Great ape interaction: Ladyginian but not Gricean

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Nonhuman great apes inform one another in ways that can seem very humanlike. Especially in the gestural domain, their behavior exhibits many similarities with human communication, meeting widely used empirical criteria for intentionality. At the same time, there remain some manifest differences, most obviously the enormous range and scope of human expression. How to account for these similarities and differences in a unified way remains a major challenge. Here, we make a key distinction between the expression of intentions (Ladyginian) and the expression of specifically informative intentions (Gricean), and we situate this distinction within a "special case of" framework for classifying different modes of attention manipulation. We hence describe how the attested tendencies of great ape interaction—for instance, to be dyadic rather than triadic, to be about the here-and-now rather than "displaced," and to have a high degree of perceptual resemblance between form and meaning—are products of its Ladyginian but not Gricean character. We also reinterpret video footage of great ape gesture as Ladyginian but not Gricean, and we distinguish several varieties of meaning that are continuous with one another. We conclude that the evolutionary origins of linguistic meaning lie not in gradual changes in communication systems, but rather in gradual changes in social cognition, and specifically in what modes of attention manipulation are enabled by a species' cognitive phenotype: first Ladyginian and in turn Gricean. The second of these shifts rendered humans, and only humans, "language ready."

communication | comparative cognition | language evolution | meaning | philosophy of language

Great ape interaction has been a model system for animal communication research for several decades. This is partly because of possible phylogenetic connections to human interaction, including language use, and also because it allows for experimental methods and naturalistic observation to be combined in a productive manner. In consequence, many advances in understanding have been achieved in the past 40 or so years (1–3). Numerous similarities with human interaction have been uncovered, such as behavioral flexibility, sensitivity to the audience's attentional state, and the use of repetition and repair when interaction fails. It is now clear that the interactions of nonhuman great apes (hereafter: great apes) are far more cognitively rich than we understood even a few decades ago. These developments make the comparison with humans even more important than it previously was—and more nuanced too. Human modes of interaction are not wholly apart from those of great apes. At the same time, there remain some manifest differences, most obviously the enormous range and scope of human expression. This is most clearly observed in language use,

but nonlinguistic human expression is also dynamic, open-ended, and flexible to an extent that exceeds what is observed in other great apes. How to account for these similarities and differences in a unified way remains a major challenge.

Many researchers now argue that further progress requires fresh approaches to cognitive description and explanation. Indeed, much research on animal behavior has been so far focused on finding relevant patterns in their behavior. With this goal, the mind can be treated as a black box: Sensory input goes in, and behavior comes out (4). This approach has proven productive, but there are now many demands to scratch beneath the surface: to ask what computational tasks are performed inside the black boxes (5–8). Furthermore, existing computational descriptions of meaning and communication in humans do not include many gradations, which limits the utility of cross-species comparisons (8, 9). So for deeper understanding, we need a framework for interaction that both specifies computational tasks and allows for gradations.

Here, we present a new analytical framework for the cognitive description of great ape interaction and the evolutionary origins of meaning in the human sense of the term, such as in language use. Specifically, we classify different modes of interaction as special cases of attention manipulation. We distinguish in particular i) the expression of intentions and ii) the expression of specifically informative intentions. We label these modes of interaction "Ladyginian" and "Gricean," respectively, and we argue that this difference is critical for current and future understanding of great ape interaction. To demonstrate, we use the distinction to develop an integrated, cognitive explanation for the most distinctive features of great ape interaction, and to differentiate some varieties of "meaning" that are continuous with one another, going beyond the classic, dichotomous distinction between natural and non-natural meaning. We address criticisms of metarepresentational approaches to interaction, and we summarize how Gricean modes of interaction have made humans, and only humans, "language ready." We conclude that with respect to the origins of language,

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the key comparisons to make between humans and other great apes are not in systems of communication as such, but rather in social cognition.

Layers of Attention Manipulation

Fig. 1 shows our "special case of" framework for classifying different modes of the intentional manipulation of attention. The conceptual distinctions we make here will in turn allow us to describe great ape gesture in a way that recognizes its cognitive sophistication, while simultaneously accounting for observable differences with human interaction.

To describe these layers, we begin at the outside and work inward. The outermost subset includes all instances of the intentional manipulation of attention. This is effectively how the concept of "intentional" expression has mostly been used in comparative cognition. We label this subset Washburnian after Margaret Floy Washburn, who pioneered the study of social cognition in a wide variety of nonhuman animals, and who argued that the difference between the human and the nonhuman psyche was a difference of degree, and not a difference in kind (11).

The second subset includes cases where individuals intentionally manipulate others' attention toward evidence of their (the focal individual's) own intentions: which could be to play, to travel, to have sex, to be groomed, and so on (see also ref. 8 on "inferential communication"). We label this subset Ladyginian after Nadezhda Ladygina-Kohts (born Nadezhda Ladygina), who was an early pioneer in the comparative study of great ape social cognition (12, 13). The difference between Washburnian and Ladyginian is that whereas Washburnian behavior aims to manipulate attention in general, Ladyginian behavior aims to manipulate attention specifically toward the focal individual's own intentions. This is possible if the target audience has social cognitive capacities able to identify others' intentions. In the next section, we shall argue that many great ape behaviors meet the description of Ladyginian interaction: They intentionally reveal intentions.

