What do Monkey Calls Mean?

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Abstract.
A field of primate linguistics is gradually emerging. It combines general questions and tools from theoretical linguistics with rich data gathered in experimental primatology. Analyses of several monkey systems have uncovered very simple morphological and syntactic rules, and they have led to the development of a primate semantics which asks new questions about the division of semantic labor between the literal meaning of monkey calls, additional mechanisms of pragmatic enrichment, and the environmental context. We show that comparative studies across species may validate this program, and may in some cases help reconstruct the evolution of monkey communication over millions of years.

Keywords: primate semantics, primate call evolution, primate implicatures, primate linguistics, evolution of meaning, evolution of communication

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The importance of monkey calls

Although numerous species use vocalizations to transmit information to conspecifics, a great deal of research has been specifically devoted to studying primate calls. The original hope was that these studies might provide clues about the evolution of human language ([1][2][3][4]). Connections to human language remain elusive, but a rich body of field experiments combined with new theoretical work has made it possible for a field of 'primate linguistics' to start emerging [5], with new insights into the structure and especially meaning of monkey calls. (Ape calls are currently less well understood.) Extant results about monkey call **syntax** (see Glossary)(i.e. rules by which monkey calls are put together) are modest, but new findings about their **semantics** (i.e. rules by which monkey calls are interpreted) have yielded precise hypotheses about what individual calls mean and how these meanings can be combined in sequences. In addition, there are striking similarities among the calls of monkey species that diverged millions of years ago. This makes it possible to use information about the evolutionary history of monkeys (obtained by DNA methods) to reconstruct the history of some calls over millions of years – which might pave the way for an evolutionary primate linguistics.

The formal approach

How should monkey calls be studied? We argue that a key idea should be borrowed from contemporary linguistics: monkey call sequences should be studied as formal languages with syntactic rules (pertaining to their form) and semantic rules (pertaining to their meaning). From the standpoint of formal language theory, it takes extraordinarily little for something to count as a 'language': any set of strings will do. But treating an object as a formal language forces one to make precise predictions about the form, use and structure of expressions. From this methodological (and terminological) stance, it does not follow that the specific rules one will uncover are similar to those of human language – for the most part, they are not. On the other hand, this methodology makes it possible to state and test precise hypotheses about the grammar of monkey communication.

Human languages as formal languages: syntax, semantics and pragmatics

In linguistics, formal *syntax* sought to specify rules that predict which strings are well-formed ([6][7]; syntax in the narrow sense is concerned with the way in which words are combined, but in a broad sense it should include questions of **phonology** and **morphology**, which pertain to the organization of sounds and words). For its part, formal *semantics* ([8][9][10]) sought to specify rules that predict in which situations a syntactically well-formed message is true. In both fields, the formal approach was integrated into a cognitive one – almost from the beginning in syntax ([7]), and in later developments in semantics ([11][12]). For our purposes, what matters is the program of analyzing natural communication systems as formal languages rather than the specific assumptions made by one framework or another, especially since the formal properties of monkey calls are very different from those of human language (see [13] and [14] for surveys of diverse formal frameworks for syntax and semantics respectively).

A key insight of contemporary studies of meaning is that the information conveyed by a sentence is not just due to its semantics, i.e. meaning as it is linguistically encoded, but also to pragmatic inferences, which are drawn by reasoning on the speaker's motives for uttering one sentence rather than another (e.g. [15]).

A textbook example involves the information conveyed by the disjunction *S or S'*. One will quickly realize that in some cases *or* appears to be exclusive (*S or S'* is true just in

case exactly one of *S* and *S'* is true), as in the sentence *I will invite Ann or Mary*, which usually gives rise to the inference that *I will invite Ann or Mary, but not both*. In other cases, by contrast, *or* appears to be inclusive (*S or S'* is true just in case *at least one* of *S* and *S'* is true). This is the case in the sentence *I doubt that I'll invite Ann or Mary*, which is understood as: *I doubt that I'll invite [Ann or Mary or both]*.

Rather than positing an ambiguity, contemporary linguistics has devised a better theory: the meaning of *or* is inclusive, but a sentence with *or* automatically evokes the corresponding sentence with *and*. As a result, if the speaker is maximally informative, and utters a sentence with *or* which is less informative than its competitor with *and*, one can infer that the latter couldn't be uttered – typically because it was false. In a simple sentence such as *I will invite Ann or Mary*, *or* will overall convey an exclusive meaning. But it will retain its bare inclusive meaning in *I doubt that I'll invite Ann or Mary* because, due to the negative expression *doubt*, the sentence with *and* is now less informative than that with *or* ([16][5]).

