Animal linguistics and the puzzle of titi monkeys alarm sequences

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Abstract

This article aims to illustrate how animal linguistics can increase our understanding of animal communication using the example of the alarm system of Black-fronted titi monkeys. Titi monkeys produce sequences composed of A- and B-calls in alarm situations. Previous biological and linguistic works investigated the semantics of these utterances but relied on a preliminary dataset. We followed up on this work by carrying out an extensive analysis of meaning at the call and sequence level, based on 18 months of field observations and experiments followed by acoustical and linguistic analyses. Our results suggest that alarm calls refer to the emotional state of the caller at the time of emission of the call. Listeners most likely attend to the proportion of BB-grams in each sequence, which provides them with information about the caller's emotional state, to infer what the predator is (aerial or terrestrial) and where it is (ground or canopy) using their world knowledge. Overall, this work suggests that the emotional states of animals can convey complex and reliable information to listeners. Our study illustrates that combining field data with linguistic analyses provides a powerful new approach to better understand animal communication.

1 Introduction

Animal linguistics, or the application of linguistic methods to the study of nonhuman animal data, is a recent approach that aims to deepen our understanding of nonhuman communication, from bird songs (e.g. Yip, 2006) to primate vocalizations (e.g. Heesen et al., 2019) and gestures (Graham et al., 2018). When exploring semantics and syntax in primate vocalizations, Schlenker et al. (2016a) proposed an approach that relies on three main pillars derived from formal linguistics: i) calls are combined into sequences that are subject to syntactic rules and can be studied under a formal syntax approach that distinguishes possible and impossible sequences, ii) there is a correlation between a call type and the context(s) in which it occurs, thus calls have a semantics and can be studied using truth-conditional semantics that establishes whether a call is true (or appropriate) in a given context, and iii) there are rules of call competition that determine which call must be chosen over another one. Overall, their approach aims to explore “the division of labor between syntax, semantics, pragmatics, and properties of the environmental context (‘world’ knowledge and context change)” (Schlenker et al., 2016a, p. 20).

Black-fronted titi monkeys *Callicebus nigrifrons* are good candidates to apply this approach and demonstrates its efficiency, since titi monkeys’ vocal communication has been described as “the maximal elaboration that can be attained by species-specific language” (Moynihan, 1966, p. 77) and that several successive theories have tried to decode its puzzling alarm system. Thus, the current work aims to illustrate how animal linguistics can increase our understanding and unveil unexpected mechanisms in a nonhuman communication system.

It should be noted that the notion of *meaning* we use here is similar to that of *natural meaning*, for which information is transmitted when there is a statistical correlation between a signal and the context (like *smoke* means fire). Thus, this work does not aim to explore *Gricean meaning* (in the sense of *intentional* communication, see for example Townsend et al., 2017) in titi monkey calls, but rather to explore the formal properties of their communication system while remaining agnostic about the underlying cognitive mechanisms.

2 First theories

Titi monkeys produce sequences composed of A-calls and B-calls in alarm situations. Cäsar et al. (Cäsar, 2011; Cäsar et al., 2012b, 2013) conducted extensive field observations followed by experiments such as predator presentations (raptor or felid models placed either on the ground or in the canopy; snake, tayra and deer models on the ground) and playbacks of titi monkey alarm sequences. They analysed the 30 first calls emitted and described the titi monkey alarm system as simplified in (1).

(1) **Cäsar et al.’s description of the different alarm sequences and their context of emission**

a. Terrestrial predator on the ground: Sequences of B-calls (B+)
b. Terrestrial non-predator animal on the ground: Sequences of B-calls (B+)
c. Caller foraging near the ground in absence of predator: Sequences of B-calls (B+)
d. Raptor in the canopy: Sequences of A-calls (A+)
e. Capuchins in the canopy: Sequences of A-calls (A+)
f. Felid in the canopy: Sequences of one single A-call followed by B-calls only (AB+)
g. Raptor on the ground: Sequences of A-calls with interspersed B-calls (A+B+)

Cäsar et al. (2012a) conducted playback experiments, in which they broadcasted A+ and B+ sequences to titi monkeys to assess the reaction of the listeners to the utterances. They obtained the results presented in (2).

(2) **Results of Cäsar et al.’s playback experiments**

a. A+ sequences make the listener look upward
b. B+ sequences make the listener look toward the speaker, as if searching for additional cues to determine the eliciting event

Using the results presented in (1) and (2), Cäsar et al. drew the conclusions detailed in (3).