The third subset includes cases where individuals intentionally manipulate others' attention toward evidence of a specific type of intention, namely informative intentions. Eating, for instance, is an intentional behavior in humans;
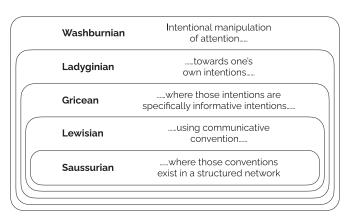
but sometimes, humans eat in an elaborated or slightly exaggerated way, perhaps accompanied by facial expressions, to suggest to others that the food is tasty, revolting, generous, or fancy. When we do this, we have a specifically informative intention that the audience learns something about the food, and we satisfy this intention by providing evidence of it, i.e., by providing evidence of the intention itself. Such behaviors are commonly called Gricean after the philosopher Paul Grice, who developed the idea that meaning in human interaction derives from the provision of evidence for informative intentions (14, 15).

This characterization of Gricean follows reformulations of Grice's original ideas developed by Strawson (16) and, in particular, Sperber and Wilson (17–19). The labels "interactional engine" and "ostensive communication" are often used more or less synonymously with how we use Gricean here (7, 20–23). What unites this family of approaches is that they all identify the roots of linguistic meaning in the expression and recognition of intentions. They contrast with "logocentric" approaches, which treat words and other linguistic phenomena as "having" or "encoding" meaning on their own.

So the difference between Ladyginian and Gricean behavior is that whereas Ladyginian behavior intentionally reveals an intention, Gricean behavior intentionally reveals specifically informative intentions. This is not a behavioral distinction but a cognitive one. Both entail informative intentions ("I want you to believe that I want to play"). The difference is how the informative intention is satisfied. With Ladyginian behavior, it is satisfied by making manifest the embedded intention ("I want to play"), while with Gricean behavior, it is satisfied by making manifest the informative intention itself ("I want you to believe that I want to play"). This Gricean approach can be successful if cognitive processes of interpretation treat others' communicative behaviors as optimally relevant for the target audience, taking into account the communicator's possible goals and the tools available to them. This may seem more "elaborate," but this does not mean that it is cognitively "demanding" or "complex" ("*Are Metarepresentational Analyses of Interaction Too Complex?*").*

Humans slide effortlessly between Ladyginian and Gricean modes of interaction in everyday life. Consider two people, Jane and Paul, walking toward one another on a relatively narrow street. Jane moves toward the right in order to make her action predictable to Paul. Such behaviors are called "coordination smoothing" (25). Jane might even move to the right in a slightly exaggerated way. Is this Ladyginian or Gricean? It depends. If Jane exaggerates her movement just to make that

Fig. 1. Graded distinctions in modes of attention manipulation. These labels each characterize behaviors deriving from underlying cognitive processes. The distinctions between these subsets are graded ("more or less") rather than categorical ("this or that"), and the shifts between them are gradual. Figure adapted from ref. 10.

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*Here, we define key terms precisely. We lean on some mainstream views about intentions from the philosophy of mind and action (24). An intention is a representation that feeds action planning and whose content includes a representation of the expected outcome of that action. Informative intentions are intentions where the outcome is a change in the mental state of another individual. Thus, a Ladyginian intention is a representation that feeds action planning with the goal to produce evidence that will guide an audience to acquire a representation whose function is to predict the actor's goals with a given behavior; and a Gricean intention is a representation that feeds action planning with the goal to produce evidence that will guide an audience to acquire a representation whose function is to predict the changes that the actor aims to make in the mind of the audience. Correspondingly, Ladyginian behavior is behavior motivated by a Ladyginian intention; a Ladyginian individual is an individual with the cognitive capacities necessary (on both the production and the audience side) to behave in ways that will cause Ladyginian intentions to be satisfied; and a Ladyginian interaction is an event where a Ladyginian individual satisfies their Ladyginian intention. Gricean behavior is behavior motivated by a Gricean intention; a Gricean individual is an individual with the cognitive capacities necessary (on both the production and the audience side) to behave in ways that will cause Gricean intentions to be satisfied; and a Gricean interaction is an event where a Gricean individual satisfies their Gricean intention.

movement easier for Paul to see, then Jane is intentionally revealing her intention to pass on the right. Her behavior is Ladyginian. If instead Jane exaggerates her movement so that Paul sees and identifies the exaggeration itself as an effort to inform him, then Jane is not simply revealing her intention to pass on the right. She is, rather, revealing her specifically informative intention that Paul believes she intends to pass on the right. This makes her behavior Gricean. In general, humans seem to make their informative intentions manifest just to the extent that it is efficient to do so, in order for the informative intention to be satisfied, but no more so.