The key to this analysis is the **Informativity Principle**, which can be stated as follows:

If the speaker uttered a sentence *S* which evokes ('competes with') a sentence *S'*, if *S'* is more informative than *S,* infer that *S'* is false *S* (for if *S'* were true the speaker should have uttered it).

In linguistics, the Informativity Principle is usually taken to follow from humans' ability to communicate cooperatively and to reconstruct the intentions of language users. But as we will see shortly, this principle doesn't require such mind-reading abilities, as it is solely based on a relation of competition among possible messages, and differences of informativity among some of them. Although it takes young children some time to correctly apply the Informativity Principle, this is primarily thought to be due to the difficulty of computing which sentences compete with a given sentence ([12][17]).

Monkey call sequences as formal languages

In primatology, observations and field experiments have established two points (e.g. [1][5]).
(i) The species under study arrange discrete calls in constrained ways.
(ii) Some calls are naturally triggered by some situations but not others. Furthermore, field experiments establish that the monkeys themselves know this correlation and thus derive information from the calls they hear.

The first point (discrete calls are arranged in constrained ways) establishes that one can study the syntax of monkey calls, i.e. the rules by which calls are combined (syntax in a narrow sense) and composed (of sounds and possibly morphemes – phonology and morphology). This falls within a more general program of animal syntax, which has led to the common claim ([18][19][20]) that many animal systems can be analyzed as a sub-class of so-called **finite-state languages**, a simple model which was briefly considered for human language but decidedly refuted in the 1950's ([5]). Most results in primate syntax are thought to be compatible with this general claim (but see [21]). Salient results, compatible with the finite-state language claim, are worth mentioning.

First, there are cases of call-internal (and thus morphological) structure: in Campbell's monkeys, the suffix *-oo* can be added to two roots, *krak* and *hok* ([22][23]). In Diana monkeys, the A call can be used alone, but it also serves to form the complex calls *LA*, *HA*, and *RA*, which are targeted as units by the operation of repetition, thus yielding *LA LA LA LA* ([5][24][25]).

Second, there are simple rules of call sequencing (syntax in the narrow sense) in various species (see [5] for an overview). Thus in Campbell's monkeys, the call *boom* usually appears as a pair at the very beginning of a sequence. Black-and-white Colobus monkey calls include *snorts* and *roars*, which may appear singly or be combined; but in the latter case, a single *snort* is followed by a series of *roars*, and the opposite pattern is not found. It is an open question whether constraints on production (or perception) could explain these patterns. And in several cases, what initially appeared as a complex syntax was re-analyzed in a deflationary fashion when call meaning was studied, as we will see below in the case of Titi calls.

The second point mentioned above (monkey calls convey information) naturally leads to the project of a semantic analysis of calls. But if the notion of an animal syntax might be uncontroversial, talk of a "primate semantics" is probably more surprising. First, we wrote above that semantics is concerned with the conditions under which a well-formed message is true. But is it appropriate to say that monkey call sequences are "true" or "false" in certain situations? The issue is terminological: observational and experimental data clearly argue for a bipartition of calls among "appropriate" vs. "inappropriate" ones in a given situation; under any name, this means that these calls have a semantics – which is unsurprising since they clearly convey information. Second, can one postulate the existence of a meaning when there is no evidence of an intention to mean something? Here there is a discrepancy between the pre-theoretical notion of meaning, which involves intentionality, and the technical notion used in linguistics, which assimilates the meaning of an expression to the bi-partition it establishes among situations in which it is true vs. false. It is this lean notion of meaning that we employ below ([5]; see [26] for a different view).

