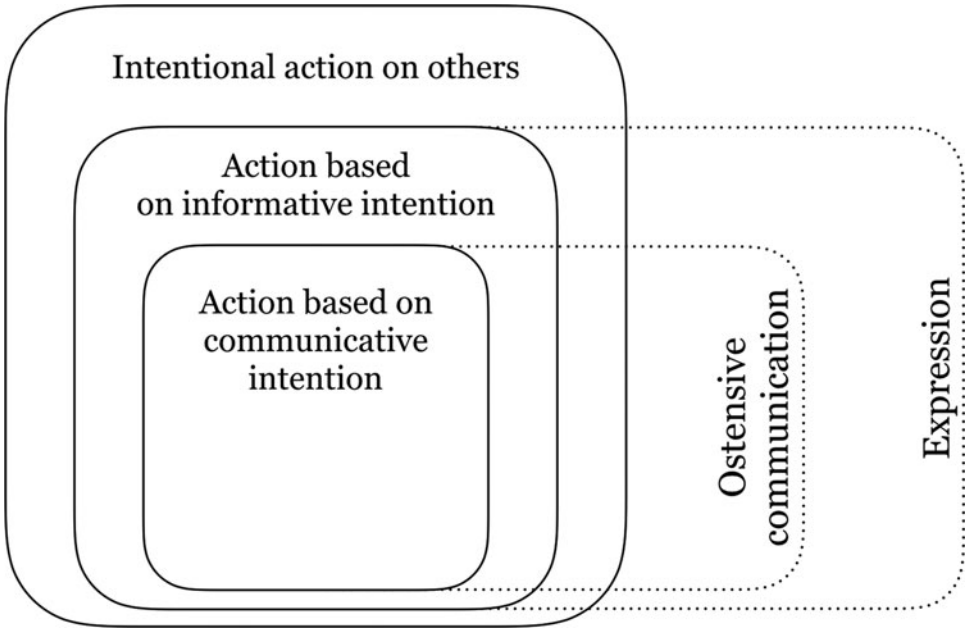

Figure 2. Embedded subsets of manipulative intention. Aligning with our functional characterisation of expression (sect. 2), here we differentiate expression as action based on informative intention, from ostensive communication, which is action based on communicative intentions.

overtly bringing attention to this informative intent – is a common feature of human social life.[5]

Such behaviour can generate a degree of shared knowledge about the actor's informative intent. In other words, it may be salient that the actor has and is acting on an informative intention. That said, this need not necessarily be the case. In fact in some cases the actor might have informative intentions but also have strategic motives to actively keep those intentions hidden or at least deniable (called "hidden authorship"; see, e.g., Grosse, Scott-Phillips, & Tomasello, 2013). A criminal who plants misleading cues in a crime scene has an informative intention and is acting on it, but simultaneously hiding that intention. A dinner guest who wishes to have more wine but, recognising it would be impolite to ask, might wait until her hosts' attention is elsewhere and then move her empty glass to a conspicuous location where it will, in due course, be noticed. Many public acts of generosity fall within this category also: Generous individuals want to be seen as generous, so they gain a positive social reputation, but often they do not want their acts of generosity to be seen as simply attempts to gain a positive social reputation, because that would immediately undermine their purpose (Berman, Levine, Barasch, & Small, 2015; Frank, 1988; Hoffman, Yoeli, & Nowak, 2015; Karabegovic & Heintz, under review; see also sect. 8.3 on punishment).

In all these cases, agents satisfy their informative intentions simply by means of providing non-communicative, or "direct," evidence for what they want to convey.[6] If, for instance, Amy puts three apples on the table with the intention of informing Barry that there are three apples, she is providing non-communicative evidence for the presence of the three apples. She can, moreover, do this without any indication that she actually has an informative intention: She can just place the apples on the table, without drawing any particular attention to the fact that she is doing this. Looking comparatively, we take it as highly plausible that nonhuman primates, and possibly some other species, have informative intentions, and satisfy them by providing non-communicative evidence (see, e.g., Genty & Zuberbühler, 2014, for a plausible example; Zuberbühler, 2018, for a review; and Warren & Call, in revision, for discussion). The key comparative questions are, in our view, whether any nonhuman species act in the ways described in the next subsection, where we consider cases where the communicator provides evidence for the informative intention itself (see Moore, 2016, 2017, 2018, for a different approach to the same issues). Such cases are sometimes called *overtly intentional*, because they involve making intentions overt; or more simply, *ostensive*.[7]

3.3. Action based on communicative intention

In this third set are behaviours performed not only with an intention to inform an audience, as above, but, more than this, to make the actor's informative intention mutually known. This is achieved, as we said above, by communicators providing non-communicative evidence for their informative intention itself.

To see the difference between this set and the one above, consider two possible ways in which Mary might satisfy her intent that Peter be informed that some berries are edible (see also Scott-Phillips, 2015; Sperber, 2000; Wharton, 2006). One way Mary might do this is to simply eat the berries in Peter's company (without Mary bringing any particular attention to the fact that she is doing this). In this case Mary has an informative intention which she acts on by providing some evidence that the berries are edible, but without giving any overt evidence that she is acting on an informative intention. As such she relies on Peter simply attending to her behaviour and drawing the inference that the berries are edible. In this case, Mary's behaviour belongs to the second embedded subset (sect. 3.2). There is however an alternative. Mary might not eat the berries at all, but instead mime eating them, perhaps with exaggerated movements and while tapping her tummy. Here she has the same informative intention, but provides evidence only about the intention itself. She does not eat the berries, after all. She provides only communicative evidence of their edibility.

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The most salient and important special case of overtly intentional behaviour is, of course, the use of conventional symbols, especially, but not only, in the context of language use (sect. 8.5). Grice's work on meaning was focused on these cases, and his crucial insight was that the sort of actions we are describing in this section – providing evidence about informative intentions – is what generates meaning. As he put it, "'*A* meant something by *x*' is (roughly) equivalent to '*A* intended the utterance of *x* to produce some effect in an audience *by means of* the recognition of this intention'" (1957, p. 385, italics added; the intention referred to here is best understood, in our analysis, as an informative intention).

That said, overtly intentional behaviour is also viable in cases where no conventions are used to communicate. After all, almost any behaviour that humans can perform, they can perform in an overtly intentional way. Sometimes we eat food, and sometimes we eat food in an overt, exaggerated, or otherwise ostensive way, to express to others that the food is tasty, revolting, generous, or fancy. Sometimes we blink, and sometimes we blink with microscopic exaggeration, such as with a slight delay in re-opening the eyes, to express, say, ironic surprise. Such deviations from otherwise non-communicative behaviour have been experimentally isolated in a number of studies, in both production and comprehension (e.g., McEllin, Sebanz, & Knoblich, 2018a; Newman-Norlund et al., 2009; Royka, Aboody, & Jara-Ettinger, 2018; Scott-Phillips, Kirby, & Ritchie, 2009; Vesper, Morisseau, Knoblich, & Sperber, 2021). Again, like language use, such behaviour is Gricean. It provides evidence about informative intentions.

We have so far presented the distinction between the three subsets in this section as categorical, but they are in fact graded and continuous (Sperber, 2019). That is, different means of manipulation can, we suggest, vary in the extent to which the actor makes her informative intention manifest. Grice's characterisation of meaning, quoted above, describes one end of this continuum; the cases described in section 3.1 represent the other end; and in between are many cases where communicators make informative intentions partially manifest. We shall return to this graded quality in section 8, where we shall suggest that it helps to generate the massive diversity of human expression. (For related but different continua see Duranti, 2015, p. 290; Sperber & Wilson, 2015; Wharton, 2009.)

In any case, informing others via the expression of informative intentions – commonly called "communicating" – has a distinctive property that is not present in the other subsets described above. Crucially, the communicator is now freed from the constraint of providing non-communicative evidence (see also sect. 5). Returning to the example above, Mary makes eye contact with Peter and mimes eating berries in an exaggerated way, with the informative intent that Peter believes the berries are edible, and in doing so she provides only communicative – and hence indirect – evidence that the berries are edible. So communication provides Mary with a second inferential route to the same conclusion. Mary intends Peter to believe that the berries are edible, and she can do this either directly, just by eating the berries, or indirectly, by making manifest her intention.

However, for this potential freedom of expression to be realised two related issues must be addressed. First, freedom from the constraint of having to provide non-communicative ("direct") evidence depends on audiences' complementary abilities to infer informative intentions, more-or-less accurately, on the basis just of whatever other, communicative evidence communicators are able to provide (see sect. 2 on the importance of complementary mechanisms). Second, expressive freedom also provides communicators with the opportunity to deceive, leaving the system clearly prone to evolutionary instability (sect. 2). To discuss how these issues are resolved, we turn now to the audience side.

4. Graded forms of social vigilance

All animal species have evolved adaptive reactions to the presence and behaviour of others. As with manipulation (sect. 3), we define these adaptive reactions functionally, recognising that the specific mechanisms can be many and varied.[8] For example, a chameleon's adaptive reaction to the presence of potential predators is (we assume) largely physiological. We focus here on cognitive means of adaptive reaction targeted at the behaviour of conspecifics. We call these cognitive means "social vigilance" (Heintz, Karabegovic, & Molnar, 2016). Again we distinguish three graded and embedded subsets (Fig. 3), and we describe their relationship to the various categories of intentional manipulation described in the previous section.

4.1. Inferences about others' intentions

The first embedded subset includes inferences based on the capacity to anticipate and respond adaptively to the intentional action of others. Humans do this routinely, of course. Others' intentions are relevant to us, such as when we decide whether to avoid or engage with them as friends, rivals, or indeed any social relationship. The capacity to behave in ways that take account of other individuals' intentions has also been experimentally documented in many studies with nonhuman great apes (Andrews, 2017; Bettle & Rosati, 2021; Call & Tomasello, 2008; Emery & Clayton, 2009). In one such experiment, chimpanzees are given the opportunity to take a piece of food from a bucket, the location of which is either known or not known by a dominant

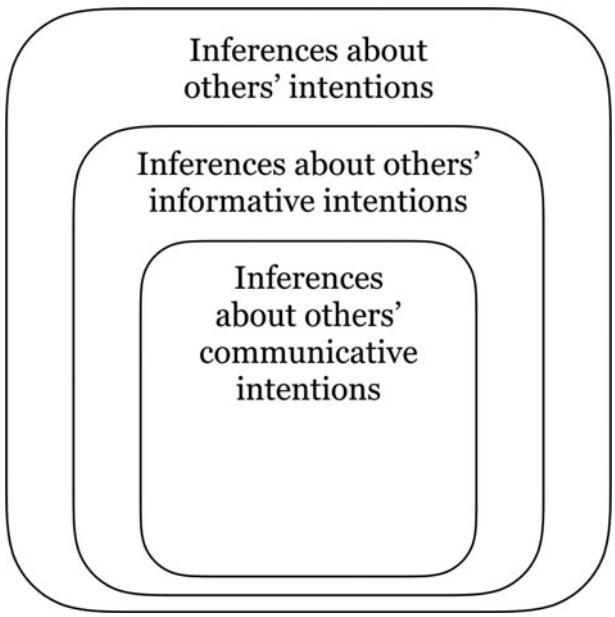

Figure 3. Embedded subsets of social vigilance. Importantly, the inferences contained in the innermost subset include interpretative inferences derived on the basis of a presumption of relevance, and also inferences about the epistemic value of what is communicated (i.e., inferences derived on the basis of epistemic vigilance; see sect. 5).

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conspecific. The key finding is that the subordinate chimpanzee is more likely to take the food if the location is unknown to the dominant (Hare, Call, Agnetta, & Tomasello, 2000). The details of exactly which intentions and other mental states great apes attribute to others remain a topic of active study; but in any case many experiments show that chimpanzees are able, in some contexts at least, to adaptively modulate their behaviour in view of what the conspecific is most likely to do, and what effects this might have on the focal individual. Similar modulations have been documented in many non-primate species. Grey squirrels, for instance, have been shown to modulate their caching behaviour as a function of the presence of onlookers, for example, moving a cache when the onlooker leaves (Leaver, Hopewell, Caldwell, & Mallarky, 2007); and ravens have been shown to guard their caches against discovery, taking into account other ravens' possible knowledge of the cache (Bugnyar, Reber, & Buckner, 2016).[9]

4.2. Inferences about others' informative intentions

In the second embedded subset are inferences about others' informative intentions. The possibility of such inferences, and their nature, depends to a significant extent on whether the informative intentions in question have been made overt (sect. 3.3) or not (sect. 3.2) by the actor, or communicator.

If an informative intention is not overt and audiences do not recognise it, then what is perceived is simply instrumental action, which like any behaviour might or might not be relevant to the observer. If, alternatively, an informative intention is not overt but is recognised nevertheless, audiences might take account of this absence of overtness, and the possible reasons for it, in their interpretation. Suppose, for instance, Claire leaves Dwight's keys on the table, with the informative intention that by virtue of seeing them Dwight does not forget the keys when he goes to work. Dwight might simply see the keys and thus remember to take them, not ever recognising Claire's informative intention, which was after all not overt. Alternatively, Dwight might recognise that Claire had an informative intention even though she did not make this overt, and he might hence infer that she thinks he is absentminded but she does not want to embarrass him by saying so explicitly. In any case, humans commonly act with informative intentions that they do not make overt, but which are sometimes recognised nevertheless. Section 8.1 on coordination smoothers and section 8.3 on expressive punishment discuss some specific examples.

Actors attempting to make an informative intention overt have a communicative intention (by definition: see sect. 3.3). If the informative intention is nevertheless not recognised, such as when, for instance, a raised hand, intended as a request to ask a question, is interpreted as a mere stretch of the arm, then that is a simple failure of communication. If, in contrast, an overt informative intention is recognised as being overt, such as when a raised hand intended as a request to ask a question is indeed recognised as a request to ask a question – if, in other words, the audience recognises that the actor has not only an informative intention, but also a communicative intention – then the audience is warranted in making an inferentially powerful presumption about the behaviour. Specifically, the audience is warranted in presuming that the behaviour is the most effective one the communicator could produce, given the communicators' goals, abilities, and the constraints acting on them. This insight is central to relevance theory (Sperber & Wilson, 1986/1995, 2002, 2007), where it is called the *communicative principle of relevance*. In the next section we describe in more detail the nature of the inferential process that is triggered, in audiences, by this recognition of communicative intent.

4.3. Inferences about others' communicative intentions

In section 3.3 we described how communicators sometime express their informative intentions overtly, with the goal to make their informative intention mutually known. Here we discuss how such stimuli are interpreted.

Language use is a paradigmatic example, and one of Grice's pioneering insights was that the interpretation of utterances is guided by prior expectations about the cooperative intent of communicators (mirroring his characterisation of linguistic meaning: see sect. 3.3).[10] Further developments in cognitive pragmatics have specified and debated the nature of these expectations in more detail. Relevance theory, for instance, describes these expectations in terms of a single assumption, that ostensively presented stimuli are optimally relevant for the intended audience, given the speakers' goals, abilities, and the constraints acting on them. Or, in other words, audiences have a strong positive prior expectation that overtly intentional behaviour is cooperative; and this prior expectation of cooperativeness in turn licenses a presumption that informative intentions are worth paying attention to, that is, are optimally relevant. Here and elsewhere, "optimally relevant" means, more precisely, that communicators strive to optimise the trade-off between cognitive effects and processing effort, subject to goals, abilities, and constraints.

Here is an example. Amy and Barry are drinking in a bar. Amy's glass, which is visible to both her and Barry, is empty. This fact is on its own unremarkable. Suppose now that Amy picks up the glass and gently waves it in front of Barry. Why would she do this? What could it possibly "mean," and how could Barry know? The relevance theory answer is that Amy's behaviour triggers in Barry a spontaneous process of interpretation, governed by a cooperative assumption that Amy's behaviour is the most optimally relevant behaviour she could perform given her goals and the circumstances. The key point here, which features in some form in all Gricean approaches, is that only with this cooperative assumption can Barry converge on the conclusion that Amy's behaviour is a suggestion that they stay for another drink. Otherwise, without this assumption, Amy's behaviour is simply mysterious. Many experimental studies have shown how prospective audiences interpret communicative behaviours under presumptions of optimal relevance (e.g., Gibbs & Bryant, 2008; van der Henst, Carles, & Sperber, 2002; *inter alia*).

This is very similar to how other specialised cognitive mechanisms "embody" knowledge about the nature of objects, magnitudes, species, and other basic, fundamental features of the human evolutionary ecology (Carey, 2009; Spelke & Kinzler, 2007). In all these cases, items perceived as being of a particular type (an object, a magnitude, etc.) trigger specific assumptions about the nature of that item. For example, items perceived as physical objects trigger assumptions that the item is physically cohesive, bonded, rigid, and cannot be acted on at a distance (Spelke, 1990). In the present case, behaviour perceived as ostensive triggers an assumption that the behaviour is optimally relevant for the audience, given the communicator's goals, abilities, affordances, and constraints. This allows a specialised, "satisficing" process of interpretation to then derive the communicator's intended meaning (Sperber & Wilson, 2002; see also, e.g., Ferreira

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& Patson, 2007, on "good enough" approaches to linguistic comprehension). This process is, moreover, spontaneous and largely unconscious, meaning that we cannot "choose" not to perform it even if we wish to. As a revealing example, consider film spoilers: Our desire to not recover the meaning of what is said does not and cannot suspend the interpretive process. Again, this is akin to the recognition of objects, magnitudes, and so on, all of which we recognise and process in spontaneous and unconscious ways. We cannot "un-see" objects, and we cannot "un-understand" what others say. All in all, spontaneous interpretation of ostensive stimuli is a functionally specialised form of social vigilance, targeted at the specific phenomenon of others' ostensive behaviour. It is, moreover, a foundational aspect of human interaction: Without it, we simply would not be able to understand each other in communication.

As with the other side of the equation (sect. 3), we have so far presented the distinction between the subsets in this section as categorical, but they are in fact graded and continuous. Specifically, there is on the audience side variation in the extent to which recognition of the actor's informative intention contributes to correct interpretation, that is, to satisfying the informative intention. Again, we shall return to these graded aspects in section 8.

5. Unleashing expression, together

We can now summarise how a system of communication predicated on the expression and recognition of informative intentions can unleash expression.

Crucially, the metarepresentational structure of ostensive communication generates a "virtual" domain generality (see also Mercier & Sperber, 2009, on virtual domain generality in cognition more broadly).[11] Communicators provide evidence of their informative intentions, which can in turn be about anything at all. Consider again the example of Mary, who makes eye contact with Peter and mimes eating berries in an exaggerated way. By doing so, she provides evidence of her informative intention that Peter understands that the berries are edible; and this intention is informative about the actual edibility of the berries only in turn. This metarepresentational structure makes the expressive domain of ostensive communication effectively open-ended (unleashed), even though the actual domain of the relevant cognitive capacities is narrow and specific: It is just the communicator's informative intentions.

This in turn has two important consequences, which together generate a further important corollary.

First, a metarepresentational structure is how ostensive communication can be expressively open-ended while still conforming to the central evolutionary constraint that communication systems are tied to narrow domains of statistical mutual benefit. In section 2 we summarised why, from an evolutionary perspective, all evolved communication systems should be tied to narrow domains of statistical mutual benefit, and we observed that human communication appears to be in flagrant violation of this constraint. Now we can state how the paradox can be resolved. The actual domain of the cognitive capacities that underpin ostensive communication is indeed still restricted to a narrow domain of statistical mutual benefit, namely the communicator's own informative intentions. At the same time, the metarepresentational structure generates an expressive domain that is truly open-ended.

Second, the metarepresentational structure of ostensive communication generates a distinction between comprehension and acceptance. Comprehension is targeted at the informative intention itself: To comprehend is to recognise the informative intention that an individual has towards another ("She wants me to believe that the berries are edible"). Acceptance, in contrast, is targeted at what the informative intention is about, that is, what is "virtual." To accept is to actually update one's own beliefs in light of what has been communicated ("The berries are indeed edible").

Together, these two consequences imply that audiences cannot actually gain from communication unless they extend a degree of trust towards the communicator. The distinction between comprehension and acceptance, and the massive open-endedness of human communication, together mean that audiences who do not extend a degree of trust towards ostensive communicators would comprehend what others want to do to their minds, but would never then update their beliefs in light of that knowledge. They would never allow themselves to gain information in communication! Peter would understand that Mary wants him to believe that the berries are edible, but Peter unless he extends some trust towards her, he will never believe that the berries are actually edible. Of course, this trust must be tentative and provisional, lest audiences be misinformed, but it must be extended in some way, just for audiences to gain from communication in the first place.

In consequence, cognitive capacities for expressing and recognising informative intentions must be complemented by further capacities that allow audiences to trust what is communicated but in a vigilant way, possibly questioning the competence or the benevolence of the communicator, and evaluating the plausibility of what is communicated. Commonly known as epistemic vigilance, these cognitive capacities are a specialised form of social vigilance, targeted at the assessment of informative intentions (Mercier, 2017; Sperber et al., 2010). They also allow audiences to identify misleading communicators, and hence adjust the attention and trust they are willing to grant in the future.

In sum, then, the open-ended richness of human communication is achieved virtually, by a combination of cognitive capacities for the expression of informative intentions, cognitive capacities for the recognition of informative intentions, and cognitive capacities of epistemic vigilance, all of which are functionally tied to one another. Thus, to properly explain the expressive openness of human communication, what must be described is: (1) how these cognitive capacities could all gradually co-evolve and be mutually supportive of one another, such that they form a communication system; and (2) the ecological reasons why they have actually done so in humans. The next section addresses these questions.

6. Co-evolutionary ecology of human communication

Many authors have observed how human communication must have co-evolved in a highly social ecology, one way or another (sect. 1). Here we identify which specific and distinctive aspects of human social ecologies can generate the co-evolution of the cognitive capacities described in sections 3 and 4, such that fully enriched ostensive communication can become uniform and stable in the population. We also provide precise description of how this co-evolution could occur in a gradual manner.

Arguably the most distinctive feature of the human cognitive niche is that it is highly social. Humans tend to live in social groups that are loosely defined but long-lasting, and comprised of both kin and non-kin. To a degree that surpasses that of

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other great apes, this social ecology generates many opportunities for win-win cooperation, and risks of exploitation. More broadly, human social ecologies involve an especially delicate balance of cooperation and competition, with substantial evolutionary pressure for behaviours that make the most of this mix (Ferriere, Bronstein, Rinaldi, Law, & Gauduchon, 2002; Noë & Hammerstein, 1995; Tomasello, Carpenter, & Liszkowski, 2007). Individuals acting in their own adaptive self-interest seek out others ("friends," "colleagues") with whom to engage in mutually beneficial enterprises, and they behave in ways that increase their chances of being chosen as a partner for joint enterprise (e.g., Barclay, 2013; Krems, Williams, Aktipis, & Kenrick, 2021). A partner choice ecology will include many limitations about who might or might not be available for a joint enterprise. It need not be a perfect market of potential partners. Still, its main feature is that individuals might gain or lose win-win opportunities depending on what others think of them. Humans have hence evolved a number of cognitive capacities adapted for this ecology, including moral dispositions, mechanisms of social vigilance that identify potential partners and opportunities for mutually beneficial interaction, an awareness of potential opportunities to exploit others, a strong sensitivity to changes in one's reputation, and so on (see, e.g., Barrett, Cosmides, & Tooby, 2010; Baumard, André, & Sperber, 2013; Curry, Mullins, & Whitehouse, 2019; Delton & Robertson, 2012; Engelmann & Tomasello, 2019; Heintz et al., 2016; McCullough, 2020; Origgi, 2004, 2005; Sperber & Baumard, 2012).

These factors collectively constitute a "partner choice" social ecology; or, possibly, an ecology of "self-domestication." This means, minimally, that it is advantageous to be selected as a partner for some joint enterprise (other than mating), and that the selection of partners for joint enterprise is based on information on past actions. Reputations are thus especially critical.[12]

In this partner choice ecology, the cognitive means of manipulation described in section 3.3, and the cognitive means of social vigilance described in section 4.3, are each adaptive. Particularly important is the role of social commitments. By providing evidence of their informative intention, informers make themselves accountable to their audience, putting their reputation at stake; and audiences can hence effectively assume the relevance of overtly expressed informative intentions. This evolutionary dynamic is, incidentally, similar to that described by partner choice approaches to fairness (André & Baumard, 2011; Barclay, 2013, 2016; Debove, André, & Baumard, 2015). In both cases, the adaptive value of maintaining one's reputation in a partner choice ecology constitutes a crucial selection pressure for psychological traits, which in turn generates prosocial behaviour. In the case of ostensive communicators, prosocial behaviour means being relevant.

The following five paragraphs elaborate this argument in more detail. They hence provide an existence proof of how and why the cognitive capacities described in previous sections could have evolved in a gradual manner (for similar but different approaches see, e.g., Cornell & Wharton, 2021; Wharton, 2006). Indeed, "lineage explanations," in which changes in the phenotype result from incremental changes, are an important constraint on theories of cognitive evolution, especially co-evolutionary theories (Calcott, 2009).

Consider a social ecology with many, varied opportunities for win-win cooperation. Here, informing others can be adaptive, because it can facilitate win-win cooperation or even create new win-win opportunities. In particular, informing others can generate common ground and hence facilitate many joint enterprises (such as, say, animal hunting, building shelter, maintaining a fire, alloparenting). Informing others can also have fitness advantages by allowing the social transmission of opaque skills to cooperative partners and kin.

These potential adaptive benefits in turn mean that it is adaptive to recognise and attend to others' attempts to gain attention (sect. 4.2). That said, attention is limited and thus should be modulated depending on whether others' attempts to inform are likely to be worth the attention indeed, that is, are revealing of relevant information. Individuals should be socially vigilant towards others' informative intentions, evaluating whether, or to what extent, the intentions are indeed cooperative. It will hence be in informers' own interests to actually be relevant for their audience, because those who intentionally attract attention but fail to do so in ways that are useful (relevant) will, in time, incur costs to their reputation and lose their capacity to manipulate their conspecifics' attention. In other words, there will be selection for behaviours that intentionally attract others' attention only when it is likely to be worthwhile for the audience to indeed pay attention (see also Dessalles, 1998).