The fourth and fifth subsets include cases where Gricean behavior is performed by the use of particular, culturally evolved tools. The fourth subset, Lewisian (after David Lewis), includes conventions such as used in nodding, pointing, or shrugging. The fifth subset, Saussurian (after Ferdinand de Saussure), includes cases where the conventions are (self-) organized in highly structured networks. These networks are commonly called "languages," and the conventions that comprise them are called "constructions" (26–28). One of Grice's great achievements was to see, and begin to describe, how linguistic meaning is predicated on the expression and recognition of intentions (14, 29). Intention reading is primordial to semantics.

This special case of framework for classifying different modes of interaction also allows us to characterize "language evolution" somewhat precisely. In the most general sense, language evolution is the study of how and why language can come to be (30, 31). We can be more specific: Language evolution critically includes gradual shifts from Washburnian modes of attention manipulation to, ultimately, Saussurian modes of attention manipulation. Gradual shifts from one Saussurian system to another are called "language change."

Great Ape Interaction: A Reanalysis

In this section, we reconsider great ape interaction in light of this special case of framework, and in light of the Ladyginian–Gricean distinction in particular. We focus on the gestural domain. Gestures are certainly not the only modality of great ape interaction—vocalizations and facial expression are also important (2, 32, 33)—but two related features of gesture make it a suitable focus for detailed analysis. First, it is the domain where the evidence for cognitively rich behavior is most compelling and uncontroversial (see below). Second, it is also where there has been greater dedicated research attention.

Great Ape Interaction Is (at Least) Ladyginian. Great ape gesture certainly has many features that collectively mark it out as cognitively distinctive. In particular, gestures are used very flexibly, with multiple different possible effects depending on the context, including the target audience's present state of knowledge, attention, and visual field (34–40). There is hence a wide consensus that great ape gesture is Washburnian, i.e., it involves the intentional manipulation of attention. But is it also Ladyginian? Again, Ladyginian behavior is more than intentional expression: It is the intentional expression of intentions (Fig. 1). Ladyginian individuals have intentions, such as to groom, to have sex, or to play, and they express these intentions intentionally. Does great ape gesture meet this characterization?

Over the past 15 y, a research agenda that in effect directly targets Ladyginian behavior has proven fruitful and productive. This agenda has been pursued in particular by a team of researchers centered at St Andrews University (1, 41–44). The main research innovation has been to focus on "apparently satisfactory outcomes": to observe and measure what reactions cause gesturers to cease gesturing. A large array of distinct gestures have been identified in this way, with names such as "Big Loud Scratch," "Grab Hold," and "Foot Present" (see here). Exactly how many gestures are present in each great ape species depends on details of definition and granularity, but there are certainly scores of them, and many seem to be common across great ape species.

We suggest that these empirical successes are evidence that great ape gesture has a Ladyginian character. The focus on apparently satisfactory outcomes effectively targets Ladyginian behavior directly. It asks, "What intentions did the gesturer reveal, which have now been satisfied by the audience?". The label "Ladyginian" has not (yet) been used to describe this approach, but Ladyginian behaviors are, we suggest, what has been targeted, and what has hence led to considerable empirical successes.

The next question is whether great ape gesture is not just Ladyginian, but also Gricean.

Great Ape Interaction Is (Probably) Not Gricean. Distinguishing Gricean and Ladyginian modes of interaction is challenging from a methodological point of view, for at least three reasons. First, the distinction is cognitive rather than behavioral: What differentiates Gricean from Ladyginian modes of interaction is not any specific behavior, but the underlying cognitive processes from which behaviors derive. Second, both Gricean and Ladyginian modes of interaction entail satisfying an informative intention. They differ just in how the informative intention is satisfied (see the previous section). Third, both Gricean and Ladyginian modes of interaction are context-sensitive: Communicators must be sensitive to what audiences can perceive and infer and take this into account in their expressive behavior.

Nevertheless, Gricean and Ladyginian modes of interaction can be distinguished empirically. In this subsection, we summarize key possible tests, inspired by research on cognitive development in human infants. This is not an exhaustive list, and none of our suggestions are intended as "the" single definitive test of Griceanism, but in each case, compelling evidence of "success" in great apes would be suggestive of Gricean behavior. Yet there is, at present, no such evidence. This is partly because the most informative tests have not yet been pursued, but also because existing descriptions and analyses of great ape interaction do not include any mention of the phenomena that would constitute the most compelling evidence. We hence conclude that great ape interaction is not ordinarily Gricean.[†]

On the production side, one approach is to contrast reactions expected from Gricean behavior and reactions expected from Ladyginian behavior. In one study with human infants, the infant requests an object and then receives it from an

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[†]This conclusion enriches and makes more precise our previous arguments (21, 22, 45). There, we argued that great ape communication is intentional ("Washburnian") but not ostensive ("Gricean"). This paper describes a mode of interaction, "Ladyginian," that is, conceptually speaking, part way between these other two.

adult, but the reasons why the request was "successful" vary in each condition: in one because the adult understood the request, and in the other because the adult did not understand the request but happened to simultaneously and accidentally knock into objects, causing the infant to receive the requested object. The second of these reactions should satisfy Ladyginian communicators, but not Griceans. The key result with human infants was that infants reacted differently to the two conditions, in particular complaining in the "accidental" condition that they (the infant) had not been understood (46). These complaints reveal that infants expect adults to recognize that they (the infant) have expressed an informative intention. In other words, infants expect adults to be Griceans. There is no similar demonstration of Griceanism in any great ape species.