While this notion of meaning is the one that comes out of formal linguistics, within primatology there has been much recent debate about the existence in primates of so-called "functionally referential" signals (the adverb "functionally" was included to avoid commitments about the psychological underpinnings of such signals). First, functionally referential signals are supposed to be context-specific, in the sense that they are triggered by some stimuli but not others (let us call this "Context specificity"). The intuition is that these specific triggers correspond (for the senders) to the reference of the signals. In addition, functionally referential signals must elicit responses even in the absence of these stimuli ([27][29][30]) (let us call this "Stimulus independence"). This is essential to show that receivers interpret the signal itself, rather the stimuli it may be associated with: even in the absence of an eagle, a monkey eagle alarm call should trigger an eagle-appropriate reaction in conspecifics. It is also often posited ([27]) that the aspect of the context that triggers the signal should be external to the caller (let us call this "Externality requirement"). The intuition is that reference should be reference *to an external reality*. Finally, functional reference is often associated with the idea that the signal should have a noun-like denotation, pertaining for instance to predator classes (eagles, leopards, etc.), but not, say, to something less concrete such as response urgency (let us call this the "Nominal requirement").

From the present perspective, Stimulus independence is indeed relevant to establish that the signal conveys information, but Context specificity, the Externality requirement and the Nominal requirement are not entailed by a semantic approach. As will be seen below, we posit several general, non-context specific calls, against Context specificity; and the meanings we posit almost never pertain directly to predator classes, against the Nominal requirement. Finally, against the Externality requirement, nothing in our approach precludes emotional meanings that pertain to the state of the mind of the caller rather than to an external event (such emotional meanings certainly exist in human language, where so-called "expressives" have been the object of detailed study – see [28] for discussion).

On the other hand, at this point our discussion says nothing of the existence of a monkey pragmatics, as the very notion of a pragmatics might presuppose cognitive abilities that go beyond the monkeys' capacities; but we will see below that there might be evidence for a monkey proto-pragmatics.

Semantic questions

What is the meaning of individual calls?

Turning to substantive semantic questions, we introduce two theoretical problems raised by three case studies. First, what is the meaning of individual calls? A rich example is afforded by Campbell's monkeys of the Tai Forest (Figure 1a). Male adults have non-predation-related call, *boom*. And they use a call *krak* to raise leopard alerts, and *hok* for raptor alerts. But as mentioned, they also have suffixed calls: *krak-oo* is used for unspecific alerts, and *hok-oo* for non-ground disturbances. The challenge is to assign meanings to *boom, krak, hok*, and *-oo*.

Further complexity is added by Campbell's call use on Tiwai Island, where leopards haven't been seen for decades: the Tai calls are used, but *krak* raises unspecific alerts (as does *krak-oo*), rather than leopard alerts. Should we conclude that meaning is subject to a kind of dialectal variation – as it is for *pants* in American English (meaning "trousers") vs. British English (meaning "underpants")?

How are the meanings of individual calls combined?

Once one understands what meaning individual calls have, it remains to ask how these meanings can be combined. Semanticists say that an expression is compositional if its meaning is derived from that of its parts. Interestingly, several monkey cases challenge compositionality ([31][5]).

In Putty-nosed monkeys (Figure 1b), which have their own non-predation-related *booms*, *pyows* alone are used for unspecific alerts, while *hacks* alone are associated with raptors (or possibly high arousal). But sequences containing a few *pyows* followed by a few *hacks* trigger group movement, rather than predator-appropriate reactions. Is the meaning of these *pyow-hack* sequences derived from the meaning of their parts, or should they be treated as a non-compositional idiom, such as *kick the bucket* (which means *die* and involves no kicking and no bucket)?

A radical compositionality problem arises in Titi monkeys (Figure 1c). With two calls (A and B) re-arranged in various ways, their sequences encode information about both predator type (cat, raptor) and predator location (on the ground, in the canopy). Do these sequences have a complex syntax, and should they be treated as very long idioms?

Semantic analyses

We argue that in almost all cases, concatenated calls each contribute their meaning independently from the others, with the result that a sequence is interpreted as the conjunction of its calls ([5][32]); furthermore, no dialectal variation in call meaning is needed. But a key ingredient, justified in three case studies ([5]), is that the interpretation of a call or call sequence can be pragmatically enriched by competition with others (see Box 1). Notably, calls are subject to a version of the Informativity Principle mentioned above: if a call *C2* is more informative than a call *C1*, then whenever possible *C2* should be preferred to *C1*. Thus if a raptor shows up, and a raptor call is available, then it should be preferred over an unspecific call; for this reason, the unspecific call may end up signifying the absence of a raptor.

Importantly, this Informativity Principle need not involve an ability to reconstruct conspecifics' intentions: its effects can be obtained as soon as a rule of competition among calls can take into account a relation of informativity. Still, the potential presence of an Informativity Principle in monkey languages and in human language raises interesting questions about their (joint or separate) evolutionary origin.