(3) **Cäsar et al.'s theory**

a. A-calls refer to danger within the canopy
b. B-calls are general alarm calls, elicited by terrestrial disturbances
c. Sequences encode type (aerial vs terrestrial) and location (ground vs canopy) of the predator using a sophisticated syntactic/semantic interface: unusual locations are encoded by a modified predator-specific sequence (namely, addition of a A-call at the beginning of the B+ sequence when the terrestrial predator is in the canopy and interspersion of B-calls into the A+ sequence when the aerial predator is on the ground)

The possibility that this species exhibits a complex syntactic/semantics interface drove linguists (Schlenker et al., 2017) to analyse this communication system using the formal linguistic approach mentioned above. The authors rejected Cäsar et al.'s theory. First, they showed that the semantics of A-and B-calls proposed by Cäsar et al. does not hold: the data exposed in (1) do not support the idea that A-calls refer to danger within the canopy, since A-calls are given to predators in the canopy but also on the ground, to aerial predators and to terrestrial predators. Similarly, B-calls can not refer to terrestrial disturbances, since they are emitted in contexts in which the threat is on the ground as well as in the canopy, and to terrestrial and aerial predators. Schlenker et al. also rejected the claim that titi monkeys exhibit a complex syntactic/semantic interface. Instead, Schlenker at al. (2017) analysed the calls using scalar implicatures, as stated in (4) and proposed the conclusions detailed in (5).

(4) **Schlenker et al.** (2016a)**'s Informativity Principle**

If a sentence S was uttered and if S' is (i) an alternative to S, and (ii) strictly more informative than S (i.e. asymmetrically entails S), infer that S' is false

(5) **Schlenker et al.'s theory**

a. A-calls do not refer to the type or location of the predator, but rather provide information about the appropriate reaction to the threat: A-calls refer to serious non-ground threats
b. B-calls are general alarm calls, referring to noteworthy events. According to the Informativity Principle, the strengthened meaning of the B-call is applicable in case there is a noteworthy event but no serious non-ground threat (or else the A- call would have been emitted)
c. Calls are individual units that reflect the state of the environment at the time of utterance of the call
d. There is no syntax: the meaning of the sequence is a conjunction of claims made by individual calls

The generalizations that fall out of Schlenker et al. (2017)'s theory are detailed in (6).

(6) **Generalizations from Schlenker et al. (2017)'s theory**

a. Terrestrial predator on the ground: noteworthy event but not serious non-ground threat, B+
b. Terrestrial non-predator animal on the ground: noteworthy event but not serious non-ground threat, B+
c. Caller foraging near the ground without the presence of predator. noteworthy event but not serious non-ground threat, B+
d. Raptor in the canopy: serious non-ground threat, A+
e. Capuchins in the canopy: serious non-ground threat, A+
f. Felid in the canopy: this is a serious non-ground threat ("non-ground" because the threat is in the canopy) so one A-call is emitted. But felid predators give up hunting after detection by their preys (Zuberbühler et al., 1999), so the predatory

threat becomes non-serious after the A-call is emitted, thus only B-calls are emitted afterwards: AB+

g. Raptor on the ground: this is a serious non-ground threat ("non-ground" because the bird attacks by flying) so A-calls are emitted. After a while, the caller realizes that the bird is not in a hunting position, because it is on the ground, thus it becomes non-serious, and the caller emits B-calls: A+B+

Cäsar et al.'s and Schlenker et al.'s conclusions were drawn using one preliminary dataset, for which the number of observations was small, and crucial experiments (namely, playbacks of AB+ and A+B+ sequences to titi monkeys) were lacking. In order to complement Cäsar et al's dataset, we conducted an extensive study involving 18 months of field observations and experiments on a wild, observer-habituated population of titi monkeys at the Santuário do Caraça, Brazil. We then conducted acoustic and linguistic analyses, and revised the conclusions proposed by Cäsar et al. and Schlenker et al., both at the call and sequence level.

3 Meaning from the caller's perspective

We recorded spontaneous alarm sequences, given to natural predator encounters and when individuals were descending near the ground to forage in the absence of predators, but also conducted predator presentation experiments. We presented 6 groups of monkeys with aerial (raptor *Caracara plancus*) or terrestrial (oncilla *Leopardus guttulus* and tayra *Eira barbara*) stuffed predators, placed either on the ground or in the canopy. We recorded the vocal reactions of the monkeys (10 first calls) and completed our dataset with alarm sequences from Cäsar (Cäsar, 2011; Cäsar et al., 2013). Description of this new dataset (N=74 sequences) is presented in (7). Our observations are mostly congruent with those of Cäsar's et al., except for the "felid in the canopy" condition (7f) for which we did not systematically observe the AB+ pattern described in (1f).