Another approach can be to motivate behaviors that are only possible among Gricean individuals. In particular, "hidden authorship" entails actively hiding an informative intention, i.e., actively hiding what Gricean behavior makes manifest. Suppose, for instance, that a dinner guest wishes to have some more wine but recognizes that it would be impolite to ask for this directly. So instead she places her empty glass in a conspicuous location where it is likely to be noticed by the host, but only when the host's back is turned. Thus, when the host sees that the glass is empty and refills it, he is not aware that by doing so he is satisfying the guest's informative intention. Even though such behavior is by definition not Gricean, it is clear evidence that individuals are aware that informative intentions can be manifest—or indeed hidden—to different degrees, depending on context and individual motivations. This makes hidden authorship a good proxy indicator that individuals are accustomed to Gricean modes of interaction. The only experimental study of hidden authorship published to date shows that 3-y-old infants (the youngest age tested) demonstrate awareness of the fact that informative intentions can be manifest or hidden to different degrees, depending on context and individual motivations (47). Again, there is no similar demonstration of Griceanism in any great ape species. Nor, to our knowledge, does hidden authorship appear in any descriptions of naturally occurring great ape interaction.

On the audience side, great apes do not ordinarily seem to expect communicators to be Gricean. In order just to comprehend Gricean behavior, audiences' cognitive processes must treat the communicative behavior as optimally relevant for them (the audience). This insight is commonly called the "communicative principle of relevance" (18). Yet results from experimental tasks widely used in comparative research suggest that while human infants indeed treat Gricean behavior as optimally relevant, great apes do not (48). In particular: i) great apes tend to "fail" the object choice task, which requires following a pointing gesture to a location (49); and ii) they do not exhibit "overimitation," in which individuals copy actions demonstrated to them even if those actions are perceivably causally irrelevant (50). Both these tendencies are, in our view, most easily explained by the absence of cognitive dispositions that are particular to Gricean interactors.

Another possible approach on the audience side is to contrast particular features of the common ground between communicator and audience. Audiences that expect communicators to be Gricean should show a strong sensitivity to the audience's prior knowledge about the communicator's knowledge. To be 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 communicative stimuli. Human infants show differential responses in these two conditions (51). Again, there is to date no similar demonstration in any great ape species.

The general point here is not that there is some fundamental cognitive barrier to Gricean interaction in great apes, or that Gricean modes of interaction are somehow cognitively "challenging" or "demanding," whatever that might mean. The general point is rather that there are several good indicators of Gricean modes of interaction, and to the best of our knowledge, these indicators are largely absent in great apes. The development of further experimental protocols of the kinds summarized above, suitable for making comparisons across species and hence for testing these conclusions more thoroughly, would be a significant advance, and hugely informative.

None of this precludes the possibility that some of the cognitive capacities necessary for Gricean interaction could, in principle, emerge in great apes living in conditions of enculturation. Indeed some studies report findings suggestive of this conclusion (52–54). However, there is a difference between, on the one hand, the presence of a cognitive capacity in the ordinarily developing phenotype of a species; and, on the other, the emergence of a cognitive capacity in specific individuals by virtue of their individual experiences. As an analogy, consider humans swinging from trees. Human bodies are not especially well-suited to this task. We lack the specialized 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 and practice. What we are suggesting is that, in great apes, the cognitive capacities for Gricean interaction may be similar: not impossible and not wholly absent, but still unspecialized, disfluent, not a regular part of the environment, and not part of the ordinarily developing phenotype. These capacities are, however, part of the ordinarily developing phenotype of humans. In short, only humans are "natural Griceans."

As a description of the cognitive basis of ordinary great ape interaction, our conclusion that it is Ladyginian but not Gricean is potentially convergent with some other analyses (8, 55–59). However, those other analyses do not make a clear distinction between Ladyginian and Gricean modes of interaction. We are arguing that this distinction is crucial. Ladyginian modes of interaction lie part way between Washburnian ("intentional") and Gricean ("ostensive").

Our arguments also contrast with accounts focused on "shared" or "we" intentionality, which has been proposed as a key cognitive difference between humans and other great apes (60). We agree that shared intentions and joint attention are more prevalent in humans than other great apes; but these phenomena are, in our view, not cognitive processes

themselves, but rather useful redescriptions of what is in need of cognitive explanation.

The Emergence of Conventions in Ladyginian Interactions. Great ape gestures exhibit some degree of cultural variation and also tend to have high levels of resemblance between form and function. In this subsection, we describe how both these qualities are to be expected in species where the common modes of interaction are Washburnian or Ladyginian, but not Gricean.