Analyzing Campbell's meanings

Let us now see how the Informativity Principle can help analyze Campbell's calls (Figure 1a; Box 1; [23]). As a first step, we take *krak* to trigger unspecific alerts, and *hok* to trigger non-ground alerts. As a second step, to analyze the meaning of the suffix *-oo*, we assume that if *R* is *krak* or *hok, R–oo* indicates a weak alert of the R-type. Thus *hok-oo* indicates a weak *(-oo)* non-ground (*hok*) alert – which is more informative than *hok*.

It is in the third step that we make crucial use of the Informativity Principle: *hok* competes with other calls, and because *hok-oo* (pertaining to *weak* non-ground alerts rather than to any non-ground alert) is more specific, the meaning of *hok* is enriched to *hok but not hok-oo*: it only applies to aerial (*hok*) non-weak *(not hok-oo)* alerts – hence the raptor uses. By the same logic, the unspecific alert *krak* competes with *krak-oo,* but also with *hok*. Due to this competition with two more informative calls, in the end *krak* can only be used for *serious (not krak-oo) ground (not hok) disturbances*. This comes very close to the leopard uses observed in Tai.

The last step is to account for the different use of *krak* on Tiwai island, where it raises unspecific alerts. Strikingly, this use just corresponds to the basic (unenriched) meaning of *krak*. The question is why this bare meaning fails to be pragmatically enriched on Tiwai. A plausible answer is that this would yield a useless meaning due to the absence of serious ground predators. Without the pragmatic enrichment, we are left with the literal and general meaning of *krak* on Tiwai island.

Analyzing Putty-nosed meanings

Turning to Putty-nosed *pyow-hack* sequences, we may treat them as (non-compositional) idioms, memorized as whole units. But this is unsatisfying because these sequences are slow and come in many varieties, depending on the number of repetitions. An alternative is to posit that these sequences have a weak literal meaning, but that it is pragmatically enriched by an Urgency Principle, which mandates that within a sentence, calls that convey information about the location of a threat come before those that don't (Figure 1b; [33]). Specifically, we take *pyows* to trigger unspecific alerts, and *hacks* to warn of (serious) non-ground, movement-related events. Semantically, then, a *pyow-hack* sequence warns of a non-ground, movement-related event, e.g. the impending movement of an attacking raptor, or of the (arboreal) monkeys themselves. But if a raptor were present, *hacks* would convey information about the location of the threat and hence (by the Urgency Principle) it should come before *pyows*. This explains why *pyow-hack* sequences are indicative of group movement; no idioms are posited, but competition principles are crucial (see [33] for a more detailed analysis). The Urgency Principle is speculative at this point, but it is noteworthy that it might explain some constraints on alert calls found in other species, notably in birds ([28][34][35]).

Analyzing Titi meanings

Let us now go back to the puzzle of Titi sequences. Due to their length and slow time course, it is unlikely that these sequences are interpreted as idioms. We explore a leaner analysis in which each call contributes its meaning independently from the others (Figure 1c; [36][37]).

Since the B-call is used in predatory and non-predatory situations alike, we take it to trigger an unspecific alert. In field experiments, the A-call triggers a *looking up* behavior, so we posit that it is indicative of serious non-ground alerts. These assumptions explain why we find B^+-sequences (i.e. a series of B-calls) in *cat on the ground* situations, and A^+-sequences (i.e. a series of A-calls) in *raptor in the canopy* situations.

But why do we find A^+B^+ (i.e. a series of A-calls followed by a series of B-calls) in *raptor on the ground* situations? A remark about hunting techniques proves essential: raptors on the ground probably attack by flying, hence the serious non-ground alerts A^+. Still, being on the ground isn't a typical hunting position, and after a while the alert stops being serious, which only leaves B as a possibility. In *cat in the canopy* situations, we find AB^+ sequences (i.e. an A-call followed by a series of B-calls), possibly because a serious non-ground danger is indicated, which then transitions to a weaker danger because a cat becomes less dangerous after detection ([1]).

If this analysis is on the right track, the apparent complexity of Titi sequences reflects the interaction between simple meanings and the evolution of the contextual environment as the sequence is produced, rather than a complex syntax/semantics interaction or very long idioms.