At this point, expression has not yet "gone Gricean" (we adopt this useful expression from Bar-On, 2013), and as such humans are not yet "language ready." This is because informative intentions are not intentionally made overt, and so expression is not yet predicated on the systematic exploitation of the audience's recognition of informative intentions (Grice's "by means of" clause: see sect. 3.3). Expression is based just on behaviours that informers expect will be relevant to others; and "comprehension" is based just on tentative assumptions that others' expressive behaviour is likely to be relevant for the same reason. These tendencies and dispositions do, however, constitute a new social ecology, and it is here that "going Gricean" is adaptive.

Crucially, in this new social ecology – in which audiences might expect others' informative behaviour to be relevant, and in which a reputation for being a good cooperator can be gained and lost – it is adaptive to make manifest informative intentions themselves, that is, make overt and common knowledge the intentions you have towards your audiences' mind. This is adaptive because, by making informative intentions manifest, informers effectively offer a credible commitment that the overtly presented behaviour will indeed be relevant for the audience; which in turn increases the probability that the informative intention will indeed be satisfied. In other words, because the overt expression of an informative intention makes that informative intention common knowledge; and because in a partner choice social ecology there is the risk of developing a reputation for irrelevance and hence of losing the possibility of influencing others' minds; then communicators are effectively committed to their behaviour being useful (relevant) for the audience. This in turn makes it adaptive for audiences to simply presume – even if just tentatively at first – that the behaviour is indeed relevant, and to interpret the behaviour in light of this presumption of cooperativeness.

The social ecology is now one in which the overt expression of informative intentions effectively commits informers to being relevant to their audience, and in which informers indeed abide by that commitment (see also Scott-Phillips, 2010; Sperber, 2013). In this new ecology, it is adaptive for audiences to evolve two kinds of specialised cognitive disposition. (1) High prior expectations that others' communicative behaviour will be relevant. These will eventually become the spontaneous presumptions of relevance described in section 4.3. (2) Forms of social vigilance that

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assess how, and to what extent, beliefs should be updated in view of others' informative intentions. These will eventually become the epistemic vigilance described in section 5. Now audiences have these two kinds of specialised cognitive disposition, individuals can inform simply "by means of" (as Grice put it) making their informative intentions manifest. This is Gricean communication proper.

Let us summarise. What we are arguing is that outside a partner choice social ecology, communication and expression are highly prone to irrelevance, deception, and instability; but within a partner choice social ecology there is selective advantage for behaviour that is cooperative (statistically speaking at least), which in the context of communication means relevant. Within this social ecology a gradual, cognitive co-evolution of specialised capacities for ostensive communication is hence possible. As with other aspects of core cognition, these capacities, which provide the foundations of human communication (sect. 5), should become part of the ordinarily developing cognitive phenotype, emerging at reliable and predictable stages of ontogeny.

There is, correspondingly, abundant empirical evidence of this reliable and predictable cognitive development in humans, both in language use and communication more broadly (e.g., Bates, 1979; Bloom, 2002; Bohn & Frank, 2019; Clark, 2003; Goldin-Meadow, 2005; Tomasello et al., 2007; *inter alia*). In the next section we consider whether, or in what ways and to what extent, the same cognitive capacities might be present in nonhuman primates.

7. Cross-species comparisons

Do any other species communicate ostensively, or in proto- or quasi-ostensive ways? How would we know? These questions are worth asking because nonhuman species, great apes and dogs in particular, sometimes appear to understand some human ostensive behaviour, at least in some specific contexts. Here we outline how this question can be addressed experimentally, we present an ecology-based explanation of key differences between human and nonhuman great ape communication, and we reinterpret some key findings in the comparative cognition of communication.

The key methodological challenge in studying ostensive communication from a comparative perspective is that ostension is ultimately a psychological construct, that is, ostension is not any particular behaviour, but rather any behaviour motivated by a particular cognitive phenomenon, namely informative intentions (sect. 3.3). This makes it impossible to fully isolate behavioural characteristics. As such it will always be theoretically possible to reinterpret any behavioural differences between experimental conditions in a non-mentalistic ('killjoy') way, so the relevant cognitive capacities are not ascribed to the individual animal participants, or species. One response to this methodological challenge has been to, effectively, abandon use of the Gricean framework in the study of animal communication (e.g., Townsend et al., 2017). In contrast, we suggest that experiments revealing the relevant intentions and interpretative processes are still possible.

In particular, the hypothesis that nonhuman primates can be sensitive to ostension *qua* ostension (i.e., sensitive to the expression of an informative intention) can be tested by contrasting two scenarios in which the *exact same* ostensive behaviour prompts spontaneous identification of different informative intentions, and hence different behavioural responses, depending only on what is in the common ground. Real-world human communication is replete with examples. Ordinary utterances such as, say, "It's raining" can, even if produced in exactly the same way in each case, be interpreted in wildly different ways depending only on the present common ground ("Take an umbrella," "Even the whether can't lighten my mood," "Your parents won't be visiting after all"). The same can be true of non-verbal means of communication, such as points and nods, not to mention spontaneous and ad hoc gestures, and indeed all human ostensive stimuli.[13]

We predict, tentatively, that if any nonhuman primates do reliably pass tasks of the type described above, it will be individuals with extensive experience of altruistic human caregivers, and not those living the natural social ecologies of nonhuman primates. Nonhuman primate social ecologies involve fewer and less frequent opportunities for interactions of mutual benefit. That is not to say such opportunities are absent, but they are much less prevalent relative to the human case, and in consequence the relevant selection pressures are not (as) present. This is, we believe, why nonhuman great apes have not evolved all of the same communicative dispositions as humans. At the same time, nonhuman primates living under captive conditions, with human caregivers who are more-or-less uniformly cooperative, could – perhaps – develop the relevant dispositions and expectations ontogenetically (see, e.g., Call, 2011, for discussion of how rearing conditions can affect chimpanzee communication). In other words, a "proto" presumption of relevance could result from non-standard life history in nonhuman apes. If so, then we should expect some recognition and interpretation of human ostensive behaviours *qua* ostensive in at least some individuals, albeit in imperfect and happenstance ways. This prediction is of course ultimately a matter for future empirical research, but it aligns with existing findings that humans differ from other great apes in dispositions of trust and cooperation (see, e.g., Jaeggi, Burkart, & van Schaik, 2010; Moll & Tomasello, 2007; Tomasello & Call, 2019).

Here is an analogy that helps to articulate this difference between specialised competences that are part of the ordinarily developing phenotype (as ostensive communication is in humans), and latent competencies that might be refined in the right ecology (as might be the case for ostensive communication in chimpanzees and some other nonhuman primates). Consider humans swinging from trees. Human bodies are not especially well-suited to this task. We lack the specialised biological apparatus of other primates and we do not develop the relevant dispositions as an ordinary part of ontogeny. At the same time, there is no absolute barrier. Some humans can swing from trees in some limited ways and to some extent, and this basic ability can be refined and enhanced with training: in other words, in the right ecology. What we are suggesting, tentatively, is that ostensive communication in other primates, living in the right sort of social ecologies, might be similar: Not impossible and not wholly absent, but still unspecialised, disfluent, not a regular part of the environment, and not part of the ordinarily developing phenotype.

This perspective on nonhuman primate cognition can help make sense of otherwise puzzling findings in the comparative psychology of communication. We highlight two examples in particular: performance in the "object-choice task," and the phenomenon of overimitation. (This is obviously not an exhaustive list of relevant comparisons. As one of many further phenomena to explain, great ape interaction tends to have a dyadic rather than triadic character; see Pika, Liebal, Call, & Tomasello, 2005.)

First, in the object-choice task a desirable object is shown to the participant, and then placed in one of the two boxes, or bins. The participant does not know which of the two boxes contain the desirable object. The two boxes are placed either side of

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the experimenter, who then points to the box with the desirable object. The participant is then free to open the boxes. Many nonhuman primates "fail" this task: In many studies nonhuman primates do not choose the indicated box at levels greater than chance (see Clark, Elsherif, & Leavens, 2019, for a recent review). We suggest that this occurs simply because the relevant cognitive processes employed by the audience are, in nonhuman primates, not ordinarily predicated on a presumption of cooperation, which in the context of pointing means communicative relevance. Dogs, in contrast, perform far better at the object-choice task (see below), as do human infants.

Second, we consider "overimitation," in which individuals copy actions demonstrated to them, including in particular those that are perceivably causally irrelevant (e.g., tapping a box before opening it, even when the tapping makes no difference to whether or how the box is opened). Intriguingly, overimitation is only consistently observed in humans, including children, and not in chimpanzees or bonobos (Clay & Tennie, 2018; Hoehl et al., 2019; Horner & Whiten, 2005; Johnston, Holden, & Santos, 2017; Lyons, Young, & Keil, 2007). This finding has prompted speculation that overimitation derives from a cognitive adaptation for acquiring generic, cultural knowledge (e.g., Chudek & Henrich, 2011; Gergely, 2013; Legare & Nielsen, 2015; Nielsen & Tomaselli, 2010). We suggest, in contrast, that overimitation is best explained as a by-product of audience presumptions of relevance. Overimitation reliably occurs only when the copied behaviour has been performed in an overtly intentional (i.e., ostensive) way (see, e.g., Király, Csibra, & Gergely, 2013, for experimental demonstration). This triggers in the audience a spontaneous process of interpretation, which is predicated on a presumption of relevance (sect. 4.3), hence delivering the (incorrect) conclusion that the demonstrated actions are useful, even if that utility is currently opaque to the audience. We are suggesting, in short, that the reason only humans reliably demonstrate overimitation is that only humans reliably interpret ostensive behaviour in terms of optimal relevance (see also Morin, 2016, pp. 244–245). We note, consistent with this interpretation, that overimitation emerges in development very soon after the emergence of ostensive communication.

Finally, dogs are also an informative point of comparison. Dogs have been subject to a long period of domestication in which humans are often prosocial towards them. In this ecology it can be adaptive for dogs to simply presume that when humans attempt to gain their attention, it is indeed worthwhile to actually pay attention. Correspondingly, dogs seem to be sensitive to some of the most salient human ostensive behaviours (see, e.g., Topál, Kis, & Oláh, 2014; Wynne, 2016, for reviews). This sensitivity, moreover, emerges early in development and is highly heritable (Bray et al., 2021). Presumably, dogs do not make the same interpretative inferences as humans, but they do show how, in the right evolutionary ecologies, it can be adaptive to spontaneously presume that others – in this case, human owners – are being cooperative when they attempt to gain attention.

8. Diversity in human expression

In this section, we suggest how the cognitive mechanisms described in previous sections underpin many otherwise diverse means of human expression. Our main goal is demonstrative: We aim to highlight how otherwise distinct means of expression and communication appear in new light when considered from the perspective of cognitive unity. We focus in particular on the examples of coordination smoothers (sect. 8.1), teaching (sect. 8.2), punishment (sect. 8.3), art (sect. 8.4), and languages (sect. 8.5). In each case, we summarise how these different means of expression each employ the common, unified set of cognitive capacities described in previous sections, but in different ways in each case. If we are right about this, then the evolutionary emergence of specialised, cognitive means of manipulation (sect. 3) and social vigilance (sect. 4), which together unleash expression (sect. 5), is a root cause of many of the most distinctive aspects of human behaviour and societies. Other domains that have been studied from a perspective broadly similar to ours include divination (Boyer, 2020), humour (Yus, 2016), emotional expression (Dezecache, Mercier, & Scott-Phillips, 2013; Wharton, Bonard, Dukes, Sander, & Oswald, 2021), literary interpretation (Cave & Wilson, 2018; Chapman & Clark, 2019), mathematical diagrams (McCallum, 2019), onomatopoeia (Sasamoto, 2019), many borderline or quasi-linguistic phenomena (Ifantidou, de Saussure, & Wharton, 2021), and others.

We will highlight in particular the importance of graded aspects of human expression. In section 3.3 we mentioned how there is a graded quality on the production side: Different means of expression can vary in the extent to which the actor makes her informative intention manifest. In section 4.3 we mentioned how there is, in turn, variation on the audience side: Recognition of the actor's informative intention can contribute to satisfying the informative intention to different degrees in each case. In the subsections below, we describe how different forms of human expression make use of these graded aspects in a range of different ways; and we suggest that in general people aim to make their informative intentions manifest just to the extent that the informative intention is likely to be satisfied, but no more so.

8.1. Coordination smoothers

To coordinate with one another in joint actions, such as dancing with a partner, maintaining a tempo, moving large objects together, and many others, individuals must be informed about each other's behaviour and likely future behaviour, often on a moment-by-moment basis (Sebanz, Bekkering, & Knoblich, 2006). This can occur passively, but individuals also behave in ways that actively facilitate the flow of information for joint action. For instance, two people may have a goal to lift and move a large table. In lifting their end of the table, each person might move in slightly exaggerated ways, in order to be predictable. Such behaviours are called "coordination smoothers": they enable predictability for coordination (Vesper, Butterfill, Knoblich, & Sebanz, 2010, 2017). Some cases of coordination smoothing are clearly communicative, such as road signs and forms of language use targeted at easing the flow of conversation ("discourse markers," "procedural meaning": see, e.g., Blakemore, 2002; Gibbs & Bryant, 2008). However, cases in which informative intentions are less overt have only recently been explicitly analysed in terms of communication and expression (e.g., Pezzulo et al., 2019).

Consider two people, Jane and Paul, walking towards one another on a relatively narrow street. Jane makes a clear movement towards one side in order to make her action predictable to Paul. This informs Paul that Jane intends to proceed on the right, and it can do so even if Paul does not recognise that Jane has this informative intention. Alternatively, Jane might exaggerate her movement to one side. This makes her informative

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intention more manifest, and Paul can hence infer that she has an informative intention that he believes she will proceed on the right, and trust in it. This raises the question: When, why, and to what extent do individuals make their informative intentions manifest? When should Jane not just clearly move, but exaggerate her movement to one side? And to what extent? Correspondingly, on the audience side: To what extent does recognition of the actor's informative intention contribute to successful coordination smoothing? These are all empirical questions whose answers depend on how individuals take into account the constraints and the affordances of the situation, and how they navigate graded dimensions of human expression.

Many results in the experimental study of joint action suggest that people indeed exaggerate or otherwise adjust their actions to the extent that it is useful to do so for the purposes of informing others; or, in other words, they make the least costly difference that is large enough to make a difference (e.g., Curioni, Vesper, Knoblich, & Sebanz, 2019; McEllin et al., 2018a, 2018b; Schmitz, Vesper, Sebanz, & Knoblich, 2018). Observers, in turn, attribute to others *commitments* to behaving in the predicted way just to the extent that those others are perceived as acting on a communicative intention (see, e.g., Bonalumi, Tacha, Scott-Phillips, & Heintz, 2020, 2021; Gibbs & Bryant, 2008). In sum, we are suggesting that coordination smoothing is a form of human expression, in which people navigate graded aspects of human expression in a competent way.

8.2. Teaching

Human teaching is richly diverse. Ethnographies of teaching reveal practices that span the full range of human expression, ranging from tolerated observation, in which a skilled individual just allows others to observe her in practice, to, at the other extreme, direct verbal statements from the teacher, which the learner is expected to internalise (e.g., Lave & Wenger, 1991; Marchand, 2010; Sugiyama, 2021). Most actual instances of teaching lie between these extremes and also include, for instance, repeated demonstration, performance, exaggeration, role-play, and countless other forms of expression (see, e.g., Kline, 2015 for a recent review). We suggest that, as with coordination smoothers, one way to organise the diversity of teaching is in terms of graded distinctions in human expression. Different means of teaching vary in the extent to which the teacher makes her informative intention manifest; and also the extent to which recognition of the teacher's informative intention contributes to successful interpretation, and hence learning.

Consider, for instance, a dance teacher (see, e.g., Downey, 2008 for cognitively informed ethnography of dance teaching). At one extreme, she might simply repeat a dance step multiple times, possibly from a range of different angles, allowing learners to observe, without any further guidance about which aspects of the movement to attend to. Here the teacher has an informative intention, and this intention is not hidden at all, but the teacher does not make the intention manifest, and the learners employ means-end relations to learn. Alternatively, at the other extreme, the teacher might openly exaggerate some of her movements and hence highlight especially relevant aspects, which would otherwise remain unnoticed. By doing this the teacher makes her informative intention manifest. This triggers in learners spontaneous presumptions of relevance (sect. 4.3), which allows them to differentiate exaggeration from the actual target behaviour, and hence identify what is especially relevant about the teacher's movements. In between the extremes are cases where the teacher makes her informative intention somewhat manifest, such as when she slows her movement but in a slight way only. In these ways and others, teaching is a phenomenon that, in its diversity, spans the two graded dimensions of human expression we highlighted above.

When should different modes of teaching be employed? Sometimes it is suitable to simply perform the target behaviour as usual and just allow observation, sometimes it is suitable to make an informative intention somewhat manifest – and sometimes it is necessary that the teacher's informative intention be made wholly manifest. In particular, by triggering learners' presumption of relevance, teachers can teach things even though what makes those things relevant is opaque to the learners (Gergely & Csibra, 2006). A real-world example is teaching the counting routine to children, who learn by presuming that the routine is relevant even though they do not yet understand its real utility. This mode of teaching is arguably crucial for conceptual change (Heintz, 2011).

This perspective on teaching, as a subclass of human expressive behaviours, contrasts with approaches that treat teaching as a distinct behaviour in need of its own gradual evolution (e.g., Csibra & Gergely, 2011; Gärdenfors & Högberg, 2017). It can also help to explain why teaching is prevalent in human societies but relatively rare in other species (see, e.g., Hoppitt et al., 2008; Thornton & Raihani, 2008, for comparative perspectives). Human teaching involves the dynamic use of unleashed expression. Analogous behaviours are observable in other species, but not with the same dynamic, open-ended, and flexible range of behaviours that are afforded by truly unleashed expression, and readily exploited by human teachers and learners.

8.3. Punishment

Punishment is not always or intuitively thought of as a means of expression. Particularly within cognitive science and cognate fields such as behavioural economics, punishment has traditionally been modelled simply as retribution or incentive, such that it discourages or deters specific behaviours. The actual delivery of punishment is then necessary only to maintain the integrity of the incentive structure. Yet the rewards and punishment that humans tend to produce are actually inefficient for this goal. That is, they do not incentivise the target behaviour well, contrary to the intuitive model (Cushman, Sarin, & Ho, 2022; Ho, Cushman, Littman, & Austerweil, 2019). The way people punish also includes an important expressive dimension (*ibid.*). More precisely, punishment is, we suggest, used to inform others that future exploitative behaviour will result in future costs (see also e.g., Sripada, 2005).

But why, then, is this expressive function not patently apparent? In other domains (linguistic communication, teaching, art) expression and communication are utterly plain to see. We suggest that punishment is usually most effective when its communicative aspects (sect. 3.3) are somewhat hidden, even though its informative aspects (sect. 3.2) are present.

The crucial point is that in ordinary social relations, punishment is credible only if the incentives behind it are perceived to be stable; but in fact, in ordinary social relations the incentives to inform are *un*stable. Specifically, they are dependent on the possibilities of future collaboration: If we are unlikely to interact in the future, I have no substantive incentive to inform you that your behaviour was unacceptable. So if the real incentives that

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motivate punishment were actually made manifest, they would be revealed as unstable and would hence undermine the credibility of punishment as a means of informing. In this respect punishment is akin to generosity. We mentioned in section 3.2 that there is a slight paradox to generosity, in the sense that while it can be motivated by an intention to advertise oneself as prosocial, this intention should not itself be too manifest, lest the act of generosity be seen as insincere. We are suggesting that a similar dynamic plays out on the punishment side: Punishment does not credibly demonstrate a willingness to retaliate against anti-social behaviour if it is perceived as being motivated only by an intention to demonstrate a willingness to retaliate against anti-social behaviour. So for both generosity and punishment, the communicative aspect should not be salient, because this undermines the very purpose of the behaviour, namely to inform others of likely future costs and benefits.

Institutional forms of punishment, in particular the legal punishments of nation states, provide a revealing contrast. In jurisprudence the communicative aspects of legal punishment have been long recognised: Punishment is described as, for instance, "a conventional device for the expression of attitudes of resentment and indignation, and of judgments of disapproval and reprobation" (Feinberg, 1965, p. 400; more recently see, e.g., Duff, 2001; Hampton, 1992; Primoratz, 1989). The expressive dimension of punishment is straightforwardly recognised in the legal domain because, we suggest, there is in this domain no real doubt that the punisher (the nation state) has a long-term, stable incentive to inform the audience (citizens) about what is unacceptable. Nation states hence have no real need to hide the communicative dimensions of their punishments.

The expressive dimensions of punishment can be investigated in much more detail. In particular, we know of no studies that focused on whether, or to what extent, people interpret or understand punishment as communicative; nor on the effectiveness of punishment as a means of expression. Such studies would form an important bridge between cognitive pragmatics and other fields, such as the newly emerging area of experimental jurisprudence (Sommers, 2021). We also know of no existing research examining the expressive dimensions of legal punishment from a historical perspective.

8.4. Art

Art is clearly expressive in some way, and audiences interpret artistic outputs in open-ended ways. Modern audiences in particular are granted a great deal of autonomy in how they engage with art, and are encouraged to develop and seek out their own, often highly personal interpretations. We suggest that, like the other examples above, the open-endedness of artistic expression derives from the natural character of human expression more broadly; and hence that the interpretations that audiences derive from artwork, which are often highly personal, are nevertheless often prompted by and derive from the same set of cognitive processes that govern more ordinary forms of communication.

Crucially, what differentiates artistic expression from ordinary behaviour is not any fundamental aesthetic quality as such, but rather the overt presentation of an object as an aesthetic experience worthy of attention. This is the conclusion reached in many lines of research and argument from at least four different fields: traditional art theory (e.g., Danto, 1964; Dickie, 1987), cognitive pragmatics (e.g., McCallum, Mitchell, & Scott-Phillips, 2020; Pignocchi, 2019), philosophy of mind (e.g., Fodor, 2012), and social anthropology (e.g., Dissanayake, 1988, 2003). The overt presentation of objects as worthy of attention is respectively labelled "Artworld," "ostensive," "Gricean," or "making special," in each of these four literatures. This consensus in turn suggests that while proclivities towards aesthetic experience might be observable in other species, the evolutionary emergence of cognitive capacities for unleashed expression, as a core part of the human cognitive phenotype (sect. 6), allows those proclivities to be expressed in overtly intentional ways, thus differentiating art from other forms of aesthetic experience.

The emergence of art institutions can further reinforce these effects. Contemporary art galleries in particular use white walls, open spaces, and other features of curation to present artworks as items to be considered and appreciated, hence triggering, we claim, the audience presumptions of relevance that are an indelible part of ordinary communication. These and other institutional effects, which can generate highly personal, even idiosyncratic interpretations, are well established in art theory. What cognitive pragmatic perspectives help to provide is description of how these effects exploit and otherwise build on the way audiences spontaneously interpret ostensive behaviour in more ordinary forms of social interaction (McCallum et al., 2020; Pignocchi, 2019).

8.5. Languages

Language use is quintessentially ostensive. Unlike some of the other means of expression described above, language use involves making informative intentions wholly manifest. We are arguing, in other words, that cognitive capacities for ostensive communication are foundational to language use: There could not be any languages or linguistic communication without the prior existence of cognitive capacities for ostensive communication (see also e.g., Levinson, 2006; Scott-Phillips, 2015; Tomasello, 2008). As we put it in section 1, natural languages *exploit* unleashed expression: not the other way around.

Languages have, of course, their own particular features that collectively distinguish them from other means of communication. In particular, linguistic communication makes ubiquitous and multilayered use of communicative conventions: phonemes, morphemes, words, grammars, and so on, which function to associate particular behaviours (speech, gesture) with particular inferences that the communicator intends to trigger in the audience. This "pragmatics-first" perspective on the nature of languages aligns with usage- and construction-based approaches to grammar, which emphasise how linguistic constructions are used as a means to provide evidence of speaker meaning (e.g., Bybee & Beckner, 2010; Goldberg, 2003; Goldberg & Suttle, 2010; Hartmann & Pleyer, 2021; Schmid, 2020; Tomasello, 2003).

Where do communicative conventions come from? In recent decades the emergence and stabilisation of communicative conventions has been documented in several real-world case studies (e.g., Brentari & Goldin-Meadow, 2017; Kegl, Senghas, & Coppola, 1999; Meir et al., 2010), and studied experimentally in the laboratory (e.g., Fay, Arbib, & Garrod, 2013; Granito, Tehrani, Kendal, & Scott-Phillips, 2019; Motamedi, Schouwstra, Smith, Culbertson, & Kirby, 2019; Raviv, Meyer, & Lev-Ari, 2019; Schouwstra & de Swart, 2014). What is commonly observed in these literatures is how behaviour that is sufficiently similar to previously successfully informative behaviour tends to be interpreted by audiences as a further token of the same type as previously used, even after just one interaction; and also how further

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repetition causes the focal behaviours to become increasingly conventional. How and why does this happen?

In answering this question, what is not often recognised is that the very same cognitive capacities that make ostensive communication possible in the first place, also play a pivotal role here. In particular, without audience presumptions of optimal relevance (sect. 4.3), behaviour that resembles past communicative behaviour is mysterious and strange. Why repeat a past behaviour, and bring attention to it?! Such behaviour is worth doing only if the attention-grabbing repetition of a past behaviour triggers in audiences the interpretation that the behaviour is being used for the same or similar purposes as previously. So past events have a role in communication not simply because of statistical learning of associations, but because alluding to past events is typically the most effective way to trigger audience presumptions of relevance, and hence interpretative inferences that are the same or similar to those triggered previously.

Furthermore, this allusion to past events will often mean that a given behaviour can afford to be slightly less complex or less elaborate than the previous version, so long as the allusion is still made. Communicative success becomes increasingly governed by the simple fact that echoing how behaviours have been successfully used in the past is the most efficient means of prompting the intended inferences in the audience. Repeated many times over, this allows gradual simplification of the stimuli; and in time helps to shape many of the features that are characteristic of natural languages, such as displaced reference, compositionality, predicate-argument structure, low levels of resemblance between form and use ("symbolism"), statistical relationships between word length and frequency of use (e.g., "Zipf's law"), and so on. These processes can, we believe, be fruitfully analysed within an epidemiological framework (e.g., Enfield, 2003, 2014; see also Scott-Phillips, Blancke, & Heintz, 2018).