One relatively well-studied process by which conventions can emerge in great apes is ontogenetic ritualization, where behavior that is initially not communicative becomes communicative by means of repeated mutual anticipation (61, 62).[‡] The classic example is the chimpanzee "nursing poke." i) The infant initially attempts to move the mother's arm to feed at her breast. ii) Once the mother has detected what he wants she raises her arm voluntarily. iii) As this process recurs over time, the mother comes to move her arm as soon as the infant begins to attempt to move it himself. iv) Eventually, the infant only needs to do the initial movement, effectively poking the mother's arm, for her to react. In general, the stages of ontogenetic ritualization are as follows:

i   Individual A performs behavior X.
ii Individual B reacts consistently with behavior Y.
iii If (i) and (ii) recur sufficiently often, then when A begins to perform X, B anticipates A's performance of X and hence performs Y.
iv A anticipates B's anticipation of X and hence produces X in a "merely" ritualized form, sufficient to elicit Y.

More recent analyses suggest that gestural conventions can emerge in a manner somewhat more dynamic than the specific steps of ontogenetic ritualization: Interactional experience and shared understanding may be more important than previously understood (63, 64). This further underlines the point that repeated interaction between great apes can generate communicative conventions.

This process is built on Ladyginian modes of interaction. On the audience side, Ladyginian individuals are able to identify others' intentions and react accordingly. On the production side, Ladyginian individuals are able to anticipate what behaviors are most likely to satisfy their informative intentions. In particular, they are able to anticipate what behaviors might elicit the desired reaction taking into account the learned expectations of the target audience. In fact it is hard to see how the mutual anticipation that underpins ontogenetic ritualization, let alone more dynamic forms of interaction, could occur without these capacities (65).

As such, Ladyginian modes of interaction can quickly generate a degree of variation between and within groups (8). Repeated Ladyginian interaction facilitates repeated mutual anticipation, and other behaviors, which, when repeated sufficiently often between the same individuals, generates a dynamic process of emergence. This process is contingent on interaction history and other sources of stochasticity. It

can hence generate forms of communication that are specific to a given community, or even just a given dyad, such as a mother-infant pair.

At the same time, the forms that these communicative conventions might take is constrained by the absence of Gricean modes of interaction. To be successful, Ladyginian behavior must provide some sort of evidence of the intention that is being intentionally expressed. One key way to do this is for the behavior to exhibit some perceptual resemblance between form and meaning (sometimes called "iconicity," although this term is used inconsistently in the literature). Processes such as ontogenetic ritualization can simplify the form that this evidence might take, but it does not remove the need to provide it. The consequence is that repeated interactions that are Ladyginian but not Gricean will tend to generate conventions that retain a degree of perceptual resemblance between form and meaning.

Explaining Attested Tendencies of Great Ape Interaction. We have identified from the empirical literature eight tendencies in great ape gestures (Table 1). These tendencies are not absolute—exceptions can be found, especially among enculturated apes—but they are clear patterns. In the previous two subsections above we elaborated on the first five of these tendencies, and described how they are best explained as the product of the Ladyginian but not Gricean character of great ape interaction. In the rest of this subsection, we elaborate on two more.

"Triadic" interaction is when attention is not simply focused on the self and the audience, for immediate social goals such as play or sex, but rather on some other, third entity, such as a distant object (row 6). "Displaced reference" is reference about phenomena remote in time and space (row 7). Both features tend to be absent in great ape gesture. In other words, great ape gesture is overwhelmingly dyadic, and overwhelmingly about the here-and-now: grooming, other apes, food, predators, travel, and so on (3, 66, 67). This is not to say that great apes "cannot" do displaced reference or triadic interaction—in fact, these features can be elicited in the right experimental contexts (39, 68)—but the tendencies are clear.

Why is this? Undisplaced reference and dyadic interactions are relatively straightforward to achieve between Ladyginian individuals, because it is possible to provide "direct evidence" of intentions when the intended state is proximate in time and space.[§] For instance, placing the relevant body part immediately in front of another individual provides direct evidence of an intention to be groomed. This is "direct" because the intention to be groomed can be inferred without raising and answering the question "what does the agent want me to know by behaving the way they do?". In contrast, it is not straightforward to provide direct evidence for intended states that are not so proximate in time and space. How do you provide direct evidence of, say, a termite nest that is not in view, or travel plans beyond the immediate moment? We are suggesting is that great ape gesture tends not to be triadic or exhibit displaced reference because these

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[‡]We define conventions in purely functional terms, as tools for coordination. Specifically, conventions are commonly known solutions to recurrent coordination problems. As a human example, which side of the road to drive on is a coordination problem, it is recurrent, and having everybody drive on the right is a commonly known solution. Since this characterization of conventions is solely functional ("What recurrent coordination problem does it solve?"), it is inclusive of whatever properties the solution might have.

[§]Precisely, we say that X is direct evidence for Y if and only if X can generate, in the audience, the inference that Y without the audience necessarily computing that the informer has the informative intention that Y. An alternative, equivalent way to characterize direct evidence is X is "direct evidence" for Y if and only if X makes Y manifest to an audience without ostension playing any role. Something is manifest to an individual at a given time to the extent that she is likely to entertain it and accept it as true (19).