As can be seen, a unifying theme of these various studies is the division of informational labor between semantics, pragmatics and the environmental context – which in the cases discussed makes it possible to maintain particularly simple individual meanings and composition rules.

Reconstructing the evolutionary history of calls

While the comparative analysis of monkey calls brings out some common theoretical themes, it also highlights numerous shared properties at the level of call form and function. In fact, comparative studies of monkey calls have long been used to reconstruct **phylogenies** (i.e. the 'family trees' of monkey species), with results that often converge with DNA methods ([38][39]). But one can turn the problem on its head and start from established phylogenies to reconstruct call evolution. This promises to offer a window into the evolution of form and meaning in simple communication systems.

Initial results are striking. *Booms* are non-predation-related calls present in many subspecies of cercopithecines, including Campbell's and Putty-nosed monkeys (Figure 2). Inspection of their distribution is strongly indicative of their presence in the most recent common ancestor of entire subgroups: *booms* probably existed several million years ago ([5][40]). Thus while comparative monkey semantics might not directly illuminate the evolution of human language, it could yield striking insights into the evolution of meaning in simpler systems.

Concluding remarks and future perspectives

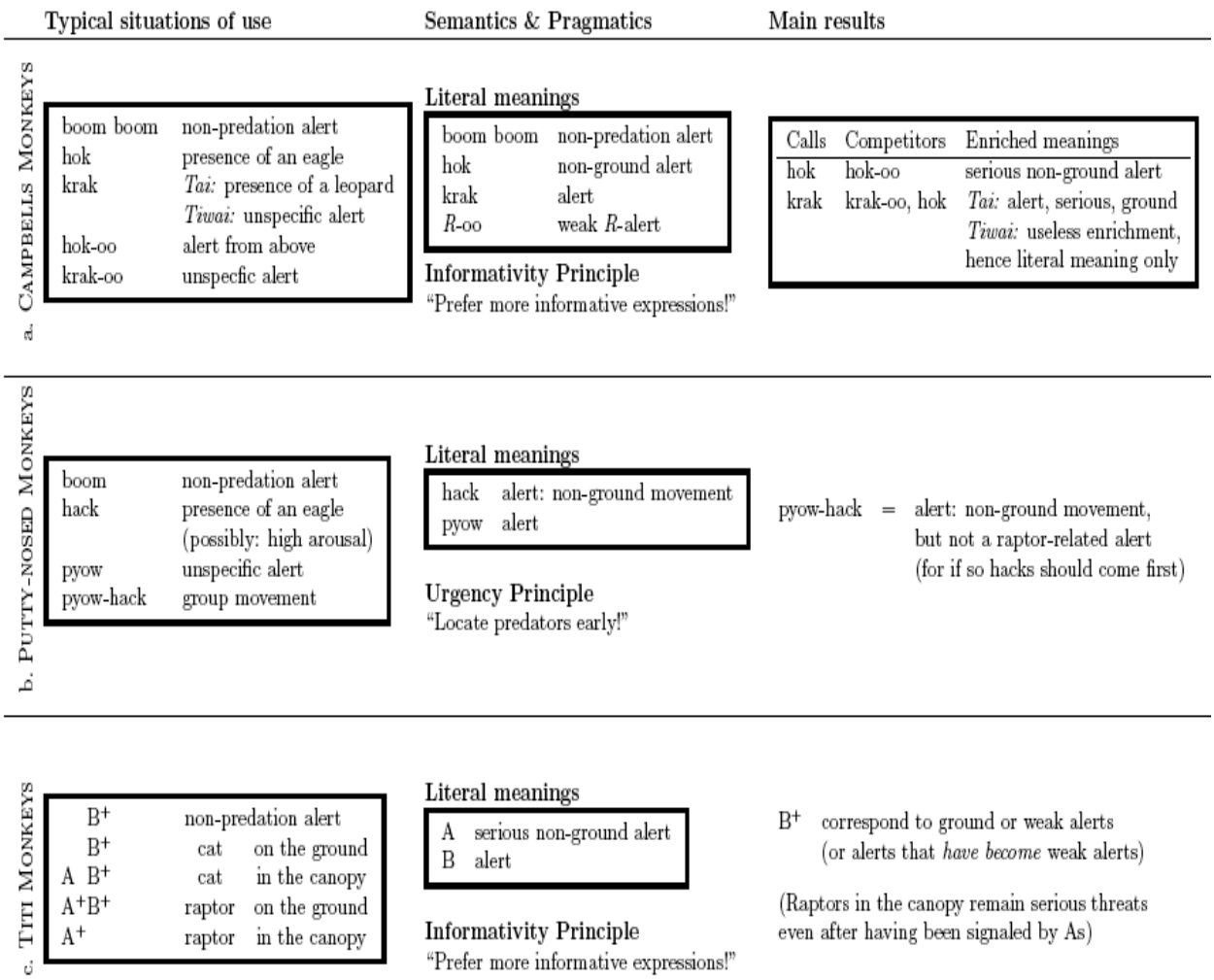
We take this discussion to suggest that general questions and tools from formal linguistics can prove fruitful in the analysis of the form and especially meaning of monkey calls. This program could be extended to other systems of animal communication as well. For instance, bird calls/songs have been argued to display interesting phonological ([41][42]), syntactic ([19][43]) and semantic ([34][35]) properties, and we mentioned in our discussion of the Urgency Principle that they might be studied from a pragmatic perspective as well. In addition, it has been argued that birds can learn morphological patterns of affixation (involving prefixes and suffixes) in artificial languages ([44]).