Finally, we note that linguistic stimuli are processed by some dedicated cognitive capacities (see, e.g., Hagoort, 2017 for a recent summary). Crucially, these capacities appear to work *in parallel with* cognitive processes of ostensive communication more broadly. On the comprehension side in particular, inference of what is said and inference of what is meant are not serial, with one following the other, but instead seem to impact on each other in a dynamic process of parallel "mutual adjustment" (see, e.g., Carston, 2002; Sperber & Wilson, 2007; Wilson, 2004 for post-Gricean description of this process; and e.g., Paunov, Blank, & Fedorenko, 2019; Spotorno, Koun, Prado, van der Henst, & Noveck, 2012; Vanlangendonck, Willems, & Hagoort, 2018 for neuroscientific evidence). Further and deeper integration of findings in psycholinguistics and cognitive pragmatics are important future research goals (Gibbs & Colston, 2020; Noveck, 2018); but in any case, the evolutionary emergence of these dedicated capacities must have followed, rather than preceded, the evolutionary emergence of ostensive communication described in section 6.

9. Conclusion: Rethinking pragmatics

Historically speaking, pragmatics has been situated on the periphery of the language sciences, appearing in textbooks usually only as a fringe topic. We have argued, in contrast, that cognitive capacities for ostensive communication are foundational, because they unleash expression on a grand scale. This in turn redefines the domain of pragmatics itself. Rather than being narrowly conceived as the study of how context influences the interpretation of utterances – which is how it is conceived in many approaches – pragmatics should be characterised as *the study of how, and the many means by which, informative intentions are satisfied*. The core questions for pragmatics are how informative intentions are made manifest, and to what effect (e.g., Allott & Wilson, 2021). Language use and other conventionalised means of expression are the most salient specific instances, and are clearly central to human sociality, but there are many others too.

Here we have grounded this rethinking of pragmatics in a broad evolutionary and cognitive context. Human communication has long posed a challenge to evolutionary biology and signalling theory, because of its versatility, diversity, and clear proneness to deception (sect. 2). We have described how this problem is resolved in humans, allowing truly unleashed expression (sect. 5); described key graded differences between the specialised capacity of mind that drives human communication and other means of social cognition (sects. 3 and 4), some of which are shared with other great apes (sect. 7); and provided a crucial proof of evolvability, by relating these graded differences to specific and distinctive aspects of the human social ecology (sect. 6). We also described how several different means of human expression each employ the relevant cognitive capacities in interestingly different ways (sect. 8). If we are right about this, then the evolutionary emergence of specialised, cognitive means of influencing other minds (sect. 3.3), and of recognising what others want to do to your mind (sect. 4.3), is a root cause of many of the most distinctive aspects of human behaviour and societies.

An essential future goal is to establish a formal foundation for this reconceived pragmatics. An important first step in the development of scientific understanding is informed description of the phenomenon of interest, recognising its full complexity while simultaneously providing some provisional order and generality. We hope to have contributed to that goal here, which is too often neglected in contemporary cognitive psychology and cognate disciplines (e.g., Doliński, 2018; Oude Maatman, 2021; Rai & Fiske, 2010; Rozin, 2001; *inter alia*). Formal models build on these descriptive foundations. In this respect Bayesian models of interaction, in which production and comprehension are modelled as interconnected planning problems over others' mental states, are a particularly promising direction (e.g., Goodman & Frank, 2016; Ho et al., 2019; Shafto, Goodman, & Griffiths, 2014). Different specific models differ in the detail and we do not subscribe to all of the assumptions made.[14] Moreover, we do not believe that any existing model is sufficiently general to cover the full range of prototypical cases of communication (e.g., pointing, gesture, language use), let alone the broader diversity we highlighted in section 8. Nonetheless, we do believe that modelling human interaction in these terms is an important and promising research direction. We hope that our description of the evolutionary and cognitive foundations of human expression, in all its diversity, will aid this agenda.

More broadly, we agree with recent arguments that the human evolutionary sciences are presently too "cognition blind" (e.g., Heyes, 2019; Morin, 2016; Singh et al., 2021), and that greater theoretical unity will be achieved by deeper consideration of the cognitive processes that underpin otherwise diverse human behaviours. The case of communication and expression is, we believe, a clear case in point. Quite commonly, particular types of expressive behaviour (e.g., language use, teaching, punishment, art) are considered each in isolation, without much consideration of the possibility that they might in fact derive from the same

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underlying biological trait: As if the evolution of running was considered in isolation from the evolution of walking, when in fact both are derived subfunctions of a unified capacity for bipedal locomotion. We have argued that the same applies here: Different types of human "expressive act" are each derived sub-functions of a unified capacity for ostensive communication.

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Notes

1. An item's *function* is the task that is causally responsible for the recurrence of the item in question (see, e.g., Millikan, 1984; Origgi & Sperber, 2000). Hearts, for example, make noise, contribute to body weight, and pump blood, among other things, but it is only the last of these that causally explains why hearts recur from one generation to the next.
2. From the perspective of evolutionary theory we are defining "expression" at the ultimate/functional level of analysis, with the goal to focus, in later sections, on its proximate manifestation in humans, and potentially other species (for elaboration of the ultimate-proximate distinction see Scott-Phillips, Dickins, & West, 2011).
3. Despite the pejorative tone of "manipulation" in everyday language, here it is used just to describe actions on others, regardless of whether those actions are pro- or anti-social.
4. This is a broad category that encompasses any intention to enable information flow. This might or might not involve representation of the audience's mental state. In particular, some animals might have informative intentions without representing the mental states they actually produce in others. For instance, a gorilla thumping his chest might associate this with the behavioural effect of conspecifics backing away, but not with the effect of them being frightened.
5. A further example is "phatic communication": pleasantries and other means of communication that serve plainly social functions, and which mainly consist of expressing a willingness to engage and to observe local conventions of politeness. Phatic communication often uses languages and other means of communication from within section 3.3, even though the informative intentions that are expressed in phatic communication bear mostly on the willingness to engage, in and of itself, rather than on what is linguistically expressed.
6. Precisely, we say that X is non-communicative evidence for Y if and only if X (might) generate, in the audience, the inference that Y without the observer necessarily computing that the informer has the informative intention of that Y. Two incidental notes about this. (1) This notion of non-communicative evidence is similar to Grice's "natural meaning" (1957). (2) Interestingly, many languages have grammatical evidential markers for information acquired in this non-communicative ("direct") way.
7. Regarding "ostension," the word is used in slightly more broad or more narrow ways in different literatures. Within pragmatics the word was first used narrowly, for the actions described in section 3.3, i.e., making an informative intention manifest (Sperber & Wilson, 1986/1995). Since then sizable literatures have developed studying ostension from many perspectives including development, evolution, and comparative cognition, and here the term is sometimes used more broadly, corresponding roughly to the actions described in section 3.2 (see, e.g., Csibra, 2010; Gómez, 1996; Moore, 2017; Sperber, 2019; Tomasello, 2008).
8. Note that our terminology here differs from Krebs and Dawkins, who used "mindreading" instead of "adaptive reaction" (1984). We have deviated from this usage because "mindreading" is also widely used in the social cognition literature to describe mechanisms rather than function, i.e., at the proximate rather than the ultimate level.
9. Throughout this article, we have avoided using the terms "mindreading" and "theory of mind," because they are so widely contested. Nevertheless, a reviewer asked us to state our view and we are happy to do so: we are mindreading "deflationists" (e.g., Jacob & Scott-Phillips, 2020). That is, we believe that these notions are best used in a minimal way, to refer just to the spontaneous recognition of mental states; and as such we believe that mindreading is much more akin to, say, visual cognition than to conscious "thinking." We think that mindreading in this deflationary sense is likely to be phylogenetically widespread, but enriched in various specialised ways in different species. The various cognitive processes we describe in this article – including mental metarepresentations, i.e., mental states about mental states (sect. 5) – are just such specialised versions of mindreading in this deflationary sense, falling within the broad functional category of social vigilance.
10. Note that the notion of cooperation used in the Gricean framework is not the same as that used in standard evolutionary theory. The evolutionary notion is about evolutionary function, and describes any behaviour that has a positive effect on another organism's inclusive fitness. The Gricean notion is about the assumptions that audiences make about the intent of the communicator. While these two notions can align with one another, and are sometimes conflated, they are different levels of analysis and not the same.
11. Both communicative and informative intentions are metarepresentations. Communicative intentions are representations of informative intentions (sect. 3.3). These informative intentions are in turn representations of the mental states to be triggered in the audience (Scott-Phillips, 2015, pp. 65–68; Sperber, 2000). Some authors assert that this metarepresentational framework for communication is excessively "complex" or "sophisticated," such that it is implausible as a description even of ordinary human communication, let alone the communication of, for instance, human infants (e.g., Bar-On, 2021; Moore, 2017; Townsend et al., 2017). These assertions remind us of Berkeley's disbelief in Descartes' (broadly correct) account of binocular vision: "But those lines and angles, by means whereof some men pretend to explain the perception of distance, are themselves not at all perceived, nor are they in truth ever thought of by those unskilful in optics [i.e. laypeople]… In vain shall any man tell me, that I perceive certain lines and angles, which introduce into my mind the various ideas of distance, so long as I myself am conscious of no such thing" (Berkeley, 1709). The point of this comparison is that phenomenologically simple phenomena (vision; communication) can have scientifically complex descriptions. Vision scientists have made tremendous progress in explaining vision by describing the visual system as implementing highly complex computations. We think we should not shy away from the idea that human communication is based on the comparatively simple ability to represent representations (see also Scott-Phillips, 2015, p. 10).
12. Three different notions of reputation can be distinguished. (1) An individual A can have a "reputation" for X in the sense that another person believes X about A (this is sometimes called an "image score"). (2) An individual A can have a "reputation" for X in the sense that a community of others all believe X about A. (3) An individual A can have a reputation for X in the sense that a community of others all believe that they all believe X about A, i.e., the notion that A is X is a common ground. Our argument in this section turns just on notions (1) and (2). Clearly, the emergence of ostensive communication, which enables open-ended communication and hence gossip, will in turn facilitate the emergence of (2) and (3), and can hence support cooperative phenomena such as indirect reciprocity (see, e.g., Nowak & Sigmund, 2005).
13. Note that the *spontaneity* of responses is especially important for future experimental design, because for a compelling test the differential interpretations of a specific stimulus should not be learned by training on that same specific stimulus. Infants have been shown to pass a third-person version of such tasks, i.e., a version in which the infant observes interaction between two other agents (Tauzin & Gergely, 2018).
14. Consider, for instance, the Rational Speech Act framework (Goodman & Frank, 2016). Here, communicative behaviours are assumed to have "literal" meanings, independent of use, from which speakers might deviate. We do not share this assumption; that is, we do not believe that there is any such thing as "literal

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meaning" so conceived. Indeed, this is one of the key points of difference between neo-Gricean approaches and the post-Gricean approach we have adopted in this article (Sperber & Wilson, 2007; see also citations in sect. 8.5, on the process of parallel mutual adjustment, which undermines the notion of literal meaning).

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Open Peer Commentary

Primates unleashed

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Abstract

Before claiming major differences between the communication systems of humans and other species, it is necessary to (1) overcome methodological limitations in the comparative study of communicative intentions; (2) account for mechanisms other than epistemic vigilance that may also sustain complex forms of communication; and (3) better differentiate between motivational and cognitive factors potentially affecting the emergence of open-ended communication.

The authors discuss how the peculiar socio-ecological characteristics of our species would have allowed us to evolve a unique set of cognitive skills necessary to "unleash expression." Although we applaud the authors' attempt to build a new theoretical framework, we are not sure how much it will advance the current state of the art from an evolutionary perspective. In particular, the authors suggest how, for unleashed expression to emerge, one would need cognitive skills to express and recognize communicative intentions, and a "partner choice social ecology" in which epistemic vigilance allows ostensive communication to become more reliable and "unleash expression."

First, studying how individuals express and recognize communicative intentions implies investigating their attribution of mental states (by recipients to signalers), which is not an easy endeavor in non-linguistic subjects (Townsend et al., 2017). In the absence of language, even complex behaviors may appear simpler, as one cannot for instance ask receivers about their inferences of others' communicative intentions. The authors briefly address this problem by suggesting to test whether nonhuman species produce different behavioral responses when exposed to the same ostensive behavior in different scenarios in which only the individuals' common ground differs. However, while such an approach may be informative about whether individuals can attribute mental states to others (see Krupenye, Kano, Hirata, Call, & Tomasello, 2016) and how they may flexibly combine this information to contextual cues and/or signals, it may still be hard to clarify what individuals understand about others' *communicative* intentions. In any case, it is at the moment not possible to exclude that species other than humans can reliably express and recognize communicative intentions.

Similarly, there are still important methodological issues to be addressed before claiming major differences in how humans and other species express and recognize communicative intentions. To date, the majority of vocal research has focused on how recipients react to vocalizations, while little is known about senders' communicative intentions (but see Crockford, Wittig, Mundry, & Zuberbühler, 2012). In the gestural modality, on the other hand, most studies focus on senders and their intentional gesture use, while there is little knowledge about how recipients interpret the senders' communicative intentions. Moreover, it is currently unknown if the interplay of different modalities might convey communicative and/or informative intentions. For example, a gesture produced in isolation may be perceived as the intent to inform others, whereas the combination of a gesture with gaze alternation between the recipient and an object might be perceived as having a communicative/ostensive function (note that these terms are used in slightly different ways across disciplines). Because most research about primate communication is unimodal (Liebal, Slocombe, & Waller, 2022), we might miss exactly those aspects of communicative interactions that would qualify them as ostensive communication. Addressing these methodological issues is therefore essential before drawing conclusions about interspecific differences.

Second, we do not think that epistemic vigilance is necessary for the evolution of open-ended communication. According to the authors, communication can only become open-ended when it is stable and mutually beneficial: Epistemic vigilance would be thus fundamental to assess the plausibility of what is communicated, reducing deception and allowing communication to thrive. However, as the authors incidentally recognize, there are several other ways in which mutual benefits in communication can be ensured, including genetic relatedness and direct reciprocity. In these systems, deception may be evolutionary disadvantageous and communication reliable even in the absence of epistemic vigilance. Moreover, communication can be seen as a form of cooperative behavior and therefore more general forms of social vigilance commonly used in cooperative interactions may also avoid the collapse of communicative systems when deception occurs. These mechanisms may be present in several species other than humans. Species engaging in complex forms of cooperation, like cooperative hunting and cooperative breeding, or some monogamous species, for instance, need to coordinate

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their actions and may especially rely on reliable trustful exchanges of communicatory signals. Therefore, it is not clear why a "partner choice social ecology" with epistemic vigilance would be a necessary prerequisite to evolve open-ended communication.

Third, the authors should better clarify whether humans, in their opinion, differ from other species in terms of cognitive skills or motivational aspects of communication. In their article, the authors suggest that, through experience with "altruistic human caregivers," nonhuman primates may acquire the ability to recognize the expression of informative intentions. This would suggest that species other than humans do have the cognitive skills required for unleashed expression to emerge, but lack the predisposition to use them. However, in the "right" socio-ecological setting (e.g., a social environment of trust and mutual benefits), also other species may show communicative dispositions similar to human ones and engage in complex forms of communication.

Finally, we consider that the ability to combine meaningful elements into new combinations with novel meanings still better explains how open-ended communication emerges, especially if "stability in the face of incentives to deceive" is effectively achieved in other species as for other forms of cooperation (see above). In the last few years, studies in vocal and gestural communication systems of birds and nonhuman primates have provided evidence of compositionality – a property that had also long been considered one of the hallmarks of human communication. Campbell's monkeys (*Cercopithecus campbelli*), for example, can combine specific alarm calls into new vocalizations with a novel meaning (Arnold & Zuberbühler, 2006, 2008), whereas Japanese great tits (*Parus minor*) react differently to single notes and their combinations (Suzuki, Wheatcroft, & Griesser, 2016). Similarly, chimpanzees (*Pan troglodytes*) may compositionally recombine gestures with signals across different modalities (see Amici, Oña, & Liebal, 2022). Therefore, compositionality may be really a key factor for the emergence of open-ended communication.

Overall, we argue that accounting for combinatorial and multimodal aspects of communication in other species is necessary to understand the complexity of their communication systems, before suggesting major differences with human means and modes of expression. Through mechanisms other than epistemic vigilance, individuals in other species can reliably communicate with each other, and some may compositionally recombine meaningful elements – a crucial property, after all, for the evolution of open-ended systems.

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The evolutionary roots of goal-directed mechanisms: A communication account

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Abstract

Unleashed expressions for cooperation are mainly based on the expected perceptual effects of behaviours and not the behaviours themselves. From an evolutionary viewpoint, this goal-directed mechanism allows for a comprehensive story for the theory proposed by Heintz & Scott-Phillips. Over the past 2 million years, this situated mechanism has been reused for tool use and the language development for hominids.

Similar to art, tool use and language, cooperation–communication from unleashed expressions represents a defining feature of human species. This fundamental issue was very well embraced by Heintz & Scott-Phillips (H&S-P) in their suggestion that human communications come from an interrelated collection of cognitive capacities devoted to the expression and recognition of informative intentions. The goal of such cognitive capacities is social adaptation in human cooperation. For example, the recognition and interpretation of body movements of others can form human expressions and the core of shared human interactions. In teaching situations, such as learning dance, the teacher can trigger unleashed expressive behaviours to deliver her or his message to the learner. I agree with this role of unleashed actions for cooperation, but the described predictive behaviour mechanism underlying such communication is misinterpreted and lacks two essential prerequisites: grounded cognition and neuronal-reuse mechanisms.

The main delusion of the target article comes from the assertion that human communication and cooperation should come from only the understanding of bodily states, and not from the expected perceptual effects of these movements (Badets, Koch, & Philipp, 2016; Kunde, Weller, & Pfister, 2018). In this view, it is important to emphasize that such communication comes from a grounded mechanism and, more precisely, a situated account. For Wilson (2002), cognition involves perception and action mechanisms, but it crucially includes the context of a real-world environment. From this perspective, perceptual information from the environment and generated from actions themselves support online cognition, especially for humans while holding a conversation (see also Barsalou, 2008). Accordingly, Pickering and Garrod (2013) suggested that, during a dialogue between

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two persons (A and B), there is a shared cognition between the perceptual information about the speech during the production of words-sequences (language production by A) and the processed information during the understanding, from a semantic level, of these words-sequences by B. For this perceptual–alignment hypothesis, the expected perceptual effect of mouth movements should represent the cognitive base in which expected information from the environment can be updated for human interaction. For unleashed communication, the best anticipative tool that humans possess is a goal-directed mechanism devoted to the processing of relevant expected perceptual effects. Consequently, for communication and cooperation, bodily states could play only a subordinate role.

For a semantic processing account and to dissociate body movements from their generated–expected perceptual effects, we recently developed a paradigm that manages a tool-use task during Arabic number processing (Badets et al., 2017, 2020). In these experiments, participants were required to use inverse pliers, such as French snail pliers, after the processing of small or large numbers. Respectively, such number presentations allow for the processing of a small or large magnitude dimensions that could interact with the movements of the pliers. Specifically, two hypotheses can be supported. First, if small and large number processing efficiently primes the hand movement towards the tool, then faster movements should be observed for the closing and opening hand movements. According to this view, closing and opening movements of the hand correspondingly implicate opening and closing movements of the pliers towards the object that are not relevant for the interaction. Second, if the pliers' movements are more essential during this task, then the interaction with numbers should be observed with the pliers' movements independent of the hand movements. The results confirmed this second hypothesis in revealing that the large number processing slowed the action to perform the closing movement with the tool and, as a result, the opening movement of the hand. Here, the interaction between a person and her or his environment does not come from body movement itself but from the expected perceptual effects of these movements, here the tool action.

From an evolutionary point of view, this tool–semantic interaction reinforces the hypothesis that human cooperation–communication and tool use developed in a conjoint manner, starting approximately 2 million years ago (Larsson, 2015). According to this theory, producing and perceiving sounds created by tool use could have played a crucial role in the development of semantics and communication in humans. For a complete description of this mechanism, Badets and Osiurak (2017) suggested that such an anticipative system has been reused during human evolution. For these authors, "a fundamental principle of the human brain is to recycle an old inherited brain network to permit adaptations to new social and/or environmental constraints" (p. 367). For Anderson (2010), it is indeed more efficient for the brain to reuse an existing neuronal area for new tasks than to evolve new networks. Consequently, to construct or to use a tool, it is highly probable that the sounds of tools have, from an evolutionary viewpoint, constituted the core perceptual information for unleashed human expressions in communication and cooperation. This perspective is speculative but posits the goal-directed mechanism for communicative acquisition for a more representative story in human evolution.

Obviously, it could be argued that claiming human communication and tool use have evolutionarily emerged conjointly (see also Corballis, 2013) affords an interesting hypothesis but lacks convincing detailed cognitive mechanisms. However, I draw attention in the commentary that a well-documented perceptual mechanism (Shin, Proctor, & Capaldi, 2010), and not a body movement mechanism, could characterize a common denominator between the two intertwined domains. Accordingly, during a dialogue, the understanding of the perceptual information of sound sequences could form the shared cognition between two persons. From an evolutionary perspective, it has been easier to reuse sounds of different tools for the emergence of such relevant perceptual information (Larsson, 2015). This goal-directed mechanism could represent the common denominator between tool use and communication and afford a more complete story of the unleashed theory suggested by H&S-P. From this perspective, we could argue that only humans are capable of vocally describing, with great and unleashed details, how they will use a tool to manage future cooperation in real-life episodes. Here, the situated account and the neuronal-reuse mechanism represent indispensable notions for a plausible evolutionary theory.

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Metarepresentation, trust, and "unleashed expression"

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Abstract

Heintz & Scott-Phillips's account of human expression leaves a number of central issues unclear – not least, whether the lack of expression in nonhuman species is attributable to their lack of the relevant metarepresentational abilities, an absence of trust, or a consequence of other factors. In place of their view, we propose a gradualistic account of the origins of human expression.

We ask Heintz & Scott-Phillips (hereafter H&S-P) to clarify several issues related to "ostensive-inferential" communication in the animal kingdom, including the relationship between ostension and contextual interpretation, the role of metarepresentation in communication, and its relationship to enculturation. Because the unclarities we raise indicate problems with their view, we propose an alternative.

H&S-P suggest that a fruitful test of whether other species understand ostension *qua ostension* would be if animals respond differently to the same ostensively produced "informative intention" in different contexts. They predict that enculturated great apes may respond in contextually appropriate ways, because they have had more occasions for "interactions of mutual benefit" (target article, sect. 7, para. 4). We agree that enculturation improves great ape communication. Nonetheless, the context-sensitivity of interpretation is not a good test of ostensive communication. Great apes in the wild interpret gestures in context-specific ways (Hobaiter & Byrne, 2014; Moore, 2014) – suggesting that contextual interpretation is not specific to enculturation. Moreover, claims about whether communication is "ostensive-inferential" are independent of contextual variation in audience responses (Bar-On & Moore, 2017; Wheeler & Fischer, 2012). For this reason, we'd like H&S-P to clarify their view of the relationship between ostension and contextually variant interpretation.

Sometimes the authors claim that what distinguishes ostensive-inferential communication from other forms is that users can independently produce and attribute "informative" and "communicative" intentions (see also Scott-Phillips, 2014). They write that the "cognitive capacities for ostensive communication are foundational, because they unleash expression on a grand scale" (target article, sect. 9, "Conclusion," para. 1). They also claim that object-choice tasks involving chimpanzees are a test of ostensive-inferential communication. Enculturated great apes do perform better in object-choice tasks (Lyn, Russell, & Hopkins, 2010). However, if enculturation makes chimpanzees better at pointing comprehension, it is unlikely that it is because it drives an ability to distinguish between informative and communicative intentions. Studies have shown that small methodological tweaks to these tasks (e.g., placing hiding locations further apart; Mulcahy & Call, 2006) also improve great ape performance. These adjustments seemingly work not because they facilitate independent comprehension of "communicative" and "informative" goals, but because they support sustained attention and prevent apes from acting unreflectively (Berio & Moore, Unpublished manuscript). A more compelling explanation of the great ape gestural data is therefore that all chimpanzees are ostensive-inferential communicators, and understand informative and communicative intent (Berio & Moore, Unpublished manuscript; Moore, 2016, 2017a), but they perform poorly in object-choice tasks because they are inattentive or unmotivated.

If we understand H&S-P's argument correctly, enculturated great apes acquire expectations of mutual benefit, and so trust the information provided by pointers. However, it's unexplained whether or how this facilitates the development of the metarepresentational understanding of communication hypothesized to unleash expression. H&S-P suggest that an understanding of metarepresentations may be widespread in the animal kingdom (footnote 9), although perhaps "enriched" in humans. Is their idea, then, that unenculturated chimpanzees distinguish between "informative" and "communicative" intentions, but remain poor at pointing comprehension only because they lack the trust to interpret humans' messages pro-socially? If so, this seemingly retracts a central claim of Scott-Phillips's earlier work (2014), in which the metarepresentational abilities needed for ostensive-inferential communication are uniquely human.

The extension of metarepresentational abilities to other species also raises further questions. If enculturated apes can acquire expectations of mutual benefit, and if their metarepresentational abilities are already in place, could their communicative abilities also be unleashed? This seems unlikely. Take Kanzi, perhaps communicatively the most sophisticated living nonhuman great ape. His productive communication is limited, although more expansive than in wild apes. While his comprehension is better than his production, it stops developing around the level of a child of 2.5 years (Savage-Rumbaugh, Taylor, & Shanker, 1998). If Kanzi has the relevant metarepresentational abilities, the combination of metarepresentations and expectations of mutual benefit surely do not suffice for unleashing expression. Dogs present another puzzling case, because they excel in object-choice tasks – yet remain limited in what they can understand and express.

We propose that what unleashes expression in humans is not a difference in our metarepresentational abilities. Such abilities are needed for ostensive-inferential communication only in limited ways, and the relevant abilities are within the ken of all great ape species (Moore, 2016, 2017a). Moreover, the development of uniquely human forms of metarepresentation seems to be language-dependent (Berio, 2021a, 2021b; Grosse Wiesmann, Friederici, Singer, & Steinbeis, 2017; Low, 2010; Moore, 2021) and acquired later than basic forms of beliefs (Newen & Starzak, 2020). Nor is what's missing in unenculturated great apes exclusively a matter of trust. Human expression was not unleashed by any radical new mechanism for communication in our species. Rather, what matters is that even enculturated great apes are domain-bound in the ways they use their skills for ostensive-inferential communication.