Table 1. Eight tendencies of great ape gestures and their explanations in terms of the Ladyginian–Gricean distinction

Observed tendency	Explanation in light of the Ladyginian–Gricean distinction
Failure in the object-choice task	Success in the object-choice task requires cognitive dispositions—specifically, presumptions of optimal relevance—that are particular to Gricean interactors.
Absence of overimitation	Overimitation may be a by-product of cognitive dispositions—specifically, presumptions of optimal relevance—that are particular to Gricean interactors.
Presence of elaboration and repair	Ladyginian capacities allow communicators to infer whether their informative intention has been satisfied, and hence to repeat or adjust behavior if necessary.
Within-species variation	At least some great ape gestures emerge through social processes that are inherently stochastic, hence leading to variation.
A high degree of resemblance between form and meaning.	Ladyginian modes of interaction are effectively tied to providing some direct evidence of the expressed intention. This ensures a degree of resemblance between form and meaning (sometimes called "iconicity").
Dyadic rather than triadic	Dyadic interaction is precisely what to expect if attention is drawn to the focal individual's behavioral intentions, i.e., if interaction is Ladyginian in character.
Absence of displaced reference	Providing direct evidence of intentions with respect to phenomena that are remote in time and space is highly impractical, if not impossible, by Ladyginian means.
Absence of the expression of anything beyond current intentions	Gricean communication, and only Gricean communication, enables "virtual domain generality." See ref. 10 for detail.

These tendencies are not absolute—exceptions can be found, especially among enculturated apes—and this list is not presented as a systematic review of the literature, but it is representative of general patterns. We elaborated on the first seven rows of this table in the previous two subsections.

features are unlikely to occur in interactions between Ladyginian but not Gricean individuals.

Ladyginian Description and Analysis. Here, we reinterpret two representative examples of great ape interaction, captured on video, as instances of Ladyginian behavior. Our goal is to show, briefly, how the concept of Ladyginian behavior enriches understanding of the natural phenomena.

Movie S1 from ref. 69: This paper develops a species-independent framework for communicative repair—behavior that fixes communicative failure or trouble—and applies that framework to great ape gesture. Language affords many means of repair, including interjections such as "Huh?" and "What?"; question words seeking clarification; partial repeats of the source of uncertainty followed by a question word; and others. However, some means of repair are not language-specific. In particular, what was meant can be repeated or reformulated, regardless of the means of communication. The interaction shown in this video provides a good example (first reported in ref. 70). A mother makes multiple attempts to initiate travel with her infant across a water pond. Between 00:03 and 00:08, she pulls on a branch that the infant is sitting on. Making the assumption that great ape gesture is Ladyginian, and hence allowing that the meaning of a particular gesture is context-dependent, we interpret this as the intentional expression of an intention to travel. The gesture is not successful: The infant does not move. At 00:15, the mother moves closer to the infant and briefly puts her (the mother's) hand on her own back. The method of observing apparently satisfactory outcomes (see above) identifies this as a commonly used gesture, named "Present Climb On" to describe its common usage: to present a body part onto which the audience is expected to climb (43). Again we make the assumption that great ape gesture is Ladyginian, and we hence interpret this momentary gesture as the intentional expression of an intention that the infant climb upon the mother's back, so that they can travel. This gesture also fails—the infant remains unresponsive—and

so between 00:20 and 00:26, the mother reverts back to the original strategy of pulling on the branch the infant is sitting on. When this too fails, the mother travels back across the pond. Now closer, the infant finally climbs onto her back.

Movie S3 from ref. 71: This paper describes beckoning gestures in --bonobos, used to garner attention and encourage others to join them. In this specific video, an arm is stretched out toward the audience, followed by a sideways, sweeping movement of the arm toward the self, in a way that is strikingly similar in form to human beckoning. Bonobos use this in particular (but not only) to initiate sexual intercourse. The gesture is first seen at 00:07. It is a large movement of the arm that is likely to attract attention. It is repeated at 00:25 and 00:38, now alongside the clear presentation of an erect penis. There is hence direct evidence of the opportunity to mate. Making the assumption that great ape gesture is Ladyginian, we interpret these behaviors as the intentional expression of an intention to have sex. To be clear, the point here is not that sex is relevant to understanding what is going on: that much is obvious. The point is the cognitive interpretation: The bonobo has an intention to have sex and intentionally expresses this intention. This is cognitively continuous with Gricean expression but not equivalent to it.

Natural Griceans Are Language Ready

Natural Griceans are species where the cognitive capacities necessary for Gricean interaction are part of the ordinarily developing cognitive phenotype. We have argued above that humans are the only species of natural Griceans. Here, we describe why a community of natural Griceans, interacting repeatedly, will straightforwardly become "Lewisians" and, in turn, "Saussureans."

The emergence of Lewisian and Saussurean modes of interaction has been widely documented in humans. In home-sign, deaf infants born to nonsigning parents develop their own visual-gestural forms of communication (72). Several sign

languages have been studied continuously from their inception, as they develop many of the characteristic features of languages (73, 74). Notably, these new languages show no absence of the features summarized in Table 1, such as displaced reference. And many studies in experimental psycholinguistics and language evolution isolate processes of language emergence in laboratory conditions (30, 75, 76). All these literatures show how, when tasked with communicating without pre-established communicative means, regularly interacting humans will readily develop a new system of conventions, which will in turn begin to exhibit many of the most characteristic features of natural languages (77).