We also argued that the adoption of a comparative perspective can yield new insights into the evolution of calls over millions of years. And in the long term, a detailed

understanding of monkey calls is certainly a pre-condition to a meaningful comparison with human language (see Box 2).

Each sub-area leads to new questions that should help orient future research, as outlined in the *Outstanding questions* box. One key issue is whether the division of labor we proposed between semantics, pragmatics and the environmental context is on the right track. In particular, we posited rules of pragmatic competition that enrich the meaning of some calls whose core informational content is by itself compatible with a broad range of situations. An alternative is to take these calls to provide specific instructions about precise actions, which might be appropriate for a broad range of situations (such as *looking around*; [45][28]). Further experimental studies should help distinguish among these proposals.

Figure 1. Data and possible theories for three monkey species: Campbell's monkeys, Putty-nosed monkeys, and Titi monkeys



Box 1. How does one argue for a semantic analysis?

It is sometimes thought that postulating meanings in monkeys is necessarily *ad hoc* because the subjects cannot be asked what they have in mind when they produce a call. This objection is based on several misconceptions.

• First, even in *human* linguistics one can't just ask subjects what the meaning of a word is: while they have intuitions about the truth conditions of sentences, the meaning of a word is a *theoretical construct* that must be supported by indirect evidence. A case in point is the word *or*, discussed in the text: speakers have no reliable intuitions as to whether the meaning they have in mind is inclusive or exclusive. Rather, it is by investigating the truth conditions of numerous sentences that linguists concluded that *or* is inclusive, and that its exclusive use is derived by the Informativity Principle. Similarly, primate semantics starts from the analysis of truth conditions; the main difference is that information about these is much harder to obtain than in adult humans. A closer point of comparison pertains to meaning in children, where experimental methods are needed to elicit truth conditions ([46]).

• Second, as in every scientific endeavor there are two main criteria of success for a theory: its parsimony; and its ability to make correct predictions ([28][45]). To be concrete, consider the case of Campbell's *krak* (Box 1a), and compare two theories:

(i) *krak* has a ground threat meaning in the Tai forest, but a meaning of general alert on Tiwai island (**Dialectal Variation Theory**);

(ii) *krak* has a general alert meaning on both sites, but is enriched by the Informativity Principle when this does not yield a useless meaning (**Uniform Theory**).

–If independent motivation for the Informativity Principle can be found, the Uniform Theory can be taken to be more parsimonious.

–More importantly, the Uniform Theory makes correct predictions that are not made by the Dialectal Variation Theory. To give but one example, the Uniform Theory explains why *krak-oo*, which has a general meaning on both sites, can be derived from *krak* + *-oo*, in particular on the view that *R-oo* signals a weak alert of the *R*-type. The Dialectal Variation Theory has difficulty with the data from Tai: since *hok* signals non-ground threats and *hok-oo* weak non-ground threats, and since (according to that theory) *krak* signals ground threats, one would expect that *krak-oo* signals weak *ground* threats – which is incorrect: even in Tai, *krak-oo* has non-ground uses.

Box 2. What is the relation between monkey languages and human language?

We argue in the text that the *methods* of formal linguistics can prove useful in the investigation of monkey languages, but that it does not follow that the latter share non-trivial *properties* with human language. There are important dissimilarities and some limited similarities between the two systems ([5][28][47][48]).