(7) **Updated description of the different alarm sequences and their context of emission**

a. Terrestrial predator on the ground: Sequences of B-calls (B+)
b. Terrestrial non-predator animal on the ground: Sequences of B-calls (B+)
c. Caller foraging near the ground in absence of predator: Sequences of B-calls (B+)
d. Raptor in the canopy: Sequences of A-calls (A+)
e. Capuchins in the canopy: Sequences of A-calls (A+)
f. Felid in the canopy: Sequences of B-calls; A-call(s) interspersed in the sequence at irregular places in 7/14 sequences (B+(A))
g. Raptor on the ground: Sequences of A-calls with interspersed B-calls (A+B+)

As presented in (1), B-calls are found in a large set of contexts, including predatory and non-predatory situations, which have nothing in common from a human point of view. These puzzling observations led both Cäsar et al. and Schlenker et al. to propose a general meaning for B-calls, as presented in (3) and (5). These claims were built on the assumption that B-calls emitted in predatory and non-predatory contexts are similar, but acoustic analyses were sorely lacking to verify and thus validate these assumptions. To investigate this possibility, we first conducted acoustic analyses on B-calls spontaneously given when the caller is foraging in low strata ("ground B-calls") and experimentally induced during terrestrial model presentations ("terrestrial predator B-calls" collected from AB+ and B+ sequences as described in (1)). We found that B-calls exhibit a different acoustic structure depending on their eliciting context, and that terrestrial predator B-calls are higher-pitched that ground B-calls (Berthet et al., 2018). These results are presented in (8).

B-calls are also emitted in response to aerial predators on the ground (A+B+ sequences). To fully grasp the meaning of the B-calls, we investigated whether these B-calls are similar to ground or terrestrial predator B-calls. We measured 45 B-calls given to aerial predators on the ground (“aerial B-calls”) and compared them to 192 ground B-calls and 113 terrestrial B-calls by classifying them using a linear discriminant analysis on mel filterbank. Our analysis confirmed that ground and terrestrial predator B-calls are distinguishable based on spectral properties. Importantly, the classification of aerial B-calls was unambiguously bimodal, with 28 aerial B-calls classified as clear terrestrial predator B-calls, and 17 classified as clear ground B-calls, confirming that aerial B-calls do not form a separate class of B-calls. Rather, aerial B-calls are a mix of lower-pitched ground B-calls, and higher-pitched terrestrial B-calls. Results are also presented in (8).

(8) **Results of our successive acoustic analyses on B-calls**

a. Terrestrial predator B-calls are higher-pitched than ground B-calls
b. Aerial B-calls are a mix of terrestrial predator and ground B-calls

As presented in (8b), ground B-calls and terrestrial predator B-calls are given to diverse situations that, again, have little in common from an observer’s point of view. Indeed, ground B-calls are given when the caller is descending near the ground and when presented with an aerial predator on the ground, while terrestrial predator B-calls are given to terrestrial predators but also when presented with an aerial predator on the ground. The fact that one context can elicit different B-call types is puzzling, and suggest that either B-calls exhibit two acoustic variants that both refer to general alerts – but this system does not seem of great relevance – or that B-calls do not function as labels as previously thought. In line with the second idea, we suggest that B-calls actually refer to the emotional state of the caller. Moreover, as presented in (8a), the frequency of the B-calls varies with the eliciting situation. Yet, the frequency of a call is highly dependent on the emotional state of the caller (Briefer, 2012), with higher arousal levels eliciting higher frequencies. If the acoustic variation of the B-call was linked to a variation in the emotional state of the caller, our data would support the hypothesis that the caller is more aroused in presence of a terrestrial predator than when it is foraging in a vulnerable position (near the ground, where terrestrial predators are likely to be) but in the absence of immediate threats. We can thus stipulate that B-calls reflect the emotional state of the caller.