Wild chimpanzees communicate fluently with a small repertoire of signs (Hobaiter & Byrne, 2014). Nonetheless, in captivity they fail to use this repertoire for solving coordination tasks, because they are poor at projecting existing skills into new contexts, to solve unfamiliar problems (Moore, 2017c). They operate in what Susan Hurley called "islands of practical rationality" (Hurley, 2003), where they can solve specific social tasks without being able to transfer the relevant skills to more general domains. Hurley thinks it is language that bridges these islands in human reasoning. This may be, but something similar also happens in enculturation. Enculturation trains attention and builds trust, but it also expands great apes' hitherto minimal communicative ecology, leading them to discover the possibility of using their communicative abilities in new contexts. This insight arose in phylogeny only after the mechanisms of ostensive-inferential communication. Nonetheless, expression in enculturated great apes remains stalled by their limited working memory, weak analogical reasoning, lack of capacity for syntax, and poor inhibition control and social learning, among other factors.

In phylogeny, a communicative mechanism common to many species (Moore, 2017b) expanded slowly. Many other abilities were relevant to this expansion. This makes expression one of many domains in which human and animal abilities are continuous (Andrews & Monsó, 2021; Laland & Seed, 2021).

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Putting the cart before the horse? The origin of information donation

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Abstract

Heintz & Scott-Phillips propose that the partner choice ecology of our ancestors required Gricean cognitive pragmatics for reputation management, which caused a tendency toward showing and expecting prosociality that subsequently scaffolded language evolution. Here, we suggest a cognitively leaner explanation that is more consistent with comparative data and posits that prosociality and eventually language evolved along with cooperative breeding.

That language is stable despite the incentive to deceive proves that humans have solved the "central problem" for the evolution of communication (Maynard Smith & Harper, 2003). We humans indeed show a cooperative attitude, which includes the *a priori* mutual expectation of cooperative intent between communicators (Grice, 1989), and, as Heintz & Scott-Phillips (H&S-P) rightly emphasize, extends well beyond communication: It is also reflected in teaching, and in fact permeates almost all our social behavior and cognition (see also Burkart, Hrdy, & van Schaik, 2009).

According to H&S-P, our partner choice ecology can explain these developments (Fig. 1, top row) because the strong ecological reliance on cooperation makes it vital to be chosen by others as a cooperation partner. The latter can be maximized by engaging in reputation management, that is, advertising one's own cooperativeness or prosociality to potential partners, which according to H&S-P is the result of a highly complex cognitive mechanism, that is, Gricean communicative pragmatics. Once evolved in the context of partner choice, this mechanism then would have become available in all the contexts where it is conspicuous today, including language.

Among nonhuman primates, partner choice is likewise widespread but tellingly, it is not based on cognitive book-keeping mechanisms (Schino & Aureli, 2009) or reputation management (e.g., in chimpanzees: Engelmann, Herrmann, & Tomasello, 2012), most likely *because* they lack language (van Schaik, 2016). In fact, reputation management is strikingly absent even in marmoset monkeys, who are renowned for their high levels of cooperation and intentional prosociality (Burkart & van Schaik, 2020; *sensu* Townsend et al., 2017) and do engage in partner choice (Brügger, Willems, & Burkart, 2021). When adult marmoset helpers were alone with immatures from their group who were not their own, they would not stop helping but even increased their food sharing tendency (Brügger, Kappeler-Schmalzriedt, & Burkart, 2018). This clearly confirmed that their motives were genuine and strong proactively prosocial rather than instrumental and serving to manage their reputation.

The high prosociality of marmoset monkeys is thus clearly not a consequence of partner choice, *pace* H&S-P. Comparative data directly comparing prosociality in a group-service paradigm among a large number of primate species (Burkart et al., 2014; Verspeek, van Leeuwen, Laméris, Staes, & Stevens, 2022) show that prosociality is best explained by reliance on allomaternal

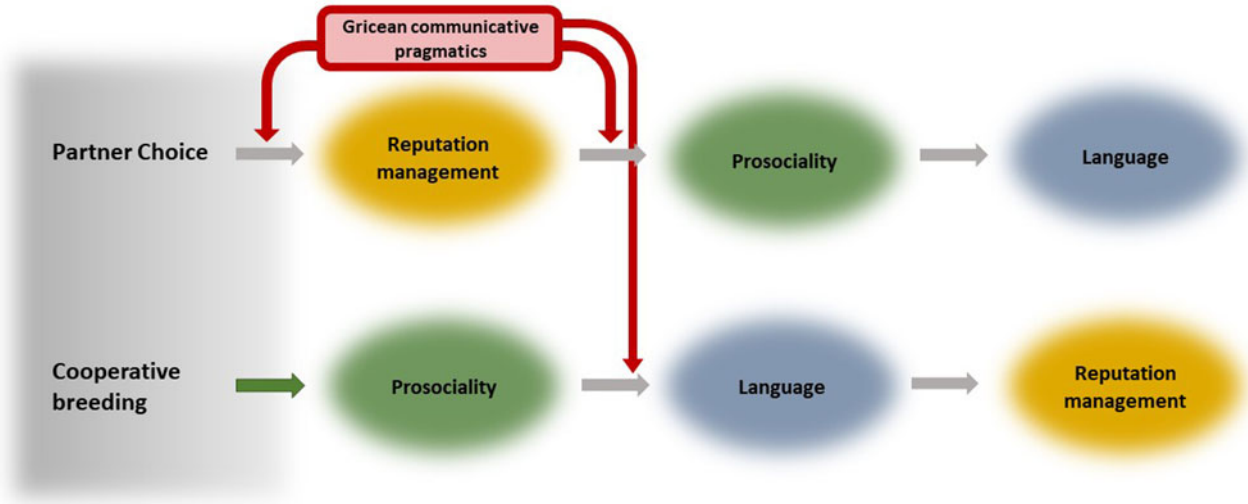

Figure 1 (Burkart et al.). Sequence of events proposed by H&S-P (top row) and in the current commentary (bottom row). The gray shading represents the socio-ecological background of our ancestors. Both proposals agree that language could only emerge once fundamental prosociality was established, but H&S-P argue it is the result of cognitively demanding Gricean communicative pragmatics (red arrow) whereas the bottom row points at comparative evidence (green arrow) that shows high allomaternal care and cooperative breeding directly facilitate the emergence of prosociality without Gricean communicative pragmatics as a precondition.

care, or cooperative breeding (when individuals other than the parents significantly help rearing offspring). Humans are cooperative breeders too (Hrdy, 2009), and when directly comparing them with the same group-service paradigm, they fall right on the nonhuman primate regression line (Burkart et al., 2014). Prosociality in humans thus does not require a uniquely human mechanism, and the claim of a cognitively demanding explanation as in H&S-P appears unwarranted (which is a more widespread problem; Adriaense, Koski, Huber, & Lamm, 2020).

Based on this primate background, we therefore propose a more parsimonious sequence than advocated by H&S-P (Fig. 1, bottom row). When our ancestors started to engage in cooperative breeding, this was accompanied by an increase in proactive prosociality, consistent with the general primate pattern (Burkart et al., 2014). This general prosocial attitude allowed the emergence of low-cost, honest cooperative signaling and thus paved the way for language evolution in our great apelike ancestors (Burkart et al., 2009, 2018, 2022). Only once language was in place, however, did reputation management become necessary on a grand scale because without, only those directly involved will know that a specific partner was non-cooperative in the past. Crucially, reputation management is only needed when one's reputation of being a good or bad collaborator can actually spread widely across a large and loose social network. Language can provide exactly this, and only when there exists a risk that deceptive behavior can be broadly advertised through gossip to everyone will it reinforce a strong concern for reputation in all group members (see also van Schaik, 2016, p. 331). In sum, only with language could a concern for reputation become strong enough to install a general prosocial attitude as suggested by H&S-P. However, because language *per se* requires such an attitude, which moreover can easily emerge in the context of cooperative breeding, this is unlikely.

Among cooperatively breeding monkeys (marmosets and tamarins), prosociality is most evident in their propensity to provide and offer food to others. However, and particularly important for the proposal above and language evolution in general, this propensity also extends toward sharing information (reviewed in Burkart, Guerreiro Martins, Miss, & Zürcher, 2018, Burkart et al., 2022). For instance, frequent vocalizations function to provide information useful to others, in particular about predators and food (Brown, Almond, & van Bergen, 2004), thus satisfying the definition of "expression" by H&S-P (target article, sect. 2, para. 1). Food-offering calls in tamarins are given for young immatures to offer food to them, but to older immatures only to indicate the location where the immatures can learn to extract food, thus engaging in teaching-like behavior (Rapaport, 2011; Troisi, Hoppitt, Ruiz-Miranda, & Laland, 2018). In fact, several marmoset and tamarin species show remarkable sensitivity to the skill level of immatures when deciding whether to advertise the presence of food and share it with them (Dell'Mour, Range, & Huber, 2009; Humle & Snowdon, 2008; Moura, Nunes, & Langguth, 2010; Sehner, van Schaik, & Burkart, 2022; Snowdon & Roskos, 2017). Critically, such teaching-like scaffolding was also reported during the vocal development of immatures (Chow, Mitchell, & Miller, 2015; Takahashi et al., 2015, 2017).

Among adults, the cooperatively breeding marmosets are more likely than independently breeding primates such as capuchin monkeys or macaques to use gaze as coordination smoothers when engaged in joint action with a partner (Miss & Burkart, 2018; Miss, Meunier, & Burkart, 2022). Although cooperatively breeding groups are closely related on average, immigration and emigration events are frequent and group membership, rather than mere relatedness, determines helping (De Oliveira Terciero, Willems, Arruda, Burkart, & Araujo, 2022). Overall, it thus very much seems that to thrive in their socio-ecological niche of cooperative breeding, marmosets and tamarins have evolved a convergent interaction engine (Levinson, 2006) that resembles the one of humans in many relevant respects (Burkart et al., 2022).

Our complementary account does not argue that partner choice and reputation management are not crucial in the human social ecology. However, the cooperative breeding of our ancestors offers a more plausible point of departure: Great apelike organisms who were more prosocial than extant great apes and had a greater inclination toward information donation.

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Immatures growing up in such an interdependent ecology would have acquired much of the cognitive infrastructure described by H&S-P (Hrdy & Burkart, 2020) before reputation management evolved.

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No unleashed expression without language

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Abstract

While the metarepresentational structure of ostensive communication may explain the unleashing of human expression, it neither explains the open-endedness of the thoughts expressed/communicated, nor how the multiply embedded nature of the metarepresentational structure invoked arose. These both require the recursivity of human language, a capacity which must be distinguished from external (public) languages and their use in communication.

Heintz & Scott-Phillips (H&S-P) give a compelling account of how expression was "unleashed" in human evolution, based centrally on the metarepresentational structure of ostensive communication, developed within a partner choice social ecology where there is selective advantage for behaviour that is cooperative. It is claimed that this structure, comprising a communicative intention to provide receivers with evidence of an intention to inform them, enables communication to be "about anything at all" (domain general) while meeting the evolutionary constraint on communicative systems of being statistically mutually beneficial to producer and receiver. The open-endedness of human expression/communication is *not* based on the open-ended combinatorial possibilities of human language: "Natural languages, in all their combinatorial richness, are a means by which we *exploit* unleashed expression, rather than being the source of unleashed

expression" (target article, sect. 1, para. 3) and so, they conclude, the evolutionary emergence of language must have followed, rather than preceded, the evolutionary emergence of ostensive communication.

While welcoming the foundational role given here to cognitive pragmatics, I think that there are two important explanatory gaps in this account and that language (in all its "combinatorial richness") is a crucial component of both. First, open-ended (unleashed) expression/communication entails open-endedness of that which can be expressed/communicated, that is, the thoughts and attitudes that are the content of our informative intentions. Here, then, is the first explanatory gap: How is it that human informative intentions can be about anything at all? Sperber (2000), whose ideas infuse the work of H&S-P, emphasizes that human *non*-metarepresentational mental representational capacities have rich and indefinitely varied contents, indicative of "a system of internal representations that is – or is equivalent to – a mental language with compositionality and recursion" (Sperber, 2000, p. 119). The word "language" is apposite here: The open-ended content of our informative intentions depends on our recursive linguistic ability, albeit so far manifest in a *language of thought*, yet to be externalized into a public system usable for communication.

Second, the pivotal metarepresentational structure of ostensive communication itself entails a cognitive capacity for recursive embedding – of representations within representations. The structure requires (at least) four levels of metarepresentation: 'Mary intends that [Peter believes that [she intends that [he believes that [the berries are edible]]]]'. In related work by Scott-Phillips and colleagues, the orders of metarepresentation humans are shown to manipulate run to seven or eight orders (O'Grady, Kliesch, Smith, & Scott-Phillips, 2015; Scott-Phillips, 2015). Here, then, is the second explanatory gap: How did this recursive property of our mindreading (metarepresentational) capacity arise? As suggested above, even without *meta*representation, our mental representational system is a language – open-ended, recursive, semantically compositional. Our capacity to represent representations has to be at least as rich as the representations it represents, and, citing Sperber (2000, p. 119) again: "the only cost-effective way to achieve this is to have the expressions of the object-language do double service as expressions of the metalanguage." By "language" what is intended here is a mental representation system that manifests a capacity for recursive (self-embedding) structures harnessed to a conceptual–intentional system. So, again, the human language capacity, as manifest in thought, specifically here as informative intentions, is presupposed by the metarepresentational structure of ostensive communication.

This is not to say that employment of a recursive language of thought is sufficient to explain the human metarepresentational capacity. A basic requirement is that representations (with their content properties) are apprehended as things in the world, which, along with dogs, trees, and rain, can be represented, but recursivity is another necessary component of the capacity.

The word "language" as used in the evolutionary literature on communication (and elsewhere) is highly polysemous, including (a) the human language capacity, (b) public languages, (c) language use, (d) linguistic communication, and (e) linguistic stimuli. H&S-P's topic is human communication and when they talk of "language" they mean those public languages that we employ in linguistic communication, with their cultural histories of usage conventions and innovations. And when they talk of the "language-ready" brain (target article, sect. 6, para. 8), they mean the evolutionary stage at which the human mind/brain was ready to use language *for communication*, thereby massively enhancing the range and fine-grainedness of the expression of informative intentions. However, this "language" talk can become misleading: H&S-P say they are providing an "adaptationist and cognitive answer to the 'Why humans?' question about language origins, that is clearly different to prominent biolinguistic approaches …" (target article, sect. 1, para. 3). But these are two quite different pursuits: While the biolinguistic programme focuses on the origin of the human language capacity, H&S-P focus on the conditions that led to the use of languages in communication.

Linguistic recursion grants us enormous computational power; Fitch (2010, p. 90) says "[it is] the means by which finite brains achieve unfettered potential expressivity." Arguably, this is the primary focus of an evolutionary account of language, with its use in communication and the ensuing cultural evolution of usage conventions as secondary. Work within the biolinguistic programme on the origins of human language unpicks the "mosaic" of components that make up language in the broad sense and isolates, as specifically linguistic, the simple but powerful recursive operation "Merge," responsible for the hierarchical self-embedding structures of human syntax. It seems to have arisen from some rewiring of the brain, whether an effect of increased brain size or a chance mutation, and proved so advantageous to planning and thinking that it was selected for as an instrument of thought (Boeckx, 2013; Chomsky, 2010; Hauser, Chomsky, & Fitch, 2002; Reboul, 2017), only subsequently exapted for use in communication. Linguistic syntax isn't designed for communicative purposes: It disallows many structures that are perfectly interpretable and so of potential communicative utility (Carston, 2015). There is mounting evidence that syntax is optimized to satisfy its interface with conceptual–intentional systems, rather than its interface with the sensorimotor systems that enable its externalization (in various forms) for use in communication, a secondary function (Chomsky, 2010).

According to H&S-P, humans were not "language-ready" until they became ostensive communicators. I would say that a species is not "ostensive-communication-ready" before it has the capacity of linguistic recursion.

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From the pragmatics of charades to the creation of language

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Abstract

We agree with Heintz & Scott-Phillips that pragmatics does not supplement, but is prior to and underpins, language. Indeed, human non-linguistic communication is astonishingly rich, flexible, and subtle, as we illustrate through the game of charades, where people improvise communicative signals when linguistic channels are blocked. The route from non-linguistic charade-like communication to combinatorial language involves (1) local processes of conventionalization and grammaticalization and (2) spontaneous order arising from mutual constraints between different communicative signals.

We applaud Heintz & Scott-Phillips's (H&S-P's) argument that the gulf between human communication and that of other animals arises primarily from the astonishing power of human social and pragmatic reasoning. We agree, too, that the unique flexibility and sophistication of natural language, in contrast to nonhuman animal communication systems, arise from a suite of cognitive abilities underlying such reasoning, rather than from any human-specific "universal grammar," encoding abstract syntactic knowledge.

From a pragmatics-first perspective, however, the question remains: What is the route from non-linguistic communication, driven by a powerful "pragmatic engine," to the creation of the astonishing complexity of full-blown combinatorial language? In this commentary, we argue that the game of charades provides a window not only into the nature of human pragmatic inference, but also into how linguistic systems can begin to emerge through a process of conventionalization (Christiansen & Chater, 2022). We suggest, moreover, that processes of cultural evolution, without further biological evolution, can lead to the creation of a full-blown language, with the spontaneous, although partial, emergence of complex syntax.

To fix our intuitions, consider a charade aimed at conveying *The Hound of the Baskervilles*, first by miming the act of peering through a magnifying glass (hoping to bring to mind Sherlock Holmes) and then imitating a dog-like baying and biting action (to bring to mind the hound). While H&S-P focus on the complementarity between mechanisms for expression and interpretation of communicative signals, we stress that successful integration of such mechanism also requires communication to be a collaborative process (see Brennan & Clark, 1996; Clark, 1996; Misyak & Chater, 2022). Thus, miming looking through a magnifying glass will only be taken to convey Holmes if the existence of the relevant association is common to all participants. Similarly, the relevance of Holmes to the target book title requires knowing that *The Hound of the Baskervilles* is a Sherlock Holmes mystery. If the observer doesn't know this then the communicative signal will likely fail. More generally, successful improvised communication requires all parties implicitly *agreeing*, given their common knowledge and goals, on a particular mapping between signals and meanings. Whatever the actor intends the charade to convey, the charade only succeeds in doing so if everyone involved interprets the charade in the same way (or closely enough for their communicative goal to be achieved). The capacity for establishing common ground, and engaging in joint reasoning in light of that common ground, is arguably crucial for coordinated social behavior of all kinds, and it is particularly central to the coordination of signal-meaning mappings underlying communication.

Charades are, of course, typically one-offs; and the charm of the game is the continual need for ingenuity and creativity from all players. But if the game is played repeatedly by the same people, conventions can rapidly become established. Thus, the magnifying glass gesture may become increasingly simplified and stylized, and its use broadened to convey detectives of all kinds, crime stories and movies, actual crimes, and so on. More generally, each new charade can build, in arbitrarily creative ways, upon the common ground of prior charades.

We have recently argued (Christiansen & Chater, 2022) that the gradual conventionalization of charades captures, in miniature, some crucial aspects of the cultural evolution of language. The linguistic signal becomes increasingly standardized and simplified over time; and the meanings conveyed can both sprawl in many directions. Thus, everyday words, such as *game*, *set*, or *shallow* have endless interlocking meanings but, as Wittgenstein (1953) stressed, with no common definitional core (e.g., consider *shallow waters*, *slopes*, *boats*, *bowls*, *spoons*, *thoughts*, etc.).

The process of erosion and simplification of form, and broadening of meaning, parallels the process of grammaticalization widely observed in comparative and historical linguistics (e.g., Bybee, Perkins & Pagliuca, 1994; Hopper & Traugott, 2003). Grammaticalization is the process by which some "content" words become so stereotyped in use, and so "bleached" of meaning, that they take on purely grammatical functions. Thus, for example, the content verb *to will* has in English also taken on a purely grammatical function (e.g., *I will eat* shifts from signaling an intention to eat, which must necessarily happen in the future, to a pure future-tense marker, irrespective of intention, as in *the temperature will rise*). Processes of simplification and erosion can also cause distinct words to collapse together, to create morphological complexity (thus, forms of *to have* have joined with verb stems to mark the future tense in many Romance languages) (Coleman, 1971; Fleischman, 1982). The creation of grammatical words and functions and the increasing standardization of their use provides the starting point for complex syntactic patterning.

The linguistic signal consists of recycled parts with partially conventionalized meanings, although always with the possibility of new and often highly creative uses (Contreras Kallens & Christiansen, 2022). Thus, we continually extend meanings using rich pragmatic inference, such as in metonymy (e.g., *take this drink to the pancakes by the window* – where *the pancakes* substitutes for *the customer with the pancakes*) and extend

meanings across domains by elaborate and partially consistent processes of metaphor (e.g., famously mappings between physical and mental objects and transportation [Lakoff & Johnson, 1980], so that we can give a person an idea, leave a worry behind, have it at the back of one's mind, etc.). Thus, the creative charade-like process remains at the heart of linguistic communication, but built on a system of conventions that has become entrenched over generations of language use.

The process of grammaticalization is, we suggest, part of the broader process of cultural evolution of language – by which linguistic forms and their meanings are continually reshaped by the multiple constraints of our perceptual, motor, and cognitive machinery, as well as the continually changing communicative challenges that we face (Christiansen & Chater, 2022). Moreover, different linguistic conventions will continually be shaping each other, through processes of similarity, analogy, and competition. If H&S-P are right, and cognitive pragmatics is prior to, and underpins, linguistic communication, it is natural to consider the patterns exhibited by natural languages not as arising from a distinctive special-purpose biological endowment for syntax (Berwick & Chomsky, 2016), but through a process of spontaneous order over generations of cultural evolution (Chater & Christiansen, 2022).

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Cognitive pragmatics: Insights from homesign conversations

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Abstract

Homesign is a visual–gestural form of communication that emerges between deaf individuals and their hearing interlocutors in the absence of a conventional sign language. I argue here that homesign conversations form a perfect testcase to study the extent to which pragmatic competence is foundational rather than derived from our linguistic abilities.

Compared to the longstanding histories of spoken languages, all known signed languages are considered to be young languages (Meir, Sandler, Padden, & Aronoff, 2010). For this reason, the study of sign languages and the social mechanisms through which they evolve provides a unique opportunity to shed light on the following questions: Which aspects of our communicative abilities are present from the very earliest stages of language emergence; and, by extension, which aspects of our cognition have been selected for as language evolved?

From the 1970s until recently, sign language linguistics focused almost entirely on sign languages that have arisen as deaf people have congregated in the context of government institutions for the deaf, primarily deaf schools (McBurney, 2012). Oftentimes such sign languages have been around for several centuries, such as Old French Sign Language and its descendent American Sign Language, but in a few cases sign linguists have been able to track the emergence of new sign language from the very start (Senghas, Kita, & Ozyurek, 2004). From 2005 onward, the field has started to investigate the many sign languages to have emerged in rural areas with a high incidence of deafness (Zeshan & de Vos, 2012). In a handful of cases, such complex gene-culture coevolution has led to longstanding rural signing communities, but in most cases the unique circumstances that lead to emergent signing varieties do not allow them to persist across multiple generations (Mudd, de Vos, & De Boer, 2020).

Emergent signing varieties are often thought to originate in homesign systems (Senghas et al., 2004); that is to say, one-off communication systems that begin and end with just one deaf individual who co-creates a visual–gestural form of communication with their hearing relatives and friends in the absence of a signing community (Goldin-Meadow & Brentari, 2017). The homesign literature thus far has focused mostly on the genesis of linguistic structures and the cognitive consequences of long-term language deprivation (see Motamedi, Schouwstra, Smith, Culbertson, & Kirby, 2019, for a recent overview). Most notably, Gagne and Coppola (2017) found that the four Nicaraguan homesigners who participated in their study were unable to pass standard false belief tasks that require the ability to predict other's beliefs and behaviors. When taken at face value, these findings are problematic for any perspective on language evolution that views our pragmatic abilities as foundational to human language (cf. the target article; Levinson, 2019). In the remaining paragraphs of this commentary, I provide an alternative view based on data from Bali: that, in everyday conversation, homesigners may demonstrate ample evidence of mentalizing abilities.

Crucially, most work on homesign has been based on small-scale case studies elicited from a small number of deaf individuals in Nicaragua and the United States. The data discussed here stem from the newly created Balinese Homesign Corpus, which includes, among other things, conversational data from 14 homesigners and their hearing interlocutors across the province of

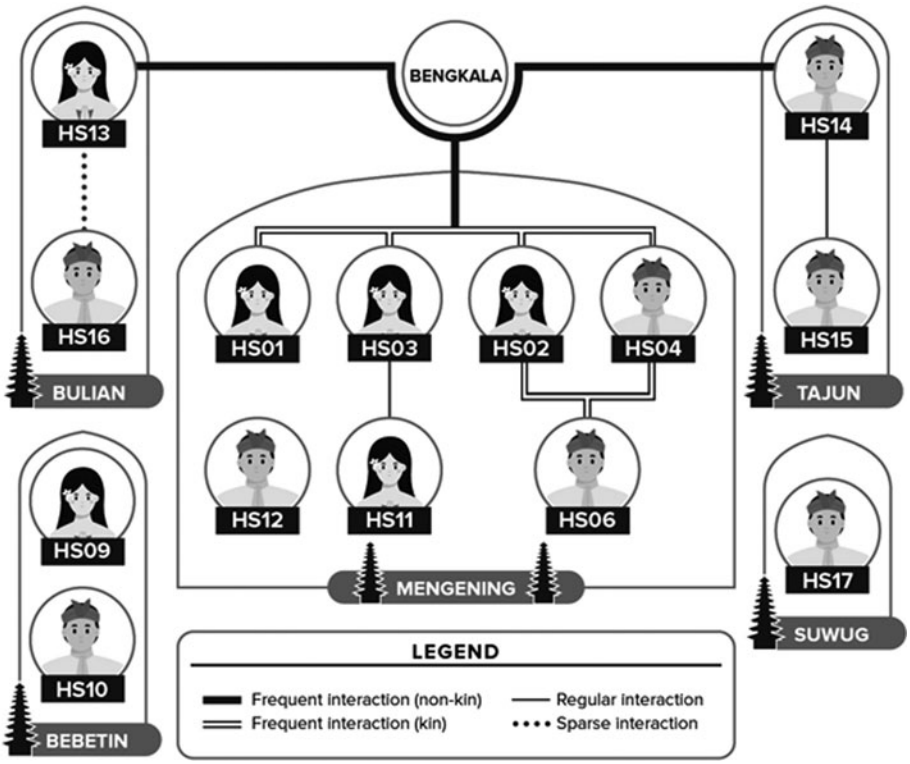

Figure 1 (de Vos). Social interaction patterns of all 14 homesigners recorded for the Balinese Homesign Corpus, including data from the villages of Bebetin, Bulian, Suwug, and Tajun as well as their relation to the Kata Kolok signing community in Bengkala.