So we know that humans do indeed readily become Lewisians and Saussureans. Why is this? What makes it possible? Here, we describe how the gradual transitions to Lewisians and Saussureans modes of interaction are based on Gricean modes of interaction.

While modes of interaction that are Ladyginian but not Gricean are inherently flexible and context-sensitive, they are also, by definition, constrained to the expression of intentions for which individuals can provide direct evidence (see above). That is, they are constrained to the expression of intentions that can be inferred without the audience needing to raise and answer the question, "What does the agent want me to know by behaving the way they do?". Good examples of intentions for which it is possible to do this are intentions to play, to have sex, or to groom.

Gricean modes of interaction are not constrained in the same way. By definition, Gricean audiences do raise and answer the question, "What does the agent want me to know by behaving the way they do?". (How? Not through explicit or conscious consideration of this question, but by means of dedicated cognitive processes that instantiate a presumption of optimal relevance. See refs. 18 and 22.) This means that Gricean communicators can satisfy their informative intention in a much wider range of ways than can Ladyginian communicators.

In particular, for Gricean communicators faced with Gricean audiences, often the most effective thing to do will be to produce a behavior that is sufficiently similar to a behavior that has previously been used to express the same or a similar informative intention. This reproduced behavior may be slightly less complex or less elaborate than the previous version, just so long as it is sufficiently similar to trigger the intended inference in an audience whose cognitive system effectively asks, "What does the agent want me to know by behaving the way they do?". Repeated many times over, this allows gradual simplification and conventionalization of the stimuli. Crucially, what is being simplified here is, by definition, evidence of an informative intention—and evidence of an informative intention need not resemble the information embedded in the informative intention. So while conventions can emerge among Ladyginian individuals (see above), conventions will emerge much more readily and more commonly among communities of natural Griceans.

So a gradual shift from Ladyginian to Gricean modes of interaction was, we suggest, a crucial step in human evolution. It shaped the human "interaction engine" into a form that rendered us, and only us, language ready. Incidentally, this shift must have enabled, or been accompanied by, further complementary changes in anatomy, physiology and cognition. These include, among others, a delicate sensitivity to timing and contingency in interaction, fine-grained control of the many muscles employed in speech and signing, changes in the vocal tract, sensitivity to subtle variation in vocalizations, long-term memory enabling the storage of linguistic constructions, and the emergence of a conspicuously white sclera in the eye. The net consequence of these changes is a natural, multimodal, open-ended fluency in face-to-face interaction, and language use in particular (78, 79).

Varieties of Meaning

Paul Grice famously distinguished natural meaning from non-natural meaning (14). This is a useful but nevertheless binary distinction, and as such it does not lend itself to gradualist approaches to the origins of meaning. It also provides no means to differentiate and organize the many varieties of meaning that exist in the natural world, as uncovered by biologists and comparative psychologists (80). Here, we enrich our special case of approach to attention manipulation, to distinguish some notions of meaning, and hence sketch some gradations that are highly relevant for the comparison between humans and other great apes (for other gradualist approaches see refs. 18, 19, 59, 81–85).

In the most general sense, meaning is a property of a relationship between an item (a "stimulus") and a cognitive system, such as an individual mind. So anything can "have" meaning, just so long as it is processed by (or "is informative for") some cognitive system. Nature is a highly opportunistic tinkerer, and where some stimulus in the world is reliably informative for a biological system, we can expect that system to evolve some sensitivity to the item, i.e., to treat it as meaningful (86).

Of the many sources of meaning in the world, only some items are produced with the function to inform. That is, only some are "representations." For instance, the location of the sun is meaningful for migrating birds, because it is informative about path and time, but it does not represent anything about path and time. In contrast, aposematism (warning coloration) represents unpalatability not because it is informative about poison or venom, but because it has the function to be informative about poison or venom. Similarly, cricket chirps represent availability for mating. This distinction is, in other terms, the classic distinction in animal signaling theory between a "cue" (informative but without the function to inform) and a "signal" (informative and with the function to inform) (87–89). Representations exist not only between organisms ("public representations"), such as in the examples above, but also within individual organisms, as part of cognitive processing ("mental representations").