When considering the case of A-calls, the picture is clearer. As presented earlier in (3), Schlenker et al. stated that A-calls refer to serious non-ground threats. However, Cäsar (2011) argued that aerial predators represent the major danger to titi monkeys, which suggests that the proposed meaning “serious non-ground threat” is redundant. We thus argued that the “non-ground” specification can be eliminated from the meaning of A-call, resulting in a simplification such that A-calls refer to serious threats (Commier & Berthet, 2019).

However, results presented in (8) suggest that B-calls are linked to the emotional state of the caller. Since A-calls are very high-pitched calls, and because they are given when the caller is facing a serious threat, we emit the hypothesis that A-calls are also related to the emotional state of the caller, and are emitted when the caller is highly aroused. Since B-calls are emitted in less dangerous situations, and because B-calls exhibit two acoustic variants, we conclude that B-calls reflect either low or medium arousal levels in the caller These hypotheses are synthesized in (9).

(9) **Meaning at the call level: our hypothesis**

a. Alarm calls of titi monkeys reflect the emotional state of the caller
b. A-calls reflect high emotional states of the caller
c. B-calls reflect lower emotional states of the caller

d. Modular theory: Acoustic structure of the B-calls indicates whether the level of stress experienced by the caller is low (low pitched B-calls) or medium (high pitched B-calls)

Since alarm calls are a reflection of the emotional state of the caller, and in line with Schlenker et al.'s theory described in (5d), we propose that the calls reflect the emotional state of the caller at the precise time at which they are uttered. If this is true, then the sequence reflects the temporal evolution of the emotional state of the caller, as detailed in (10).

(10) **Sequence encoding: the caller emits calls that reflects its emotional state at the time of emission**

a. Caller descending near the ground: vulnerability to potential terrestrial predator, low arousal: low-pitched B+

b. Terrestrial predator on the ground: noteworthy threat that is easy to escape from, medium arousal: high-pitched B+

c. Aerial predator in the canopy: serious threat, high arousal: A+

d. Terrestrial predator in the canopy: noteworthy threat that is easy to escape, medium arousal with anecdotal peaks of excitement: B+(A)

e. Aerial predator on the ground: serious threat at first, the caller then realizes that it is not that serious (because not in a hunting position or because it is a fake model that does not move): A+B+ (high- and low-pitched B-calls)

Contrary to the previous proposals of Cäsar et al. and Schlenker et al., this theory can also account for irregularities of the calling patterns, like the one presented in (10d): these irregularities can be due to sudden changes in the arousal, which can be explained by the experimental paradigm (e.g. previous experience of the caller with this model, the fact that the model does not move), the presence of human observer and their distance to the caller, the presence or absence of conspecifics and the changes in the audience, the movement of the caller toward or away from the model, etc.

4 Meaning from the listener's perspective

We ran an extensive field study to investigate what information was extracted by listeners at the sequence-level, and what mechanisms they used to decode information (Berthet et al., 2019). We conducted predator presentation as detailed above, recorded the vocal reaction, completed this dataset with that of Cäsar et al. and extracted the first ten calls of each sequence. Each of the N=50 sequences was then characterized by 15 metrics referring to the composition, ordering, temporal structure and complexity of the sequence[1]. We conducted a multimodel inference to investigate whether each metric conveyed information about predator type and/or location. In order to identify the mechanisms used by listeners to extract information from the vocalizations, we conducted playback experiments. We broadcasted the recorded alarm sequences to other individuals, coded the gaze reaction of the subjects and conducted multimodel inference to investigate whether gaze direction of listeners was influenced by i) the origin of the sequence (i.e. the location and type of the predator that elicited the broadcasted sequence) and ii) the metrics characterizing the sequences used as playback stimuli. We present the main results of this study in (11) and our resulting conclusions, in (12).

(11) **Results from Berthet et al., 2019**

a. Several sequence metrics encode for predator type or predator type and location

[1]It must be noted that this analysis was conducted before we investigated the acoustic variants of B-calls. Thus, this study did not consider whether B-calls of the sequences were high- or low-pitched B-calls.

b. Listeners look more upward and less toward the speaker when listening to sequences recorded from encounters with an aerial predator/a predator in the canopy
c. Listeners strongly react to the proportion of BB-grams (i.e. the proportion of combinations of 2 B-calls) of the sequence: they look more upward and less toward the speaker when listening to sequences containing a smaller proportion of BB-grams
d. Sequences recorded from encounters with an aerial predator/a predator in the canopy contain a smaller proportion of BB-grams than sequences recorded from encounters with a terrestrial predator/a predator on the ground