Buleleng, Bali (see Fig. 1). This area of Bali is of particular value for understanding how homesign may jumpstart the grammars of emergent signing varieties, because it is also home to Kata Kolok, a rural sign language that has been acquired naturally by at least six subsequent generations (de Vos, 2012; Lutzenberger, 2022).

While there is plentiful evidence for grammatical complexity in homesign systems, the homesigners and their interlocutors in the Balinese Homesign Corpus communicate using the full range of semiotic strategies available to them (see also Safar, 2019). An important communicative strategy to ground the meaning of their utterances builds on the local gesture culture (Nyst, 2019). This includes highly conventionalized forms of quotable gestures, also known as emblems, being co-opted for more diverse meanings. For example, the Balinese conventional gesture to insult men by comparing them with female genitalia has actually attained a neutral, normalized meaning of "woman" or "wife" in Kata Kolok (Marsaja, 2008). As has been well-documented for spoken languages, such a semantic shift is engendered by interlocutors using this form in conversational settings in which the new intended meaning can be derived from the situational context.

Homesigners also ground their utterances in what they understand to be shared knowledge between themselves and their hearing interlocutors by inventing novel signs based on cultural practices. For example, the way a particular fruit is normally peeled or cut becomes a way of referring to that fruit. Similarly, homesigners will point to locations that they know their interlocutors will make similar associations with, such as pointing to someone's homebase to refer to that individual. Lastly, in conversational settings, deaf homesigners will monitor their interlocutor's understanding of what is being expressed by responding to situations in which positive feedback by way of nodding is discontinued, or in which non-understanding is signaled through a puzzled facial expression by their interlocutor. Subsequent utterances are tailored to deal with the source of communicative trouble, supplementing their initial expression with additional forms to make themselves understood (Safar & de Vos, forthcoming). All in all, our observations of homesigners in their everyday social interactions indicate an ability to capitalize on semiotic resources to help build rapport with their interlocutors and re-establish mutual understanding when needed. This means that prior indications of the limited mentalizing abilities of homesigners may be indicative of a task effect, or alternatively a result of the extent to which their hearing interlocutors in Bali engage with homesigners using visual communication from the get-go.

The remaining questions then are to understand the extent to which the quality of social interaction and subsequent cultural learning boost or impede pragmatic competence, and by extension, the extent to which such abilities have indeed been shaped by human evolution. The Balinese Homesign Corpus represents the world's first extensive collection of homesign conversations, which enable us to pursue fundamental questions on the nature and origins of cognitive pragmatic competence.

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Teaching unleashes expression

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Abstract

I propose that the evolution of teaching has been central in extending manipulative intentions. Demonstrating may be the evolutionarily first form of expression that is productive, ostensive, and involves informative intention. Demonstration also involves theory of mind. Then pantomime goes a step further and involves a communicative intention. Pantomime can thereby function as displaced communication used for more complex expressions.

I propose that the evolution of teaching has been a central factor in unleashing expression. Heintz & Scott-Phillips (hereafter H&S-P) argue that extending manipulative intentions is the main evolutionary mechanism behind the expansion of human communication (sect. 3 in the target article). In my opinion, analyzing the evolution of teaching may help us understand what drove the expansions of intention from (a) intentional action to (b) intentional action on others, then to (c) action based on informative intention and finally to (d) action based on communicative intention. I focus on the roles of demonstration and pantomime in the evolution of teaching.

The basic level is intentional action. When a young chimpanzee watches an adult cracking nuts, the young understands the adult's intention to obtain the nut and tries to emulate the actions (Tomasello, 1999), that is, obtain the same result for itself.

The next step is intentional action on others. The example used by H&S-P of an orangutan mother using the offspring as a physical tool is, in my opinion, very odd. Much more natural examples are found in elementary teaching situations, for example, when a chimpanzee mother changes the position of a hammerstone in the hand of her young so that it can better hit the nut (Boesch, 1991) or when a father ties the shoelaces of his daughter. This involves a simple form of theory of mind because the "teacher" acts on the assumption of a goal of the "student."

The third step – action based on informative intention – is achieved in teaching contexts by *demonstrating*. This involves intentionally showing somebody else how to perform a task or to solve a problem. It is a central element in "natural pedagogy" and seems to be present in all human societies (Csibra & Gergely, 2009). Demonstrating, as separate from ordinary action, may be the evolutionarily first form of expression that is productive, ostensive, and involves informative intention (Gärdenfors & Högberg, 2017, 2021).

Two central aspects of demonstration that separates it from mere action are that (1) the demonstrator makes sure that the learner *attends* to the series of actions, and (2) the demonstrator's *intention* is that the learner can perceive the right actions in the correct sequence (Gärdenfors, 2017, 2021). As regards criterion (2), Csibra and Gergely (2009, p. 149) point out that "human communication is often preceded, or accompanied, by ostensive signals that (i) disambiguate that the subsequent action (for example, a tool-use demonstration) is intended to be communicative and (ii) specify the addressee to whom the communication is addressed."

Criteria (1) and (2) entail that demonstrating builds on elements of a theory of mind both for the teacher and for the learner (Gärdenfors & Högberg, 2017, 2021). Unfortunately, these components are disregarded by H&S-P. The most efficient (and the typical) way to satisfy (1) is that the teacher and the learner achieve *joint attention*, but other means of making the learner attend are also possible. Criterion (2) presumes that the teacher understands the lack of knowledge in the learner and that the learner experiences that there is something to learn.

The final step – action based on communicative intention – is achieved by *pantomime*. In many teaching situations, the teacher cannot perform the action that the learner is supposed to perform because then the learning opportunity is foregone. For example, teaching somebody how to knap a Levallois flake when only one core is available cannot be made by demonstration because once the flake is made the earlier state of the core cannot be reproduced. The main difference between pantomime and demonstration is that in pantomime the mimer performs the movements of the actions in the task without actually performing the actions.

Understanding the intention of a pantomime is cognitively more demanding than understanding a demonstration. The meaning of a demonstration is clear as soon as the addressee understands that it is performed in a teaching context. For a pantomime, the addressee must also understand that the teacher intends the pantomime to *stand for* a real action and that the teacher intends the addressee to realize this. Unlike demonstration, pantomime is thus not primarily an action, but a representation of an action. In that sense, pantomime is more ostensive than demonstration. Pantomime fulfills the following criterion (Zlatev, Persson, & Gärdenfors, 2005):

Communicative sign function: The agent intends for the act to stand for some action, object, or event for an addressee, and for the addressee to realize that the act is a representation.

Pantomime therefore involves an intention to communicate and it may be the evolutionarily earliest form of action involving such an intention. Once the communicative function of pantomime has been established, it can be exapted to other forms of

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communication, such as planning and story-telling. In such uses pantomime becomes a displaced form of communication (Gärdenfors, 2017; Hockett, 1960).

The upshot is that following the evolution of teaching along the steps outlined here may reveal a lot about how various forms of expression were unleashed. The expansions of the activities and cognition involved in going from one level of teaching to the next are quite natural and it thus provides a motivation for the embedded forms of manipulative intention presented by H&S-P. It also shows how the different forms build on increasing demands on a theory of mind. I am not claiming that the evolution of teaching is the only way to understand the different forms of manipulative intentions, but the analysis outlined here shows one prominent evolutionary road – perhaps the major one.

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Conflict of interest. None.

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Loosening the leash: The unique emotional canvas of human screams

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Abstract

We use screams to explore ideas presented in the target article. Evolving first in animals as a response to predation, screams reveal more complex social use in nonhuman primates and, in humans, uniquely, are associated with a much greater variety of emotional contexts including fear, anger, surprise, and happiness. This expansion, and the potential for manipulation, promotes listener social vigilance.

Heintz & Scott-Phillips (H&S-P) present an evolutionary and cognitive account of the uniquely open-ended and enormously rich expressive diversity of humans, facilities which, they contend, are underpinned by an interrelated suite of cognitive capacities that serve in the production and recognition of informative intentions. They maintain that while natural selection in nonhuman species constrains communication to "narrow domains of statistical mutual benefit," the cognitive facilities they identify "unleash" human expression. We suggest that these same cognitive devices may be relevant to the human expansion of several classes of nonverbal vocalizations used in far more restricted contexts in other species.

Screams are a particularly interesting category of vocalizations to explore some of the ideas presented in the target article. Across a broad range of species, these vocalizations show remarkable evolutionary stability with respect to acoustical form and function. When in the grasp of a predator, many species of animals scream (Caro, 2005; Högstedt, 1983; Wise, Conover, & Knowlton, 1999). Screams appear to have evolved, originally, to startle the predator and increase the probability of the caller's escape. As a natural example of the well-studied acoustic-startle response (Davis, 1984), the sonic features of screams employed in this context elicit a particular affective state in the predator. The vocalizations are, at this stage, expressive, in H&S-P's sense, because they serve to generate a "psychological reaction" in the predator.

However, in some highly social nonhuman primate species, the contexts in which screams occur, and their acoustical forms, have diversified over the course of evolution, shifting from limited predator–prey interactions to more complex and nuanced agonistic conflicts relating to the dominance relationships among conspecific group members (reviewed in Gouzoules, 2005; Gouzoules & Gouzoules, 2011). These screams recruit aid from allies, usually matrilineal kin. The vocalizations are communicative, in H&S-P's sense, in that they are stimuli (more precisely, signals) that function to generate a reaction by the means of stimulating complementary mechanisms of interpretation within the agonistic context. Evidence points to the conclusion that monkeys appear to recognize that production of vocalizations like screams follows rules of sender–receiver directionality that correspond to the dominance hierarchies in their social groups (Cheney & Seyfarth, 2007, p. 268). The cognitive processes these nonhuman primates use to perceive conspecific screams are considerably more complex than in the predator-startle context (reviewed in Schwartz, Engelberg, & Gouzoules, 2020). Chacma baboons (*Papio ursinus*), for example, show particular interest when they hear played back sequences of dominance grunts from a subordinate individual followed immediately by submission screams from a dominant group member, an occurrence that would characterize a rank challenge (Bergman, Beehner, Cheney, & Seyfarth, 2003). Upon hearing a conspecific scream, monkeys seem to make use of a mental representations of the identity of the vocalizer and the nature of a social interaction, and they contextualize this information within their knowledge of kinship and dominance relationships among individuals (for additional details and examples, see Gouzoules, 2005).

In our species, an evolutionarily conserved mammalian vocal–emotion system is augmented by a speech articulation complex that includes direct neural connections from motor cortex to the musculature controlling the larynx, yielding a "dual pathway vocal production" system (reviewed in Bryant, 2021). The ramifications for human affective signaling are immense because this system allows substantial emancipation of emotion from the

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evolutionarily original production context of vocalizations. In humans, uniquely, screams are associated with a much greater variety of emotional contexts including fear, anger, surprise, and happiness (Anikin, Bååth, & Persson, 2018; Engelberg, Schwartz, & Gouzoules, 2021; Frühholz, Dietziker, Staib, & Trost, 2021). These emotional displays do not ineluctably represent automatic embodiments of internal states: Humans are endowed with remarkable capacities for the volitional and flexible control of expressions, abilities aligned with those allowing speech (Fitch & Zuberbühler, 2013). As a result, signalers are likely to produce natural expressions in a variety of socioemotional contexts, some of which derive primarily from internal states, while others are driven more by cultural norms or strategic motivations, including manipulation (Scherer, 2013). Humans can use screams voluntarily and deliberately to attract attention and, also, spontaneously and involuntarily when the caller is threatened, startled, or even experiencing sudden joy, and it is not always possible to distinguish these two situations (Engelberg et al., 2021). Of note, the degree to which listeners accurately perceive different emotions from screams varies across contexts which, given the evolutionary saliency of screams (they almost inevitably attract attention), places a premium on social vigilance of the sort proposed in the target article and by other authors (e.g., Bryant, 2021).

The added social complexity of screams that is seen in monkeys and, in humans additionally, the enhanced level of intentionality involved in their production, promotes social vigilance. Listeners must attend to the acoustic variation among screams to make inferences about the caller's intentional actions and subsequent behaviors (in humans), even if, in the case of monkeys, they cannot infer informative or communicative intentions. In primate screams, then, we see a communicative context in which, relative to their evolutionary precursors, both the cognitive capacities for goal-directed communication and correlated capacities for social vigilance have advanced along the graded scales described by H&S-P.

Thus, human scream production and usage suggests novel functions in this evolutionarily conserved call type, make them a fascinating subject for understanding nonlinguistic emotional communication in our species. We focused here on screams, but laughter (e.g., Gervais & Wilson, 2006) and tearful crying (e.g., Vingerhoets & Bylsma, 2016) represent additional examples where human expression has expanded beyond that shown by any other species. We suspect that H&S-P might not agree with the extrapolation of their term "unleashed" to include the expansion of human nonverbal expression, but they might agree that, in the case of screams, the leash has been loosened.

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The co-evolution of cooperation and communication: Alternative accounts

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Abstract

We challenge the proposal that partner-choice ecology explains the evolutionary emergence of ostensive communication in humans. The good fit between these domains might be because of the opposite relation (ostensive communication promotes the evolution of cooperation) or because of the dependence of both these human-specific traits on a more ancient contributor to human cognitive evolution: the use of technology.

Humans' seemingly unique communicative system was likely the result of selection pressures arising from a unique environment. If so, then any selective scenario for the emergence of human communication must explain why it evolved in humans and not in any other animal species (Hurford, 1998). Heintz & Scott-Phillips (H&S-P) propose a feasible and detailed answer to the understudied question of what ecology promoted the emergence of ostensive communication in human evolution. While we

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agree that H&S-P's proposal, according to which ostensive communication evolved in a partner choice ecology, is a plausible account, we believe that there are alternative scenarios that also deserve serious consideration.

If the explanandum is the evolutionary relation between two seemingly human-specific behavioral traits, ostensive communication and hyper-cooperativity, then another possibility is that ostensive communication, rather than emerging out of a highly cooperative ecology (as H&S-P suggest), was itself the chief driver of distinctive forms of cooperation among humans. Human cooperation is uniquely flexible in at least two related senses. First, our cooperation often requires planning on the basis of displaced or detached representations, because it pursues goals that are not immediately realized (Brinck & Gärdenfors, 2003). Second, our cooperative goals are open-ended, that is, the scope of possible goals is not innately prespecified. Paleoarcheological evidence suggests that the foraging behavior of the genus *Homo* involved a relatively wide range of flora and fauna (e.g., Roche, Blumenschine, and Shea, 2009), often requiring the invention of novel means for obtaining and processing food. Whether in the form of hunting or confrontational scavenging (Toth & Schick, 2015), this type of foraging necessitated sophisticated levels of collaboration.

We suggest that such flexibility of human cooperation would not be possible without a similarly flexible communicative system. Symbolic communication allows humans to transmit open-endedly propositional content about displaced entities (Hockett, 1960). This in turn could facilitate collaborative foraging, coalition building, negotiating benefit sharing, reaching agreements, and many other cooperative activities. Therefore, contrary to H&S-P's proposal that a cooperative, partner choice ecology explains the reliability and flexibility of ostensive communication, it is possible that it was ostensive symbolic communication that promoted new levels of cooperation and partner choice among hominins. This account, of course, raises the question of how ostensive communication evolved in the first place – just like H&S-P's proposal would demand an explanation for the original emergence of partner choice ecology. While H&S-P characterize their account as co-evolutionary in nature, their description of the incremental emergence of Gricean communication (target article, sect. 6) presupposes highly structured win-win cooperation among humans from the very beginning of this process.

A second alternative possibility regarding the evolution of cooperation and ostensive communication is that a third, and more ancient, factor drove the evolution of both of these human-specific traits. We propose that hominins' extensive reliance on technology, and especially on "recursive" technology that effectively separated means from ultimate ends, could be one such factor. Much of our knowledge about the behavior of hominins comes from the study of Paleolithic tools. While this might simply be because of a preservation bias, it provides us with relatively direct and verifiable evidence about some aspects of cognitive evolution of early humans. The Oldowan lithic industry from about 2.7 Ma already produced stone tools that are not seen elsewhere in the animal kingdom (Roche et al., 2009). Some of these tools, like the hammerstone, were used to make other types of tools, like flaked artifacts, which were in turn used for animal butchery and possibly woodworking (Toth & Schick, 2015). Such recursive toolmaking, which also involved transporting and storing of tools (Shick, 1987), could have contributed to the co-evolution of communication and cooperation in various ways.

It has been suggested that the Oldowan technology relied on communicative demonstration for the transmission of the knapping skill from experts to naïve learners (Gärdenfors & Högberg, 2017). Moreover, the Acheulean technology, from approximately 1.76 Ma, involved even more cognitively demanding skills to make symmetrical handaxes and cleavers, and likely depended on more complex forms of communication (Gärdenfors & Högberg, 2017; Morgan et al., 2015). Thus, the advent of new technologies, with increasingly long sequences of necessary steps that made human actions and tools "opaque" to naïve observers, might have led to the evolution of novel communicative means to convey skills and generic knowledge to novices (Csibra & Gergely, 2011). Such an action-based communication system could have emerged gradually, and without the need of recruiting arbitrary symbols, because its contents derive from the natural meaning of the demonstrated actions, and (unlike communicating via established channels, such as speech) it demands making the communicative nature of the demonstration manifest, which is the very point of ostensive communication. Besides, the function of teaching technology fulfills all criteria that an account for the evolution of symbolic communication would have to meet (Laland, 2017). Thus, increasing dependence on recursive tool use and toolmaking could have promoted the evolution of ostensive communication.

Reliance on technology would also create an ecology that fosters collaboration and novel social structures at many levels. As soon as tools are seen as valuable items for themselves and are stored for later exploitation, the rights for their use (i.e., their ownership) becomes a social issue, creating entitlements and obligations, as well as novel opportunities for sharing. The reliance on special technological expertise necessitates division of labor and fosters mutualistic and reciprocal cooperation. (E.g., building shelters and the control of fire in hearths might demand collaboration, possibly involving complementary roles.) These types of pressure together can create an ecology in which, as H&S-P rightly suggest, participating in joint enterprises is adaptively beneficial. Importantly, however, producing such an ecology already requires flexible communication, not just for transferring technological knowledge to others but also to maintain the social ecology that in turn maintains the technology that is needed by humans to survive. This perspective, unlike that of H&S-P's, is truly co-evolutionary and may also be supported by tangible paleoarcheological evidence.

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What semantic dementia tells us about the ability to infer others' communicative intentions

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Abstract

As Heintz & Scott-Phillips rightly argued, pragmatics has been too commonly considered as a supplement to linguistic communication. Their aim to reorient the study of cognitive pragmatics as the foundation of many distinctive features of human behavior finds echo in the neuropsychological literature on tool use, in which the investigation of semantic dementia challenges the classical semantics versus pragmatics dissociation.

Heintz & Scott-Phillips (H&S-P) stressed that humans possess cognitive means of adaptive reaction targeted at the behavior of conspecifics: Humans cannot un-understand what others say. The neuropsychological literature on tool use in semantic dementia corroborates and extends this perspective in indicating that humans cannot un-understand what others "expect." This literature provides insights into the neurocognitive bases of the ability to infer others' communicative intentions, which can contribute to make human evolutionary sciences less "neurocognition" blind.

Tool-use disorders – also called apraxia of tool use (Osiurak & Rossetti, 2017) – are traditionally assessed by asking patients to show how to use familiar tools presented in isolation (i.e., single tool-use/pantomime tasks; Table 1). These tasks are considered to investigate semantic knowledge about tool function (Goldenberg & Hagmann, 1998). Others suggest that these tasks engage sensorimotor knowledge about tool manipulation (e.g., Rothi, Ochipa, & Heilman, 1991), but we limit our discussion to the semantic dimension. The rationale is that the mere presence of a tool should be enough to activate the corresponding semantic knowledge and, thus, help the patient use the tool appropriately. Although these tasks appear simple at first glance, individuals, including healthy ones, frequently hesitate about the actions to perform and ask the clinician for more information about what is expected. Indeed, the absence of associated objects makes the task ambiguous and obliges the individual to infer the clinician's expectations or communicative intentions in H&S-P's terms. After all, if you frequently use newspapers to light fire, what would you do if a clinician asked you to show how to use them? Would you pretend to light fire with them or read them? To find the correct answer, you must infer that the clinician may expect that the demonstration involves the most frequent usage of newspapers. So, you would have to pretend to read them, otherwise your demonstration could be considered as pathological. These tasks are much more than simple tool knowledge tasks and illustrate how semantic knowledge and cognitive pragmatics are intertwined. The study of semantic dementia is particularly enlightening on this point.

Table 1. (Osiurak and Federico). Neuropsychological tool-use tasks

Task	Description
Pantomime of tool use	The individual demonstrates the use of a tool[a] presented in isolation without holding it in hand.
Single tool use	The individual grasps a tool presented in isolation and shows how to use it.
Real tool use	The individual actually uses a familiar tool with a familiar object (e.g., pounding a nail with a hammer).
Novel tool use	The task can consist of using familiar tools in a non-conventional way (e.g., driving a screw with a knife) or in selecting, making, and/or using novel tools to solve mechanical problems (e.g., extracting a target out from a box by folding a wire to create a hook).

[a]The term tool will be hereafter used for the implement that performs an action (e.g., hammer) and the term object for the recipient of the action (e.g., nail).

Semantic dementia is a variant of frontotemporal dementia, which is characterized by an inaugural atrophy of the polar temporal lobes that are known to play a critical role in semantic cognition (Lambon Ralph, Jefferies, Patterson, & Rogers, 2017). At the onset of the disease, patients lose knowledge about unfamiliar things. Thus, they can name a giraffe as a dog with a long neck. Then, even knowledge about familiar things is lost. Patients can name a dog or any four-legged animal as "Ruben," their dog. Their interpretation of their environment becomes progressively guided by their episodic memory, which generates communicative disorders. They become egocentric (Snowden et al., 2001; see also Moreaud et al., 2008) and this egocentrism becomes also visible in single tool-use/pantomime tasks. For example, if a patient with semantic dementia is asked to demonstrate how to use a colander, the patient may be unable to name it or give details about its function, but can say it is useful for changing the oil of a car. This response can be explained by the observation that the patient has been occupied with car repair for the past several weeks. This idiosyncratic and egocentric type of reference is very common in semantic dementia.

One may consider that the difficulties reported in semantic dementia in single tool-use/pantomime tasks reflect nothing else than the selective loss of knowledge about tool function, which prevents the patients from using familiar tools appropriately. If so, then semantic dementia should be characterized by a general tool-use disorder that also impacts the real use of tools presented with objects (i.e., real or novel tool use; Table 1) as in some patients with left brain damage (for a review, see Osiurak & Reynaud, 2020). However, evidence indicates that

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semantic memory is neither necessary nor sufficient for real tool use (Baumard et al., 2019; Buxbaum, Schwartz, & Carew, 1997). This is also true for patients with semantic dementia, who obtain quasi-normal performance in real tool-use tasks (Baumard et al., 2016) or when they use familiar tools in their everyday life (Bozeat, Lambon Ralph, Patterson, & Hodges, 2002a; Lauro-Grotto, Piccini, & Shallice, 1997). These patients have also "normal" performance on novel tool-use tasks (Hodges, Bozeat, Lambon Ralph, Patterson, & Spatt, 2000; Lesourd et al., 2016; Table 1), which suggests that their technical-reasoning skills are spared, allowing them to reason appropriately about mechanical actions that involve tools and objects. In fact, their good technical-reasoning skills explain why they can use familiar tools with their corresponding objects (i.e., real tool-use tasks) even if they cannot name or give details about them. The presence of both tools and objects makes the task "more mechanical-oriented," leading them to reason about the mechanical actions that they can generate from their presence, as in novel tool-use tasks. In this case, the clinician's expectations have not to be included in the equation. By contrast, patients with semantic dementia meet difficulties in single tool-use/pantomime tasks that are strongly linked to the severity of semantic deficits (Bozeat, Lambon Ralph, Patterson, & Hodges, 2002b; for a review, see Osiurak et al., 2021). In sum, these patients have no tool-use disorders strictly speaking. Instead, it is the artificial nature of the single tool-use/pantomime tasks that obliges the individual to include the clinician's expectations in the equation and that makes the task difficult for a patient with a loss of semantic knowledge.

These findings, which challenge the classical semantics versus pragmatics distinction, are in line with H&S-P's perspective by suggesting that there is no reason to see cognitive pragmatics as peripheral to linguistic communication. Semantic dementia tells us that semantic memory supports the ability to infer others' communicative intentions, which complements their perspective by building a bridge with the neurocognition domain. Semantic dementia is characterized by lesions to the polar temporal lobes, which are known – as also illustrated here – as playing a key role in semantic cognition. Evidence also indicates that these brain regions are part of the mentalizing network (Gallagher & Frith, 2003), thereby drawing an interesting link between semantic cognition and the ability to understand others' intentions.

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Structuring unleashed expression: Developmental foundations of human communication

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Abstract

The target article highlights the sources of open-endedness of human communication. However, the authors' perspective does not account for the structure of particular communication systems. To this end, we extend the authors' perspective, in the spirit of evolutionary extended synthesis, with a detailed account of the sources of constraints imposed upon expression in the course of child development.

Heintz & Scott-Phillips strongly argue that the cognitive capacities required for unleashed communication are *adaptations* to a "partner choice" social *ecology*. This emphasis on adaptation and ecology puts them roughly within the purview of modern evolutionary synthesis (Huxley, 2010). However, arguments against both the adaptationist paradigm and the program of modern synthesis have been accruing systematically for a long time (e.g., Gould & Lewontin, 1979; Sober, 1982; Walsh & Huneman, 2017) and resulted in several alternative proposals, out of which the extended evolutionary synthesis is one of the

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most prolific (Laland et al., 2015; Pigliucci & Müller, 2010). Evolutionary extended synthesis positions at its center the study of development (developmental bias and plasticity) and niche construction. These are precisely the elements that we argue that the authors overlooked in their proposal, and which can provide important details not only about how expression becomes "unleashed," but also how it can become highly structured to enable the emergence of symbolic communication systems, such as language.