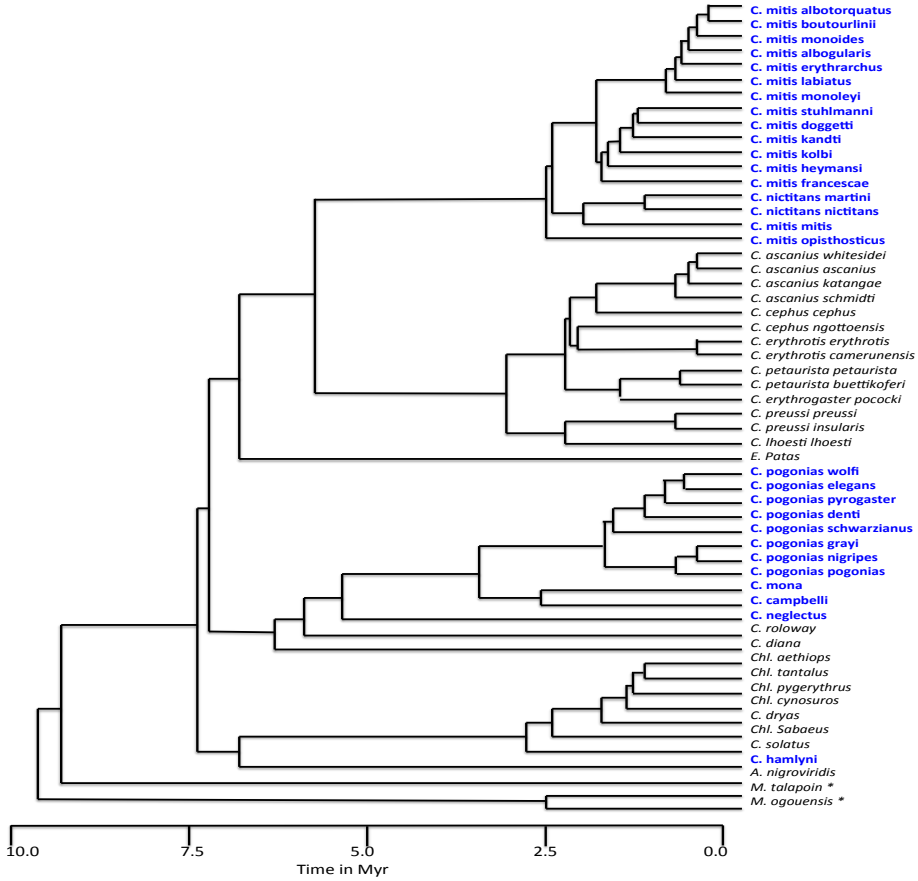
• **Morphology and syntax**: word-internal and sentence-internal structure is extremely limited in the species we have studied (but see [21]): calls are limited to two components (e.g. *krak*+-*oo*), and there is no evidence that sequences have a complex structure. By contrast, human language has arbitrarily complex words (e.g. *anti-dis-establish-ment-ari-an-ism)*, and highly sophisticated syntactic structures ([6][7][48]). Furthermore, monkey languages display numerous cases of call repetition, which have no equivalent in human language.

• **Semantics**: unlike most human words, call meanings that have been posited so far usually pertain to threats, although this is partly due to a selection bias (for female social calls, see [24][25]). Call-internal composition seems to exist in Campbell's monkeys (*krak-oo*) and possibly beyond, but remains limited ([28][32]). There is no real evidence of non-trivial composition of meaning sequence-internally, as each call can be taken as an individual sentence, interpreted independently from the others.

• **Pragmatics**: while there is no clear evidence for an ability to represent communicative intentions in monkeys, we postulated in the text an Informativity Principle that is similar in form to one found in human language, but their evolutionary relationship is unclear.

When monkey languages are better understood, one would need to ask whether any similarities they bear to human language arose by **convergent evolution** (in case similar properties developed independently in humans and in monkeys) or could result from **evolution from common descent** (in case similar properties are inherited from the communicative system of the most recent common ancestor of monkeys and humans).