There are many varieties of public representation in the world. Of these, a subset derive from an intention to have a cognitive effect on others (they are intentional). Our special case of framework for attention manipulation provides a way to differentiate these varieties (Table 2). In cases of meaning$_W$ (Washburnian), individuals intend to act on others' mental states but do not have any particular motive to reveal this intention. Many clothing choices, for instance, are made to express certain attitudes—rebelion, professionalism, and conformity—without necessarily advertising this intention. In cases of meaning$_L$ (Ladyginian), individuals intentionally reveal their intentions. We argued in previous sections that most great ape gesture has meaning$_L$, and we now have

Table 2. Varieties of intention-based meaning

Variety	Possible examples in nonhumans	Examples in humans	Examples of deceptive use in humans
Meaning$_W$ (Washburnian)	Arguably, many animal behaviors have meaning$_W$, which has been widely investigated under the term "intentional" (94).	Gray suits mean$_W$ professionalism. Expensive cars mean$_W$ wealth. Generous behavior means$_W$ prosociality.	An expensive car used to supposedly display wealth, but which was in fact borrowed from a relative. A more complex example is leaving false clues, such as to deceive a detective. This is Washburnian because it is intentional, but it is not Ladyginian or Gricean because the intention is not revealed (on the contrary, it is actively hidden). And this is deceptive because the "clues" are in fact misleading.
Meaning$_L$ (Ladyginian)	The ordinary gestural interactions of great apes, such as described in the "Great Ape Dictionary."	Moving to one side on a narrow street means$_L$ an intention to pass on that side. In partnered dance, some movements mean$_L$ an intention that the partner perform a particular further movement.	Feints. When a sportsperson (footballer or boxer) moves their shoulders, that can be observable evidence of an intention to move in a particular direction. Thus, sportspeople sometimes produce behaviors that appear to provide evidence of an intention to move in a particular direction, when in fact they are about to move in an opposite direction.
Meaning$_G$ (Gricean)	Possibly the gestural interactions of some enculturated great apes.	Pantomime. Pointing. All language use: "cat" means$_G$ feline animal.	Lying. Gricean expression is wholly open-ended. This leaves audiences vulnerable to being misinformed, and so cognitive capacities for Gricean communication must be complemented by cognitive capacities for "epistemic vigilance," with which audiences evaluate the relevance of others' communicative behavior.

In the most general sense, meaning is a property of a relationship between an item and a cognitive system. There are many varieties of meaning so understood. This table lists and provides examples of three intentional varieties of meaning. Note that meaning$_G$ is equivalent to Grice's notion of meaning$_{NN}$ (NN for "non-natural"): We have used G instead of NN to align this table with the labels used in Fig. 1.

growing "dictionaries" listing the meanings$_L$ of specific great ape gestures (43). Humans also use meaning$_L$ often, such as in many instances of "coordination smoothing" (25). Finally, in cases of meaning$_G$ (Gricean), individuals intentionally reveal a specifically informative intention. Meaning$_G$ is another name for Grice's "non-natural meaning," or meaning$_{NN}$. These three varieties of meaning are special cases of one another (Fig. 1), and as such they are a key source of evolutionary gradualism between humans and other great apes. The third variety, meaning$_G$, provides the foundation for all pragmatics and semantics (23, 90–92).

Many animal signals are not intentional. They are public representations, but they do not have any of meaning$_W$, meaning$_L$ or meaning$_G$, all of which emerge from interactions among individuals with particular social cognitive capacities. So for any given public representation, it is an empirical question whether it has meaning in these senses. In this paper, we have focused on great ape gestures and argued that they ordinarily have meaning$_L$ and not meaning$_G$. In contrast, great ape vocalizations are a case that was previously thought not to meaning in any of these senses, but which is now being rethought (33).

Are Metarepresentational Analyses of Interaction Too Complex?

The framework we have presented here is inherently "metarepresentational" (48, 94). Washburnian, Ladyginian, and Gricean modes of interaction all entail "representations about representations." Metarepresentational frameworks for interaction are sometimes criticized on the grounds of cognitive implausibility (9, 56, 82, 95). The main critique is

that metarepresentational frameworks excessively intellectualize what is actually an ordinary, everyday activity.

This critique mistakes phenomenological simplicity for descriptive simplicity. When René Descartes first proposed that depth perception could be achieved by triangulating between two eyes and the target object, some of his contemporaries complained that this was implausible because triangulation is too complex, or too intellectualized, as a description of ordinary 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" (96). The subsequent history and successes of vision science have shown how this worry was wholly mistaken. Tremendous progress has been made by describing the visual system as implementing highly complex geometric computations. We see no reason why the same should not be true in the case of communication, with the difference that here the computations entail metarepresentations. In general, there is no reason why phenomenologically simple processes—such as vision and communication—must have scientifically simple descriptions.

Conclusion: What Are the Best Comparisons for Language?

The distinction between Ladyginian and Gricean is, we believe, essential for current and future understanding of

great ape interaction. With this, it may be possible to explain both the similarities and the differences with human communication in a unified way. Specifically, present data suggests that great ape interaction tends to be Ladyginian but not Gricean. The distinctions we have made here also sketch some gradualism in the origins of meaning and hence connect empirical discoveries about the social cognition of nonhumans with theories of communication and meaning from linguistics.

A crucial takeaway point is that with respect to the origins of language, the key comparisons to make between humans and other great apes are not in systems of communication as such, but rather in social cognition, and specifically in means of attention manipulation (Fig. 1). Communication systems in nonhuman primates share some surface similarities with natural language, but there are also many important dissimilarities which collectively constitute strong evidence against evolutionary continuity (10). Evolutionary continuity can rather be identified and described in the domain of attention manipulation, with relatively small differences between humans and other great apes. With the key notion of Ladyginian interaction, we hope to have helped understand these small but consequential differences.

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