The target article draws the continuity between different forms of human expression, moving the search for foundations of the unleashed communication, that is, the generativity of communication systems, outside the properties of language itself. This opens up new avenues for asking more adequate questions about systems of communication. Here we want to ask, what makes language in particular a suitable tool for such an open-ended expression. While various means of human expression – art, dance, or improvised gestures – can convey meaning, language seems to be the only system effectively allowing for communication both unlimited and precise. We argue that the authors' framework cannot account for the emergence of the structure of unleashed communication visible in language. Here we focus on the inclusion of a crucial factor: External sources of linguistic structure present in development that go beyond the authors' focus on social ecology on an evolutionary scale.

Human infants are born into a social world. Interactions with caretakers are the primary source of experiences for a newborn, as well as the context for their agency. These include language utterances of particular structure, crucially – closely tied to action (Rączaszek-Leonardi, Nomikou, Rohlfing, & Deacon, 2018). In fact, children learn basic linguistic structures much earlier than they are able to use them for communication in the same way as adults do (Bruner, 1985). Importantly, the caretakers' actions themselves also often exhibit a communicative structure. As evidenced in research on early semantic development, infants' behaviors, such as reaching and pointing, are treated as ostensive by caregivers to build sensible "events" or "narrations" around them. This way, action first, children learn about possibilities of expression that can be effective in social situations. "Events" rather than being entirely created on the fly are culturally sanctioned routines, adapted to a situation (Bates, Camaioni, & Volterra, 1975). It is within such interactions that experiences of being expressive and effects of this expression on partners appear and are progressively shaped toward communicative and linguistic modes. Yet the child may be perfectly unaware of this and treat pointing gestures just as a reliable way of getting what they want. It is only when pointing becomes unreliable and produces different results depending on the context (most importantly, receiver's attention and knowledge; Liszkowski, Carpenter, Henning, Striano, & Tomasello, 2004) that the child starts to become aware of the intricacies of communication. Thus two kinds of cultural enactments scaffold the developmental progression: interactive routines leading to various expressions being integrated for purposive co-action (Rączaszek-Leonardi, Nomikou, & Rohlfing, 2013; Rossmanith, Costall, Reichelt, López, & Reddy, 2014) and using a highly structured language by a parent, in concert with the routines, which scaffolds skillful linguistic participation. In both cases, it is shareable structures, historically shaped by culture, that are central for developmental language emergence in interaction (Bruner, 1983).

Finally, these public, physical structures are crucially *replicable*. The authors are certainly correct in highlighting that one of the purposes of conventionalization is to turn attention to the communicative intention of a particular action (target article, sect. 8.5, para. 3). As importantly, however, conventionalization ensures the replicability of expressions and serves as one of the key sources of constraints on unleashed expression. Over the course of development, via overimitation (target article, sect. 7, para. 8) and co-action, utterances (spoken or signed) are nudged toward these culturally sanctioned forms stabilizing their functions, which make up a *language*. In turn, all this depends on the physical, public, and shareable nature of the signs that can be abstracted away from a particular situation in which they are produced and repeated under nearly any circumstances.

A fully unleashed expression would prevent successful message transmission because of the multiplicity of possible meanings. Introducing structure and constraints that ensure replicability, a "leashing" of expression of sorts, restricts informative intentions of communicators that cannot be "about anything at all" (target article, sect. 5, para. 2). Open-endedness of some elements of a communication system needs to become suspended, so that they are produced and interpreted as natural signs (Bar-On, 2021, p. 15), for the system to remain unleashed. This is possible via the developmental pressures described above. The evolutionary perspective of the authors needs a complementary account of the developmental and environmental structures that enable and stabilize communicative abilities. While the roots of expressive communication could be observed in the open-ended improvised expressions, identifying the key processes from other timescales at the level of individual and language development allow for an adequate, interaction-specific balance of "leashed" and "unleashed" parts of communication. We argue that this contribution may serve as a valuable extension for the proposed framework.

The processes described above indicate that the focus on the ecological interactions and on the evolutionary timescale may lead to averaging out crucial processes that accompany the unleashing of expression. On the other hand, taking care to analyze the developmental processes substantiates the authors' claims about the appearance of relevant cognitive capacities at "reliable and predictable stages of ontogeny" (target article, sect. 6, para. 11) and highlights that this results from a network of dynamic processes supported by other individuals and the cognitive niche that humans have constructed in order to master language use.

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Ostensive communication, market exchange, mindshaping, and elephants

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Abstract

Heintz & Scott-Phillips's hypothesis that the topic range and type diversity of human expressive communication gains support from consilience with prior accounts of market exchange as fundamental to unique human niche construction, and of mindshaping as much more important than mindreading. The productivity of the idea is illustrated by the light it might shed on why elephants seem to engage in continuous social communication for little evident purpose.

Heintz & Scott-Phillips's (H&S-P) complex hypothesis, according to which the topic range of human communication and the diversity of human expressive signals is derived from cognitive foundations in partner discrimination for shared enterprises, is rich in its implications and consilience of evidence. It naturally complements Ofek's (2001) defense of the thesis that the origins of human ecological dominance and expansion of community scales lie in market exchange and specialization traced to the Upper Pleistocene. Indeed, Ofek's account arguably provides the evolutionary foundation for H&S-P's story, with prehistoric markets (e.g., hearth maintenance) constituting the constructed niche in which ostensive communication of intentions for partner matching became adaptive. H&S-P's thesis also comports smoothly with Zawidzki's (2013) argument that human mindreading – inferring stable latent intentions from observed behavior – is a relatively difficult, unusual, and special-purpose capacity that relies on more ubiquitous and basic processes of mind*shaping*, that is, mutual co-adjustment of intentional interpretations to support coordination and cooperation. Mindshaping is a plausible basis for the shared attention and presumption of relevance in communication that, according to H&S-P, are required for successful ostension. Mindreading is not. This conceptual complex of market exchange, mindshaping dynamics, and ostensive communication of intentions (with the "unleashing" of expressive power that derives from it according to H&S-P), might furnish a complete general theory of human ecological specialness.

This speculation invites tests based on comparative psychology. H&S-P mainly consider evidence from great apes, presumably on the usual grounds that they provide the best available behavioral evidence about capacities of our most recent nonhuman ancestors. On the other hand, they recognize that dogs attend to expressed human intentions in ways that chimps don't, and attribute this to the fact that dogs are adapted to the human-constructed niche in which general cooperative commitment to communicative relevance is a valid presumption. This does not hold in the more individualistic and purely competitive social ecology of chimps. It is not clear that a similar obstacle applies to the much more cooperative dispositions of gorillas. Here is an instance where Ofek's foundational account might be usefully invoked: Gorilla foraging in verdant rainforests involves no pressure for evolution of market exchange.

Given the general significance of evolutionary convergence, it is a good exploratory strategy to look beyond apes and consider other large-brained social animals that are more intensely cooperative. Elephants are particularly potentially relevant in the context of H&S-P's account, because, unlike any extant apes, they engage in communication at a level of frequency that approaches that of humans. Elephant subsonic rumbling, along with trunk gesturing and touching, is clearly communicative. It is an intriguing puzzle that although researchers are beginning to decipher the meanings of some elephant signals associated with group traveling decisions and greeting rituals, elephants "chatter" continuously when they are together, even when their circumstances are apparently uneventful. Unlike songbirds or (perhaps) dolphins, elephants do not need to continuously signal their locations to keep rapidly traveling groups connected.

H&S-P's emphasis on the power of *human* language as being derived from unleashed expression neither implies nor requires the assumption that language is unique to humans. Indeed, it may be an *attractive* feature of their account that it re-directs attention, in explaining human specialness, from the McGuffin of human linguistic structural complexity. There is no convincing reason to *assume* that elephants lack language: Their communication system has sufficient acoustic variation and regularity, and information appears to spread among them with surprising efficiency and specificity (Ross, 2019). However, there is no evidence that their communicative expression is unleashed. It might be leashed not by lack of language but by the fact that they are *too* relatively and reliably cooperative to be motivated to attend as closely to subtle differences in expressed intentions as successful humans must do. Matriarchal elephants have status hierarchies but are not competitive about them.

As H&S-P discuss, chimps are, compared with humans, relatively uninterested in one another's dispositions to cooperate, and this blocks unleashing of their expressiveness. Elephants appear to be primarily preoccupied with food, water, babies, and one another's emotions. For them, the first two topics of concern reduce to interest in collective travel decisions. This, along with their relative imperviousness to predation and the ecological uselessness of deception to them, may have prevented them from developing promiscuousness of shared attention to a wide range of aspects of the non-social external environment, which could block unleashed expression.

An element of irony may lurk here. If H&S-P are right, then humans are distinguished by devoted attention to expressions of conspecifics' beliefs and preferences. Yet in elephants we might have a species in which individuals are even *more* relatively preoccupied with one another's attitudes – but *too much* so to get traction for unleashed expression. Elephants, before humans came along to shatter their peace, may not have been under enough pressure to care about relevance; perhaps their conversation is mostly obsessive phatic communication. It is a tribute to the productivity of H&S-P's intriguing perspective that it frames this novel hypothesis about the elephant puzzle.

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Illustrating continuity between linguistic and non-linguistic human communication and expression

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Abstract

This commentary presents two illustrations, from the world of poker, of the continuity between linguistic and non-linguistic communication and expression, in support of Heintz & Scott-Phillips's account of the evolution of human expression and communication. I also come across the presumption of relevance in the context of a poker table.

It seems very tempting, almost obvious, to attribute the uniquely wide scope of human communication to cognitive capacities for generating or harnessing the combinatorial power of language. But Heintz & Scott-Phillips (H&S-P) emphasize instead as foundational such capacities for "ostensive communication." These "unleash expression on a grand scale" (target article, sect. 9, para. 1). My aim here is to supplement their account of the evolution of language and of other aspects of human sociality with two exhibits from the poker world, which support their view by illustrating especially the continuity between linguistic and non-linguistic communication and expression in a quite striking manner.

The first also illustrates what human communication can do even without language and its combinatorial power. In July 2016, in the Main Event of the 2016 World Series of Poker in Las Vegas, Stacy Matuson is faced with a decision for all her chips after Will Kassouf's bet, who is now talking to her relentlessly, notably offering "if you fold and show [your cards] I will show [my cards]." When he is prohibited by a floorperson from saying another word, Kassouf just repeats this same message by miming the sequence, accompanied by suitable facial expressions. A TV commentator for ESPN, Norman Chad, puts it thus: "Now he's talking without speaking! He's pushing it." Indeed, despite not having violated the prohibition, Kassouf ends up getting penalized by the tournament director, apparently for "taunting" Matuson. Intuitively, Chad sees continuity, then, as possibly does the tournament director.

To find footage of this online, use "nine-high like a boss" as a search phrase. Incidentally, after a player's request for Matuson to arrive at a decision is approved by the floor, Chad adds something else of interest here: "Usually I'm in favor of calling the clock, but she has been under siege most of the time from Will Kassouf – I would have given her a little more room." Come to think of it, why "under siege"? As opposed to, say, merely "distracted" by Kassouf's behavior at her table? Why could she not have closed this communication channel that brings only deception? Because, H&S-P might comment, we presume relevance and comprehend spontaneously and involuntarily (target article, sect. 4.3; such an unconditionally trusting stance can be viable normally because the message still awaits epistemic vigilance, see target article, sect. 5). Meanwhile, "speech players" like Kassouf, even the less intrusive ones, appear bound to develop a reputation for irrelevance, but it should not be as detrimental here as it typically was in human evolutionary history according to H&S-P, because it can remain linked to the game setting. Or at least that's what I would think, based on some experience in the poker room of a casino.

Later, Kassouf almost made it into the "November Nine": the last nine survivors, out of 6,737 tournament entrants, would return months later to play out the so-called final table, for about 25 million dollars in remaining prize money. Such an interruption, to build anticipation for the final, was practiced until 2016. Thus one could prepare by using TV footage of one's opponents. A poker-behavior ("tells") author translated into more than half a dozen languages, Zachary Elwood, offers testimonials on his website from a finalist he helped with this in 2013 and one in 2015 (hardly anyone makes the final twice – too much in poker depends on luck), adding "as far as I know, I'm the only person who's ever been hired to study tells in such a high-stakes setting" (Elwood, n.d.). Now, the reason I am trying to document Elwood's leading expertise is that my second exhibit comes from his writing. From part one of a two-part piece:

> I started thinking more about a general behavioral theory I had introduced in my second book, *Verbal Poker Tells*. The theory applies to verbal behavior, but as I worked through the footage, I started seeing how the theory was actually part of a larger theory, affecting not just verbal behavior but also physical tells. (Elwood, 2015a)

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Again, when he is describing one aspect of his new larger theory (I should note he is presupposing the popular No-Limit Texas Holdem poker format):

> [P]layers with very strong hands don't like to draw attention to themselves early in a hand, when the pot is small. Rather, they will tend to be silent and not make ostentatious movements. Wording the tendency […] in terms of ostentatious behavior, lets us see the verbal behavior tendencies as just one part of the overall tendency not to draw attention, no matter the type of behavior, verbal or physical. (Elwood, 2015b)

Once the pot of contested chips is big, tendencies change (2015b). But my point here is not to really present this theory. Rather, it is the continuity that Elwood came to see, after perhaps starting out cutting nature at a false joint, so to speak, between verbal and non-verbal tells. And while some or most examples of "ostentatious behavior" he provides (Elwood, 2015b), such as unprompted smiling, or reaching for chips before one's turn, though expressive, may not quite qualify as ostensive-communicative, H&S-P emphasize that how much an intention to inform is made overt is a matter of degree. Sometimes it is even strategically better to hide it (target article, sects. 3.2 and 8.3). This can naturally apply at a poker table.

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Expression unleashed in artificial intelligence

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Abstract

The problem of generating generally capable agents is an important frontier in artificial intelligence (AI) research. Such agents may demonstrate open-ended, versatile, and diverse modes of expression, similar to humans. We interpret the work of Heintz & Scott-Phillips as a minimal sufficient set of socio-cognitive biases for the emergence of generally expressive AI, separate yet complementary to existing algorithms.

In recent years, artificial intelligence (AI) systems powered by machine learning have demonstrated human-level capabilities in a variety of games (Brown et al., 2018; Jaderberg et al., 2019; Moravčík et al., 2017; Silver et al., 2018), and are increasingly finding applications in the real world (Grigorescu et al., 2020; Hwangbo et al., 2020; Mandhane et al., 2022). Despite this progress, AI remains specialists, lacking the breadth of competence across diverse tasks, which is characteristic of human intelligence (Chollet, 2019; Hutter, 2000; Legg et al., 2007). Training large models with large, diverse datasets of interactive behavior appears to be a promising direction for increased generality, both in the language domain (Brown et al., 2020) and in 3D simulated worlds (Abramson et al., 2020; Baker et al., 2019; Team, Open Ended Learning et al., 2021). On the other hand, it is unclear whether a purely data-driven approach can scale toward open-ended intelligence. This motivates interest in algorithms designed for general learning from scratch, such as in emergent communication (Foerster et al., 2016; Lazaridou et al., 2016) or never-ending learning (Mitchell et al., 2018).

The versatility of human social interaction provides a powerful lens through which to study the general capabilities of AI, dating back at least as far as Turing (1950). To partner with diverse individuals across a wide range of tasks necessarily requires flexible modes of expression, adapted on the fly with new conventions and commitments (Bard et al., 2020; Dafoe et al., 2020). Indeed, domain-agnostic social intelligence may even be a sufficient iterative bootstrap to reach individual general intelligence, via cultural evolution (Henrich, 2015; Team, Cultural General Intelligence et al., 2022). The question of how to unleash expression in AI is therefore timely and relevant. Research in this direction could even provide new insights into the evolutionary psychology of language, echoing recent links between AI and neuroscience (Macpherson et al., 2021; Savage, 2019).

We argue that the target article can be interpreted as a minimal set of socio-cognitive biases that may lead to improved versatility in AI, particularly in interaction with humans. Following the model of reinforcement learning algorithms (Sutton et al., 2018), we identify desirable properties of the environment and of the agent, inspired by the co-evolutionary ecology of human communication. We relate these perspectives to existing approaches in AI, showing that they are relatively underrepresented, and thus provide valuable inspiration for future research.

In the social environment, partner choice ecology is perhaps the main driver for the evolution of ostension and inference. These capabilities underlie all human communication and expression because they enable humans to influence and decode the intentions of others. Partner choice social ecology develops these capabilities whenever humans can select their teammates. In harmony with these observations, partner choice catalyzes artificial learning agents to find the tit-for-tat solution to Prisoner's Dilemma, a strategy that not only plays cooperatively, but also encourages others to cooperate (Anastassacos et al., 2020). Human feedback can itself be seen as a form of partner choice, when humans choose which AI models they would prefer. Indeed, social interaction with humans in the loop promotes generalizable and robust AI (Carroll et al., 2019; Jaques et al., 2018). These works are a proof of concept that partner choice is important for generally expressive AI, and there is much yet to explore.

The paradigm of emergent communication has shown great promise in training artificial agents, both in situations where incentives are aligned, and in settings requiring negotiation or partial competition (Lazaridou et al., 2020). Typically, the

symbols used for communication do not have any pre-existing semantics. Rather their meaning emerges during training, leading to "code-model" communication (Scott-Phillips, 2014). Various studies (Bouchacourt et al., 2019; Kottur et al., 2017; Resnick et al., 2020) have found that the resulting protocols are not human-interpretable and do not share the structural features of human language. On the other hand, humans are capable of devising generalizable protocols in a zero-shot or few-shot manner (Kirby et al., 2008; Scott-Phillips et al., 2009).

We argue that this lacuna can be resolved if Gricean pragmatics is viewed as a fundamental objective in the design of agent algorithms for emergent communication. There is already promising work in this direction (Eccles et al., 2019; Kang et al., 2020; Pandia et al., 2021), but pragmatic reasoning is still often regarded as a supplementary bolt-on. Inverting this viewpoint would put inference and ostension at the heart of AI learning algorithms. For instance, an agent with an inverse model of its own policy may use this to infer the communicative intention of others on the fly, a simulation of simulation theory (Gordon, 1986; Heal, 1986). Alternatively, one might hope such a model is constructed implicitly during the course of meta-learning across a population of partners (Gupta et al., 2021; Strouse et al., 2021). Furthermore, such approaches can easily be combined with data-driven language models (Lowe et al., 2020).

There is a close relationship between pragmatic capabilities and theory of mind, a topic that has received some attention in the AI literature (Moreno et al., 2021; Rabinowitz et al., 2018). The ability to infer the beliefs of others has been shown to aid convention-building, leading to more generalizable conventions across diverse agents (Foerster et al., 2019; Hu et al., 2019, 2021). Moreover, when agents are incentivized to manipulate the learning of others, they achieve greater success across a variety of games, including when communication is useful (Foerster et al., 2017; Jaques et al., 2019; Yang et al., 2020). As they strive for more general and versatile agents, algorithm designers could benefit greatly from understanding the cognitive bases for punishment and teaching in humans.

We conclude with an example of real-world importance. Autonomous vehicles (AVs) have the potential to make transportation safer and more convenient. To optimize for safety in interactive situations, the AV must both predict other road users, and be predictable to other road users. In other words, AVs require ostension and inference capabilities (Dolgov, 2021). Existing AV systems use data from human drivers to generate human-like plans and to predict other road users' behavior (Sadigh et al., 2020; Tolstaya et al., 2021). However, such data may not be enough if the behavior of others is strongly influenced by the autonomous car itself, particularly in previously unseen scenarios. Hence, just as in the target article, we come to the need for a metarepresentational framework, a means of reasoning over the representations that an AV induces in other road users. Already, there exists communicative hardware for AVs (Habibovic et al., 2020), alongside plans to elicit online human feedback as a guide (Team, Open Ended Learning et al., 2021). Ostensive communication may be a key ingredient for safe autonomous driving in highly interactive urban environments.

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The scaffolded evolution of human communication

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Abstract

Heintz & Scott-Phillips provide a useful synthesis for constructing a bridge between work by both cognitive scientists and evolutionary biologists studying the diversity of human communication. Here, we aim to strengthen their bridge from the side of evolutionary biology, to argue that we can best understand ostensive communication as a scaffold for more complex forms of intentional expressions.

While the Darwinian revolution has taken much of the force from the idea that humans are separate from the rest of nature, there is no doubt that one of our unique traits is the diversity and open-endedness of our means of expression; constituting something of a major transition in the evolution of our hominid ancestors. Yet, in order to begin an evolutionary investigation into how and why this happened, we require an integration of many sources of data from different fields that have hitherto largely operated independently. It is just such an empirical synthesis that has been offered in the present target article by Heintz and Scott-Phillips (H&S-P). They provide what is effectively a breakdown of the components of human communication to enable an evolutionary reverse-engineering approach for understanding the evolution of this rich, diverse, and open-ended capacity of humans and allowing us to begin the construction of a bridge between the work of evolutionary biologists and cognitive scientists interested in human communication.

Yet we maintain that this bridge could be strengthened on the evolutionary side. The authors maintain, similarly to Heyes (2019), that evolutionary biologists have remained "cognition blind" – failing to adequately take into consideration the progress computational cognitive science has made in understanding the mind, and instead relying upon needlessly simplistic and mechanistic "hardware" (as opposed to "software') models. While this is certainly true to some extent (Morin, 2016), the criticism can cut both ways and we should likewise not underestimate the blindness of many cognitive scientists towards the resources of modern evolutionary biology. As an example for "cognition blindness," H&S-P argue that the common division of expressive behaviours such as language, instruction, and the like, which they maintain could be seen as part of a single cognitive capacity for ostensive communication. However, by using the analogy of running and walking as subfunctions of a more general capacity for bipedal locomotion it should be clear that the division of capacities into subfunctions is not because of a blindness to cognitive

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mechanisms. It is the tried-and-proven evolutionary method of reverse engineering to make sense of the phylogeny of different functional capacities of organisms. But it remains still too rare an occurrence that the teleonomic question is asked regarding what cognition is – or particular cognitive capacities such as communicative ability are – *for*, especially in the case of humans. There is thus a need for further attention on both sides.

In particular, we think that the bridge between evolutionary biologists and cognitive scientists could be strengthened by considering recent work on "scaffolding" in evolution (Caporael, Griesemer, & Wimsatt, 2014; Sterelny, 2006; Veit, 2022). Scaffolding refers to traits that facilitate the evolution or for that matter the development of other traits, and may then themselves eventually be lost or repurposed, which could have happened in the evolution of the distinct modes of human expression. If the diversity of human forms of expression has a common evolutionary origin, we would then expect to trace back the evolutionary history to find something like a common scaffold, one that was eventually discarded or at least transformed. While this terminology is not used by H&S-P, their proposal that ostensive communication is the common functional core of human communication can be better understood as the claim that direct ostensive communication (i.e., action grounded in communicative intentions) served as an evolutionary scaffold for the evolution of more complex intentional capacities, such as those they describe.

Ostensive communication can additionally be seen as a developmental scaffold as much as an evolutionary scaffold. While development should not be taken to track phylogeny, it can still provide evidence regarding the evolutionary functions and origins of traits; in this case human communication. In the early stages of human development, communication very much proceeds by overtly intentional actions such as pointing (Camaioni, Perucchini, Bellagamba, & Colonnesi, 2004; Grassmann & Tomasello, 2010), a behaviour that decreases as an individual learns more complex forms of intentional expression. The evolution of humans has not yet led to discarding the older mechanism, suggesting that it is of central importance. This indicates that the simpler intentional actions serve to scaffold the development of more complex communication within the learning history of an individual, as well as the evolutionary history of a lineage. These dual lines of support lend further credence to the proposed importance H&S-P place on the cognitive mechanisms they describe.

Finally, in investigating this proposal, we urge for more research into the distribution and development of more complex forms of intentional expression in other species. Particularly in our close relatives, the great apes, their capacities may provide useful clues regarding human evolution and why the structures of great ape societies give rise only to prototypical forms of these capacities. As the authors discuss, it seems that apes are able to develop some traits when raised in more altruistic or cooperative human environments, but their natural social contexts seemingly prevent it. A nice example of this type of ability comes from the observations by Russon and Andrews (2011) on orangutans at Camp Leakey. Here, they catalogued repeated instances of orangutans spontaneously "pantomiming" (i.e., gesturing in which the meaning is "acted out" by the orangutan). Where communication initially failed, some individuals would attempt to rectify the failure through seeking the attention of their audience, and subsequent repetitions or elaborations. These are arguably examples of an individual working to make their communicative intention clear; of ostensive communication. While this context differs of course from orangutan natural social ecology, it provides a nice example of the potential ways in which more complex forms of communication can be scaffolded and thus provides some insights into how they could have gradually emerged in our lineage.

We think that understanding the evolution of human communicative abilities through the framework of evolutionary scaffolding will help us to strengthen the bridge between work on the evolution of animal communication and the cognitive science of human communication, as well as suggest ways for the integration and cross-collaboration of future work.

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The central problem is still evolutionary stability

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Abstract

We applaud Heintz & Scott-Phillips's guiding metaphor of "unleashing leashed expression," and we value the unified explanation for the emergence of not only language, but also other forms of unleashed expression, such as multimodal communication. We are more critical of the authors' discussion of the selection pressures acting towards unleashed expression, which are proposed to hinge on partner choice ecology.

In their target article, Heintz & Scott-Phillips (H&S-P) effectively confirm that the central problem for the emergence of domain-general, open-ended communication (including language) is its evolutionary stability. Their account is one of the rare few that takes this challenge seriously and does not presuppose human communication to be special. H&S-P rightly observe that "all

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evolved communication systems should be tied to narrow domains of statistical mutual benefit" (target article, sect. 5, para. 4), with human communication being no exception, as it also adheres to this evolutionary, behavioural–ecological constraint. The crucial exception, they propose, is that for humans this narrow domain is the domain of informative intentions – and it is these informative intentions that can in turn be domain general ("virtual domain generality"). This solution has a main advantage of offering an elegant and productive connection between the evolutionary considerations and the explanatory apparatus of cognitive pragmatics. It also has a main downside of pushing the real problem one level deeper: Why is it that the domain of informative intentions happens to afford statistical mutual benefit to humans (including prehistoric hominins), if it does not for anyone else (including our ape cousins)?