Figure 2. Call evolution: the example of *boom*



Phylogenetic tree of cercopithecines (from [40] and [5]), with boldfaced names in blue for species that have *booms*. It seems very likely that the most common recent ancestor of the top blue (= *mitis*) group (which lived about 2.5 million years ago) had *booms*, since all of its descendants do; and similarly for the most recent common ancestor of the middle blue group (*C. pogonias*, *C. mona*, *C. campbelli*, *C. neglectus*).

Trends

• Data gathered in field experiments provide detailed information about the form and function of monkey calls, especially the situations that trigger them and the information that conspecifics derive from them.
• While monkey calls radically differ from human language, their form and meaning can be illuminated using general tools from formal linguistics (morphology, syntax, semantics).
• Meaning studies should explain how monkey calls can encode information, thanks in particular to three components: the literal meaning of calls, knowledge of the environmental context, and some rules of competition among calls according to which more informative calls are normally preferred to less specific ones.
• Evolutionary connections between monkey calls and human language are unclear, but within monkey species the evolutionary history of calls can sometimes be traced over millions of years.

Outstanding Questions

• Phonology: The sound system of monkey calls should be investigated for itself, but also to determine whether some syntactic constraints are reducible to properties of the articulatory/perceptual system.
• Morphology: Beyond Campbell's and Diana monkeys, can further cases of call-internal structure be found?
• Syntax: Can monkey syntax be analyzed by way of 'finite-state' languages, and if so which subclass of these is appropriate? Is there evidence for a level of sentence structure beyond the concatenation of individual calls?
• **Lexical semantics**: What constraints are there on possible call meanings? Which of these constraints come from limitations of monkey conceptual abilities? Do calls provide information about the environment, or about *actions* to be taken, as is standard in game-theoretic studies of meaning?
• **Combinatorial semantics**: Can all call sequences be analyzed with a minimal rule of combination, with each call contributing its meaning independently from the others? If not, what happens when syntactically complex expressions are interpreted: is their meaning compositional or non-compositional?
• Competition-based pragmatics: Can direct evidence be provided for principles of competition among calls, such as the Informativity and Urgency Principles? Should one re-analyze unspecific alert calls as having instead *specific* meanings about *actions*, e.g. 'look up' (if a threat comes from above) and 'look around' (if the threat is unspecified or comes from below)?
• Intentional pragmatics: How much does primate pragmatics involve a theory of mind? In particular, are there audience effects whereby monkeys adapt their calls to the perceived belief state of their audience?
• Evolution: Can the evolution of further calls (such as cercopithecine *booms*) be traced over millions of years? Can formal analyses of meaning evolution (especially within **evolutionary game theory**) explain the contemporary use and/or the evolutionary emergence of some call systems?

Glossary

Combinatorial semantics: field of semantics concerned with the literal meaning of complex expressions in language – and by extension the object of study of this field.
Convergent evolution: the independent evolution in two species of a feature that was not present in their most recent common ancestor.
Evolution by common descent: the existence in two species of a feature that they inherited from their most recent common ancestor.
Evolutionary game theory: branch of game theory concerned with the ways in which some strategies come to dominate others in social change or in biological evolution.
Informativity Principle: pragmatic principle that specifies that if a certain expression evokes a more informative one, the speaker can utter the less informative expression only if he is not in a position to utter the more informative one, usually because it is false.
Lexical semantics: field of semantics concerned with the literal meaning of elementary expressions in language – and by extension the object of study of this field.
Morphology: field of linguistics concerned with the internal structure of words in language – and by extension the object of study of this field.
Phonology: field of linguistics concerned with the organization of sounds in language – and by extension the object of study of this field.
Phylogeny: evolutionary relationships among various species. A phylogenetic tree represents these relationships by way of a tree-like diagrams (as in Figure 2) in which the descendants of a given species appear under it in the tree (or to its right, as in Figure 2).
Pragmatics: field of linguistics concerned with the various ways in which the literal meaning of an expression can be enriched by reasoning on the speaker's reasons for choosing it over alternative expressions; by extension, the object of study of this field.
Finite-state languages: formal languages that can be recognized by finite state machines, which just contain a list of states and a specification of which state to go to when reading a given word. This model was shown in the 1950's to be insufficiently rich to handle human languages.
Semantics: field of linguistics concerned with the literal meaning of expressions in language; by extension, the object of study of this field.
Syntax: field of linguistics concerned with the structure of sentences in language, in particular with the rules according to which words are put together to form sentences (in a broad sense, syntax is concerned with all constraints on the form of sentences); by extension, the object of study of this field.

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