(12) **Conclusions from Berthet et al., 2019**
a. Sequences encode predator type and location
b. Listeners can extract information about predator type and location from the sequences
c. Information is transferred through the proportion of BB-grams of the sequence

But if alarm sequences are mere reflections of the temporal evolution of the arousal state of the caller, how can we explain that alarm sequences convey information about the predator type and location of the predator? As shown in (12), sequences are decoded by listeners using the proportion of BB-grams. This suggests that listeners do not process the alarm sequence call by call, but rather synthesize information by using the proportion of BB-grams. We thus postulate that listeners extract the overall level of stress experienced by the caller during the situation. We did not have the opportunity to conduct playback experiments to determine whether low- and high-pitched B-calls were discriminated by listeners in titi monkeys yet. However, several studies suggest that, in nonhuman animals, listeners can extract emotional information from the acoustic structure of the calls (e.g. Manser et al., 2002). Thus, we postulate that, in addition to relying on the proportion of BB-grams, listeners also process the acoustic structure of the calls to assess the overall emotional state of the caller – a statement that remains to be tested in the field. Listeners could then infer the eliciting situation using their world knowledge, as detailed in (13).

(13) **Sequence decoding: the listener extracts the proportion of BB-grams and uses world knowledge**
a. Low-pitched B+: maximum proportion of BB-grams, reflecting a low arousal level of the caller. The listener infers that the caller is near the ground
b. High-pitched B+: maximum proportion of BB-grams, reflecting a medium arousal level of the caller. The listener infers that there is a terrestrial predator
c. A+: minimum proportion of BB-grams, reflecting a high arousal level. The caller infers that there is an aerial predator in the canopy
d. B+(A): high proportion of BB-grams, reflecting a medium arousal level with some peaks of excitement. The listener infers that there is a terrestrial predator in the canopy
e. A+B+: low proportion of BB-grams, reflecting a high arousal that slowly decreases over time but still exhibit some sudden peaks of excitements. The listener infers that there is an aerial predator on the ground

5 Conclusion

The titi monkey system appears to rely on a division of labour between semantics (with the natural meaning of A- and B-calls being linked to the emotional state of the caller) and on pragmatics (with the listener extracting information about the type and location of the predator from the emotion-related sequences, by using its world knowledge). Although based on several observational and experimental datasets, and inferred from rigorous analyses, these conclusions remain to be tested in the field, through playbacks (e.g. by broadcasting artificial sequences with varying proportion of BB-grams) or other innovative measurements, such as the use of thermography to track emotional changes in the caller (e.g. Ermatinger et al., 2019).

Overall, our work suggests that an emotional reaction from an individual can convey reliable and complex information to listeners about the external world, provided that they use their world knowledge to process it. This confirms that the traditional dichotomy between referential signals (i.e. signals that convey information about the external world) and affective signals (i.e. signals that are linked to the emotional state of the caller) is wrong: the affective property of a signal depends on mechanisms of call production in the caller, while the referential property of a signal depends on the listener's ability to extract information from events (Seyfarth & Cheney, 2003).

Here, we remained agnostic about the cognitive processes that may be used by titi monkeys when communicating about alarm situations. First, we investigated meaning as a correlation between a signal and an event, regardless of the intention of the caller. Second, our work suggests that the Informativity Principle of Schlenker et al. (2016a) is not required to explain the vocal behaviour of titi monkeys, limiting debates on the cognitive capacities needed by the caller to apply this concept (Jäger, 2016; Schlenker et al., 2016b). Third, the world knowledge used by titi monkeys to extract information from the sequences does not require any high cognitive process, such as theory of mind or empathy: a simple associative learning between the alarm sequences and the eliciting event can account for it. Of course, we do not exclude the possibility that titi monkeys possess high cognitive processes, but the current data do not need such claims to be explained.

Overall, this work demonstrates that methods from animal linguistics can be highly beneficial to the study of animal communication. Indeed, by applying methods and concepts from ethology and linguistics on several field datasets, we built clear hypotheses that i) clarified a puzzling behaviour, ii) could not have been reached with linguistic or biological analysis only, iii) do not make high claims about the cognitive capacities of the species and iv) highlight new communication mechanisms in a nonhuman species. Animal linguistics represents a powerful new tool to study animal communication and future research should benefit from this approach, to explore the diversity of communicative systems, investigate the similarities and differences between human language and animal communication, and eventually understand better how communication evolved over time.

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