Here, H&S-P's answer – "expression can be unleashed in partner choice social ecologies" (target article, sect. 1, para. 3) – is perhaps plausible, but not new and not demonstrated to be superior to existing alternatives. Although the authors do not expressly refer to the biological markets theory by this name (BMT, Noë & Hammerstein, 1995), their solution is essentially a BMT account combined with the idea, originally developed by Dessalles (1998), of individual reputations hinging on being a relevant communicator. In sum, language and early forms of prelinguistic communication become a device for the honest signalling of one's usefulness in a competitive market of potential cooperative partners. Both those proposals need additional assumptions to make them work. As one example, scaling up BMT to account for the evolution of cooperation in hominins would presuppose starting from already very advanced cognitive–normative capacities for tracking the relative prices of numerous kinds of commodities across different timeframes (Witteveen, 2021). In turn, reputations based on relevance are vulnerable to the winner-take-all effect, that is, the entire group converging on a single or a few most relevant speakers (contemporarily best illustrated by social media celebrities), unless additional constraints are in place, such as constraints on the accessibility of social links (Dessalles, 2020). Even more importantly, H&S-P claim that "to a degree that surpasses that of other great apes, [the human] social ecology generates many opportunities for win-win cooperation, and risks of exploitation" (target article, sect. 6, para. 2) – but they stop short of making a convincing argument why and how this should be true of the evolutionary history of our species. That is, what specific "opportunities for win-win cooperation" would distinguish the *ancestral* evolutionary ecologies of *Homo* from those of *Pan*, in a way leading to lineage-specific pressures on cooperative partner choice? The target article somewhat generically mentions "animal hunting, building shelter, maintaining a fire, alloparenting" (target article, sect. 6, para. 6), and then pedagogy, but without developing convincing links to existing evolutionary accounts focusing on such interdependence (e.g., Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012 or Bickerton & Szathmáry, 2011; cf. also Beecher, 2021). Finally, H&S-P do not consider probably the most plausible account of the evolutionary emergence of cooperation and prosociality in humans: the cooperative breeding hypothesis (CBH; e.g., Burkart et al., 2014). First, CBH explains a very early start of the ontogenetic development of human cooperative dispositions (including dispositions for cooperative communication), something with which interdependence-based accounts struggle (Tomasello & Gonzalez-Cabrera, 2017). Second, it has a rare degree of empirical support from extant primates, because cooperative breeding is known to underlie a suite of cooperative behaviours in callitrichid monkeys, including teaching, foodsharing, and joint vigilance (Burkart, Hrdy, & Van Schaik, 2009).

What we see as a particular advantage of the target article is the choice of its guiding metaphor: unleashing expression (otherwise leashed to narrow domains of statistical mutual benefit). This is an apt metaphor whose heuristic value should be fully appreciated. Standard accounts of language origins typically work with, perhaps more intuitive, metaphors of transformation or even accretive development; that is, they focus on the communicative–cognitive skills that need to be added to (or reworked from) generalised ape cognition, or on the accretive increases in the complexity of communication systems. Reframing the question from *developing* into *unleashing* expression prioritises the ultimate-level perspective of behavioural ecology and signalling theory over the proximate-level perspective of implementation, and it foregrounds a behavioural–ecological "leash" as the main factor that is responsible for the rarity of language-like systems in nature. This approach is correct, because selection could not possibly promote the cognitive skills for language-like communication without first removing the evolutionary constraints for its emergence. In similar spirit, we have previously proposed a different metaphor, of domain-general communication resting on a "platform of trust," without which such domain-general communication must collapse (Wacewicz & Żywiczyński, 2018). However, an additional advantage of "unleashed expression" is the implication that expression is something not inherently missing but rather very much latently present in nonhuman apes. This seems to be in line with much recent primatological research, which suggests that "the most important limitation to the evolution of human-like language was indeed the motivation to share information, rather than the cognitive ability to do so" (van Schaik, 2016, p. 423). Finally, we strongly support "expression" as an explanatory target that extends beyond language to other forms of rich communication and activities such as teaching. We agree with the authors that despite their superficially very different manifestations, language, pantomiming, declarative pointing, or teaching all form a natural kind, as all of them are types of domain-general "information donation," subject to the same behavioural–ecological constraints.

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On the murky dissociation between expression and communication

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Abstract

The authors present an ambitious attempt to outline the gradual evolution of the cognitive foundations of ostensive communication. We focus on three problematic aspects of the distinction between *expression* and *communication*: ambiguity in the distinction's central principle of "complementary mechanisms," inconsistencies in the application of the distinction across taxa, and the dismissal of mentalizing in nonhuman primates.

The authors propose a fundamental distinction between *expression* and *communication*: They refer to "expression" as behavior whose function is to induce an intended reaction in the other and reserve "communication" for behavior whose function is to generate an intended reaction by means of stimulating evolved *complementary mechanisms* of interpretation in the other. This distinction ascribes the status of communication to the waggle dance in honeybees because the behavior of the signaler triggers an evolved complementary interpretive mechanism that induces the receiver's response (to visit a particular location). Crucially, the authors dismiss nonhuman primates' intentional use of gestures as *not* communication because although they induce responses in the recipient, and the authors concede that informative intentions may drive the signaler's actions, primates may lack the capacity to represent the mental states their signals create in others. In their view, "a gorilla thumping his chest might associate this with the behavioral effect of conspecifics backing away, but not with the effect of them being frightened."

This distinction between communication and expression creates three interpretative problems. First, contrary to the authors' proposal, the gorilla chest-beating display may qualify as communication because it (and other intentional gestures by nonhuman primates) may indeed trigger an evolved mechanism of interpretation in the recipient. Chest-beating is a species-specific signal typically used in agonistic contexts (although juveniles also use it in play) to intimidate others by conveying strength. In this sense, chest-beating is not so different from other species-specific signals, such as red deer roaring, commonly used in male–male contests. It is thought that such signals evolved precisely because opponents can interpret them as a reliable indicator of the signaler's strength. Thus, production and interpretation of gorilla chest-beating and other nonhuman primates' intentional gestures are likely to have evolved (or developed during ontogeny) as complementary systems.

Second, if nonhuman primates' intentional use of gestures does not qualify as communication on the grounds that signalers do not mentalize their effects on others, it is unclear why the honeybee dance constitutes communication. Bee signalers and recipients have evolved a fixed but complementary system of signal decoding, where mentalizing is unlikely to play a role. Therefore, the assertion that bees engage in true communication seems to hinge on the complementary nature of their system. However, the authors do not present a precise explanation of the factors which make a mechanism "complementary" that can be mapped onto behavior occurring at various levels of cognitive engagement. The authors argue that nonhuman primates' intentional gestures are expressive but not communicative, because although the signal can generate a desired behavioral reaction, it does so by "trigger[ing] a mixed set of mechanisms that may not be complementary in the relevant way." This distinction seems to imply that for mechanisms to be "complementary," they must be symmetrical in their level of cognitive engagement. In other words, the honeybee's dance uses fixed signal encoding and decoding, thus the signaler and the recipient engage with the communication in a cognitively similar manner. In contrast, the gorilla's chest-beating display may consist of informative intention from the producer, while the recipient may engage only with a behavioral reaction to their own emotional response of fright: One engages at a more complex level of cognition than the other. In our view, however, for informative gestures (like chest-beating) to be selected and maintained in the evolved repertoire of the species, they must successfully induce their intended reaction in the other often enough to remain sufficiently beneficial for fitness and survival. This makes it more likely that species-specific display gestures achieve their effect by inducing specialized functional mechanisms, whether they are cognitively symmetrical or not, that account for their sufficient degree of success and stability rather than inducing an unspecified "mixed set of mechanisms."

Third, nonhuman primates' intentional use of gestures may qualify as communication after all, even when mentalizing is required. We are uncertain as to how the authors substantiate the assertion that the displaying gorilla does not knowingly intend to induce a frightened state, when there is relevant evidence that apes are aware of some causal psychological mechanisms mediating their intended effect on their conspecific. Significantly, before presenting a species-typical gesture that displays relevant information about the context of their subsequent behavior – for example, an "arm-raise" gesture to inform a conspecific partner that the ensuing hitting behavior is meant in play – apes first check and make sure that their addressee is positioned so that they have *perceptual access* to the behavioral display (Tomasello, Call, Nagell, Olguin, & Carpenter, 1994). In fact, signalers facilitate perceptual access by engaging in tactile gestures (e.g., throwing objects, poking, touching of distal body parts), or by moving into the line of sight of an individual to ensure that they see and attend to a visual gesture (Liebal, Call, & Tomasello, 2004). This audience-sensitive, selective use of visual gestures indicates that apes can monitor the

other's perceptual orientation and intentionally modify their own signaling behavior in response. This competence establishes the preconditions for mentalization of informative intention; apes engage with the relevant psychological mechanisms of the other that are necessary for and involved in perceiving the gesturing ape's informative behavior. Furthermore, apes' coordinated use of "attention-getters" together with the subsequent display of species-specific gestures that encode relevant information has been posited as convincing evidence of non-verbal intentional communication in apes (Tomasello & Call, 2019; Warren & Call, 2022).

It appears to us that the relevant and intriguing question for evolutionary cognitive science is to further explore and characterize the underlying cognitive mechanisms and functional adaptations that serve apes' capacity for intentional communication. In particular, we should investigate whether and to what degree this rudimentary communicative system can be considered a proto-form or evolutionary precursor of ostensive communication proper as it emerged in humans. The authors attempt to identify how the relevant cognitive capacities that serve ostensive communication may have evolved in a gradual manner. We feel, however, that the theoretical distinction and definitions proposed to differentiate between expression and communication fail to serve this purpose and lead to more confusion than clarity in how these definitions can be applied to nuanced behavior across taxa.

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Authors' Response

Being ostensive (reply to commentaries on "Expression unleashed")

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Abstract

One of our main goals with "Expression unleashed" was to highlight the distinctive, ostensive nature of human communication, and the many roles that ostension can play in human behavior and society. The commentaries we received forced us to be more precise about several aspects of this thesis. At the same time, no commentary challenged the central idea that the manifest diversity of human expression is underpinned by a common cognitive unity. Our reply is organized around six issues: (1) languages and their cultural evolution; (2) the pervasiveness of expression in human behavior; (3) artificial intelligence and ostensive communication; (4) communication in other animals; (5) the ecology and evolution of ostensive communication; and (6) biolinguistics and pragmatics.

Our target article presented human expression as a diverse and rather muddy phenomenon, replete with graded differences between specific cases. This muddiness is, we believe, characteristic of great ape expressive behavior in general, and human expressive behavior especially: Humans have a large and wide range of social goals, and a large and wide range of means of expression with which to satisfy these goals. Language use is but one important special case: Not apart from other means of human expression, but continuous with them.

In aiming to identify the common foundations of this diversity, three goals were especially paramount in our minds:

(1) Specify the cognitive capacities that underpin human communication.
(2) Demonstrate that these capacities are evolvable under plausible assumptions.
(3) Describe how these capacities can generate massive behavioral diversity.

Box R1 summarizes our main contributions to meeting these goals. The concept of ostension plays an especially important role. Indeed, one of our main hopes was to contribute to "pragmatics-first" accounts of language origins, which emphasize how ostensive communication must be prior – in ontogeny and phylogeny – to the emergence of language and languages. More broadly, the diversity of expression enabled by ostension raises an important set of empirical questions for cognitive science. In particular, when, how, and why do people choose the particular means of expression they do? (See Box R2.)

The commentaries enriched and challenged many aspects of this thesis, in original ways. Our reply is organized around six core issues:

(1) *Languages and their cultural evolution*. What role, if any, does ostensive communication play in the cultural evolution of languages?
(2) *The pervasiveness of expression in human behavior*. What new insights and understanding are gained by an expressive perspective on human behavior?
(3) *Artificial intelligence and ostensive communication*. What prospects are there for the development of intention-based models of communication?
(4) *Communication in other animals*. What forms or precursors of ostensive communication might be found in other species?
(5) *The ecology and evolution of ostensive communication*. What ecological factors, distinctive of humans, are necessary to trigger the gradual evolution of ostensive communication?

Box R1. Summary of key ideas

Here we summarize our contributions to meeting the three goals stated in the Introduction: (1) to specify the cognitive capacities that underpin ostensive communication; (2) to demonstrate that these capacities are evolvable under plausible assumptions; and (3) to describe how these capacities can generate massive behavioral diversity.

Regarding the specification of the key cognitive capacities, we drew heavily on Deirdre Wilson and Dan Sperber's relevance theory and its subsequent enrichments, while also paying more attention to the production side than is typically the case in that literature. We highlighted in particular: (a) *On the communicator's side, the capacity to satisfy their informative intentions by means of making them – the intentions themselves – manifest*. An act of ostensive communication consists in intentionally attracting the audience's attention to evidence about one's own informative intentions. By doing this, communicators trigger audiences' interpretative processes. (b) *On the audience's side, the capacity to identify the communicators' informative intentions, i.e., what is meant*. This is achieved by spontaneous presumptions of relevance. In other words, audiences recognize and interpret ostensive stimuli with cognitive capacities that, in effect, embody an assumption that ostensive stimuli are the most effective means available to the communicator for revealing her particular informative intentions. (c) *Also on the audience's side, the capacity to modulate trust in what is meant*. Thus, audiences update their beliefs in view not only of their interpretation of others' ostensive behavior, but also in view of the broader, validating context, which includes the trustworthiness of the communicator and the plausibility of what is interpreted. We described how these cognitive capacities collectively constitute a communication system that can be both evolutionarily stable and truly open-ended at the same time, and we discussed similarities and differences with the communication of other species.

Regarding evolutionary plausibility, we specified one way by which the above capacities can co-evolve with one another. The essential idea is that in a partner choice ecology, it is often adaptive to draw others' attention to whatever will allow them to "acquire" information; and that once audiences effectively presume that this expressive behavior is done cooperatively, then drawing attention to evidence of one's own informative intentions will itself be sufficient to generate the intended inferences in the audience. In fact, this unleashes expression. We think this specific evolutionary path is very plausible, but it is presented in the first instance as an existence proof of how and why the necessary cognitive capacities could have evolved in a gradual manner.

Regarding massive behavioral diversity, we highlighted five specific examples in the target article: language use, coordination, teaching, punishment, and art. We described some of the ways in which these cases are each very different from one another, and the underlying cognitive unity. Some of the commentaries provide further good examples, such as the non-verbal cues used by poker players to influence one another's thought processes (**Stehberger**), movements used by car drivers to reveal their intentions to other drivers (**Tolstaya et al.**), and screaming (**Gouzoules et al.**). Recognizing that this diversity has common evolutionary and cognitive foundations generates new questions for future empirical research (Box R2).

(6) *Biolinguistics and pragmatics*. What is the root source of open-endedness in natural languages?

R1. Languages and their cultural evolution

Language use is the most salient specific mode of ostensive communication. In previous work, we have argued that from a pragmatics-first perspective there are thus two basic questions for language evolution (Scott-Phillips, 2017). (1) How and why did humans evolve ostensive communication? (2) How do collections of communicative conventions develop, and how and why do they evolve, culturally, to take the forms that they do? Our target article was aimed mainly at question (1), with only passing remarks on question (2). Four commentaries (**Chater & Christiansen**; **de Vos**; **Rorot, Skowrońska, Nagórska, Zieliński, Zubek, & Rączaszek-Leonardi [Rorot et al.]**; **Veit & Browning**) justly picked up where our article left off, elaborating and debating answers to question (2).

Chater & Christiansen phrase the question this way: "what is the route from non-linguistic communication, driven by a powerful 'pragmatic engine,' to the creation of the astonishing complexity of full-blown combinatorial language?" Sketching their answer, they describe how communicative conventions are continually recreated and reshaped in the course of ordinary interaction (see also Christiansen & Chater, 2022). We very much agree; but we also think this picture can and should be enriched further, in two particular ways.

First, what *cognitive* capacities drive these processes? As **Chater & Christiansen** point out, there is by now a large amount of literature on how grammar and symbols emerge from behavior in interaction – but where do those behaviors themselves come from? We believe that the cognitive capacities described by relevance theory (target article, sects. 3.3 and 4.3) provide a good answer to this question: "the very same cognitive capacities that make ostensive communication possible in the first place, also play a pivotal role here" (target article, sect. 8.5). Second, what is the most useful framework with which to describe and analyze the evolving system of communicative conventions? This is an important question, because without any answer it is hard, if not impossible, to describe how individual behavior (language use) generates population-level phenomena (languages): this is sometimes called the "problem of linkage" (Kirby, 1999, p. 19). Somewhat in contrast to other frameworks for cultural evolution,

Box R2. Where is ostension?

Generally, the many and different means of human expression are described and studied in largely independent literatures (target article, sect. 8). The diversity is daunting and empirical research tends to focus on specific cases in isolation. Yet viewing diversity as different solutions to the same problem – satisfying informative intentions – generates new and important questions for empirical research.

One especially important question is, when and why do people decide that the best means to satisfy their informative intention is to make it overt? That is, when do people provide evidence of their own informative intention, rather than evidence of whatever it is they want to inform others about? Part of the answer must be that in some cases it is hard or impossible to provide direct evidence of whatever it is that the communicator wants to inform the audience of, e.g., absent entities or past events (see also target article, endnote 6). Still, there are cases when ostension – in the narrow sense (target article, endnote 7) – is used even when direct evidence could be provided: for an example see target article, section 8.2.

One approach to the question might be to treat ostension as something "special" and perhaps cognitively "costly" or "complex," and hence as something to be used only when other, more "simple" or "basic" cognitive processes do not suffice. In contrast, we argued that the ordinarily developing human cognitive phenotype includes competence with ostensive communication, i.e., with each of the various cognitive capacities entailed by the expression and recognition of informative intentions. Thus, we suggest that humans tend to make their informative intentions manifest to the extent that is optimal; and that others interpret this behavior assuming optimality, given the communicator's goals, and the affordances and constraints acting on them. The empirical literatures we surveyed in section 8 of the target article provide many findings consistent with this view, but the issue has not yet been investigated in a wholly unified way.

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we mentioned in the target article that we believe an epidemiological framework is likely to be a fruitful approach (see Claidière, Scott-Phillips, & Sperber, 2014; Scott-Phillips, Blancke, & Heintz, 2018). We would be interested to know how Chater & Christiansen view these important issues.

In section 6 of the target article we asserted that cognitive capacities for ostensive communication emerge early and reliably in ontogeny, and we cited some books and articles that, we believe, collectively summarize a diverse and compelling range of data in support of this conclusion. **de Vos** enriches this point substantially. She identifies that a natural testbed for this claim is homesign: Visual–gestural forms of communication that emerge in the absence of any language. de Vos hence describes how the universal aspects of communicative competence we identified in our article can and do facilitate the creation and conventionalization of commonly known mappings between form and function, and hence in due course the emergence of new languages. This process can occur at many different levels of analysis, from individual households and small communities to whole nation states. de Vos provides description of the specific example of Balinese homesign, expanding the range of natural case studies beyond more commonly studied cases, in particular Nicaraguan Sign Language and Al-Bedouin Sign Language.

We think, furthermore, that findings derived from the study of homesign and new sign languages are of high importance not only for language evolution, but also for language learning. If infants are competent ostensive communicators "from the beginning," so to speak – which is to say, very soon after they actively engage in the social world, at around 9 months of age – then what changes over time in the process of language learning is not the development of any core competence with ostensive communication as such, but rather (a) greater knowledge of the means by which those around them express and recognize informative intentions, especially conventional means; and (b) greater sensitivity to the possible motives, goals, and objectives of communication partners. Accordingly, any apparent weaknesses in infant pragmatics are explained not by any weaknesses in communication *qua* communication, but rather by changes in (a) and (b) that occur as infants grow. This picture aligns squarely with **de Vos**'s arguments that studies that supposedly show pragmatic and/or socio-cognitive "deficits" in homesigners are likely better explained as task effects. Further empirical findings consistent with this idea can be found in several other literatures such as, for instance, discourse pragmatics (e.g., Ateş & Küntay, 2018; Hughes & Allen, 2013; Salazar Orvig et al., 2010; Skarabela, 2007; Skarabela, Allen, & Scott-Phillips, 2013).

Both **Veit & Browning** and **Rorot et al.** make similar empirical points to those above, but they argue for different theoretical and terminological frames, which they believe provide greater or enhanced understanding of the empirical issues. Specifically, Veit & Browning emphasize "scaffolding," in which traits facilitate the evolution or development of other traits and are later lost or repurposed, while Rorot et al. emphasize the conceptual tools afforded by an "extended" evolutionary synthesis. Naturally, we see merit in the framing we adopted, which is rather classical in its evolutionary and cognitive perspectives, but we certainly don't object if other scholars find benefit in translating our claims into other terms.

For instance, **Veit & Browning** restate one of our main claims as a claim that core cognitive capacities of ostensive communication "scaffold" many important means of human interaction, such as coordination smoothing and punishment. We agree this is an insightful presentation. Indeed one of us has previously used the language of scaffolding to describe how processes of cultural evolution build upon panhuman cognitive capacities (Heintz, 2014). **Rorot et al.**'s preferred frame is the extended evolutionary synthesis. The relative merits of this theoretical frame have been debated within evolutionary biology at some length and this reply is not the place to regurgitate those arguments (see, e.g., Laland et al., 2014; Lewens, 2019); but we think we are on safe ground not adopting it explicitly. After all, even the most enthusiastic advocates of the extended evolutionary synthesis agree that more classical approaches are always able, in principle, to provide explanatory accounts of biological phenomena (Scott-Phillips, Laland, Shuker, Dickins, & West, 2014).

Empirically, **Rorot et al.** assert that our approach "*cannot* account for the emergence of the structure of unleashed communication visible in language" (italics added). We agree that our paper *does not* do this, because it does not aim to; but that does not mean that our framework *cannot* account for the emergence of language structure. On the contrary, other commentaries – in particular by **de Vos** and by **Chater & Christiansen** – show how this issue can be approached from the perspective we presented. Rorot et al. describe how development plays a key role in this process, helping to scaffold the emergence of languages: and in doing so they support and reinforce, rather than challenge, the picture developed in the target article.

R2. Pervasiveness of expression in human behavior

The modulation and flow of attention is ubiquitous in human interaction. Four commentaries enrich this point. Three elaborate some further, diverse cases of human communication and expression (**Tolstaya, Gupta, & Hughes [Tolstaya et al.]**; **Stehberger**; **Gouzoules, Engelberg, & Schwartz [Gouzoules et al.]**), and one adds new arguments for the deep, pervasive, and often unidentified role of pragmatics in ordinary interaction (**Osiurak & Federico**).

Tolstaya et al. introduce the example of driving. It is plausible to us that drivers use movements of their vehicles not just to achieve travel, but also to actively reveal their intentions to other road users. For instance, drivers wishing to change lanes in stationary traffic sometimes turn their wheels, not simply in advance of movement but also with the goal of indicating to drivers their wish, or intention, to enter the other lane. Accordingly, it is also plausible that road users are sensitive to these behaviors *as expressive behaviors*. If so, then self-driving cars, absent artificial intelligence able to duplicate human intention-reading and attention manipulation, might deviate from the behavior of human-driven cars in ways that are subtle but of high importance for predictability and hence safety. Whether this speculation is correct is a matter for future empirical research, with important implications for technological development.

Stehberger highlights the world of poker as a domain in which many of the aspects of human expression we described in our target article play important roles. As we described, ostensive communication is an important special case of expression, in which one individual (the "communicator") directs the attention of another (the "audience") to their (the communicator's) own informative intentions in a specifically overt way. However, often in human interaction it can be beneficial to not communicate ostensively as such, but rather to direct others' attention and simultaneously hide, or at least not make overt, this goal. In the target article we called this "hidden authorship." We also

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discussed how both generosity and punishment sometimes entail keeping informative intentions at least somewhat hidden (sects. 3.2 and 8.3). Some of the behaviors employed in poker are excellent further examples. There are obvious misaligned interests between poker players, and many betting decisions are made on the basis of what individuals believe others know, or what they believe that others believe about what others know. In consequence it is sometimes useful for poker players to attempt to inform, or direct the attention of other players, without overtly drawing attention to this goal. Doing this well is a difficult and advanced skill. So too is noticing others' attempts to direct attention, and making betting decisions that take into account what you believe others have revealed in their actions at the table, or are attempting not to reveal. Stehberger also describes how poker players exploit the fact that interpretation of ostensive stimuli is spontaneous and cannot be prevented even if interpretation is against the audiences' own interests. This is akin to the case of film spoilers, which we mentioned in section 4.3: Our desire to not recover the meaning of what is said does not and cannot suspend the interpretive process. All in all, Stehberger's commentary highlights how a deeper understanding of a common mode of human interaction – in this case, a competitive game – can be gained from the broad and pragmatic perspective we developed in the target article.

Gouzoules et al. discuss the enlightening example of screams. We are especially glad for this because of emotional expression is an obviously major means of human and nonhuman expression which we did not discuss in the target article. Gouzoules et al. describe how capacities of scream production tend to first evolve with the expressive function to startle potential predators, and how in some highly social species the forms and functions of screams have diversified over the course of evolution, creating selection for "complementary" capacities of comprehension, hence forming a communication system. Gouzoules et al. further describe how screams can hence be sometimes expressive but not necessarily communicative (such as to startle predators), and at other times they are properly communicative (such as when used to recruit aid). In humans this diversity is extended even further, because in addition to using screams as emotional communication, humans can use screams in an unleashed way to ostensively communicate that, for instance, something is inducing emotion. This is different from the spontaneous, non-ostensive communication of emotion itself. Gouzoules et al. wonder if we would not agree with the extrapolation of the term "unleashed" to include human nonverbal expression; but far from disagreeing, we very much welcome this, as it helps to further demonstrate the real pervasiveness of expression and communication in human life.

Osiurak & Federico provide an interesting example of how human interaction is so much governed by the expression and recognition of informative intentions that it can easily lead scientific investigation astray, if we are not alert to its effects. They point out how tasks used to assess dementia overlook the ostensive nature of experimental instructions to participants, failing to recognize how standard tasks used to assess dementia, which entail consideration of the experimenter's expectations, can be challenging for patients with a loss of semantic knowledge. Patients with semantic dementia of tools usually do not lack the mental representations needed for using tools; rather, they lack knowledge about the means used in ostensive communication to communicate about tools. Thus, behaviors that have been assumed to derive from a general tool-use disorder might in fact result from disorders that principally affect pragmatic communicative capacities. We do not have expert knowledge in this area but this analysis seems very plausible to us. Indeed, we think that many experimental protocols in psychology have pragmatic aspects that have consequences that are not always taken into account in the interpretation of data. Further examples include the Wason selection task, used to assess reasoning skill (e.g., Sperber, Caro, & Girotto, 1995); verbal false-belief tasks commonly used to assess infant mindreading (e.g., Helming, Strickland, & Jacob, 2014; Siegal & Beattie, 1991); and cross-cultural experimental games used to assess prosocial preferences (e.g., Baumard & Sperber, 2010; Heintz, 2013). In all these cases, and apparently also in the case described by Osiurak & Federico, the experiments entail ostensive communication between investigator and participant. This communicative interaction is often not the simple and innocent process it sometimes appears to be. It is a social interaction with its own dynamics, and if scientists are not alert to these dynamics and their consequences, then the data they acquire may not be as revealing of the target phenomenon as intended.

R3. Artificial intelligence and ostensive communication

Tolstaya et al. survey the literature on generality in artificial intelligence, pointing out that specialization remains the norm: There is still very little artificial intelligence that displays a breadth of competence across otherwise diverse tasks. We argued in the target article that ostensive communication is both a very general skill and a very specialized one. It is very general in the sense that the effective domain of the relevant cognitive capacities is unlimited. At the same time, ostensive communication is a very specialized skill, in the sense that the relevant cognitive capacities all have their own specific and narrow domains. Accordingly, we described how the metarepresentational structure of ostensive communication generates virtual domain generality from narrow specialization (target article, sect. 5). Tolstaya et al. intuit that this approach provides a new way to address the problem of generality in artificially intelligent communication. It also, we believe, reframes one of the basic challenges for artificial intelligence, namely how to replicate human language use. There are countlessly many artificial intelligence language models that replicate human language use with varying degrees of success, but none (to our knowledge) is based on a pragmatics-first foundation, with communicative conventions employed as an enrichment of the expression and recognition of informative intentions. We believe this challenge is deeper and far harder than presently appreciated; but were it to be addressed, it would fundamentally change the prospects for artificially intelligent communication.

The key engineering challenge is that ostension is not any specific behavior, it is any behavior motivated by a particular cognitive phenomenon, namely informative intentions (target article, sect. 3.3). Thus, in order to artificially replicate ostensive communication, what will be necessary are pairs of social agents who have (1) goals with respect to each other's internal ("mental") states, and (2) models of each other's goals, and the means by which those goals might be satisfied. Some limited progress has been made in this direction using Bayesian approaches (e.g., Ho, Cushman, Littman, & Austerweil, 2021), in which a communicator's behavior is modeled as efficient planning with respect to an audience's beliefs, and comprehension as inverse planning of the same, that is, for what goals could this behavior be the most efficient means? In this way, communicative behavior is modeled as a type of action whose costs and benefits (for the

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communicator) turn on its impact on the belief states of other agents; and comprehension is modeled as a reactive process whose costs and benefits (for the audience) turn on how informative this process is about the communicator's goals. The modeling of language use, as one especially important form of ostensive communication, will, in turn, be based on the use of words and other linguistic items *in the service of* these deeper goals. As **Tolstaya et al.** suggest, such approaches would be radically different from the present cutting-edge; but if successful they could lead to major advances in the development of open-ended communication in artificial agents. Or to put the point in negative terms: We do not believe that artificial intelligence will achieve human-like competence in language, and human communication more broadly, unless and until it meets the difficult engineering challenges presented by ostensive communication.

R4. Communication in other animals

Plainly, there are cognitive differences of some sort between human and nonhuman communication. **Veit & Browning**, **Amici & Liebal**, and **Warren, Call, & Gergely (Warren et al.)** all emphasize that exactly what these differences are and where they come from are important empirical questions. We agree, and we argued that the most informative comparisons from an evolutionary perspective will be those focused on social cognition, and more precisely on means of attention manipulation (see also Scott-Phillips & Heintz, 2023). We further suggested that (1) ostensive communication, in its full richness, is part of the ordinarily developing cognitive phenotype of humans and not part of the ordinarily developing cognitive phenotype of nonhuman great apes, and (2) differences between the social cognition that underpins ostensive communication, and the social cognition of other great apes, are graded and relatively few. Three commentaries raise questions on clarification or skepticism about these claims (Warren et al.; **Berio, Newen, & Moore [Berio et al.]**; Amici & Liebal). One further commentary broadens the range of species considered to raise some important issues about the mappings between species' social ecologies and the nature of their communication (**Ross**).

Warren et al. attribute to us some views that we do not hold. In particular, they assert that we do believe the gestures of nonhuman primates are not communicative: "the authors dismiss nonhuman primates' intentional use of gestures as not communication"; "The authors argue that nonhuman primates' intentional gestures are expressive but not communicative…." Yet we do not claim this and in several places we say the opposite. Here are two things we did write: "Living things communicate in a great variety of ways, from the quorum sensing of bacteria, to songbirds, to the gestural and vocal communication of primates…"; "The gestural communication of nonhuman great apes is more diverse and flexible than most other cases…." One reason Warren et al. seem to attribute to us the contrary view is the following sentence, which they quote and take issue with: "a gorilla thumping his chest might associate this with the behavioral effect of conspecifics backing away, but not with the effect of them being frightened." Yet, when the passage is quoted in full, it is clear that this is a hypothetical example used to motivate a conceptual distinction, with no empirical claim either way (target article, endnote 4). Warren et al. attribute to us the certain view that gorilla chest thumping is not communicative: But we did not express any such view, we do not have any such view, and we do not believe the relevant passage suggests such a view. Whether chest thumping or any other behavior achieves a communicative function, and whether it does so in a specifically ostensive way, are empirical questions to be resolved for each given case.

More substantively, **Warren et al.** question the distinction we drew between communication and expression. In some respects this distinction is unusual. After all, if an informative intention is satisfied, then there is successful "information transfer," and so perhaps "expression" could be equated with "communication." However, it is useful to maintain a terminological distinction between (1) behavior or traits the function of which is to inform, and (2) behavior or traits the function of which is to inform by the specific means of triggering inferences whose function is, complementarily, to identify and process the behavior or trait. Without this distinction then we have no way to distinguish communication proper from, say, mimicry and other behaviors or traits that could be called "psychological coercion." Put simply, communication is the product of complementary traits: one on the production side and one on the interpretation side (Maynard Smith & Harper, 2003; Scott-Phillips, Blythe, Gardner, & West, 2012). In the target article we specified it this way, "By 'complementary,' we mean that each mechanism can perform its function only in conditions when the other mechanism is in place…. This characterisation is solely functional in nature, and not mechanistic." The important general point here is that a functional approach allows empirical questions to be asked and addressed in an open way, without prior assumptions or commitments. Warren et al. seem to question this, stating that "the authors do not present a precise explanation of the factors which make a mechanism 'complementary' that can be mapped onto behavior occurring at various levels of cognitive engagement" – but the distinction being drawn is not a mechanistic one, it is functional. We strongly support the empirical research agenda of investigating cognitive similarity and cognitive difference between humans and other species, especially other great apes; and we believe that this research agenda will both enrich and be enriched by functional clarity.

Berio et al. ask some specific questions of clarification, which we are happy to answer. First, they press us on "the relationship between ostension and contextually variant interpretation." They point out, rightly, that contextual variation is widely documented in animal communication. However, our suggestion was not simply contextual variation: It was contextual variation (1) in response to specifically ostensive stimuli (where ostensive is used in the narrow sense employed in the target article; see in particular endnote 7) and (2) dependent on what is in the common ground. The contextually variable response should "make sense of" the ostensive stimulus *in light of* the common ground, and in particular in light of the audience's prior knowledge about the communicator's knowledge. To be even more precise, one suitable test would be experiments in which the independent variable is the audience's knowledge of the communicator's knowledge, and the dependent variable is the audience's reaction to ostensive stimuli produced by the communicator. We mentioned in the target article that human infants have been shown to pass a version of such tasks where the infant observes interactions between two other agents (Tauzin & Gergely, 2018). Further experimental protocols, suitable for comparisons across species, would be hugely informative, and would complement existing studies on the production side showing that chimpanzee pointing behavior can be dependent on what is or is not in the common ground (e.g., Bohn, Call, & Tomasello, 2015; Tauzin, Bohn, Gergely, & Call, 2020).

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Second, **Berio et al.** summarize one of our claims as follows, and take issue with it: "If we understand H&S-P's argument correctly, enculturated great apes acquire expectations of mutual benefit, and so trust the information provided by pointers." This is not exactly our argument. What we claim is that enculturated great apes learn to assume that behavior that overtly demands attention is likely to indeed be worth paying attention to (and to some extent, this claim is reinforced by the points that Berio et al. make about attention in the object-choice task). It is important to distinguish "assuming that something is worth paying attention to" and "trust": the former is about expecting relevance, while the latter is about accepting what is meant. Relatedly, Berio et al. ask if we claim that "unenculturated chimpanzees distinguish between 'informative' and 'communicative' intentions, but remain poor at pointing comprehension only because they lack the trust to interpret humans' messages pro-socially." Again, not exactly. What we claim is that unenculturated chimpanzees tend not to recognize communicative intentions because doing so requires the specific cognitive disposition to presume that behavior that demands attention is indeed likely to be worth paying attention to. In humans this disposition is built into (or "embodied") in the way our attentional systems work (sect. 4.3). We raised the hypothesis that, while this interpretative mechanism is not part of the ordinarily developing cognitive phenotype of other species, a corresponding disposition could be acquired ontogenetically, in the right ecology.

Amici & Liebal make four main points. We agree with some and not with others. First, they emphasize the methodological challenges of investigating cognitive capacities of ostensive communication in nonhumans, and hence caution against hasty conclusions. We fully agree. Second, they assert that epistemic vigilance is not necessary for the evolution of open-ended communication. This is not true. Arguing otherwise, Amici & Liebal point out that many communication systems are evolutionarily stable without cognitive mechanisms of epistemic vigilance. Yes indeed, but this is not a counter-argument to the facts that (1) epistemic vigilance is necessary for any distinction between comprehension and acceptance, and (2) this distinction between comprehension and acceptance is critical to the stability of truly open-ended communication (target article, sect. 5). Third, Amici & Liebal ask us to "better clarify whether humans… differ from other species in terms of cognitive skills or motivational aspects of communication." It is both (target article, sect. 7). It is cognitive skill, because the cognitive capacities that underpin ostensive communication are not part of the ordinarily developing cognitive phenotype in nonhuman great apes. It is also motivational, because it is not the case in nonhuman great ape social ecologies that attending to others when they attempt to attract attention will necessarily prove beneficial. Here dogs provide the most revealing contrast: They spontaneously presume that when humans attempt to gain their attention, it is indeed worthwhile to actually pay attention and expect relevance, even if that relevance is not initially clear.

Fourth and perhaps most fundamentally, **Amici & Liebal** maintain that "the ability to combine meaningful elements into new combinations with novel meanings still better explains how open-ended communication emerges." We highlighted two major challenges for this focus on structural and combinatorial features of different species' communication systems (target article, sect. 1), and Amici & Liebal's reassertion of this perspective does not directly address either challenge. First, this focus says very little about quasi- and non-linguistic means of communication and expression. Second, it does not address the fundamental problem of how (how just possibly?) a communication system can be both stable and open-ended. Amici & Liebal summarize some recent findings of compositions in primates and we fully agree that these findings are valuable and important (Scott-Phillips & Heintz, 2023), but it does not follow that a focus on combinatorics provides a "still better" explanation of the evolution of truly open-ended communication.

Ross's observations and speculations about the ecologies and communication systems of other species are interesting and relevant: A true diversity of examples and case studies is very welcome. In particular, Ross raises the intriguing hypothesis that elephant communication may be "leashed" in part because there is insufficient divergence of interests within elephant communities, and hence there has not been selection on cognitive capacities necessary to deal with the challenges and complexities of a social ecology where there are not only very high potential gains to cooperation, but also high risks of exploitation. This contrast highlights how the evolution of ostensive communication requires not only cooperation and relatively sophisticated social cognition, but also the potential for divergent interests and conflict (target article, sect. 5).

Ross also comments on the possible contrast between "mindreading" and "mindshaping" (see also Zawidzki, 2013). Approaches to the evolution of human communication that emphasize metapsychology, including ours, are sometimes criticized on the grounds that they are too cognitively "rich" or "intellectualized." Two endnotes in the target article address this worry (9 and 11). In particular, we use the notion of mindreading in a broad, minimal, and deflationary way, to refer just to the spontaneous recognition of mental states, which we believe may be present in many species. If others use "mindreading" in richer ways, such as to describe the conscious analysis of others' mental states, then we don't object to a different term for the more deflationary notion, and "mindshaping" may indeed be suitable. In fact it may have the advantage of highlighting "action" on mental states. Whatever the terminology, we certainly agree that cognitive capacities to recognize and shape others' mental states must ultimately serve behavior and action.

R5. Ecology and evolution of ostensive communication

Five commentaries raise questions about the ecology and evolution of human cognition, and communication in particular (**Badets**; **Burkart, Sehner, Brügger, Adriaense, & van Schaik** [**Burkart et al.**]; **Gärdenfors**; **Mussavifard & Csibra**; and **Wacewicz & Żywiczyński**). In the target article we described how the cognitive capacities that underpin ostensive communication can evolve in a gradual way, and become stable cognitive adaptations in a partner choice ecology. What we did not do is describe in detail why *humans in particular* occupy the relevant social ecology; and hence the deep evolutionary reasons why it is humans, and not any other species, that have traversed the evolutionary path toward language.

So as **Wacewicz & Żywiczyński** put it, our article pushes the issue "one level deeper." Why, they ask, does the expression and recognition of information intentions afford fitness benefits "to humans (including prehistoric hominins), if it does not for anyone else (including our ape cousins)?." We do not believe anybody yet knows the answer to this question in detail, but our target article did contain a sketch. Prompted by Wacewicz & Żywiczyński, here we elaborate a little more.

A partner choice social ecology has two key prerequisites. (1) An environment in which there are opportunities for win-win and win-lose ventures, such that it is adaptive to cooperate with

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others, but not always and not necessarily so. These opportunities may be present in the social ecologies of several species, but they are present to a greater degree, and with more diversity, in the human case (target article, sect. 6). (2) Social cognitive capacities that allow individuals to assess whether entering a cooperative venture with someone will be beneficial at all; and whether it might be more beneficial to enter it with someone else if possible. We called this "social vigilance." Social vigilance is commonly achieved by reading and representing others' mental states, which we assume is common to great apes and perhaps several other species and taxa (target article, sect. 4).

These two elements together generate selection pressure for the social cognitive capacity to provide credible evidence to others that a cooperative venture is indeed a win-win opportunity; and also for capacities of reputation management. One of the main contributions of our target article is a description of how these selection pressures are on their own sufficient to trigger a gradual co-evolution of the cognitive capacities necessary for ostensive communication. None of this is to deny, as **Burkart et al.** point out, that forms of partner choice take place in many other species, including several primate species. The difference is just degree and span. In humans, partner choice – characterized as above – is more ubiquitous and involved in many more diverse tasks than in other species. There is more mutual dependency (or "interdependence" as **Wacewicz & Żywiczyński** put it), and we have evolved more specific cognitive dispositions to handle both its opportunities and its dangers. **Ross** notes how this emphasis on the breadth of human partner choice aligns with a common view about the origins of human ecological dominance, namely that it lies in the expansion of community scales, market exchange, and specialization traced to the Upper Pleistocene.

So the relevant domain of partner choice in humans is broad, covering a wide range of possible interactions. It probably includes hunting, parenting, technological development, and many others. Three commentaries elaborate supposed alternatives, but these are, we think, both better understood as special cases of partner choice. **Burkart et al.** stress cooperative breeding, **Gärdenfors** suggests that teaching may be an especially important domain, and **Mussavifard & Csibra** argue that extensive reliance on technology, where the causal relations between object and goal are hard to perceive, creates a need for pedagogical demonstration. These activities all provide opportunities for cooperative ventures, which can be beneficial for the self, or not, depending on the context and available partners. (Shall I leave my offspring with this person? Is it to my advantage that this person acquires skills I can demonstrate?) In the target article we mentioned also animal hunting and building shelters. We have no strong views about which types of cooperative venture exercised the most significant role during evolution. Our claim is that an open social ecology, such that there is a high degree and wide span of partner choice, occupied by a socially vigilant species, makes possible the gradual evolution of the cognitive capacities that underpin ostensive communication (see Fig. R1).

The ecological breadth of partner choice maps onto the functional breadth of human communication. Debate over the evolutionary origins of human communication, and language in particular, is too often focused on which of many different types of human communication – gossip, sexual advances, teaching, and so on – had the greatest relative importance during evolution. Some of the commentaries, such as by **Gärdenfors**, seem to reinvigorate this debate. However, a focus on relative importance misses the point that the great boon of ostensive communication is its functional diversity.

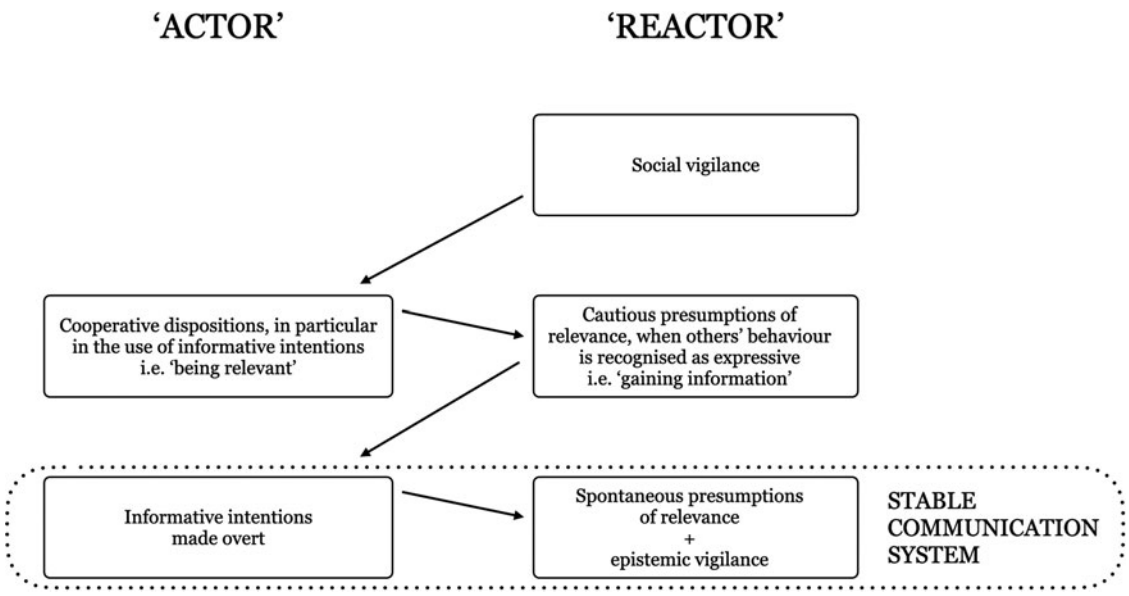

Figure R1. *Whence ostension? Summary of a plausible and gradual co-evolutionary path to ostensive communication* (see also target article, sect. 6). Specifications of plausible, co-evolutionary paths, such as this, are important contributions that go beyond imagining just-so stories: They are a necessary exercise for any cognitive capacity thought to be species specific. The numbers below refer to the four arrows in the figure, from top to bottom: in each case, organisms of the type described in one box constitute a selection pressure for organisms of the type described in the next box. (1) In a partner choice ecology – this comprises socially vigilant others and sufficient opportunities for win-win and win-lose ventures – it is adaptive to have intentions that are both informative (i.e., directed at others' mental states) and cooperative (i.e., targeted at being useful for others). (2) When informative intentions are recognized as such, it is adaptive to presume, even if cautiously at first, that these intentions are cooperative: This is what allows individuals to actually "gain information" from communication. (3) When others make cautious presumptions of relevance, then making one's informative intentions overt is an efficient and adaptive means to trigger the intended inferences in the audience, and hence satisfy one's informative intention. (4) Cognitive capacities that deliver spontaneous presumptions of relevance can then evolve as an interpretative mechanism distinct from epistemic vigilance.

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It is as if the evolution of bipedal locomotion was discussed just in terms of the relative importance of running, jogging, and walking, when in fact what has been selected for *is functional diversity itself*, and the large range of behavioral possibilities thus enabled (Origgi & Sperber, 2000). So we agree with Gärdenfors that the evolution of human communication must precede through different modes of attention manipulation, enabling some behaviors (e.g., a hammering action) to "stand for" others (e.g., hammering itself) – but we disagree that this is specific to teaching.

Finally, three commentaries make observations either enriching or challenging the specific evolutionary path we sketched in the target article. **Badets** proposes that the evolution of human communication may have proceeded alongside tool cognition. This is an intriguing suggestion, to find one unique origin for both human-specific communicative capacities and tool use. Moreover, there is a sense in which expression does indeed involve using tools – words and other linguistic "constructions" – to act on the world: It is just that, with communication, the part of the world acted upon is psychological states and the tools are, correspondingly, epistemic. But other than this general observation we do not have any strong or specific views on how communication and tool cognition relate to one another. **Mussavifard & Csibra** suggest that rather than partner choice and cooperation causing the evolution of ostensive communication, ostensive communication may facilitate cooperation. However, there is an important asymmetry between ostensive communication and cooperation. Ostensive communication is necessarily a type of cooperation, but cooperation is not necessarily a type of communication. We therefore agree with Mussavifard & Csibra that ostensive communication can promote cooperation, indeed we wrote as much in endnote 12. The point we insisted on is just that there is no ostensive communication at all without a specific type of prior cooperation. **Burkart et al.** attribute to us the view that partner choice requires Gricean cognitive pragmatics for reputation management, hence causing a tendency toward showing and expecting prosociality in communication; but this is not exactly our proposal and we do not much recognize our account in their figure. What we argued is that an ecology of partner choice will select for specific forms of cooperative behavior in expression, which in turn enables the gradual evolution of ostensive communication (see Fig. R1).

R6. Biolinguistics and pragmatics

We share with **Carston** the view that cognitive pragmatics is foundational to language use, and that relevance theory provides the most cognitively plausible description of the relevant capacities (e.g., Carston, 2002a, 2002b; Wilson & Carston, 2006). Looking beyond this point of agreement, her commentary highlights a point of difference that echoes major divisions in linguistics itself (see, e.g., Harris, 2021; Scholz, Pelletier, Pullum, & Nefdt, 2022). Channeling what is sometimes called the biolinguistic perspective – according to which "language" is most properly conceived of as a cognitively internal device of recursive symbol manipulation – Carston argues that language must logically *precede* ostensive communication (see also e.g., Berwick & Chomsky, 2016; Carston, 2000; Murphy, 2020).

In making this argument **Carston** raises two particular issues for our "pragmatics-first" approach. One is that the metarepresentational structure of ostensive communication itself entails a cognitive capacity for recursive embedding (in this case, recursive embedding of mental states), and where is that to come from if not language? Our answer is that recursive embedding is not distinctive of language. It is present in other cognitive domains also, including some that, unlike ostensive communication, are shared with other species. Visual processing is the clearest example (see Fig. R2). So we can agree with Carston that a species is not "ostension-communication-ready" before it has some cognitive capacity of recursion that might be co-opted from one domain to another; but we need not and do not agree that this capacity must be specifically linguistic.

The other, related issue raised by **Carston** is the open-endedness of human communication: From where does it come? In answering this question, it is important to distinguish two things: (i) what can be mentally represented; and (ii) the expression of what is mentally represented. Our target article was focused on how (ii) is achieved. Carston suggests, in effect, that without "language" then (i) is a very small set indeed, and hence that (ii) is redundant unless and until there is language. We demur. As we see it, many species have mental representations they do not express: All mammals, for instance, must represent food and sex in some way, yet not all make expressions about these things. So we see no reason to make *a priori* assumptions about the limitations of (i). Furthermore, we should not necessarily expect communication even when (i) is large, for evolutionary and game-theoretic reasons we elaborated in section 2 of the target article. Thus in our view, the problem is not so much what can be mentally represented in principle; the problem is the stability of any expression of what is mentally represented. We described our solution to this problem in section 5 of the target article.

Let us conclude by making more vivid this contrast between the biolinguistic perspective and the pragmatics-first approach

Figure R2. *Recursive embedding in visual processing*. Here, visual processing spontaneously groups the Xs into groups of recursively embedded 3 × 2 sets. This 3 × 2 structure is present at three levels of analysis, and could in principle recur without limit. The figure is inspired by Jackendoff and Pinker (2005).

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we have advocated. Consider this recent passage by Noam Chomsky, Ángel Gallego, and Dennis Ott, from the introduction of an overview of the biolinguistic program:

> "Only humans appear to possess a mental grammar… that permits the composition of infinitely many meaningful expressions… *Universal Grammar* (UG) is a label for this striking difference in cognitive capacity between 'us and them'… What is it, and how did it evolve in our species? While we may never find a satisfying answer to the latter question, any theory of UG must meet a criterion of *evolvability*: the mechanisms and primitives ascribed to UG… must be sufficiently sparse to plausibly have emerged as a result of what appears to have been a unique, recent, and relatively sudden event on the evolutionary timescale" (Chomsky, Gallego, & Ott, 2019, p. 230).

Our target article would seem to have addressed exactly these issues. We described in some detail how truly open-ended expression is made possible by a relatively sparse set of human cognitive capacities for ostensive communication; we described how these capacities meet the important criterion of *evolvability*; we addressed the equally important criteria of *gradualism* and *stability*; and we highlighted some of the most important similarities and differences between "us and them." We are thus tempted to say: If Universal Grammar is but a label for the set of cognitive capacities that allow open-ended expression in humans, then our target article contained many arguments that in fact, Universal Grammar is ostensive communication.

We are well aware, of course, that key words such as "grammar" and "expression" are used in different ways depending on prior assumptions about the nature of "language," and these prior assumptions strongly affect how empirical issues are framed (Scholz et al., 2022). Nevertheless, the contrast seems to us revealing; and, furthermore, suggestive of an original perspective on linguistic generativity. Specifically, the generativity observed in syntax and semantics – the focus of many existing research agendas – may in fact be derivative on the generativity of unleashed expression. Social cognition as the root of grammatical open-endedness. Developing this idea in detail is a major future challenge for the pragmatics-first approach: With, we believe, the potential to re-frame many fundamental issues in original and innovative ways.

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